The role of language experience in neural reorganisation and functional connectivity in deaf individuals

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Dedication

To the memory of my Deaf teacher, mentor, and friend, Tatiana Davidenko.

While no longer with us, you will always continue to inspire and guide me and many others.

All my work will forever be a tribute to you.

Illustration by Anastasia Moskvicheva

Abstract

Studies of deaf individuals, especially deaf children, suggest an association between language and cognition. Deafness also causes brain reorganisation in the auditory cortex and beyond, including changes in functional connectivity. It is often noted that such changes may be driven by either sensory or language experience, but the latter is rarely measured explicitly. The primary aim of this thesis is to investigate the effects of language proficiency and sensory experience on brain reorganisation and cognition in deaf individuals. The underlying hypothesis is that in addition to effects driven by deafness, language proficiency, shaped by varying developmental language experiences of deaf individuals, contributes to changes in neural activity and functional connectivity during different cognitive states and has a role in behaviour.

The thesis uses fMRI data acquired from deaf and hearing participants during executive function tasks (working memory, planning, switching, inhibition) and a resting-state session. The first study showed that language proficiency is associated with behavioural performance during switching and neural activity during the execution of the planning task, demonstrating its role in behaviour and brain reorganisation in deaf individuals during executive processing. Subsequent studies showed that state-dependent functional connectivity in deaf individuals can be associated with language proficiency, including changes between cognitive networks involved in task execution.

This work furthers our understanding of how language proficiency can shape brain organisation and cognition. It highlights the role that language, independently of its modality (signed or spoken), has in brain function and executive processing. It also demonstrates that associations between language and cognition are present and detectable in deaf adults. Language and cognition in deaf individuals are intertwined in both childhood and adulthood, and successful language development in any modality can support cognitive and neural processing behaviourally and in the brain.

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1 General introduction

Throughout the years, considerable attention from researchers in the fields of psychology and cognitive neuroscience has been devoted to the relationship between language and cognition in both children and adults (Emmorey, 2002; C. L. Harris, 2006; Kroll, 2015; Perlovsky, 2009; Perszyk & Waxman, 2016; Stocco et al., 2014; Stocco & Prat, 2014; Vygotsky, 1962; Woll & Wei, 2019). In recent years, studies of individuals with developmental language disorders and studies of bilinguals have been used widely to investigate complex links between language experience and cognition in behaviour and in the brain (Clegg et al., 2005; Emmorey et al., 2008; Kroll et al., 2012, 2014; Kroll & Bialystok, 2013; Manor et al., 2001; Ullman & Pierpont, 2005). This thesis aims to explore the effects of sensory experience and language proficiency in cognition and brain reorganisation in deaf individuals. This is a predominantly bilingual (Ann, 2001) population with a unique experience of language acquisition and language use throughout life. Early language experiences and subsequent proficiency in spoken and signed language in deaf individuals vary significantly (Mayberry et al., 2002). Unlike children with developmental language disorders or hearing bilinguals, deaf individuals may develop deficits in their ability to learn language and experience delays in language acquisition due to lack of language exposure early in life. The extensive variability in language backgrounds and language proficiency outcomes in this population allows us to answer fundamental questions about cognition and language in relation to behavioural and brain function, that otherwise would be more difficult to investigate in other populations due to confounding factors or lack of variability in one of the aspects. Moreover, understanding the relationships between language and cognition in deaf individuals can add valuable perspectives on education policies and interventions (Marschark & Knoors, 2012).

For hearing individuals with no developmental language disorders or traumatic isolating experiences in childhood, language acquisition naturally starts at birth due to instant language exposure (E. Clark, 2009; Saxton, 2017). Hearing children appear to share a basic knowledge of their native language's grammar by the age of five (Saxton, 2017). Unravelling the links between aspects of language development and other cognitive modules, and especially their interactions later in life, may be challenging in a typical population due to possible ceiling effects in language performance. For instance, there is evidence of ceiling effects in judgements on linguistic violations in hearing adults: hearing college students show ceiling effects in their sensitivity to grammatical violations (Wulfeck et al., 1991), dyslexic and non-dyslexic adults perform at ceiling level on a morphosyntactic judgement task (Rispens et al., 2006). In contrast, in deaf individuals, grammatical judgements performance in participants with different age of sign language acquisition as their first language has been shown to change with the age of acquisition (Boudreault & Mayberry, 2006).

Disentangling language-related effects on cognition and brain function in those who were deprived of natural language due to social isolation, or in individuals with developmental language disorders can lead to confounding effects related to social and neural development (Curtiss, 2014; Liégeois et al., 2014; Mayes et al., 2015).

In contrast to the above-mentioned populations, deaf children are born with a full capacity for acquiring language in a similar way and through the same milestones as their hearing peers (Bellugi, 1988; Chamberlain et al., 1999; Mayberry & Squires, 2006; Meier, 1991; Morgan & Woll, 2002; Newport & Meier, 1985), and it is only due to purely environmental reasons (lack of full access to a natural language) that they may not develop language to the same level. In addition, deaf individuals regularly use lipreading and visual cues, and many of them use sign language as their preferred language of communication. Deaf individuals represent a unique heterogeneous population with varying language experiences that have a significant impact on their life and development. The consequences of insecure language development on cognition and neural organisation can be studied by using various techniques, including behavioural and neuroimaging techniques. One of the main aims of this thesis is to explore the effects of language experience on cognition and brain reorganisation in deaf individuals, using language proficiency as a proxy for language experience. Language proficiency has been used in literature before to investigate the effects of language experience on cognition, for instance, in spoken language bilinguals with different language backgrounds (Bonfieni et al., 2019). Other fundamental dimensions of language experience include the age of acquisition and language exposure (Bak, 2016; Kaushanskaya et al., 2020; Luk & Bialystok, 2013), which are also commonly used in the literature on bilingualism, multilingualism, and deafness (Mayberry et al., 2002; Twomey et al., 2020). The decision to use language proficiency as a proxy for language experience throughout this thesis is motivated by an idea similar to that proposed in the literature on bilingualism: while bilingualism is often described in binary terms and measured as a categorical variable, it is a continuous, rather than a categorical, phenomenon (Luk & Bialystok, 2013). Recording proficiency allows for a more sensitive approach, as it can be measured by tasks providing continuous data based on performance. Using continuous measures has been suggested to particularly benefit studies of potential cognitive benefits of language experience in bilingualism in adults due to the ability to detect smaller effects (Kremin & Byers-Heinlein, 2021). Similarly, the complex language backgrounds of deaf individuals also may not be successfully reduced to only categorical measures, and the importance of continuous language proficiency measures for studies on language proficiency has been emphasised in the literature on deafness before (Schönström & Hauser, 2022).

Language effects are often considered secondary to the effects of sensory deprivation in neuroimaging studies of deaf individuals, or they are strictly controlled by recruiting a group with homogeneous language backgrounds. Research on deafness and the brain has shown that deafness leads to significant reorganisation in the auditory areas (Andin et al., 2021; Bottari et al., 2014; Cardin et al., 2013; Ding et al., 2015; Finney et al., 2001, 2003; Karns et al., 2012; MacSweeney, Woll, Campbell, McGuire, et al., 2002) (see *1.2.1. Cross-modal reorganisation in sensory-deprived cortices in blindness and deafness*). This type of reorganisation can have a functional role in cognition in deaf individuals, such as advantages in performance in a working memory task (Ding et al., 2015). Studying language-related effects on brain organisation in deafness is not possible without taking into account the sensory experience of this population. This thesis aims to answer questions about the influence of sensory and language experience on cognition and brain reorganisation in deafness, highlighting the role of the experience of deafness and language proficiency specifically in executive function (see *1.2. Executive function in hearing and deaf individuals*) and functional connectivity (see *1.4. Functional connectivity in deaf and hearing individuals*).

1.1. Language experience and language processing in deaf and hearing individuals

In this section of the introduction, I will describe language variability in deaf individuals, highlighting the importance of early language acquisition for language development in childhood and later in life. Then I will discuss how signed and spoken languages are organised in the brain and describe the effects of age of acquisition and sensory experience on language development in the brain. These questions are relevant for each of the studies presented in this thesis, as they are investigating the effects of sensory experience and language proficiency on functional processing in the brain across several networks, including the language network.

1.1.1. Different pathways to language

Hearing children acquire language naturally through exposure from birth (E. Clark, 2009; Saxton, 2017). Although some children may experience delays or difficulties in the process of language acquisition due to neurological conditions, such as developmental language disorders (DLDs), on average hearing children acquire the basic structure of their first language that allows them to use it in many different scenarios and ways by the age of five (Lewis, 1972; Matthews & Krajewski, 2019; McCarthy, 1943; Saxton, 2017).

Deaf individuals typically do not have the same environmental experience in terms of language exposure as their hearing peers do. This is due to the fact that more than 90% of deaf children are born to hearing, non-signing parents (Mitchell & Karchmer, 2004). This, combined with different approaches to early intervention and deaf education, leads to great variability in language backgrounds and proficiency in deaf individuals. Within this population, native signers appear to be a homogeneous group due to the consistent and positive influence of the language background of the family (Johnston, 2004). Other deaf children acquire their first language through many different pathways leading to various outcomes in terms of the success of acquisition. This is due to an interaction of several factors, from those that vary from individual to individual, such as the age of language exposure (Mayberry et al., 2002; Newport et al., 2001), to more general factors, such as language and educational policies (Grosjean, 2008; van den Bogaerde & Baker, 2002; Woll, 2013).

The diversity of development language pathways in deaf children has great implications for their language use and variability in language proficiency in both childhood and adulthood (Boudreault & Mayberry, 2006; Emmorey, 2002; Mayberry, 1993, 2010; Mayberry & Eichen, 1991; Meier, 2016; Meier & Newport, 1990; Newport & Meier, 1985) and for other developmental outcomes (Murray et al., 2020), including higher-order cognitive functions (Botting et al., 2017; Figueras et al., 2008; Marshall et al., 2015), and neural processing of language (MacSweeney, Waters, et al., 2008; Mayberry et al., 2011).

1.1.2. Early language access and language variability in deaf individuals

The age of acquisition of a language is a crucial factor in the language development of a child. Our understanding of language development in deaf children and in the general population has been advanced by studying various populations of deaf children with different language experiences. Native signers have received major attention throughout the history of research on the topic: they acquire language through similar milestones to hearing children acquiring a spoken language (Emmorey, 2002; Morgan & Woll, 2002; Newport & Meier, 1985; Schick, 2003), which demonstrates that it is *environmental* factors, such as lack of language access, that lead to varying degrees of language proficiency in deaf children. Language access refers to the ability of a child to receive and process the linguistic signal (Hall, 2020). In deaf children of hearing parents, language access is typically hindered by the lack of naturally accessible visual language in the environment and leads to varying levels of language proficiency in comparison to their native signing or hearing peers and variation in age of language acquisition.

The importance of early language access and age of acquisition for various areas of development, including various communication skills, has been noted and investigated by researchers for many years, often with similar (Brill, 1960), or better, adjustment, communication, and achievement outcomes for deaf children of deaf parents in comparison to deaf children of hearing parents (Meadow, 2005; Stevenson, 1964). A study of 105 deaf children of deaf parents and 337 deaf children of hearing parents with an average age of 14 (Stuckless & Birch, 1966) showed that for the majority of measures described in the study (reading, written language, and even speechreading), deaf children of deaf parents had significantly higher scores than deaf children of hearing parents, while other measures did not differ between the groups (Stuckless & Birch, 1966).

As noted in the book 'Language Acquisition by Eye' which provides a review of similar studies (Chamberlain et al., 1999), early research did not directly measure sign language skills in native and non-native signers. In more recent studies, researchers have been able to investigate the effects of age of acquisition on sign language proficiency in deaf signers with varying ages of acquisition (Mayberry & Fischer, 1989; Newport, 1990; Newport & Supalla, 1990).

Maybery and Fisher (Mayberry & Fischer, 1989) showed that college students who were native signers performed a narrative shadowing task better than late learners of sign language. Sentence recall scores declined with the age of acquisition in deaf signers. A different study (Mayberry & Eichen, 1991) focused on deaf adults with a minimum of 20 years of signing experience, replicating the sentence recall results found in the previous work. There was no correlation with length of experience, which emphasises the importance of timely exposure to language.

Elissa Newport (Newport, 1990) described the performance of 30 deaf adult signers on a battery of tests on sign language morphology and reported a consistently small decline in morphology scores in deaf early signers (4-6 years old at the time of exposure), suggesting that age of acquisition effects can be present even if acquisition happened at an early age (before the age of 7). Effects of acquisition have been found between native signers, early signers, and late signers (those who were exposed to sign language after the age of 12), all of whom had at least 30 years of sign language communication experience. Native signers outperformed early signers, who outperformed late learners. Multiple regression analyses have shown that the effects of age of acquisition were differentiated from the effects of length of experience with the language, with the observed effects, such as a decline in morphology scores, being due to age and not the years of exposure. These studies have great implications, as participants in the study had at least 30 years of experience with a sign language. Similar to what was found by Mayberry and Eichen (Mayberry & Eichen, 1991), the years of use did not correlate with performance on tasks on morphology, demonstrating that timely exposure to a language is crucial for its development and that years of exposure do not make up for these effects completely even in adults with decades of experience with the language. It should be noted that the authors did not find the effects of age of acquisition on basic word order, suggesting that age of acquisition affects certain aspects of grammar in different ways. Similarly, Emmorey and colleagues (Emmorey et al., 1995) found that native signers were more sensitive to errors in verb agreement and aspect in American Sign Language in comparison to early and late signers, who did not show this sensibility, but all three groups were sensitive to errors in aspect morphology.

Other studies have shown the age of acquisition effects on other aspects of linguistic processing, such as lexical identification, with native signers being faster at recognising signs than non-native signers (Emmorey & Corina, 1990), and non-native signers requiring more information for sign recognition (Morford & Carlson, 2011).

Deaf adults (the study sample had an age range from 37 to 72 years old) who acquired language early in life showed better language learning performance in learning a second language than those who had little experience of language in early childhood and acquired the same language as their first language at adult age (Mayberry, 1993).

Native signers have near-native grammaticality judgement skills in English, which is their second language, while non-native signers who also have English as their second language perform less accurately and slower in the same task (Mayberry & Lock, 2003). Another study of 55 deaf individuals (Freel et al., 2011) used the American Sign Language – Sentence Reproduction Test (ASL-SRT) (Hauser et al., 2006) to measure signing skills in deaf university students and correlated it with their skills in English. Signing skills were correlated positively with reading skills, and native signers had more proficient bilingual abilities than non-native signers. Both native signing and maternal education significantly predicted bilingual abilities (in American Sign Language and written English). Maternal education has been shown to be important for American Sign Language and reading skills in deaf children in a previous study, but the quality of mother-child communication was a stronger predictor (Calderon, 2000).

Studies show that regardless of the language modality – signed or spoken – of the first or second language of an individual, those who were exposed to language in infancy learn a second language successfully, while those who did not have a full language experience and access in early childhood perform poorly when learning a second language (Mayberry et al., 2002).

In her review on cognitive development in deaf children (Mayberry, 2002), Rachel Mayberry concluded that language difficulties that are present in a large proportion of deaf children, are 'completely preventable and caused by a lack of exposure to accessible linguistic input at the right time in human development, namely infancy and childhood'.

Taken together, work on language acquisition in deafness demonstrates how deaf native signers benefit from language access from birth due to the language-learning abilities being supported by early language acquisition. The majority of deaf children are born to hearing parents and have language access difficulties due to environmental factors, with many being exposed to a signed language – a language fully accessible to them due to its visual modality – at school or in adulthood, when the critical period for language development has passed (Mayberry et al., 2002; Mayberry & Lock, 2003). Work on language development and proficiency in deaf children and adults emphasises that the effects of delay in language acquisition on language abilities in the first and second language in deaf individuals are long-lasting, as they are also detected in adulthood (Emmorey et al., 1995; Mayberry, 1993; Mayberry & Eichen, 1991; Newport, 1990), which is an important consideration for this thesis.

1.1.3. The role of language modality, language access, and sensory experience in language processing in the brain

1.1.3.1. Spoken language processing in the brain

One of the most important questions about language processing in the brain in the field of deafness-related neuroscience and beyond is how the human brain processes sign language. Before answering this question, it is important to understand what had been known about language processing prior to the studies looking at sign language.

The research that led to the discovery of language areas in the brain was clinical studies of patients who demonstrated language difficulties after a stroke or an injury. One of the earliest and most-known observations was related to the difficulties in producing speech in individuals with lesions in the left inferior frontal gyrus (an area often referred to as 'Broca's area') (Broca, 1861). The next major discovery related to language processing in the brain was made by Carl Wernicke who described the area of the brain involved in speech comprehension in the left posterior temporal lobe (often called ‘Wernicke’s area’) (Wernicke, 1874). Finally, the visual word recognition area was discovered in the left angular gyrus (Déjerine, 1891). These findings resulted in an initial neurological account of the location of the language processing areas in the brain.

Major limitations have been raised concerning different aspects of language processing that were not accounted for by the initial descriptions even before the existence of functional imaging techniques, and the understanding of the role of these areas in language processing has been consistently revisited and updated (Binder, 2017; DeWitt & Rauschecker, 2013; Flinker et al., 2015; Tremblay & Dick, 2016). Neuroimaging techniques, including positron emission tomography (PET) and functional magnetic resonance imaging (fMRI), allow scientists to precisely localise the areas related to specific processes, including aspects of language processing, such as language comprehension and production. Neuroimaging studies have suggested the contribution of additional brain areas to language processing, such as the anterior temporal lobe, the left superior median frontal lobe, the anterior insula, the left inferior temporal occipital junction, and the cerebellum, as well as regions in the right hemisphere (see Stowe et al. (2005) for a review; see Hertrich et al. (2020) for a review suggesting a more 'core' language network comprising parts of inferior frontal gyrus, premotor cortex, upper temporal lobe, and a temporo-parietal interface, and Hagoort (2017) for another recent review on the architecture and temporal dynamics of the spoken language processing areas). Moreover, the typical ‘comprehension’ and ‘production’ areas are involved in both language perception and production tasks (Price, 2012). Figure 1.1 provides an illustrative sketch of the location of language-related activations from the studies co-authored by Cathy Price, who wrote a review on the PET and fMRI studies of speech, spoken language, and reading (Price, 2012).

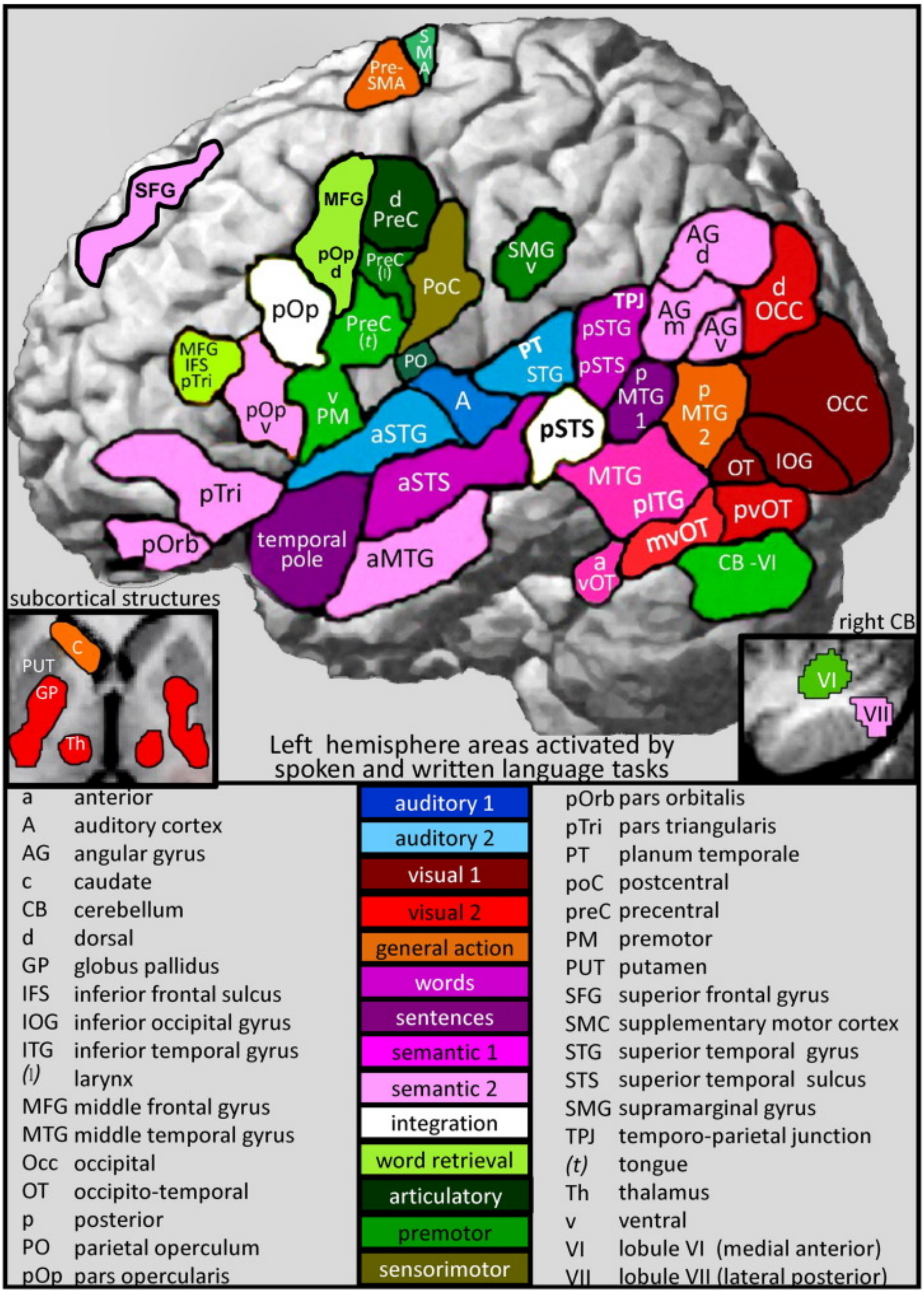

Figure 0.1. An illustrative sketch of the location of language related activations. Based on data from Price (2012). No changes were made to the illustration. Open Access under Creative Commons (CC) BY 3.0 license (https://creativecommons.org/licenses/by/3.0/). From 'A review and synthesis of the first 20 years of PET and fMRI studies of heard speech, spoken language and reading', by Cathy J. Price (2012): https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3398395/.

The anatomy of language processing has been conceptualised into a framework of language processing of the brain – the dual-stream model. It suggests that two systems with distinct functions are involved in language processing in the brain: a dorsal stream and a ventral stream that connect perisylvian language areas (Hickok & Poeppel, 2004, 2007). According to this model, the superior temporal gyrus subserves the early cortical stages of speech perception. The dorsal stream extends towards the inferior parietal and posterior frontal lobe, while the ventral stream is located in the middle and inferior temporal cortices. The dorsal stream is involved in the sensory-motor aspects of language processing, while the ventral pathway is involved in higher-level conceptual and semantic processes related to speech comprehension.

Friederici et al. (2017) note that our understanding of the neural basis of language processing is still under debate and propose that this is due to ill definitions of what 'language' means. Many studies on language processing equate language to 'speech' or 'communication'. The authors propose that language should be described rather as a 'biologically determined computational cognitive mechanism that yields an unbounded array of hierarchically structured expressions' and support their definition with evidence from recent neuroimaging studies (Friederici et al., 2017). Importantly, they emphasise that speech is just one way of externalising language, one of the other ways being sign language.

1.1.3.2. Sign language processing in the brain

Similar to how scientists learned about spoken language in the brain first by studying patients with brain lesions, the first researchers who studied sign language processing in the brain looked at signers with brain lesions in the areas of interest and quickly established that the left hemisphere dominance is preserved in signers (Corina, 1998). Six patients with damage to the left hemisphere experienced difficulties in sign language processing but no problems with non-linguistic visuo-spatial processing and the aphasiac behaviour in these patients matched with the expected distributions in the Broca's and Wernicke's areas (Poizner et al., 1990). The first studies of neural organisation for language in deaf signers suggested that language processing in the brain is modality-independent and generally left-lateralised (Corina, 1998; Hickok et al., 1998a, 2001; Poizner et al., 1990). Sign language and speech in hearing and deaf individuals activate very similar left hemisphere regions during object naming (Emmorey et al., 2003), sign comprehension (Petitto et al., 2000), sentence comprehension (MacSweeney, Woll, Campbell, McGuire, et al., 2002; Neville et al., 1998), lexicosemantic processing (Leonard et al., 2012), and other functions (see Corina & Knapp, 2006; Emmorey, 2002 for a review).

Within the left hemisphere, there is evidence of specific involvement of the left inferior and superior parietal lobule (SPL) in sign language perception, rehearsal, and production (Braun et al., 2001; Buchsbaum et al., 2005; Emmorey et al., 2007; L. Li et al., 2016). A PET study by (Emmorey et al., 2007) showed that the left temporal cortex and the left inferior frontal gyrus are recruited for the overt naming of objects in American Sign Language (ASL) and in English in 29 deaf signers and 64 hearing speakers of English. Their results revealed that while similar left hemisphere areas support language production in both modalities, certain regions in the left parietal lobe are more engaged in sign production in comparison to speech production. The authors concluded that the observed activation in the supramarginal gyrus and the superior parietal lobule is linked to modality-specific processing of sign language, namely, phonological processing and monitoring of motoric output. There is also other evidence of the left supramarginal gyrus being important for phonological processing in sign language (Cardin, Smittenaar, et al., 2016; Corina et al., 1999; MacSweeney, Capek, et al., 2008).

However, the left hemisphere dominance for sign language has been questioned by neuroscientists due to the visuo-spatial features of sign language and the fact that the right hemisphere is the dominant hemisphere for spatial processing (Heilman, 1985; Ringman et al., 2004). Studies have shown that linguistic and visuo-spatial abilities are dissociated in the brain of deaf signers (Hickok et al., 1995) while some discourse processing deficits can be caused by damage to the right hemisphere (Hickok et al., 1999). The latter finding agrees with the studies of spoken language processing in hearing individuals as the right hemisphere is also involved in spoken language discourse processing (Beeman, 1993; St George et al., 1999). In relation to the hypothesis that visuo-spatial aspects of sign language processing can engage the right hemisphere to a greater extent, one study (Emmorey et al., 2002) has shown greater right hemisphere involvement in producing classifier constructions, while another did not find such effects in the left hemisphere (MacSweeney, Woll, Campbell, Calvert, et al., 2002). It has been suggested by (Campbell et al., 2008) that the observed effect was due to the task requirements (production vs comprehension) and greater mapping demands on the regions in the right parietal lobe.

Other authors have suggested the involvement of the right hemisphere in syntactic processing by describing activations in the right hemisphere which occur when deaf and hearing native signers are watching videos of sentences in sign language (Neville et al., 1998). However, it is difficult to drive conclusions from this study due to the methodology constraints. It has been noted (Hickok et al., 1998b) that the presentation of the English sentences was word-by-word and lacked prosodic information in contrast to the natural presentation of sentences in American Sign Language. Moreover, a subsequent study that employed a different methodology (sentence-long utterances presented face-to-face in both languages) has not found differences in the extent of hemisphere recruitment (MacSweeney, Woll, Campbell, McGuire, et al., 2002).

Many researchers study questions related to the influence of language modality on language reorganisation in the brain by conducting experiments with hearing native signers who represent a population with a typical sensory experience and no delay in language acquisition. Hearing native signers are born to deaf parents and, similarly to deaf native signers, acquire sign language from birth but do not have the same sensory developmental experience of being deaf. Two PET studies of hearing children of deaf parents who used Swedish Sign Language showed different findings: in the first study (Söderfeldt et al., 1994), no significant differences have been found between spoken and signed language processing, while in the second study with a more advanced design (Söderfeldt et al., 1997), sign language comprehension resulted in greater activation of the posterior and inferior temporal and occipital areas (visual areas), while spoken language comprehension activated the superior temporal cortex (auditory areas) more. This finding reflects differences in the modalities of the two languages, however, as expected, both languages recruited similar perisylvian regions. This demonstrates that the differences in language processing between the two languages arise from the differences in the modality of the input rather than functional processing. The findings agree with other studies, for example, (MacSweeney, Woll, Campbell, Calvert, et al., 2002), or a study by Karen Emmorey and colleagues (Emmorey et al., 2014), which found greater activations in the superior temporal cortex bilaterally for speech and bilateral occipital-temporal cortex for sign language in a group of hearing native signers.

Overall, studies on sign language processing in the brain typically focus heavily on the following questions: Do sign language and spoken language engage the same brain regions? Do hearing and deaf individuals process language differently? It is generally believed that signed languages make use of the same left perisylvian regions of the brain that spoken language recruits and that differences between signed and spoken language arise from their input modalities (Campbell et al., 2008; Rönnberg et al., 2000).

1.1.3.3. The effect of age of acquisition on language processing in the brain

Age of acquisition has great implications for various processes, including language processing in the brain. Rare examples of so-called 'feral children' prove that linguistic isolation leads to impoverished language development when it comes to grammatical structures: for example, Genie, who was kept in isolation since she was an infant up to her adolescence and demonstrated extensive vocabulary but did not develop age-appropriate syntax. The presence of few syntactic markers in her speech and a general lag in syntactic development in comparison to her vocabulary development (Fromkin et al., 1974) point to the effects of missing the critical period of language acquisition (Friedmann & Rusou, 2015). There was evidence that Genie's language was right-lateralised, while she was strongly right-handed, and it was hypothesised that Genie's left hemisphere lost the ability to acquire language function (Curtiss, 2014; Fromkin et al., 1974). Genie's case gave rise to new ideas and hypotheses about language development, including neural development, but systematic studies with large samples are necessary to drive conclusions about the effects of late language acquisition on the brain. Deaf individuals who often acquire their first language late due to lack of language access resulting from environmental factors are a population where these effects can be detected.

While this thesis reviews and investigates evidence related to functional brain studies, it is important to mention that delayed first language acquisition in deaf individuals also affects the structural development of the brain, with changes in tissue concentration in the occipital cortex (Pénicaud et al., 2013). This area has been linked to the recruitment of language processing in deaf individuals with a late age of language acquisition (Mayberry et al., 2011).

MacSweeney and colleagues (MacSweeney, Waters, et al., 2008) investigated phonological processing in deaf signers and found that late deaf signers activated the left inferior frontal gyrus more than native deaf signers in a phonological judgement task in British Sign Language and in English, which the groups encountered at a late age (upon entering primary school). A major finding from this study was that the effect extends onto neural processing from both first and later learned languages. Another study that used a grammaticality judgement task and a phonological judgement task in American Sign Language found the opposite pattern, with signers with earlier sign language acquisition onset activating the left posterior superior temporal cortex more (Mayberry et al., 2011). They also activated the left visual cortex more.

Earlier I discussed that the effects of the modality of language in language organisation in the brain are often studied in hearing signers to compare individuals with the same sensory experience. The effects related to the age of acquisition in the brain may also be difficult to disentangle from the effects of the sensory experience of deafness (Neville & Bavelier, 2002). One study, aimed at controlling for this factor (Twomey et al., 2020), examined the effect of age of acquisition (early/late) and hearing status (hearing/deaf) on the neural system supporting language in 52 hearing and deaf proficient signers who watched British Sign Language sentences or strings of meaningless signs while being in an fMRI scanner. The differences in hearing status will be described in the next subsection. The authors found the effect of age of acquisition in the occipital part of the left intraparietal sulcus in both hearing and deaf signers (late > early acquisition). It suggests that both hearing and deaf late learners use more shallow visual processing resources when watching sentences and non-linguistic sign input, as suggested by (Mayberry et al., 2011). Another effect of age of acquisition was found in a regions-of-interest analysis in the deaf group only, in the left posterior superior temporal cortex, with activation greater for early signers than for late signers for signed sentences. For hearing signers, who all had robust first language acquisition, the responses did not differ between early and late signers and were similar to responses in deaf early signers. The study argues that the left posterior superior temporal cortex only shows a 'native-like' response in a later learnt language if there is robust early language experience.

A previous study of hearing signers by (A. J. Newman et al., 2002) showed recruitment of the right angular gyrus in early hearing but not late hearing signers for viewing ASL sentences.

Discrepancies in patterns of brain activity for early and late deaf signers (MacSweeney, Waters, et al., 2008; Mayberry et al., 2011), and early and late hearing signers (A. J. Newman et al., 2002; Twomey et al., 2020) across the studies, point to the importance of methodological choices and accounting for differences in language proficiency and sensory experience in conducting and interpreting studies on the influence of different factors on language processing in the brain.

1.1.3.4. The effects of sensory experience on language processing in the brain

In the study discussed in the previous subsection by Twomey and colleagues (2020), the main findings were related to differences between early and late signers, rather than hearing status. Hearing status was significant for areas of the superior temporal cortex in both hemispheres, mainly in the middle superior temporal cortex, and for both British Sign Language sentences and nonsense sign sequences, suggesting that the main effect of hearing status was not related to language processing and was related to hearing participants suppressing task-irrelevant auditory activity. They also found a significant interaction between hearing status and stimulus type in the left precentral gyrus, but the interaction was driven by the opposite patterns of activations in the two groups but the differences in activation were not significant. The presence of the latter effect suggests differences in the recruitment of the left prefrontal cortex for language between deaf and hearing signers in sign language perception, but more research is needed to investigate these effects (Twomey et al., 2020). Overall, the main findings in this study were related to differences between early and late signers, rather than hearing status (see discussion below).

Another way of studying the effect of sensory experience in the brain is by comparing groups of deaf participants with different language experiences to hearing controls. Cardin et al. (2013) compared a group of deaf native signers, a group of deaf non-signers who grew up using spoken language and did not know any sign language, and a group of hearing non-signers. In such a comparison, the effects arising from the sensory experience of deafness would be present in both groups of deaf participants but not in the hearing group. Watching sign language stimuli activated the right posterior superior temporal cortex in both groups of deaf signers in this study, suggesting that this is a plasticity effect driven by the sensory experience of deafness, rather than the language experience of the participants. There were linguistic effects in the left superior temporal cortex and in the left superior temporal sulcus that were driven by experience with sign language in deaf signers and not their sensory experience.

In a different study, on linguistic and non-linguistic working memory, Cardin and colleagues (2018) showed activation for working memory for signs vs objects in deaf individuals in the bilateral superior temporal cortex. The authors suggest that rather than it being a language effect, it is a consequence of the sensory experience of deafness, as the effect was present for working memory of both signs and non-signs and it is unlikely that only deaf participants verbalised their responses, causing superior temporal cortex activations (see Cardin et al. (2018) for a discussion).

Taken together, these studies indicate that changes in linguistic processing in the brain can be driven by the sensory experience of deafness and arising plasticity effects, and we can dissociate these effects by comparing different populations.

1.1.4. Conclusion

One of the major discoveries in the field of sign language research and the neurobiology of language in general has been the fact that sign language processing largely relies on the same brain areas as spoken language, such as the core language network of the left perisylvian regions in the brain. Nevertheless, differences in aspects related to the modality of the input, such as aspects of phonological sign processing, have been described. There is also an indication of the effect of hearing status on language processing in the brain.

Both behavioural and neuroimaging studies described in this section demonstrate the importance of early language acquisition for the development of successful linguistic processing in deaf individuals. The timing of first language acquisition influences both the functional (Mayberry et al., 2011) and neuroanatomical brain development (Pénicaud et al., 2013). These findings have great implications for educational and political practices that can aid parents of deaf children in constructing home and school environments that lead to better developmental outcomes and highlight the risks of linguistic deprivation (Humphries et al., 2014). In the context of this thesis, research studies on language processing in deafness contributed to developing hypotheses that take into account the importance of language access and subsequent language proficiency. The research questions explored in the following chapters were raised with the intent to add to the discussion of the effects in neural processing resulting from varying scenarios of language development, following that language acquisition experiences have been shown to have long-range outcomes for language proficiency in adulthood (Cormier et al., 2012; Emmorey, 2002; Mayberry, 1993, 2010;

Mayberry & Lock, 2003). Taken together, the evidence presented above suggests a need to consider various factors, such as hearing status and different dimensions of language experience, when studying the effects of deafness and language in cognition and brain reorganisation (Lyness et al., 2013).

1.2. Executive function in hearing and deaf individuals

Executive function is a term that refers to a set of complex and interrelated mental processes that underlie cognitive control of goal-directed behaviour (Best & Miller, 2010; Buss & Lowery, 2020; Diamond, 2013). Executive function develops from early childhood, with rapid changes from birth to the age of 5 (Buss & Lowery, 2020), but continues to develop through adolescence (Selemon, 2013; Zelazo & Carlson, 2012). It is critical for many aspects of human functioning, and it has been shown to be related to language development (Im-Bolter et al., 2006), mathematical abilities (Bull & Scerif, 2001), and academic achievement (Best et al., 2011).

Executive function has been known to be impacted in different populations, especially in children with neurodevelopmental disorders (see Sun & Buys, 2012; Zelazo, 2020 for reviews). Deaf native signers, both children and adults, can demonstrate performance in executive function tasks that is not different from the performance by their hearing peers (children: Marshall et al., 2015; adults: Cardin et al., 2018), but generally, deaf children show deficits in executive function (Beer et al., 2014; Burkholder & Pisoni, 2003; Figueras et al., 2008; Jones et al., 2020; Kronenberger et al., 2013). Critically, studies have shown that performance in executive function tasks is mediated by language in deaf children (Botting et al., 2017; Merchán et al., 2022) (see *1.2.6. Executive function and deafness* for a detailed discussion). Understanding how the relationship found between executive function and language in deaf children manifests later in life and in the brain has great implications for the fundamental understanding of the interactions between these cognitive processes. Moreover, it is unclear whether delays in language acquisition in deaf individuals remain to affect different aspects of executive function in adulthood.

In two of the three studies presented in this thesis (Chapter 2 and Chapter 4), I will investigate the three core executive functions *(working memory, inhibition,* and *cognitive flexibility),* as well as *planning,* which is often considered a higher-order executive process that is built on the foundation of the core executive functions. These studies are aimed at contributing to the existing literature on the effects of sensory and language experiences on executive function by investigating behavioural and neural processes in deaf and hearing individuals.

In this subsection of the introduction, I will introduce components of executive functions and will reference models of their conceptualisation and development. Then I will give an overview of the specific components of executive function that will be investigated in the studies presented in this thesis, namely, working memory, inhibition, switching, and planning. I will define each of these executive function components, describe the most common tasks measuring them, including the tasks that were used in this thesis, and explain the importance of each executive function for developmental outcomes and their relationship to other cognitive abilities. I will also provide an overview of the neural mechanisms behind executive processing. Finally, I will demonstrate how executive function has been linked to language abilities and deafness, the two main topics of investigation in this thesis. Throughout the thesis, I will predominantly focus on non-verbal executive function: the tasks chosen for the studies presented here deliberately do not include any linguistic components in their stimuli because the knowledge of English and British Sign Language varied across our participants.

1.2.1. Definitions

Executive function (or executive functions, often also referred to as ‘cognitive control’ or ‘executive control’) is a term used to describe complex top-down mental functions that are responsible for the control of cognitive processes and behaviour (Best & Miller, 2010; Buss & Lowery, 2020; Diamond, 2013). They are involved in achieving a particular goal through coordination of several subprocesses (Elliott, 2003). Even when used in a singular form, the term ‘executive function’ acts as an umbrella term that defines several separate cognitive processes. The concept of executive function can be defined in different ways, but coordination, control, and goal-oriented behaviour are integral to executive processing (Elliott, 2003). Indeed, these terms are included in many of the definitions proposed over the years (from Delis, 2012):

‘Executive function (EF) serves as an umbrella term to encompass the goal-oriental control functions of the PFC [prefrontal cortex]’ (Best et al., 2009).

‘Executive function is considered to be a product of the coordinated operation of various processes to accomplish a particular goal in a flexible manner’ (Funahashi, 2001).

‘Executive control involves the active maintenance of a particular type of information: The goals and rules of a task’ (Miller & Cohen, 2001).

Due to differences in conceptualisation and operationalisation of executive function, researchers that study components of executive control often name different sets of what they consider to be executive functions (Demetriou et al., 2019). Baggetta and Alexander (2016) conducted a review of studies on executive functions to describe how they are conceptualised and operationalised in current research. Within 106 studies reviewed, they found 25 different attributes used to describe the composition of executive function, with some of the attributes referenced only once (e.g., on-line processes (C. A. Clark et al., 2010) or self-regulatory abilities (R. Kelly et al., 2011). They also described four major spheres of influence of executive function: goal-directed behaviours; action and thoughts; cognition; and self-regulation of behaviours, cognition, and emotions (Baggetta & Alexander, 2016).

Some of the most well-known executive functions models are the older cognitive models that focus on attentional control (Demetriou et al., 2019), such as the models proposed by Alan Baddeley (Baddeley & Hitch, 1974), Michael Posner (Posner, 1980) and Tim Shallice (Shallice & Burgess, 1991). The earlier models described executive functions as a single system or resource (V. Anderson et al., 2010), for example, the 'central executive' (Baddeley, 1986) or 'supervisory system' (Norman & Shallice, 1986). Later models suggested that executive processing relies on several distinct components (Baddeley, 1998; Miyake et al., 2000; Shallice & Burgess, 1996) although some researchers still favoured a unitary view (Duncan et al., 1996). Brain studies (Fair, Dosenbach, et al., 2007) and models of executive function development (Buss & Spencer, 2018; Zelazo et al., 1997) have been substantial contributors to the reconceptualization of executive functioning in recent decades.

One of the most dominant accounts of executive function composition comes from the work of Miyake and colleagues (2000). They highlight the core three executive function components: *working memory/updating* (constant monitoring and rapid attention/deletion of working memory contents), *shifting/cognitive flexibility* (shifting flexibly between tasks or mental sets), and *inhibition* (deliberate overriding of dominant or prepotent responses). These components, according to the authors, can provide valuable insights into the nature and organisation of individual differences in executive function (Miyake & Friedman, 2012), although there can be other executive functions including 'higher-level concepts' like planning (Miyake et al., 2000). Using factor analysis, Miyake et al. (2000) identified working memory, shifting, and inhibition as clearly separable but related executive functions. This theoretical framework views executive function as a system consisting of multiple interrelated components, and the nature of their interactions is described as ‘unity and diversity’ (Miyake et al., 2000). Unity of executive function presupposes the existence of common mechanisms across different components, as reflected by the fact that the core executive functions are moderately correlated and show activation in overlapping brain areas, but there are clear neural and correlational dissociations between them (He et al., 2021; Saylik et al., 2022; see Friedman & Miyake, 2017 for a review).

1.2.2. The development of executive function

Executive function rapidly develops during infancy and continues developing and strengthening throughout childhood and into early adulthood (Best & Miller, 2010; de Luca & Leventer, 2008). Adele Diamond proposed that executive function consists of distinct components with their own developmental trajectory and rate (Diamond, 2006, 2013). In agreement with Miyake and colleagues (2000), she considers working memory, inhibition, and shifting to be the main components of executive function. They are developed in infancy and act as the foundation for more complex, higher-order executive skills (Demetriou et al., 2019), such as planning, reasoning, and problem solving (Diamond, 2013), which fully develop at a later stage (Cuevas & Bell, 2014).

There are studies that suggest a more unitary account of executive function in preschool children (C. Hughes & Ensor, 2007; Shing et al., 2010; Willoughby et al., 2010 but see Lerner & Lonigan, 2014 for evidence for a 'multi-dimensional' construct with distinct components in preschool children). There has been partial support for an integrative, or hierarchical, account of executive function development in children, following Miyake and colleagues' (2000) framework, with the model being a good fit for children from 8 to 13 years old (Lehto et al., 2003), and older children (Huizinga et al., 2006), but in the latter study it was true for working memory and shifting, but not for inhibition (see Best & Miller, 2010 for a review). Overall, following the review of studies of executive function in different ages by Best and Miller (2010), inhibition seems to show a unique pattern of development, with significant advances during earlier years of life and less change later, while working memory and shifting develop more gradually. Creating a comprehensive integrated developmental theory of executive functions is a challenging task due to the multi-component nature of executive function (Buss & Spencer, 2018), despite there being a substantial amount of literature on the topic, especially studies of children up to the age of five (Best & Miller, 2010).

Overall, components of executive function may be at least partially distinct in children, but the degree of unity and diversity would vary from age to age, and evidence needs to be considered across all age groups (Best & Miller, 2010).

Other accounts of executive function development are also mostly non-unitary. The Cognitive Complexity and Control (CCC) theory suggests that different components of executive function integrate and interact so that a person can achieve a goal or solve a problem (Zelazo & Frye, 1997, 1998). Zelazo and Frye (1998) emphasise the role of language, suggesting that the development of a complex rules-based system in childhood provides a foundation for complex cognitive skills. This theory can bring important considerations into the studies described in this thesis, as it proposes a direct link between language development and executive processing.

Zelazo and colleagues (Zelazo et al., 1996) also emphasise the ability of children to reflect on their own experiences which is important for solving some executive function tasks. The authors use the Dimensional Change Card Sorting Task (DCCS, Frye et al., 1995) to demonstrate how children at the age of three do not switch to sorting the cards according to a new rule (e.g., by colour instead of by shape), while four- and five-year-olds can successfully switch to the new rule. Here, the use of private speech can aid the reinforcement of the rules, further emphasising the role of language in this theory.

Using the same DCCS task, Buss and Spencer (2018) proposed a Dynamic Field Theory (DFT) of executive function that can integrate different components underlying executive function. Their model of executive function development includes visual-cognitive and dimensional attentional systems that are responsible for developmental changes in dimensional attention (Buss & Spencer, 2018). Crucially, the Dynamic Field Theory model allows linking the dynamics of the model to changes in the brain. The authors emphasise that in order to be able to formalise a theory of executive function development, it is crucial to not only understand the development of each component but also their interaction over time and include both behavioural and neuroimaging evidence in the analysis.

1.2.3. The components of executive function

1.2.3.1. Working memory

Working memory is one of the most researched cognitive systems that have a key role in cognition. Some researchers do not include working memory in the list of executive functions by suggesting that these cognitive processes are closely related but are separate due to different theoretical and experimental origins (García-Madruga et al., 2016).

Working memory can be defined as a cognitive system that 'actively holds information in mind to facilitate cognitive operations' (Spencer, 2020). Working memory has a strictly limited capacity (Cowan, 2010). Its capacity is similar in signed and spoken language (Andin et al., 2013; Boutla et al., 2004; see Rudner, 2018 for a review on working memory in linguistic and non-linguistic manual gestures and Rudner et al., 2009 for a review on working memory, deafness, and sign language). Different tasks of working memory capacity include complex-span tasks (Redick et al., 2012) and updating n-back tasks (Kirchner, 1958) (see Redick & Lindsey, 2013 for a review). The complex span paradigm has been used in working memory studies for many years (A. R. A. Conway et al., 2005; Daneman & Carpenter, 1980), with n-back tasks being more common in recent years. The complex span paradigm combines the recall of items while also performing a secondary processing task. In the n-back tasks, participants decide if the item that they are currently presented with matches the item that had been presented *n* items back.

A meta-analysis by Redick and Lindsey (2013) suggested that complex span and n-back tasks should not be used interchangeably but other researchers noted that low correlations among different factors do not provide evidence for the existence or absence of a common construct. Using latent factors analysis, Schmiedek et al. (2014) showed that both types of tasks are valid indicators of working memory, consistent with a hierarchical model of working memory, with a general working memory factor on top. A latent variable approach and confirmatory factor analyses support the concept of a general working memory capacity factor common for these types of tasks (Wilhelm et al., 2013).

Visual working memory, which is of particular interest for this thesis, is a cognitive system that holds visual information during short-term delays and compares visual items that cannot be simultaneously foveated (see Luck & Vogel, 2013 for a review). It can be studied with the use of different secondary tasks that may involve verbal resources or spatial integration. Visuo-spatial working memory can be tested by a spatial integration task that involves a presentation of a series of grids with several squares filled in colour, and participants are instructed to mentally combine the squares into a shape (Fedorenko et al., 2007). Such a task would be involving spatial processing resources rather than the use of verbal working memory, in contrast to arithmetic or linguistic paradigms (Fedorenko et al., 2007).

Working memory is subject to individual differences and is closely related to other higher-order cognitive functions, such as fluid intelligence (Engle et al., 1999; Fukuda et al., 2010; Kane et al., 2007). Crucially, it is also linked to academic attainment: working memory is a more powerful predictor of academic success than IQ at the start of formal education (Alloway & Alloway, 2010) and mathematical achievement in children (Bull et al., 2008).

1.2.3.2. Inhibitory control

Inhibitory control relates to the ability to control, suppress, or *inhibit* a response to goal-irrelevant stimuli in order to achieve a goal (Diamond, 2013; N. P. Friedman & Miyake, 2004; Nigg, 2000). It rapidly develops earlier in life, throughout infancy and preschool years, with significant improvements in response inhibition from 3 to 6 years old (Wiebe et al., 2012). While the more dramatic improvements take place early in life, inhibitory control continues developing throughout childhood and adolescence (Best & Miller, 2010) and is critical for cognitive development. Some authors suggest that the development of inhibitory control precedes more complex cognitive functions (Klenberg et al., 2001).

The organization of inhibitory control can be seen through either a unitary or a two-factor model. Most researchers divide inhibitory control into response inhibition and interference control (N. P. Friedman & Miyake, 2004; Nigg, 2000; Wiebe et al., 2008), although the two measures often show strong positive correlations.

Response inhibition (also sometimes called 'behaviour inhibition' or 'motor inhibition' (Tiego et al., 2018); see Tiego et al. (2018) for an overview of components of inhibitory control) relates to the suppression or inhibition of a prepared or initiated action or response (Miyake et al., 2000; Raud et al., 2020). It is often studied with behavioural tasks employing stop-signal paradigms (Logan & Cowan, 1984), where participants, while pressing a button, prepare for a sudden stop following a short stop signal delay on a minority of trials, or go/no-go paradigms (Trommer et al., 1988), where participants respond to most of the stimuli by pressing a button (go-trials) and have to control (inhibit) the response to a few of the stimuli (no-go trials). In these tasks, participants prepare or initiate a response and have to stop (inhibit) it. Both paradigms require a large number of trials before a stop or a no-go trial appears in order to lead the participants to make commission errors – pressing the button in the trials where they are not supposed to. Reaction times or correct trials can also be tracked but are not usually used as a measurement of inhibitory control (Meule, 2017). Recently it has been suggested that the stop-signal and go/no-go task paradigms capture different mechanisms, with the go/no-go paradigm relating to 'action restraint' and the stop-signal paradigm reflecting 'action cancellation' (Schachar et al., 2007) and the tasks involving different neural dynamics (Raud et al., 2020) and being differently affected by additional factors, such as, for example, exposure to negative stimuli (Littman & Takács, 2017).

The other component of inhibitory control – interference control (also called 'attentional inhibition' or 'interference suppression') – refers to the ability to resist interference from distracting stimuli (Tiego et al., 2018). Interference control is commonly measured with reaction time conflict tasks such as the Stroop task (Stroop, 1935), the flanker task (Eriksen & Eriksen, 1974), or the Simon task (J. R. Simon, 1969) that is used in this thesis. These tasks require selective attending and responding to one aspect of the stimuli with ignoring other, distracting characteristics. For example, in a typical Simon task, participants are asked to respond to one feature of the stimulus (usually colour) with their right or left hand. The stimuli are presented at different parts of the screen: either on the same side as the required response (congruent trials) or on the opposite side (incongruent trials). The interference effect is then measured by the differences in reaction time between the two conditions. Such tasks are designed to be applicable to different age ranges and even if the Stroop task typically involves reading, it can be modified to use with children who do not have the reading skills required for doing the task successfully (Gerstadt et al., 1994). The Stroop task is the most difficult task out of the three, while Simon is the one showing the earliest maturation (Ambrosi et al., 2020).

Inhibitory control has been linked in preschool-age children to theory of mind, even when controlling for age, gender, verbal ability, motor sequencing, family size, and performance on pretend-action and mental state control tasks (Carlson & Moses, 2001). In 3-year-old children, performance on a non-verbal inhibitory control task was explained by language abilities (Watson & Bell, 2013). The same pattern of association between inhibitory control and language outcome has been demonstrated longitudinally in 3-year-olds after one year (Gandolfi & Viterbori, 2020). Inhibitory control has been associated with math skills and math achievement in preschool children from ethnic minority backgrounds and in early adolescents (Oberle & Schonert-Reichl, 2013).

1.2.3.3. Cognitive flexibility

Cognitive flexibility is the ability to switch flexibly between tasks, mental sets, rules, responses, and strategies (Davidson et al., 2006; Miyake & Friedman, 2012; Zelazo, 2015). There are other names for this executive function, such as shifting, set-shifting, mental set-shifting, mental flexibility, attention switching, or task switching.

Cognitive flexibility tasks for very young children (under 3 years of age) are rare due to their complexity (Cuevas & Bell, 2014) and because cognitive flexibility, even when memory demands are very low, has a longer developmental progression (Davidson et al., 2006). It is argued to build on the other two core executive functions, working memory and inhibitory control (Diamond, 2013).

Shifting tasks are typically designed in a similar manner and always involve two phases: forming a mental set with an association between a stimulus and a response and shifting to a new mental set that is in conflict with the first set (Garon et al., 2008). While forming the first set, participants ignore distractors and hold the set in their working memory. Shifting tasks differ on the working memory demands and the amount of conflict between the sets (Garon et al., 2008). The conflict can also appear at different stages – at the perceptual (attention shifting) or at the response stage (task shifting) (Rushworth et al., 2005), with some tasks involving different forms of shifting to different extents (Garon et al., 2008). The most widely used paradigm is the task-switching paradigm (Kiesel et al., 2010; Vandierendonck et al., 2010), used in this thesis, where participants switch between two or more tasks and the switching produces a measurable cognitive cost – the 'switch cost' calculated as the difference in reaction times and/or error rate between switch trials and repetitions (Jersild, 1927; Spector & Biederman, 1976; Vandierendonck et al., 2010).

A meta-analysis showed that cognitive flexibility predicts reading and math performance in children (Yeniad et al., 2013), and it has also been linked to high-school science and math achievement in Chinese adolescents (J. Li et al., 2020).

1.2.3.4. Planning

Researchers often limit *core* executive functions to the three components discussed above (working memory, inhibition, and cognitive flexibility/shifting; see Miyake et al., 2000). It has been suggested that these core executive functions serve as a foundation for other, higher-order executive functions, such as reasoning, problem-solving, and planning (Collins & Koechlin, 2012; Cristofori et al., 2019; Diamond, 2013; Lunt et al., 2012).

Planning is largely believed to be a more complex aspect of executive function that may require activation of other executive functions, such as inhibitory control and working memory (Carlson et al., 2004; Hackman et al., 2015; Hartshorne & Germine, 2015; Miyake et al., 2000). The ‘problem-solving’ framework gave planning a large role, as it defines executive function as a macro-construct that includes four phases of problem-solving, with planning being the second phase, among problem representation, execution, and evaluation (Zelazo et al., 1997).

Planning is most commonly measured with so-called ‘tower tasks’. The participant is instructed to solve a puzzle that has a defined starting state and a defined goal state with the fewest number of possible moves. The Tower of Hanoi task invented by a French mathematician Edouard Lucas in 1883 (Hinz, 1992) involves disks of different sizes that are stacked on three pegs, and the task was to move the disk from the left peg to the right one while aiming to do it by the fewest possible number of moves and adhering to specific rules: 1) only move one disk at a time and 2) not to place a larger-sized disk on top of a smaller one. The task has been modified over the years, and now many versions of the tasks exist. The other task that is commonly used for assessing planning abilities is the Tower of London task (Shallice, 1982) (used in this thesis) which was used to assess skills associated with frontal lobe deficits in patients. Like the Tower of Hanoi, this task requires the individual to arrive from the starting configuration to the target one in the fewest number of moves, and the rule is that only one object can be moved at a time. The number of pegs or balls/beads could be manipulated by the researcher.

It has been suggested that tower tasks do not measure just planning abilities, but other processes as well, such as working memory and inhibition (Hill & Bird, 2006). In a study that specifically looked into the contribution of working memory and inhibition to performance in the tower tasks, working memory and inhibition explained over half of the variance in the Tower of London-Revised task (Welsh et al., 1999), while another study found working memory, inhibition and fluid intelligence to be accounting for variance in the Tower of Hanoi tasks, but only fluid intelligence accounted for variance on the Tower of London task (Zook et al., 2004). These findings agree with the frameworks that highlight the importance of low-level executive function components in building the foundation for higher-order executive functions, such as planning (Carlson et al., 2004; Hackman et al., 2015; Hartshorne & Germine, 2015; Miyake et al., 2000).

In terms of the timeline of development, planning was suggested to be developing similarly to theory of mind (Atance & O'Neill, 2001). Researchers have found a link between the two, with planning competence related to false-belief task performance (Bischof-Köhler, 1998; Perner & Lang, 2000), but it has been noted that the study did not control for age and verbal ability, as well as differences in inhibitory control that could be relevant for the planning task used. Another study that has taken these into account showed that while inhibition task results were significantly related to both theory of mind and planning, the planning abilities did not share any variance with theory of mind (Carlson et al., 2004).

Planning abilities undergo substantial development in childhood and adolescence at the ages of 4, 5-8, and 9-12 and continue to improve until ages 15-17 (de Luca et al., 2003; Juric et al., 2013; Luciana, 2003; Luciana et al., 2009), although on harder problems the performance can continue improving into the early 20s (Albert & Steinberg, 2011).

Planning abilities have been shown to have a larger impairment in children exhibiting arithmetic difficulties (Sikora et al., 2002), suggesting a relationship between these skills. Children with a specific reading comprehension deficit performed poorly in a planning assessment, with the difference staying significant after controlling for phonological processing (Locascio et al., 2010).

1.2.3.5. Other executive functions and the cool versus hot distinction

The executive function components discussed in this thesis are related to goal-directed mental processes that require critical analysis and conscious cognitive control. They have traditionally been the focus of research on executive function and are referred to as 'cool' or 'cold' (Peterson & Welsh, 2014). Working memory, inhibition, cognitive flexibility, and planning are all part of this subgroup of executive function and more often appear among the 'core' executive functions, with the exception of planning. Nevertheless, other mental processes that are often included among the components of executive processing should be mentioned to give a more complete overview of the topic and the state of the field.

Other executive functions fall into a separate group of so-called 'hot' executive functions. As one may deduct from the name, hot executive functions involve emotional behaviour, such as motivation- and reward-related components. A degree of independence has been suggested in terms of behavioural performance in cold and hot executive functions (Cardoso et al., 2015). One of the mental processes that can be considered a hot executive function is decision-making, as it involves emotional processing (Chan & Stevens, 2008; Fonseca et al., 2012; Happaney et al., 2004). Even though not everyone includes decision-making on the list of executive functions, it has been linked to cognitive control (Steinbeis & Crone, 2016), and both decision-making and executive functions are subserved by the prefrontal cortex (Koechlin, 2014). Recently, there has been an increase in research interest in relation to decision making (Kerr & Zelazo, 2004). Decision-making is often measured with the Iowa Gambling Task (Bechara et al., 1994), and researchers have been trying to assess whether, and to what extent, it reflects executive processing. A study using structural equation modelling concluded that the Iowa Gambling Task is 'a multi-trait task involving novel problem-solving and attentional domains to a greater extent, and executive functioning to a lesser extent' (Gansler et al., 2011).

Recently, researchers have proposed a model that describes the organisation of executive functions in the brain according to the hot versus cool distinction, with the lateral prefrontal cortex along with the dorsal anterior cingulate cortex being more relevant for cold executive functions, and the medial-orbital prefrontal cortex along with the ventral anterior cingulate cortex, as well as the posterior cingulate cortex being more related to hot executive functions (Salehinejad et al., 2021).

1.2.4. The neural underpinnings of executive function

Early research on executive function and the brain showed strong evidence that executive function is critically dependent on the prefrontal cortex of the human brain (Baddeley, 1986; Kolb & Whishaw, 1998; Stuss et al., 1986), to the point that the terms 'executive function' and 'frontal lobe function' could be used synonymously (Elliott, 2003). The prefrontal cortex is also known as the association cortex of the frontal lobe, and it is a part of the brain that experiences the greatest expansion both in evolutionary terms and in brain maturation in individuals (Fuster, 2002), with significant maturation happening in adolescent years (Gogtay et al., 2004), continuing to 25 years of age (Arain et al., 2013), rather than earlier in life, as in regions involved in attention, sensory processing, and language development (Best & Miller, 2010). Structurally, the volume of the prefrontal cortex and its thickness are associated with better executive performance, according to a meta-analysis of structural neuroimaging studies (P Yuan & N Raz, 2014).

Developments in neuroimaging techniques, methods, and theories, as well as studies of populations with neurological disorders, have led to suggestions that the frontal cortex is functionally and anatomically linked to the striatum (Alexander et al., 1986; Elliott, 2003). In recent literature, it has been actively suggested that executive function is not exclusively linked to frontal areas of the brain but rather involves a more extensive network of frontal-cortical and subcortical circuitries (Leh et al., 2010).

In relation to specific executive function components and their localisation in the brain, working memory has been linked to activity in the prefrontal cortex (Petrides et al., 1993; see D'Esposito et al., 2000 for a review), as well as in other areas, such as the parietal cortex (Passingham & Sakai, 2004). Memory load and its behavioural measure are associated with activity in dorsolateral and left inferior regions of the prefrontal cortex in a linear manner (Braver et al., 1997). In another study, effects of memory load were found in the dorsal prefrontal cortex only in the encoding period of the task, but not during the delay or response stages (Rypma & D'Esposito, 1999).

The architecture of working memory and its implications for behaviour have been also studied in participants with brain lesions, showing that dorsolateral prefrontal cortex damage is associated with deficits in the manipulation of verbal and spatial knowledge, and the left hemisphere was shown to be critical for manipulating information specifically in working memory (Barbey et al., 2013). The common finding is that the dorsolateral prefrontal cortex plays a crucial role in working memory, and it has been suggested that it aids in the maintenance of information by directing attention to internal representations of stimuli and motor plans (Curtis & D'Esposito, 2003).

Over the years, neuroimaging studies provided evidence for activations for working memory in multiple regions in sensory, parietal, and prefrontal cortices (Christophel et al., 2017). It is suggested that working memory shows a gradient pattern in brain activations, with sensory areas encoding low-level sensory features and prefrontal regions processing more abstract and response-related aspects (Christophel et al., 2017).

Inhibitory control is impaired in patients with frontal lobe damage (M. A. Conway & Fthenaki, 2003; Floden & Stuss, 2006). Literature highlights the crucial role of the right inferior frontal cortex in response inhibition (Aron et al., 2004; Garavan et al., 1999; Konishi et al., 1999). Inhibitory control has also been suggested to operate across several functionally distinct regions within the prefrontal cortex, with damage to the lateral prefrontal cortex being related to inhibitory control in attentional selection, while damage to the orbitofrontal cortex being related to inhibitory control in affective processing (Dias et al., 1997).

Cognitive flexibility has been shown to involve a distributed network of regions, including the prefrontal cortex, anterior cingulate cortex, posterior parietal cortex, and the basal ganglia in a study involving a task-switching fMRI paradigm (Leber et al., 2008). Lesions to the frontal lobe and basal ganglia have been shown to impair different aspects of cognitive flexibility (Eslinger & Grattan, 1993). A meta-analysis of brain regions associated with different types of tasks described an extensive network of fronto-parietal regions, including the inferior frontal junction and posterior parietal cortex as those active in different types of switching, while the dorsal portion of the premotor cortex and frontopolar cortex for specifically perceptual switching, as opposed to response and content switching (Kim et al., 2012). The left dorsolateral prefrontal cortex, left posterior parietal cortex, and pre-supplementary motor area were involved in rule representation and rule-switching in both children and adults (Wendelken et al., 2012).

Finally, planning, as investigated through the Tower of London task, has been shown to activate the dorsolateral prefrontal cortex, the anterior part of the cingulate cortex, the cuneus and precuneus, the supramarginal and angular gyrus in the parietal lobe, and the frontal opercular area of the insula (Lazeron et al., 2000). The same study investigated the activations in individual subjects, and the dorsolateral prefrontal cortex was activated in each of them. In a different study, the activations in the prefrontal cortex were modulated by the cognitive load, with both left and right prefrontal cortices being equally activated for moderate and difficult problems, but activation on the right being differentially attenuated during easy-problems solution (S. D. Newman et al., 2003). This led the authors to suggest that the right prefrontal cortex is responsible more for the generation of the plan, while the left prefrontal cortex is more involved in the execution. An overview of lesion studies on planning with the use of the Tower of London task and a meta-analysis of 31 neuroimaging datasets (Nitschke et al., 2017) suggest that the mid-dorsolateral part of the prefrontal cortex specifically is involved in planning bilaterally. Other regions reported include frontal eye fields, supplementary motor area, precuneus, caudate, anterior insula, and inferior parietal cortex in addition to left rostro-lateral prefrontal cortex activations. Another fMRI study (O. A. van den Heuvel et al., 2003) found activations in the dorsolateral prefrontal cortex, striatum, premotor cortex, supplementary motor area, precuneus, and inferior parietal cortex, with the increase in activity in these regions being associated with the increase in load.

1.2.5. Executive function and language development

The relationship between executive functions and language is one of the major themes of this thesis. The existence of a relationship between executive functions and language has been highlighted by a variety of studies on developmental disorders (e.g., attention deficit hyperactivity disorder: Barkley, 1997), with developmental language disorder being the most relevant for this thesis, as it suggests a causal link between language development and executive functions outcomes in a population with a unique developmental experience specifically in relation to language.

In children with developmental language disorders, age, severity, and persistence of their disorder determine whether they show deficits in executive function, particularly in interference control and working memory (Blom & Boerma, 2020). Deficits in inhibition and working memory are present in both monolinguals and bilinguals with developmental language disorder (Boerma & Blom, 2020). Updating and inhibition correlate with linguistic and narrative measures in children with developmental language disorder (Marini et al., 2020). In a different study, children with developmental language disorder performed on par with their typically developing peers in tasks on inhibition but had lower scores in working memory, updating, monitoring, and verbal fluency measures (Ralli et al., 2021).

In individuals with Down Syndrome, reported deficits in verbal components of the working memory system have been shown to be independent from their general verbal abilities deficits (Lanfranchi et al., 2010), suggesting that hearing or speech impairments are not a cause of the memory deficits in this population (Jarrold & Baddeley, 2001). Contrary to this conclusion, in another study on individuals with Down Syndrome and Williams Syndrome, verbal development was correlated with cognitive flexibility and working memory (Landry et al., 2012). The authors suggest, in agreement with Lev Vygotsky's verbal mediation framework (Vygotsky, 1962, 1978), that verbal development is a strong predictor of cognitive flexibility and working memory in individuals with Down Syndrome and Williams Syndrome.

Difficulties in language, communication, and social function are among the main characteristics of autism spectrum disorder (American Psychiatric Association, 2013; Frith, 2003; Prelock & Nelson, 2012). According to parent reports, executive processing in children with autism spectrum disorder is strongly linked to deficits in communication (Gilotty et al., 2002). It has been suggested that children with autism spectrum disorder may not be using verbal mediation, or inner speech, while solving tasks (Joseph et al., 2005; Whitehouse et al., 2006). The mediating role of language has been demonstrated in specific components of executive function, such as working memory, when assessed both directly and indirectly (Akbar et al., 2013). However, another study looking into the relationship between executive function, language, and social performance did not find strong associations between these factors (Landa & Goldberg, 2005), while describing defects in individuals with autism spectrum disorder in components of language (expressive grammar, figurative language) and executive processing (planning, spatial working memory). Other components of language processing, such as vocabulary, syntax, and pragmatics have been related to working memory, shifting, and inhibition in individuals with autism spectrum disorder (L. Friedman & Sterling, 2019). It is evident that the profiles of executive function and language skills can be very mixed in this population, but it is commonly suggested that the lack of inner speech can be a significant limiting factor in the development of various executive function components in individuals with autism spectrum disorder (Pellicano, 2012), while other authors note that directionality of the relationship between language and executive function is still unclear, and interventions that target linguistic abilities improve executive function, and vice versa (L. Friedman & Sterling, 2019).

Since Vygotsky's proposal that language and shared communication assist children in their cognitive development (Vygotsky, 1962), more researchers highlighted the importance of language in the facilitation of different cognitive functions, including executive function (e.g., the Cognitive Complexity and Control (CCC) theory by Zelazo & Frye, 1997, see section 1.2.2 above). Nevertheless, the developmental relationship and interactions between executive function and language abilities remain unclear due to contradicting evidence. In a study of children with varying language abilities, including children at risk of dyslexia, executive function but not language predicted later attention and behaviour ratings, and the latent variables approach showed little evidence of strong reciprocal influences between executive function and language (Gooch et al., 2016). Executive function can predict language development (Im-Bolter et al., 2006; McEvoy et al., 1993), and language can facilitate performance in executive function tasks in children (Brace et al., 2006) and has been shown to have direct and indirect effects on later executive function development (Kuhn et al., 2014).

Investigating the relationship between executive function and language is one of the main themes of this thesis. Studying executive function and language in deaf individuals can provide insights into the nature of this relationship from a population with a unique language experience that arises from environmental constraints rather than neurodevelopmental processes.

1.2.6. Executive function and deafness

Deaf children are often reported to experience delays in developing executive function (Beer et al., 2014; Boerrigter et al., 2023; Botting et al., 2017; Burkholder & Pisoni, 2003; Figueras et al., 2008; M. S. Harris et al., 2013; Hintermair, 2013; Jones et al., 2020; Kronenberger et al., 2013) and other cognitive domains (C. M. Conway et al., 2011; Gottardis et al., 2011; Gremp et al., 2019; Kritzer, 2009; Santos & Cordes, 2022). When designing studies on executive function in deafness, researchers often compare children with cochlear implants to hearing controls (Kronenberger et al., 2013), compare children with cochlear implants to non-implanted deaf children and hearing controls (Figueras et al., 2008), or treat implanted and non-implanted deaf children as a single group (Botting et al., 2017; Merchán et al., 2022). Independently of the approach to group composition, studies including large samples of deaf children with varying language backgrounds generally show that deaf children perform lower than their hearing peers on a variety of tasks tapping into different cognitive functions, such as visuo-spatial working memory, planning, inhibition, and cognitive shifting (Botting et al., 2017; Figueras et al., 2008; Kronenberger et al., 2013).

Based on the evidence of delays in sequence learning in deaf children, Conway and colleagues (2009) proposed *the auditory scaffolding hypothesis* (C. M. Conway et al., 2009): auditory experience is suggested to support the development of temporal and/or sequencing abilities due to the inherently temporal and sequential nature of sound signals. Furthermore, it has been proposed that a lack of auditory input may negatively affect processing capacities beyond the auditory system and lead to more extensive delays in cognition, affecting also executive function (C. M. Conway et al., 2009; Kral et al., 2016). *The auditory connectome model* (Kral et al., 2016) suggests an association between sensory deprivation and cognitive abilities but explains it through the neural connection between the auditory regions and other areas in the brain. According to Kral and colleagues (2016), changes to these connections and sensory loss may lead to 'downstream, distal, cognitive effects' on such aspects as working memory and attention. Such ideas have been collectively labelled as *the auditory deprivation hypothesis*, in an opposition to *the language deprivation hypothesis* (Hall et al., 2017). The auditory scaffolding hypothesis has been criticised for confounding the auditory experience with language experience in deaf children. Children with cochlear implants who showed lower implicit learning performance than their hearing peers were born to hearing parents (C. M. Conway et al., 2011). Hall and colleagues (2018) suggested disentangling the effects of language and auditory deprivation on implicit sequence learning by including a group of deaf native signers in the analysis, addressing the theoretical issues of the study. They found no compelling evidence for reliable group differences between native deaf signers, oral cochlear implant users, and hearing children (Hall et al., 2018). In a study on executive function, Hall and colleagues (2018) used a parent report measure BRIEF (Behavior Rating Inventory of Executive Function) (Gioia et al., 2000) and performance-based assessments, and reported that deaf native signers had lower scores on the inhibition and working memory subscales of the parent reports relative to hearing controls, though not to test norms (Hall et al., 2018). Deaf native signers did not perform worse than children with cochlear implants or hearing children on the performance-based assessments, and for many parent-reported executive function components, they had higher scores than children with cochlear implants. The scores on the inhibition and working memory subscales in the hearing group were also atypically high, which can be attributed to the recruitment area being next to a major university. It should be noted that one study (Kalback, 2004) demonstrated that performance-based measures of language predicted the performance-based measures of executive function more than the language measures predicted BRIEF ratings developed to measure everyday behaviour associated with executive functioning. Several performance-based studies on working memory in children and adults suggest that these skills are not impaired in native and/or early deaf signers (Andin et al., 2013; Boutla et al., 2004; Marshall et al., 2015), and inhibitory control skills are mediated by receptive vocabulary, but not deafness, in deaf children (Merchán et al., 2022). Research on self-reported executive functions in deaf college students does not reveal significant population differences between hearing and deaf students but suggests that native signers from deaf families may have an advantage over deaf students from hearing families (Hauser et al., 2008). The above-mentioned theories emphasising the role of auditory perception in cognition would suggest that if we do observe deficits in executive function in deaf individuals, these would be explained by hearing loss. While deaf children have been shown to perform worse in executive function tasks, in studies that controlled for language abilities, performance in executive function tasks is often found to be mediated by language (Botting et al., 2017; Merchán et al., 2022), or associated with it (Figueras et al., 2008). This leads to a conclusion that the effects arise between higher-order processes, with *language* deprivation leading to deficits in cognition, rather than *auditory* deprivation (Hall et al., 2017). The fact that studies with deaf children with varying language backgrounds show the link between language abilities and executive function performance and native signers often do not demonstrate deficits in these domains indicates that it is language experience that impacts executive function in deaf children (Figure 1.2), although the exact nature of this relationship and its progression at other ages is unclear. Being able to describe the long-lasting effects of early language experience on executive function is critical for our understanding of the complex relationships between executive function and language. This thesis attempts to do so by studying a population that often experiences impoverished language access and subsequent delays in language and executive function development.

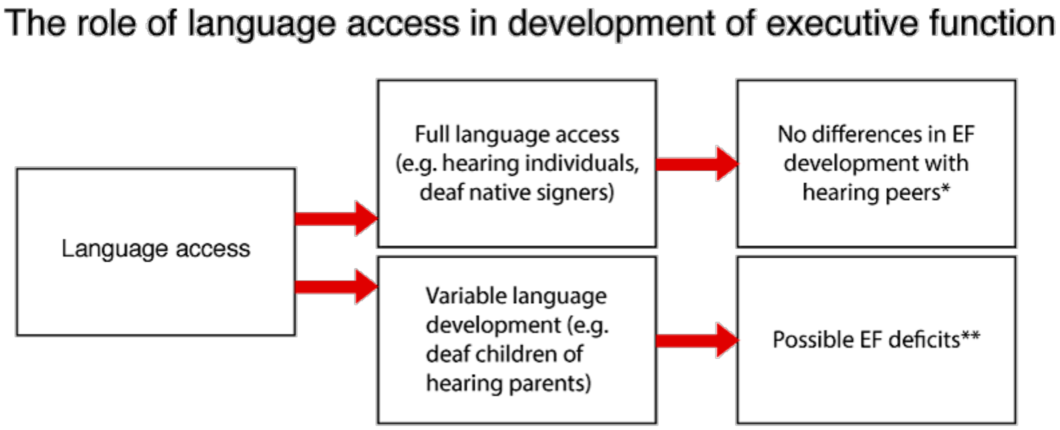

Figure 0.2. Possible pathways for the influence of early language experience on executive function development. EF=executive function. *Marschal et al. (2015) **Figueras et al. (2008); Botting et al. (2017); Merchán et al. (2022).

Specific components of executive function can reveal important interactions with language development. Working memory has been actively studied in relation to deafness and has been shown to be intact in deaf native signing children (Marshall et al., 2015). Visuo-spatial working memory specifically is intact in deaf adolescents with an unspecified language acquisition background, while phonological and writing spans are affected in this population (Alamargot et al., 2007). In deaf children with cochlear implants, both verbal and visual working memory skills are below hearing children's (Cleary et al., 2001). Critically, working memory ability and language ability are related in children with cochlear implants (Pisoni & Cleary, 2003; Pisoni & Geers, 2000).

In deaf adults, working memory performance, investigated with lexical item tasks, is not different from that of the hearing controls (Boutla et al., 2004; Rudner et al., 2007, 2013). A study using a digit-based operation span task instead of linguistic stimuli (Andin et al., 2013) also did not find differences in performance between deaf signers and hearing non-signers on a digit-based operation working memory task but found differences in their short-term memory, in agreement with previous evidence. This means that overall working memory processing capacity is not impacted by short-term memory storage differences in these populations, even in digit spans. The study by Andin and colleagues (2013) also highlighted that working memory tasks provide a better measure of cognitive function in deaf participants due to simple digit-span tests being affected by the phonological similarity effect (M. Wilson & Emmorey, 1997) that can explain differences in short-term memory between different modalities (Rudner et al., 2009). It is important to note that in the Andin et al. (2013) study all deaf participants were native or early (< 3 years old) signers, with only one participant learning sign language before the age of five.

Changes in the brain that arise from altered sensory experiences are contributed to the effects of cross-modal plasticity. Cross-modal plasticity refers to the process in which brain regions that typically process sensory information from one modality start processing information in a different modality (Merabet & Pascual-Leone, 2010; Rauschecker, 1995, 2002). There are two theoretical accounts of cross-modal plasticity, one of them suggesting that the sensory-deprived regions preserve their initial function but adapt to processing input from another modality (preservation of function) (Pascual-Leone et al., 2005; L. Renier et al., 2014; Ricciardi et al., 2009). The other account (functional change) suggests that sensory-deprived areas in the brain can also change their function (see Bedny, 2017 for a review). The evidence that leads to that account is of particular interest to this thesis, as some of it comes from the study of working memory in deafness, where deaf participants recruited auditory cortices for visual working memory (Andin et al., 2021; Buchsbaum et al., 2005; Cardin et al., 2018; Ding et al., 2015). In one study, bilateral recruitment of the superior temporal gyrus also correlated with behavioural performance (Ding et al., 2015), emphasising the functional relevance of the involvement of the auditory cortex in cognition. While the auditory cortex in hearing individuals is believed to store information in working memory (sensorimotor theories of working memory: D'Esposito & Postle, 2015), in deaf individuals it seems to also have a cognitive role.

In Cardin et al. (2018), there was no evidence of working memory for sign language recruiting specific brain regions: activations related to working memory were found in the superior temporal cortex of deaf individuals independently of the linguistic content of the stimuli, suggesting that working memory for sign language involves brain areas responsible for visuo-spatial and language processing in deaf people. Moreover, in that study, the activity in the fronto-parietal areas typically recruited for working memory was weaker in deaf individuals (Cardin et al., 2018). Taken together, the findings in the fronto-parietal and auditory regions from Cardin et al. (2018) suggest a redistribution of cognitive load between these areas.

A more recent study on working memory used a sign-based n-back task in deaf signers and hearing non-signers and did not replicate the finding of differences in fronto-parietal areas in deaf individuals (Andin et al., 2021) but also showed plasticity effects in bilateral temporal regions for high-resolution linguistic stimuli, suggesting a use of a verbal strategy in solving the task in the deaf group, while occipito-parietal regions had stronger activation in the hearing group and for low-resolution stimulus, pointing to a visual strategy. The reorganised region of the secondary auditory cortex in the deaf group did not show increased involvement for higher load, suggesting a more general role in sensory-perceptual processing in this task.

The evidence from studies on working memory and deafness that supports functional shift for working memory in the auditory cortices of deaf individuals and redistribution of resources between the fronto-parietal and temporal areas should be reconsidered in light of recent research, including research conducted by our group throughout the duration of my doctoral program. This research has been published (Manini et al., 2022), and Chapter 2 mentions the main findings relevant to the topic of this thesis and this section in particular.

1.2.7. Conclusion

Evidence from studies of neurodevelopmental disorders often links executive functions with language. Disentangling neurodevelopmental and environmental effects and determining directionality has proven difficult in these populations. The existing research in deaf children suggests that in this population if deficits relating to executive function arise, they are driven by a lack of language access. There is no research on the effects of language on executive function in deaf adults, apart from evidence from studies that do not find differences between native and early signers with no developmental delay and hearing adults. This thesis directly addresses this lack of literature on deaf adults, aiming to provide insights into the effects of language experience on executive function at a later stage of development, analysing behaviour and brain function (Chapter 2 and Chapter 4). It also explores the effects of sensory and language experience on functional connectivity between different areas in the brain in deaf adults during different cognitive states (Chapter 3 and Chapter 4), including the execution of executive function tasks (Chapter 4).

1.3. The role of sensory experience in brain reorganisation

The studies presented in this thesis are part of a larger project focusing on changes in brain organisation that are related to the sensory experience of deafness. The analysis and findings related to the processing of executive function in the brain and changes driven by the experience of deafness are described in detail in a paper from our research group, where the analysis was predominantly conducted by Dr Barbara Manini (Manini et al., 2022). The methods and results relevant to this thesis are summarised in Chapter 2. Most of the analyses described in this thesis are on changes in functional connectivity and consider both the sensory experience of deafness and language experience (Chapter 3, Chapter 4), therefore functional connectivity will receive a larger introduction and discussion throughout the thesis, with the next section of the introduction being dedicated to it. Nevertheless, understanding the effects of sensory experience on functional brain reorganisation is crucial for the research presented in this thesis, as the interpretation of the effects of sensory experience on functional connectivity would not be complete without considering findings on cross-modal plasticity in visual and cognitive tasks in deafness. Here I will give a brief overview of these findings because the more relevant studies have been covered in the subsections above and will be discussed throughout the thesis. A thorough account of the mechanisms guiding cross-modal changes in the brain is given in a review authored by our research group (Cardin et al., 2020). I will focus on studies of congenitally and early deaf and blind individuals, to provide an account of brain reorganisation in populations that did not have experience with the auditory or visual modality from birth or very early childhood, similar to the deaf participants recruited for the studies presented in this thesis.

1.3.1. Cross-modal reorganisation in sensory-deprived cortices in blindness and deafness

Blind and deaf individuals do not receive sensory input from the environment from all modalities. Understanding how the brain adapts to reconstructing the environment from other modalities provides insights into the ability of the brain to change and can aid interventions. In blind individuals, visual cortices respond to other modalities, i.e., sound and touch (Amedi et al., 2003, 2007; Collignon et al., 2007).

Changes in brain function in deaf individuals are of particular interest to this thesis. It is long-established that the auditory cortex in deaf individuals responds to other modalities, such as vision and touch (Bottari et al., 2014; Cardin et al., 2013; Karns et al., 2012; MacSweeney, Woll, Campbell, McGuire, et al., 2002). Such changes in deaf and blind individuals are called cross-modal plasticity, a phenomenon referring to the adaptation of sensory cortices to processing input in a different modality.

There are two theoretical accounts of cross-modal plasticity that are described in detail in our review (Cardin et al., 2020) and summarised here:

- *Functional preservation.* There is substantial evidence of changes in the sensory cortices of blind and deaf individuals where sensory regions preserve their initial function while shifting to processing in a different modality (e.g, voice identity processing in face processing in blind individuals: Benetti et al., 2017; visual rhythm processing in the auditory cortex in deaf individuals: Bola et al., 2017; spatial processing in blind individuals: Collignon et al., 2011; see also Pascual-Leone et al., 2005; Renier et al., 2014; Ricciardi et al., 2009). Preservation of function can also be observed for higher-order functions such as language, following the evidence of recruitment of superior temporal regions for sign language in deaf native signers but not in hearing native signers (Cardin et al., 2013; Cardin, Orfanidou, et al., 2016; MacSweeney, Woll, Campbell, McGuire, et al., 2002; Twomey et al., 2017) (see Corina & Knapp, 2006) and the evidence of recruitment of regions that process visually-presented letters in sighted individuals for letters presented in Braille (Burton et al., 2002; Sadato et al., 1996) or through sound (Striem-Amit et al., 2012).

- *Functional change.* This process refers to a change in function in the same sensory cortices (see Bedny, 2017 for a review). There is evidence of functional change in working memory (Amedi et al., 2003), maths (Kanjlia et al., 2016), and language processing in the visual regions in blind participants (Amedi et al., 2004; Bedny et al., 2011, 2012, 2015; Röder et al., 2002), and in deaf individuals for visual working memory (Buchsbaum et al., 2005; Cardin et al., 2018; Ding et al., 2015) (see the discussion above).

Taken together, evidence from these studies suggests that plasticity in the visual and auditory cortices of blind and deaf individuals, respectively, can manifest differently in the same regions. The mechanisms allowing these processes to co-exist are unclear, but they could be supported by distinct populations of neurons, cytoarchitectonic layers in the same region, or by the same underlying function, as was suggested in our review (Cardin et al., 2020). Further studies of cross-modal plasticity in deaf and hearing individuals, as well as using animal models, can shed light on the mechanisms of cross-modal plasticity in the sensory-deprived brain.

1.3.2. Reorganisation in the other parts of the brain in deaf and blind individuals

In both deaf and blind individuals, changes in the brain caused by altered sensory experience are not limited to sensory-deprived cortices. In blind individuals, the activations for low-demand listening conditions are reduced in the auditory cortex (A. A. Stevens & Weaver, 2009). There is contradicting evidence for auditory motion processing in planum temporale (F. Jiang et al., 2014, 2016; Poirier et al., 2006). The sound processing is stronger in the occipital cortex (in agreement with the cross-modal plasticity evidence presented in the section above) but reduced in the medial temporal cortex (van der Heijden et al., 2020). The planum temporale shows different patterns of activation for binaural spatial processing between blind and sighted individuals (van der Heijden et al., 2020). Other studies did not find changes in brain activity for sound localisation and auditory motion processing in blindness (Gougoux et al., 2005; Poirier et al., 2006; Weeks et al., 2000). In relation to somatosensory cortices, regions of the secondary somatosensory cortex (S2) were deactivated by a non-Braille tactile discriminative task, and the occipital regions were activated in the blind, while sighted participants demonstrated an opposite pattern (Sadato et al., 1998).

Deaf individuals show greater recruitment of the motion-selective area MT/MST (the medial temporal/medial superior temporal cortex) during monitoring moving stimuli in comparison to hearing controls (Bavelier et al., 2000). In an event-related brain potentials (ERPs) study, of a visual attentional task, deaf participants displayed significantly larger effects in the occipital regions in both hemispheres (Neville & Lawson, 1987). While both deaf and hearing individuals recruited the fronto-parietal network for short-term memory processing, deaf signers activated passive memory storage areas in the frontal brain areas more than hearing controls during linguistic memory short-term memory encoding, but generally showed less strong activation than hearing controls in a number of regions including the dorsal aspect of the inferior parietal cortex, cerebellum, and the left middle temporal gyrus (Bavelier et al., 2008). During recall, signers activated twice as many voxels in the fronto-parietal short-term memory regions as hearing controls (Bavelier et al., 2008).

Cardin et al. (2018) showed that while deaf native signers, hearing native signers, and hearing non-signers all activated the fronto-parietal areas typically recruited for working memory tasks for linguistic and non-linguistic working memory processing, deaf participants recruited several fronto-parietal regions less. The study demonstrates that recruitment of the superior temporal cortex for working memory can be accompanied by weaker engagement of the fronto-parietal network for working memory. In a study on visual working memory for signs that also found cross-modal reorganisation of auditory cortices in deaf signers, there was no evidence for weaker activation of fronto-parietal areas in deaf signers (Andin et al., 2021). There was also weaker activation in the visual cortices in the deaf group, suggesting different strategies for solving the task (linguistic for the deaf group and visual for the hearing group, as the stimuli were linguistically meaningful just for one of them).

Taken together, these findings indicate that there is evidence of plasticity effects in the intact sensory systems and in higher-order cognitive areas, but this evidence is inconclusive. Higher imaging resolution and methodologically optimised studies for detecting subtle differences can shed light on these discrepancies (van der Heijden et al., 2020).

1.3.3. Conclusion

Cross-modal plasticity is a process where modality-specific brain regions (e.g., auditory cortices in hearing individuals and visual cortices in sighted individuals) start processing input from a different modality in individuals who do not receive input from the 'typical' modality of that region. There are two theories of cross-modal plasticity: functional preservation and functional change, the former is supported by the evidence of the sensory regions keeping their function, while the latter suggests that these regions can also take on higher-order cognitive functions. In our review of these theories, we conclude that physiological and anatomical mechanisms can support the co-existence of these mechanisms in the brain (Cardin et al., 2020). There is also evidence of changes in the non-sensory cortices of deaf and blind individuals, suggesting that brain reorganisation in sensory deprivation is not limited to the auditory and visual cortices.

The theories of cross-modal plasticity and brain reorganisation in the sensory-deprived and non-deprived cortices in deaf and blind individuals can be supported by evidence from functional connectivity studies, described in the next section and in Chapter 3 and Chapter 4 of this thesis.

1.4. Functional connectivity in deaf and hearing individuals

The studies described in this thesis use behavioural and neuroimaging methods to answer questions relating to brain reorganisation, executive function, and language in deafness. Most of the research presented in this thesis (Chapter 3 and Chapter 4) focuses on the exploration of functional connectivity in the brain. Here I present an account of the history and basic notions in functional connectivity research, together with a review of relevant literature.

1.4.1. Functional connectivity in the brain and its measures

Recently, the interest in studying the connectivity patterns of organisation of the whole brain has been growing, with new techniques and analysis methods emerging in the field of cognitive neuroscience. Connectivity in general relates to the study of interactions between different brain regions. There are different types of connectivity in the brain (from Lang et al., 2012):

- *Anatomical connectivity,* or *structural connectivity*. Structural connectivity is used for discovering synaptic contacts between neurons or fiber tracks that connect neurons in distant areas of the brain. These connections are typically stable in short time scales, but a large degree of plasticity can be observed over time. Structural connectivity describes physical connections or interactions between anatomical areas of the brain and is often researched using diffusion magnetic resonance tractography methods (see Yeh et al., 2021 for a recent review on structural connectivity mapping using diffusion MRI).
- *Functional connectivity.* Functional connectivity measures the linear temporal correlations, or temporal dependency, between activation patterns in different, anatomically separated, but functionally linked regions in the brain. The statistical dependencies can fluctuate substantially over small periods of time (milliseconds to seconds), with electroencephalography (EEG) and magnetoencephalography (MEG) being used to estimate fluctuations over a timescale of milliseconds and fMRI capturing patterns occurring over a timescale of seconds (Britz et al., 2010). The durations of stable functional network emergence in the brain typically start in phases of approximately 10 seconds and greater (Chu et al., 2012).
- *Effective connectivity.* Effective connectivity aims to investigate causal interactions between populations of neurons. It is a method that can create

visualisations of directional effects within a network. See Friston (2011) for a review on functional and effective connectivity.

Functional connectivity is commonly studied with the use of resting-state functional MRI (Biswal et al., 1995). The core difference between the typical fMRI paradigms and resting-state fMRI is that previously scientists studied mostly how brain areas respond to the stimulus (that can often be a cognitive task). A graduate student Bharat Biswal decided to do something drastically different and asked participants *not* to do anything in the scanner and just lie still. Contrary to what could be suggested – the brain activity at rest being mostly unstructured – it was evident that there are correlations in fluctuations of brain activity in the regions that are known to function together. Different regions of the sensorimotor system in the brain fluctuated synchronously without an explicit sensorimotor task (Biswal et al., 1995). This story is often described as the beginning of the study of resting-state connectivity (Shen, 2015).

Resting-state fMRI measures spontaneous low-frequency fluctuations (< 0.1 Hz) in the BOLD (blood-oxygen-level-dependent) signal (Cordes et al., 2001). The BOLD signal is the basis of both task-based and functional connectivity fMRI methods but there are significant differences between the two approaches. Task-based fMRI requires the presence of a task or an activity (e.g., finger-tapping), while resting-state fMRI does not require explicit input or engagement. Signals that are often treated as noise in task-based fMRI – low-frequency spontaneous fluctuations in the BOLD signal – are treated as meaningful in resting-state fMRI, thus it improves the signal-to-noise ratio. Some of the clear advantages of the resting-state fMRI are that it does not require performing each task separately to investigate separate functions (e.g., language and visual networks can be studied within one session of resting-state fMRI) and that different populations (e.g., children, patients with low IQ or even those in a coma) can be studied without the need to perform difficult cognitive tasks.

Recently, functional connectivity studies have started to incorporate task-based connectivity into the analysis. Coactivation of different brain areas can be studied by analysing time fluctuations both at rest and during the execution of a task. Resting-state network topography is generally believed to be preserved (S. M. Smith et al., 2009) although functional connectivity does reconfigure to accommodate task demands (Gonzalez-Castillo & Bandettini, 2018). These processes are known to be small but, despite their small size, they have functional relevance (e.g., task-related changes in network organisation increase the prediction accuracy of cognitive tasks; Cole et al., 2021) (see Chapter 4 for a more thorough discussion of task-related connectivity changes).

Functional connectivity can be analysed with the use of different analyses, such as seed-based analysis, independent component analysis, and graph theory measures. There are other approaches that will not be covered here, such as regional homogeneity analysis (see Azeez & Biswal, 2017 for a review of resting-state analysis methods).

One of the most common approaches to functional connectivity analysis that is also of particular importance for this introduction, as it is the method employed in this thesis (Chapter 3 and Chapter 4), is based on **seed-based connectivity measures** (Biswal et al., 1995; Fox et al., 2005). This model-based method involves selecting a region of interest (ROI) in the brain and calculating linear correlations of this region with other voxels in the entire brain or with other regions. This method is entirely dependent on user-defined regions of interest. The most common metric for this type of analysis is *seed-based connectivity maps* but there are other measures, such as *generalised psycho-physiological interactions* (gPPI) maps. Both analyses will be used in this thesis (seed-based connectivity maps in Chapter 3 and Chapter 4, and gPPI in Chapter 4).

Seed-based connectivity maps are computed as the Fisher-transformed bivariate correlation coefficients between an ROI BOLD timeseries and BOLD timeseries of individual voxels or other regions of interest (Nieto-Castanon, 2020). gPPI measures task-modulated effective connectivity between an ROI and every other voxel or another region in the brain by using a separate multiple regression model for each target voxel/region BOLD timeseries (Nieto-Castanon, 2020). It measures changes in functional association strength covarying with the experimental factor in tasks and is used for event-related designs. The model includes the selected task effects convolved with a canonical hemodynamic response function, the seed ROI BOLD timeseries, and the interaction term specified as their product (PPI term). gPPI generates a map of regression coefficients associated with the interaction term. The full description of these methods can be found in the 'Handbook of functional connectivity Magnetic Resonance Imaging methods in CONN' (Nieto-Castanon, 2020).

An alternative approach to measuring functional connectivity in the brain is the employment of the **Independent Component Analysis (ICA)** (van de Ven et al., 2004). It is a statistical method that uses mathematical algorithms to decompose signals from the whole brain into independent components. Unlike seed-based analyses, where single interactions between the seed region and the rest of the brain are analysed, ICA looks at multiple voxel-to-voxel interactions at once. It is a data-driven method that is based on a blind source separation algorithm that allows measuring whole-brain connectivity with all components considered. Results from seed-based and ICA studies are generally similar but not identical and conceptually different (van de Ven et al., 2004), with seed-based measures reflecting a sum of ICA-derived within-network connectivities and between-network connectivities (Joel et al., 2011).

The increasingly popular approach in connectivity analysis is the employment of **graph theory** tools (Rubinov & Sporns, 2010). Graph theory is used to apply mathematical models of complex network functions to brain data. Graph theory is looking at the relationships between nodes (brain regions) and edges (connections) in a brain network. It evaluates various graph parameters (e.g., average path length, clustering coefficient, levels of modularity) that can reflect different aspects of connectivity in the brain. The major difference between the seed-based approach and the graph theory approach is that seed-based analysis focuses on the strength of correlation, and graph theory aims at investigating the topological properties of brain networks. The stability of graph theory metrics over time has not been established (Dimitriadis et al., 2017; Garrison et al., 2015; Hallquist & Hillary, 2018) (see Fornito et al., 2013 for a discussion on the key issues associated with graph theory models).

1.4.2. Large-scale brain networks

If initially the networks in the brain were defined by their activations during tasks, with the introduction of resting-state fMRI they could be defined in the absence of explicit tasks, and the brain regions would show similar patterns of activations when at rest and during task execution, maintaining the signature of functional organisation. The fluctuations within networks are present even when the subject is sleeping or under anesthesia.

Infant studies suggest that some networks, such as sensorimotor or auditory, are established fairly early (as early as at birth). Other networks may take much more time to develop (W. Gao et al., 2015). The study by Gao and colleagues (2015) shows that while activity in some core regions of the default mode network is synchronised in the first year of life, some refinements continue for at least another year. This could be seen as in agreement with the fact that children learn to recognise their own reflections between 20 and 24 months of age (Amsterdam, 1972).

Some developmental and neurocognitive conditions are associated with the disruption of specific networks. For example, the default mode network is affected in Alzheimer's disease, depression, autism, and schizophrenia (D. Zhang & Raichle, 2010).

The most often- and consistently-reported resting-state networks in the brain include the motor network, the occipital networks, the default mode network, the attention networks, the executive-control network and the sensorimotor network (D. M. Cole et al., 2010; M. P. van den Heuvel & Pol, 2010).

The sensorimotor network

The sensorimotor network, or the somatomotor network, is one of the robust brain networks that has been identified by the first resting-state functional connectivity study of Biswal et al. (1995): the BOLD fluctuations in left motor cortex were found to be correlated with the right motor cortex. Generally, high correlations are observed between the motor regions (left and right precentral gyri: Lowe et al., 1998) and somatomotor regions, anterior and posterior to the central sulcus. It extends to the supplementary motor area, and certain auditory regions may also be included in the sensorimotor network in studies that explore resting-state functional connectivity (e.g., the superior temporal gyrus) (Uddin et al., 2019).

The visual network

The visual network includes the occipital lobe, with striate and extrastriate cortex, and may additionally include the lateral geniculate nucleus of the thalamus (Uddin et al., 2019).

The auditory network

The auditory network is not always defined as a separate network but is believed to involve the bilateral superior temporal cortex (Mantini et al., 2007).

The salience network

The salience network consists of the dorsal anterior cingulate cortex and anterior insula (Menon & Uddin, 2010). It has a key role in detecting salient events and regulating the switching between other networks, it is critical for rapid changes in behaviour, the generation of appropriate responses, and cognitive control (Menon & Uddin, 2010). The network is often described as the ventral attention network (VAN), or the latter can be defined separately as the temporo-parietal junction and the ventral fronto-parietal cortex (Corbetta et al., 2008; Downar et al., 2000).

The dorsal attention network

The dorsal attention network includes the superior parietal lobule extending into the intraparietal sulcus, middle temporal area (MT+), and the putative frontal eye fields, and can additionally include ventral premotor cortex and other regions, such as the right dorsolateral prefrontal cortex and superior colliculus (Uddin et al., 2019). It is synonymous with the 'dorsal fronto-parietal network' (Corbetta & Shulman, 2002) that has a role in visuo-spatial attention and applying top-down selection for sensory stimuli and linking them with responses (Corbetta et al., 2008). The dorsal and ventral attention networks are believed to be interacting systems, and the interaction patterns are dependent on the task demands (Vossel et al., 2014).

The control network

The control network, or the executive network, involves the lateral prefrontal cortex, the middle frontal gyrus (including rostral and DLPFC), and the anterior inferior parietal lobule, extending into the intraparietal sulcus. Additional regions may be the midcingulate gyrus, as well as the dorsal precuneus posterior inferior temporal lobe (anterior to MT+), the dorsolmedial thalamus, and the head of the caudate (Uddin et al., 2019). This network is critical for executive function.

The default mode network

The default mode network (DMN) was initially described by Raichle colleagues (2001). It involves the posterior cingulate cortex, medial prefrontal cortex, and the posterior extent of the inferior parietal lobule, along with regions including the inferior frontal gyrus, middle temporal gyrus, superior temporal sulcus, and parahippocampal cortex. The additional possible regions are areas dorsal and ventral to the posterior cingulate, the precuneus and retrosplenial cortex, hippocampus superior/middle frontal gyrus, ventral frontal cortex, anterior temporal lobes, and temporo-parietal junction (Andrews-Hanna et al., 2014; Buckner et al., 2008; Spreng et al., 2013; Uddin et al., 2019; Yeo et al., 2011). The default mode network demonstrates increased activity only when the subject is not performing a task, thus it is often also referred to as a 'task-negative network' (Fox et al., 2005). It has also been noted that this network participates in social cognition (Spreng & Andrews-Hanna, 2015) and self-referential processes (Buckner et al., 2008; Sheline et al., 2009).

The language network

Similar to the auditory network, the language network is not always defined as a separate network. The language network of the brain, also called the left perisylvian language network, involves the inferior frontal gyrus pars triangularis and opercularis (so-called ‘Broca’s area’), the middle frontal gyrus, posterior regions of the superior and middle temporal gyri (so-called ‘Wernicke’s area’) and temporal regions, namely the superior temporal sulcus and the anterior temporal lobe (Jackson et al., 2016; Price, 2012) and other additional, less consistently reported regions can include dorsal areas such as the superior frontal gyrus extending into the pre-supplementary motor area and the frontal pole (Branco et al., 2020). Some authors suggest that the language regions in the brain can be divided into a core language network and additional areas that support communication (Hagoort, 2017). There is also evidence for including some right homologue areas in the network (Muller & Meyer, 2014; Vigneau et al., 2011).

1.4.3. Functional connectivity in deafness

In the following subsection, I will review the existing studies on brain connectivity in relation to deafness, focusing on studies of functional connectivity in congenitally and early deaf individuals. Most of the studies published to date investigate the effect of the sensory experience of deafness on resting-state functional connectivity.

1.4.3.1. Functional connectivity in deaf individuals at rest

One study of functional connectivity in deaf individuals investigated topographic tonotopic-like large-scale patterns at rest specifically in the auditory cortex, rather than on the whole-brain level. The findings suggest significant spatial similarity in the tonotopic organisation in the deaf and hearing groups (Striem-Amit et al., 2016), suggesting that large-scale tonotopic-based functional connectivity in the auditory cortex does not require sensory experience to develop. Later studies on functional connectivity in deafness at rest focused more on the connectivity between the auditory cortices and other areas in the brain and have found significant differences between deaf and hearing individuals (Andin & Holmer, 2022; Bonna et al., 2021).

One of the first comprehensive works on resting-state functional connectivity in deaf individuals is the study by Bonna et al. (2021) employing whole-brain graph-theory measures across 264 regions of interest divided into 13 large-scale networks in 21 early deaf and 21 hearing participants. The authors investigated global network segregation and integration in deaf and hearing individuals. Functional global network integration relates to cooperation between different networks, while segregation describes connectivity in specialised networks.

The edge-wise analysis by Bonna et al. (2021) demonstrated weaker connections between the auditory and somatomotor networks, as well as between the visual network and other regions in the brain that were not included in any of the large-scale networks in the deaf group. The authors suggested, among other options, that reduced connectivity between the auditory and somatomotor networks may be a reflection of a lack of usage of spoken language. Stronger functional connectivity was found in the deaf group between the default mode network and the subcortical network, the default mode network and the fronto-parietal network, the fronto-parietal network and the visual networks, and between the memory and the somatomotor networks. These results demonstrate changes in functional connectivity that extend beyond the sensory-deprived auditory areas. The authors suggest that stronger connectivity between the fronto-parietal network and visual regions could be related to the superior performance of deaf individuals in visual tasks (Bavelier et al., 2000) or sign language use. The evidence of the enhanced connectivity of the default mode network to other networks was proposed by the authors as reflecting the integratory role of this network in cognitive processing that could be enhanced in deaf participants as a compensatory mechanism.

Whole-brain graph theory measures indicated that the overall modularity of functional networks was lower, and variability was higher in the deaf group. The authors suggest that it could reflect variation in different factors in the deaf group (such as the use of spoken language, for example).

Finally, there were also changes in the modular group-level organisation of brain networks in deaf and hearing participants in several networks, especially task-related networks. The fronto-parietal module was significantly different between the groups, with the salience network having a larger contribution to it in the deaf group. The 'multi-system' module incorporating various networks in the hearing group (somatomotor, salience, auditory, cingulo-opercular, ventral-attention, subcortical, and cerebellum) was also different between the groups, with the salience and ventral-attention networks contributing to it more in the hearing group. In the deaf group, the salience network was more associated with the fronto-parietal module, while the ventral attention module was associated more with the default mode module. The default mode module was larger in the deaf group as a result of this contribution from the ventral-attention nodes (as opposed to these nodes contributing to the multi-system module in the hearing group). The visual module was the most similar between the groups and mostly included visual network nodes.

In conclusion, the study by Bonna and colleagues (2021) demonstrated changes in functional connectivity between different networks in deaf individuals, including changes in non-sensory, task-related networks. Some of these changes have been proposed to be linked to language use or sensory experience but were not directly disentangled in this study, while others have been proposed to be related to sensory deprivation and/or compensatory mechanisms in cognitive or visual processing arising from the sensory experience of deafness.

Dell Ducas and colleagues (2021) investigated functional and structural connectivity in a group of native or early deaf signers, with a focus on networks outside of the auditory cortex that are related to cognitive control. The deaf group had increased functional connectivity in a number of non-sensory networks (salience, dorsal attentional, and fronto-parietal). Higher connectivity of the attention networks, similarly to the argumentation in Bonna et al. (2021), was proposed to be reflecting compensatory mechanisms arising from lack of auditory input, while the increased connectivity in the non-deprived sensory networks (visual and somatomotor) could be attributed to these sign language use.

The default mode network in the study by Dell Ducas et al. (2021) had higher connectivity with the non-deprived sensory networks (visual and somatomotor) but lower connectivity with the language network in deaf individuals, reflecting a different pattern from the one observed in the study by Bonna et al. (2021).

Dell Ducas et al. (2021) highlight the changes in the default mode network, salience, dorsal attention, and the fronto-parietal networks, as well as in the non-deprived sensory networks in deaf individuals, focusing on their role in responding to environmental stimuli and visual input.

One of the latest studies on functional connectivity in deafness investigated connectivity in the large-scale brain networks in early deaf signers using the independent component analysis (ICA) (Andin & Holmer, 2022). This analysis allowed the authors to fully characterise large-scale networks in the brain of deaf signers and compare connectivity at rest and network organisation between the groups. In this study, nine components were characterised in the two groups, and changes in functional connectivity were found in four (the left control, default, ventral somatomotor, and attention networks), with the majority of differences arising from temporal regions. These regions, in a seed-to-voxel analysis, showed increased connectivity to a number of areas in the cingulate, insular, superior temporal cortices, as well as cuneus, precuneus, supramarginal gyrus, supplementary motor area, and cerebellum (crus 1) in the deaf group. The opposite pattern, with the hearing group having increased connectivity to these temporal areas, was found in the hippocampus, middle/superior frontal gyrus, precentral gyrus, postcentral gyrus, and cerebellum (crus 8).

Taken together, the results suggest that network composition can be different between different networks in individuals with unique sensory experiences. The networks that do not show compositional differences between the groups may still exhibit significant changes in functional connectivity in deaf individuals. For instance, while the salience network did not differ between the groups in composition, some of its areas showed differences in connectivity with the superior temporal cortex, in agreement with the study by Ding et al. (2016) (discussed below). The authors propose that some of the differences observed between the groups may arise from language use or visual attention changes (Bavelier et al., 2006).

The most recent study that explored resting-state functional connectivity in deaf individuals describes connectivity changes throughout the brain in association with the sensory experience of deafness and performance in executive function tasks (Cardin et al., submitted). The analysis was conducted across 400 regions of interest, and there were 239 between-group differences in connectivity, with 221 of them including a region in the auditory network, suggesting that the auditory cortex in deaf individuals undergoes substantial functional changes. This finding agrees with the point made by Andin and Holmer (2022) in their study which also found a large number of altered connections specifically in the auditory cortices of deaf individuals at rest. The connectivity between the auditory and somatomotor networks was reduced in deaf individuals, replicating the results of the Bonna et al. (2021) study. The authors proposed that if reduced connectivity reflected a lack of spoken language use in the deaf group, it would be plausible to expect enhanced connectivity between the visual and somatomotor areas in the deaf group of native and early signers. Therefore, the authors suggest that the changes in connectivity between the auditory and somatomotor regions could rather arise from a general principle of functional reorganisation of the sensory cortices, considering similar findings of decreased connectivity in blind individuals between the visual and somatomotor regions (Burton et al., 2014; Y. Liu et al., 2007; C. Yu et al., 2008).

The auditory network showed increased connectivity to the salience network in deaf individuals, in agreement with the findings from Ding et al. (2016) and Andin and Holmer (2022). This connectivity pattern may be explained by plasticity effects related to the reallocation of attention in deaf individuals (Manini et al., 2022).

1.4.3.2. Functional connectivity in deaf individuals during task execution

Increased functional connectivity between the auditory cortex and the dorsal visual cortex was found when deaf participants were performing a task with dynamic visual stimuli that activated the auditory regions (Bola et al., 2017). The study used a psychophysiological interaction (PPI) analysis – a method measuring task-related changes in functional connectivity – and demonstrated that the high-level auditory cortex and the dorsal visual stream (V5/MT cortex) had increased functional connectivity in deaf participants during the visual task. The coupling was present only when deaf participants performed the task on visual rhythm discrimination, but not during the control task (simple flashes with a constant interval).

In a recent study, Andin et al. (2021) also showed increased functional connectivity between the auditory cortex and visual cortex in deaf signers during a visual working memory task.

Another study (Que et al., 2018) used three types of stimuli to investigate cross-modal plasticity and functional connectivity alterations: words, sign language sentences, and lip-reading sentences. The deaf participants showed a response to all types of visual stimuli in the right superior temporal cortex. During the visual condition (non-linguistic stimuli), there were increased connections of the right superior temporal cortex to the left occipital cortex and right thalamus. During watching language stimuli, deaf participants showed strong connectivity between the superior temporal cortex and visual areas, as well as with the anterior temporal cortex and inferior frontal gyrus. The superior temporal cortex activity when watching language stimuli was functionally connected to both the visual cortex and the frontotemporal areas in deaf participants. It was also highly corrected with the learning of sign language.

Shiell et al. (2015) found that the posterior superior temporal gyrus (STG) region that was reorganised for visual motion in early-deaf participants had increased functional connectivity with a region in the calcarine fissure during visual motion, suggesting that visual information arrives from the visual cortex to the reorganised superior temporal gyrus through corticocortical connections (Shiell et al., 2015). The connectivity between the superior temporal gyrus and the intracalcarine cortex correlated negatively with the duration of hearing aid use, emphasising the role of sensory experience in connectivity changes in deafness.

One study investigated *effective* connectivity in deaf individuals during visual motion perception using dynamic causal modelling (Benetti et al., 2021). Deaf individuals had increased effective connectivity between the reorganised superior temporal cortex and a portion of the middle occipito-temporal cortex (hMT+/V5), and between the reorganised superior temporal cortex and the intraparietal sulcus, in comparison to hearing controls, suggesting that the reorganised superior temporal cortex is a part of the network dedicated to visual motion perception.

1.4.3.3. Functional connectivity changes and executive function in deaf individuals

Functional connectivity patterns can be investigated in relation to the cross-modal reorganisation observed in the auditory cortex of deaf individuals. The superior temporal cortex (STC) in deaf individuals has been shown to be activated during visual working memory tasks (Cardin et al., 2018; Ding et al., 2016). It was hypothesised that the superior temporal cortex may be incorporated into the cognitive network responsible for executive processing, as it is actively engaged in these processes. Indeed, deaf individuals have shown increased connectivity between frontal regions and the superior temporal cortex during rest (Cardin et al., 2018), with activity in the left superior temporal cortex being positively correlated to activity in fronto-parietal regions, such as pre-supplementary motor area and dorsolateral prefrontal cortex. The hearing participants, including hearing signers, did not show such patterns, which indicates that the results are caused by the sensory experience of deafness rather than sign language knowledge.

In a study in which deaf participants were compared to hearing participants on a visual working memory task (Ding et al., 2016), enhanced functional connectivity was found during rest between the superior temporal gyrus (STG) and brain regions of the salience network, the bilateral anterior insula and dorsal anterior cingulated cortex. Furthermore, the functional connectivity of the superior temporal gyrus predicted the performance in the working memory task in the deaf group. This can be interpreted as another manifestation of this region's involvement in the working memory process and the control network.

The main aim of the study by Cardin et al. (submitted) was to investigate functional connectivity and its changes in relation to behavioural performance in executive function tasks on working memory, inhibition, and switching. When the behavioural performance in executive function tasks was added as a covariate in the analysis on resting-state connectivity, the differences in connectivity between the auditory network and the default mode, visual, control, and language network were not significant. Instead, differences were arising from regions belonging to other networks, particularly the salience/ventral attention and the default mode networks. Critically, performance between tasks was not different between the groups, suggesting that changes in connectivity between large-scale networks may reflect differences in underlying neural mechanisms of achieving similar performance in deaf and hearing individuals.

1.4.3.4. Functional connectivity and language in deaf individuals

Wang and colleagues (2015) investigated functional connectivity patterns of the visual word form area (VWFA) in deaf individuals, using the visual word form area as the seed of interest in their analysis of resting-state data (X. Wang et al., 2015). In hearing individuals, the visual word form area has been shown to have preferential functional connectivity during rest to the core language regions (W. D. Stevens et al., 2017). In the Wang et al. (2015) study, there were no differences in location or strength of activation in the visual word form area between the groups, but functional connectivity patterns were different, with the deaf participants showing reduced resting-state connectivity between the visual word form area and the auditory speech perception area in the left anterior superior temporal gyrus. At the same time, the intrinsic functional connectivity between the visual word form area and a fronto-parietal network, the left inferior frontal gyrus, and occipito-parietal regions did not differ. The authors propose that their findings reflect the influence of the experience of spoken language use on the computation of the correspondence between the visual word form and speech.

In a study that used graph theory measures to study resting-state connectivity in deaf adolescents, the group of deaf adolescents demonstrated increased resting-state connectivity between the limbic system and the visual and language regions (W. Li et al., 2016). Decreased connectivity was found between the visual and the language regions, which the authors attributed to the 'inferior' reading and speaking skills of the participants, but they did not test these skills directly. A graph theory analysis did not show changes in small-worldness property, but eight regions involved in visual, language, and auditory processing were identified as hubs only in the deaf adolescents.

In a study investigating the default mode network neural activity and functional connectivity in deaf individuals (Malaia et al., 2014), in a partial correlation analysis based on ICA, deaf signers showed increased connectivity within default mode network regions, namely, between posterior cingulate/precuneus and left medial temporal gyrus. In the right hemisphere, deaf participants showed increased functional connectivity between the inferior parietal lobe and medial temporal gyrus. The authors suggest that the connectivity patterns in the deaf groups may reflect the effects of sign language processing. The study did not explicitly measure sign language abilities or included a group of hearing signers in the analysis, which could help disentangle sensory effects from language effects or establish a statistical link between language experience and functional connectivity. Moreover, the study did not seem to regress out the effect of task and analysed the task and no-task conditions together. Disentangling the effects of task state and sensory and language experience could help in interpreting the effects found in this study further.

Two studies of functional connectivity in deaf individuals included a measure of language proficiency in their analysis, one in written language (Y. Li et al., 2013) and the other in sign language (Holmer et al., 2022). The former (Y. Li et al., 2013) compared two groups of deaf participants (congenitally deaf and those with acquired deafness) and one group of hearing controls on the intra- and inter-regional synchronisation in the superior temporal cortex. Congenitally deaf individuals showed enhanced connectivity between the middle superior temporal sulcus (mSTS) and posterior STS, in comparison to the group with acquired deafness, that could be attributed to visual language processing resulting from cross-modal changes in the middle superior temporal sulcus. Both congenitally deaf individuals and those with acquired deafness had weaker connectivity of the middle superior temporal sulcus with the anterior superior temporal sulcus, and the connectivity between these regions was positively associated with their language skills tested in written language.

The other study by (Holmer et al., 2022) explored the relationships between resting-state connectivity of language-related regions (bilateral inferior frontal gyrus and posterior superior temporal gyrus) to the rest of the brain and sign language skills in a group of deaf individuals using seed-to-voxel connectivity analysis. Phonological awareness and sentence processing skills were measured in deaf individuals. The authors also included non-verbal cognitive ability in some of the analyses as it correlated with performance on the phonological awareness test. The authors reported a correlation reflecting stronger connectivity between the right inferior frontal gyrus and the left middle frontal gyrus/frontal pole in participants with faster phonological processing abilities. The relationship did not remain significant after non-verbal cognitive ability was included in the analysis, possibly reflecting the importance of the fronto-parietal network in executive processing rather than language-related effects (Holmer et al., 2022).

Sign language sentence processing was negatively correlated with the connectivity between the left inferior frontal gyrus and sensorimotor language-related regions. The authors propose that those deaf individuals who had lower sign language sentence processing scores could use non-linguistic motor representation as a compensatory mechanism for their poorly defined language representations. Alternatively, this could reflect larger involvement of language-control functions for language-based motor representations. This study highlights the importance of using different language assessments for investigating language-related effects in deaf individuals. Taken together, the two last studies described in this subsection demonstrate that connectivity between language-related regions and other regions may reflect language proficiency in either written (Y. Li et al., 2013) or sign language (Holmer et al., 2022).

1.4.3.5. Other studies of connectivity in the brain and deafness

The studies described above used fMRI-based approaches and the most common analysis methods (e.g., seed-based functional connectivity and ICA) in studying functional connectivity in deafness. This thesis employs fMRI-based measures of functional connectivity, focusing on seed-based functional connectivity between different networks, therefore fMRI studies of congenitally or early deaf adults that focus on connectivity between different networks receive larger attention throughout this work, but functional connectivity in deafness has also been studied using other techniques and analyses.

There are studies investigating developmental aspects of functional connectivity in deafness. Deaf infants demonstrated increased resting-state functional connectivity between the primary auditory cortex (A1) and the right insula and superior temporal gyrus (S. Wang et al., 2019). The authors explain the increased connectivity associated with auditory and language networks as a compensatory mechanism.

Another study looked into the amplitude of low-frequency fluctuations (ALFF) and regional homogeneity (ReHo) in deaf infants (Xia et al., 2017). They showed a decreased amplitude of low-frequency fluctuations and regional homogeneity in the auditory and language regions in the brain when compared to hearing infants. For example, they had increased amplitude of low-frequency fluctuations in the left Heschl's gyrus, left superior temporal gyrus, left inferior frontal gyrus, left inferior frontal gyrus, left inferior prefrontal gyrus, and left dorsolateral prefrontal cortex. At the same time, the opposite pattern was observed in the right occipital lobe and right angular gyrus, with increased amplitude of low-frequency fluctuations in deaf infants. In terms of regional homogeneity, deaf infants showed decreased regional homogeneity in the left superior temporal gyrus, left inferior frontal gyrus, left inferior prefrontal gyrus, left dorsolateral prefrontal cortex, left medial frontal gyrus, and left temporal polar gyrus. Similarly, increased regional homogeneity was observed in the left occipital lobe in the deaf group.

There are also studies of structural connectivity, not investigated in this thesis, which can provide valuable insights for interpretations of other findings. Deaf adolescents showed decreased grey matter connectivity within the auditory and visual systems, as well as connectivity between language and visual systems (B. Liu et al., 2015). At the same time, increased grey matter brain connectivity was found between auditory and visual systems.

Cheng et al. (2019) investigated white matter connectivity in the language-related pathways in a group of deaf native signers, hearing signers of American Sign Language, and three individuals who experienced language deprivation in childhood using diffusion tensor imaging (DTI) (Cheng et al., 2019). White matter connectivity was not influenced by the experience of language acquisition in a different modality in groups without language delay, and both showed leftward laterality in the language pathways. Critically, changes in white matter microstructure were detected in the individuals with early language deprivation.

Structural connectivity linked to the functional recruitment of the temporal voice area by face stimuli in deaf individuals was analysed by Benetti and colleagues (Benetti et al., 2018). The authors investigated the structural connectivity between occipital, fusiform, and temporal regions that typically support voice- and face-selective processing. Although functional reorganization has been demonstrated for face processing in the temporal cortex of the deaf, the macroscopic properties of these connections did not change. At the same time, both occipito- and fusiform-temporal connections showed significant microstructural changes (fractional anisotropy reduction, radial diffusivity increase). The authors believe that the functional reorganisation of auditory regions builds on intrinsic and mostly preserved anatomical connectivity between auditory and occipital areas.

1.4.3.6. Functional connectivity in populations with varying hearing levels and types of deafness

The above-mentioned studies investigated connectivity mostly in early or congenitally deaf participants. There are other studies of functional connectivity in different populations with hearing loss, one of them being older individuals. One study investigated functional connectivity between auditory and visual cortices during audio-visual processing in older participants with varying degrees of hearing loss (Puschmann & Thiel, 2017). This group showed an increase in connectivity between the auditory cortex and the right motion-sensitive visual area MT+ when processing audio-visual input. Hearing loss modulated resting-state connectivity between the right area MT+ and parts of the left auditory cortex, suggesting that the changes in coupling between the visual area and the auditory cortex are associated with an increasing degree of hearing loss.

One of the subgroups of the deaf population that has been studied extensively over recent years is individuals with cochlear implants. Studying functional connectivity in individuals with cochlear implants may be a challenge due to the incompatibility of these devices with fMRI. One commonly-used alternative technique is functional near-infrared spectroscopy (fNIRS). Chen et al. (2017) compared functional connectivity in a group of post-lingually deaf users of cochlear implants with hearing controls while they were performing tasks on visual (visual discrimination) and auditory (passive listening task) stimulus processing. The deaf group showed reduced intra-modal functional connectivity within auditory and visual areas and increased cross-modal functional connectivity between the left auditory cortices and visual cortices in both hemispheres (represented as differences in connectivity between visual and auditory areas) in both visual and auditory processing. Cross-modal functional connectivity for auditory more than visual stimuli was associated with better speech recognition abilities in one of three speech recognition tasks. The study was exploratory and had several potential limitations (such as the presentation of visual stimuli during the auditory task or comparing a passive task with an active discrimination task) but it replicated the findings of increased functional connectivity between auditory and visual areas during sensory processing described in the paragraph in a study of older individuals with hearing loss (Puschmann & Thiel, 2017).

Other possible ways of investigating functional connectivity in deafness include studies of unilateral hearing loss (B. Liu et al., 2015; Shang et al., 2020) and individuals with different degrees and causes of deafness (Y. Zhang et al., 2018). For example, causal resting-state connectivity is different between auditory regions and between auditory and other sensory (visual and somatomotor) and higher-order (default mode and ventral attention) networks in individuals with post-lingual mild-to-severe sensorineural (caused by damage to cells in the cochlear and/or the auditory nerve) hearing loss (Y. Zhang et al., 2018). In a different study, the group with unilateral (left-sided) sensorineural hearing loss showed altered functional connectivity in the auditory system, the recognition network, the language network, and the visual network (B. Liu et al., 2015).

These studies will not be considered when interpreting the results of the studies presented in this thesis as the environmental and linguistic experiences of the above-mentioned populations are different from those of congenitally deaf individuals, while the work presented in this thesis focuses on the experience of congenital and severe-to-profound deafness. Nevertheless, work with populations with other types and levels of deafness demonstrates that sensory experience influences functional connectivity between various brain networks during sensory processing and at rest and that the changes in connectivity can be associated with language-related abilities in spoken language (L.-C. Chen et al., 2017) and the language network (B. Liu et al., 2015).

1.4.4. Conclusion

Functional connectivity studies provide us with an opportunity to study the patterns of connectivity between regions across the brain and the formation of large-scale networks in the brain, including sensory networks (e.g., auditory) and networks directly involved in the execution of executive function tasks and language processing.

The majority of studies on brain reorganisation in deafness focus on crossmodal plasticity effects, and few have explored functional connectivity in relation to deafness at the level of the whole brain (Andin & Holmer, 2022; Bonna et al., 2021; Cardin et al., submitted). Moreover, while there have been studies of modality-specific language effects on functional connectivity in deaf individuals (Holmer et al., 2022; Y. Li et al., 2013) to the best of our knowledge, no existing studies have explicitly described the effects of language experience independently of the modality and in a large variety of large-scale brain networks. The review of literature presented in this introduction demonstrates that deaf individuals exhibit changes in functional connectivity between different types of brain networks, and some functional connectivity changes are modulated by language (Holmer et al., 2022; Y. Li et al., 2013). Further research is needed to support existing results and create a comprehensive picture of functional connectivity organisation in the deaf brain, as well as its relationship with major environmental factors affecting development in deafness, namely, sensory deprivation and language access.

1.5. Summary and research questions

The evidence provided in this chapter shows that deaf children who are not born to deaf parents often do not acquire their first language due to limited access to language in childhood in the same way as hearing children do. Early and congenital deafness is often related to insecure and delayed first language acquisition, and these effects are significant and detectable in deaf adults, showing the detrimental consequences of lack of language exposure on proficiency in both first and/or second language, whether it is signed or spoken (Cormier et al., 2012; Mayberry, 2007). This has important implications for the research questions investigated in this thesis.

I demonstrated in this chapter how research on deafness provides insights into how unique sensory and linguistic experiences affect cognition and brain organisation. It also has the potential to reveal interactions between aspects of language, cognition, and brain reorganisation. Associations between executive processes and language have been suggested by a large body of research, especially in atypical populations and individuals with developmental language disorders (Akbar et al., 2013; D. M. Hughes, 2006; Marton, 2008). In contrast to some of these populations, the brain of deaf individuals has a full capacity to acquire language through the same milestones and to the same level of fluency as the hearing brain within the critical period (Mayberry & Squires, 2006). Insecure or delayed language acquisition in deaf individuals is a result of environmental conditions rather than neurological factors. This allows scientists to conduct research that can answer questions about the nature of the relationship between language and cognition. Evidence demonstrates that executive processing is largely intact in deaf native signers (Marshall et al., 2015) and that language skills in deaf children are related to executive function (Botting et al., 2017; Figueras et al., 2008; Merchán et al., 2022). It is unclear whether this association is preserved and/or detectable later in life.

We know that the age of first language acquisition influences the neural basis of language processing (MacSweeney, Waters, et al., 2008) and brain structure (Cheng et al., 2019; Pénicaud et al., 2013) in deaf individuals. The sensory experience of deafness results in crossmodal plasticity effects in populations with different language experiences, and these effects may manifest differently. It is unclear how language experience affects brain reorganisation independently of language modality in this population. Effects of language proficiency evaluated continuously, rather than through a binary opposition of groups, have not been described in relation to crossmodal plasticity effects in deaf individuals in visual cognitive tasks. In **Chapter 2** of this thesis, I will explore the effects that *general, modality-independent* language proficiency in deaf individuals may have on behavioural and neural responses in executive function tasks, especially in the typically reorganised temporal regions of the brain.

In **Chapter 3** and **Chapter 4**, I will investigate the effects of sensory experience and general, modality-independent language proficiency on functional connectivity in deaf individuals during rest and during the execution of executive function tasks.

Functional connectivity has been shown to be different between groups of deaf and hearing individuals across multiple brain networks (Andin & Holmer, 2022; Bonna et al., 2021; Cardin et al., submitted). To the best of my knowledge, the effects of sensory deprivation and language experience have never been investigated together in a single study of functional connectivity in deafness by using a modality-independent measure of general language proficiency in a population with heterogeneous language backgrounds. If measured explicitly, language experience can provide unique insights into how language shapes functional associations in the brain of deaf individuals (Holmer et al., 2022; Y. Li et al., 2013). The main purpose of this thesis is to explore the associations between sensory experience, language experience, and cognition in deaf individuals using behavioural and neuroimaging techniques.

2 The role of language proficiency in executive function tasks in deaf individuals

The between-group fMRI analyses of the data from executive function tasks described in this chapter have been performed by Dr Barbara Manini, who was a postdoctoral researcher at the Deafness and Neural Plasticity Lab at the University of East Anglia (UEA) and University College London (UCL). The between-group behavioural analyses and all language-related analyses have been performed by myself. Some of the results discussed in this chapter have been accepted for publication and can be accessed online. My role as one of the first authors involved making contributions to study preparation, data collection, data analysis, and writing up. Some of the results discussed in this chapter have also been presented at international conferences.

Poster presentations:
Vinogradova, V., Manini, B., Woll, B., Eimer, Cardin, V. (2021). Language modulates executive function performance and neural activity in reorganised areas in deaf individuals. *Cognitive Neuroscience Society Annual Meeting.*

Vinogradova, V., Manini, B., Woll, B., Eimer, Cardin, V. (2020). Language experience in deaf individuals is linked to behavioural performance and neural reorganisation in the auditory cortices during planning and switching tasks.*Society for Neurobiology of Language (SNL) Annual Meeting.*

Publications:
Manini, B., Vinogradova, V., Woll, B., Cameron, D., Eimer, M., & Cardin, V. (2022). Sensory experience modulates the reorganization of auditory regions for executive processing. *Brain*. https://doi.org/10.1093/brain%2Fawac205

Talks:

Vinogradova, V., Manini, B., Woll, B., Eimer, Cardin, V. (2021). Language experience modulates functional connectivity at rest in deaf individuals. *Slide Session, Society for Neurobiology of Language (SNL) Annual Meeting.*

2.1. Introduction

This chapter aims is to investigate the effect language proficiency has on non-verbal aspects of executive function in deaf adults, both behaviourally and in the brain. The association between language and cognition, and especially executive function, has been the focus of multiple investigations and debates in the fields and subfields of psychology, cognitive neuroscience, language, and educational sciences (Bialystok, 2015; Chang, 2020; L. Friedman & Sterling, 2019; Gooch et al., 2016; Hall et al., 2018; Henry et al., 2015; Kaushanskaya et al., 2017; Nichols et al., 2020; Olsson et al., 2019). The majority of the studies investigating the relationship between language and executive function focus on populations that demonstrate language delay or deficits due to neurological disorders or other non-environmental reasons, such as children with developmental language disorders, previously known as specific language impairments, and autism spectrum disorder (Akbar et al., 2013; L. Friedman & Sterling, 2019; Weismer et al., 2018). Deaf children often experience language delay resulting from limited access to language from the environment, given that more than 90% of them are born to hearing, non-signing parents (Mitchell & Karchmer, 2004). These children's language development significantly differs from the language development of their hearing peers or deaf children from deaf families (native signers) (Lu et al., 2016). Environmental factors, such as the inability to fully access natural language in the auditory modality and the absence of visual language input in the visual modality, lead to differences in age of acquisition and the subsequent effects of age of language exposure on language and literacy development in deaf children (Mayberry, 2007). The effects of age of acquisition are detectable in older age in this population and have been found for both signed and spoken language proficiency (Boudreault & Mayberry, 2006; Cormier et al., 2012; Emmorey et al., 1995; Mayberry, 1993, 2002, 2007; Mayberry & Lock, 2003). Critically, among individuals who acquired sign language as their first language at different ages, native signers perform better than early sign language learners, while early learners perform better than late learners (Mayberry, 1993).

Language development and language access have been linked to executive function in deaf children (Botting et al., 2017; Figueras et al., 2008; Marshall et al., 2015; Merchán et al., 2022). The language scaffolding hypothesis suggests that successful language acquisition in deaf children provides the necessary foundation for other cognitive skills, including executive function (Hall et al., 2017). Evidence for the support of this hypothesis comes from studies of deaf children with different language backgrounds. Native signers do not show deficits in working memory and do not differ in performance from hearing controls, while non-native signers perform less accurately in some executive-loaded non-verbal working memory tasks (Marshall et al., 2015). Vocabulary scores predicted scores in these tasks when all children were considered together, highlighting the importance of language access independently of the language modality. Implanted and non-implanted deaf children born to hearing parents have shown disadvantages in other executive function tasks, tapping into impulse control, inhibition, working memory, and cognitive set-shifting (but not planning and problem-solving), in comparison to hearing controls (Figueras et al., 2008). These differences disappear when receptive language skills are taken into account, highlighting, once again, that differences in performance are a consequence of delayed language acquisition. Moreover, global executive function ability and language ability are highly correlated in hearing and deaf children (Figueras et al., 2008). In a different study (Botting et al., 2017), deaf children with varying language backgrounds showed lower performance scores in all executive function tasks, apart from design fluency: executive-loaded visuo-spatial working memory, cognitive shifting, planning, and inhibitory control. Botting and colleagues (2017) conducted a mediation analysis on executive function and language scores and established that language mediated the composite executive function score but not vice versa. Lately, similar findings were published from a study on language and inhibitory control in deaf children: a group of children with and without cochlear implants showed a lower range of receptive vocabulary and weaker interference abilities, but the interference effect was mediated by receptive vocabulary, and not deafness (Merchán et al., 2022), highlighting the critical role of language performance in relation to executive function performance.

Most research on the relationship between language and executive function in deaf individuals focuses on deaf children, and not on adult populations, especially not adults whose language backgrounds do not fall within the commonly accepted oppositions: for instance, native signers or deaf individuals who use only spoken language for communication. Such compositions of participant groups allow researchers to compare deaf individuals with a typical language development trajectory – native signers whose families provide them with language input in a fully-accessible modality from birth and act as role models – to deaf individuals with no such background. The majority of deaf individuals do not come from deaf families (Mitchell & Karchmer, 2004) and have highly variable language experiences and skills: some of them can successfully rely on spoken language in their daily life and have limited or no knowledge of sign language, some of them may choose to predominantly use sign language and become very proficient in it. Different scenarios may lead to higher or lower levels of usage and proficiency in languages in both modalities, resulting in a high variation and degree of bilingualism (Grosjean, 2010; Padden, 1998; van den Bogaerde & Baker, 2002). This chapter investigates the influence of language proficiency on executive function in adult deaf individuals whose language backgrounds reflect the wide spectrum of language proficiency in deaf individuals (van den Bogaerde & Baker, 2002; Woll, 2013). In order to do so, we have adopted an approach that allows us to measure language proficiency in deaf participants independently of their preferred language by assessing their *best* language instead. This has not been done in literature before, to the best of our knowledge. Although there are examples of developmental studies assessing deaf children's preferred language, they only assess them in one language (Botting et al., 2017), while we have compared the performance of those of our participants who are bilingual in each of the languages they use. This methodological choice allows us to investigate how general language proficiency, independent of the language modality or preference, influences executive function.

We suggest that if the nature of the relationship between executive function and language in deaf individuals is that language mediates executive function skills, as has been proposed by the language scaffolding hypothesis and the studies described above, then insecure language background would affect executive function performance negatively. On the other end of this spectrum, high language proficiency would suggest successful language acquisition and lead to a faster and more accurate performance in executive function tasks.

Finally, given the proposed link between language and executive function, we can investigate what role language experience plays in brain reorganisation. Neural reorganisation of sensory and non-sensory regions in deaf individual has been described for working memory but not for other executive function components. During working memory task execution, deaf participants activate temporal cortices more (Andin et al., 2021; Cardin et al., 2018; Ding et al., 2016) and fronto-parietal areas less (Cardin et al., 2018; see Andin et al., 2021 for a study that did not corroborate the finding of such reorganisation in a different working memory task), suggesting that plasticity effects can extend to cortices outside of the sensory-deprived areas (Cardin et al., 2018). Changes in brain structure have been detected in deaf individuals with a delay in language acquisition, also outside of auditory areas (Pénicaud et al., 2013). In hearing individuals, structural changes are also present in relation to language acquisition (Richardson & Price, 2009). Several studies described changes in brain function in linguistic processing tasks in connection with the age of acquisition in deaf individuals (MacSweeney, Waters, et al., 2008; Mayberry et al., 2011; Twomey et al., 2020). Given the observed behavioural relationships between language and executive function, and the evidence of the age of acquisition effects on brain function in deaf individuals, we suggest that neural reorganisation for executive processing in the brain of deaf individuals may be related to their language proficiency levels, considering the influence of age of acquisition on language proficiency later in life (e.g., Emmorey et al., 1995; Mayberry & Eichen, 1991).

2.2. Methods

2.2.1. Participants

29 deaf and 20 hearing individuals participated in the study. We did not have a specific language experience as inclusion criteria for the deaf participants and recruited deaf individuals with any language acquisition background to reflect the natural linguistic heterogeneity observed in this population. Hearing participants were all native English speakers with no knowledge of sign language. The inclusion criteria for deaf participants were the age of onset of deafness (congenital, or up to three years) and degree of hearing loss (severe or profound). The first language of deaf participants could be either British Sign Language (BSL) (or a sign language from the BSL family, such as Australian Sign Language, or Auslan), English, or both. Language background, onset, and cause of deafness of all deaf participants who took part in the study are reported in Table 2.1. All participants were right-handed (self-reported),

with normal or corrected-to-normal vision, and had no history of neurological conditions.

One participant was excluded from the studies described in this thesis due to their mean hearing loss being lower than the pure-tone average (PTA) of 65 dB across three speech frequencies: 500 Hz, 1000 Hz, and 2000 Hz (Brant et al., 1996; Kodera et al., 1977; Kronenberg et al., 1992), meaning that they did not fit the inclusion criteria of severe or profound deafness. Datasets from two more participants have been completely excluded from all analyses described in the thesis due to excessive motion during the whole duration of the fMRI session (see *2.2.5. fMRI data preprocessing* section). Data from one more participant have been excluded from the analyses described in this chapter also due to excessive motion in the scanner. The reasons for the exclusion of participants from analyses of specific tasks are described in Appendix Table 2.1 and *2.2.10. Statistical data analyses*.

The final sample size of the deaf group for the analyses presented in this chapter was 25. The mean pure-tone average (PTA) of these participants in the 500-1000-2000 Hz speech frequency range was 94.33dB (*SD* = 7.86dB), with the range for the better ear being 66.67-105 dB and the range for the average of both ears being 78.33-105 dB. It should be noted that the maximum recorded value for each participant was set at 105 dB, but the majority of participants were not able to hear the signal at 120 dB in the speech frequencies (13 participants). The threshold of 105 dB was chosen for consistency. If the maximum threshold recorded is used in the analysis, then the average PTA in the speech frequency range for the group is 98.21 dB (*SD* = 11.48 dB), the range in the better ear is 66.67-118.33 dB, and the range for the average of both ears is 78.33-118.33 dB. Participants could provide the audiometer data if they had records available, or their hearing was assessed during the behavioural session. Audiogram data were missing from four participants, but they were all congenitally severely or profoundly deaf (self-reported). The cause of deafness for three of them was genetic, and one was unknown. None of the participants relied on hearing when communicating with the researchers.

Table 2.1. Questionnaire data on the deafness and language background of the deaf participants included in the analysis of the executive function tasks

Deafness onset	**Cause of deafness**	**BSL**	**Sign language acquisition**	**Preferred language**
Birth	Unknown	Yes	Native	BSL
Birth	Other	Yes	Early	BSL
Birth	Genetic	Yes	Native	BSL
Birth	Genetic	No	N/A	English
Birth	Genetic	Yes	Native	BSL
Birth	Genetic	Yes	Native	BSL
< 3 years	Meningitis	Yes	Early	BSL
Birth	Genetic	Yes	Early	English
Birth	Genetic	No	N/A	English
Birth	Unknown	Yes	Late	English
Birth	Genetic	Yes	Native	BSL
Birth	Unknown	Yes	Late	English
Birth	Mother had rubella	Yes	Late	English
Birth	Unknown	Yes	Late	BSL
Birth	Genetic	Yes	Native*	BSL
Birth	Mother had rubella	Yes	Early	English
Birth	Genetic	No	N/A	English
Birth	Genetic	Yes	Native	Auslan
Birth	Genetic	Yes	Native	English
Birth	Genetic	Yes	Late	English
Birth	Mother had rubella	No	N/A	English
~ 3 years	Genetic	Yes	Native	BSL
< 3 years	Meningitis	Yes	Late	BSL
Birth	Genetic	Yes	Early	BSL
Birth	Mother had infection	Yes	Early	BSL

Note. *The participant learned BSL from an older sibling. Two participants learned BSL after they learned a different sign language from the same family: Australian Sign Language (Auslan) and South African Sign Language.

Participants were recruited through public events (e.g., festivals and scientific talks), social media, and the participant databases of the Deafness, Cognition, and Language Research Centre (DCAL) at University College London (UCL) and the School of Psychology at the University of East Anglia (UEA). All procedures followed the standards set by the Declaration of Helsinki and were approved by the ethics committee of the University of East Anglia's School of Psychology and by the Norfolk and Norwich University Hospital (NNUH) Research and Development Department.

Participants travelled to the University of East Anglia and the Norfolk and Norwich University Hospital to take part in the study. All participants included in the study communicated with the researchers through their preferred language: BSL or English (through lipreading). A BSL interpreter was provided if a participant requested one.

The study included a behavioural session and a scanning session. The sessions could be conducted on the same day, or different days, depending on the availability of the participant. All participants provided written informed consent, and all deaf participants had the opportunity to read the information sheet or watch the signed version of it in BSL. Most deaf participants travelled to Norfolk from other counties and were reimbursed for the travel and accommodation. All participants were compensated for their time.

The deaf and hearing participant samples for each task were matched on age, gender (deaf: 16 females, 9 males; hearing: 15 females; 5 males), non-verbal reasoning, and visuo-spatial working memory span. The differences in age, gender, non-verbal reasoning ability and visuo-spatial working memory were not significant between the groups in any of the task samples. The demographics and the results of the pre-screening tests for the participants included in the analyses presented in this chapter are displayed in Table 2.2.

Table 2.2. Demographics and pre-screening tests for the participants included in the analyses of executive function tasks

			Age			**Gender**	**WASI**		**Corsi**	
	Group	*N*	*Mean*	*Range*	*SD*		*Mean*	*SD*	*Mean*	*SD*
Full sample	hearing	20	37.50	18-66	16.85	15f/5m	57.47	8.02	5.40	1.10
Full sample	deaf	25	41.68	19-66	14.38	16f/9m	59.68	8.51	5.30	0.78
Working memory	hearing	19	38.47	18-66	16.72	14f/5m	57.83	8.10	5.47	1.08
Working memory	deaf	24	41.38	19-66	14.60	15f/9m	59.96	8.58	5.38	0.70
Planning	hearing	19	36.95	18-66	17.13	14f/5m	57.56	8.25	5.44	1.11
Planning	deaf	21	40.81	19-63	13.65	13f/8m	59.67	9.19	5.26	0.82
Switching	hearing	20	37.50	18-66	16.85	15f/5m	57.47	8.02	5.40	1.1
Switching	deaf	23	40.30	19-63	13.93	14f/9m	59.87	8.76	5.39	0.71
Inhibition	hearing	15	40.33	18-66	17.09	12f/3m	57.57	9.05	5.43	1.21
Inhibition	deaf	22	40.59	19-66	14.87	14f/8m	60.05	8.84	5.43	0.70

Participants had to be excluded from the analyses of individual tasks. The reasons for exclusion are described in Appendix Table 2.1. One hearing participant did not complete the behavioural session and their responses were coded as missing in the non-verbal reasoning assessment and the visuo-spatial working memory task.

Table 2.3. Between-group comparisons on demographics and pre-screening tests for the participants included in the analysis of the executive function tasks

	Hearing	**Deaf**	**Age**			**Gender**		**WASI**			**Corsi**		
	N	*N*	*df*	*t*	*p*	X^2	*p*	*df*	*t*	*p*	*df*	*t*	*p*
Working memory	19	24	41	0.61	.55	0.6	.44	38	0.34	.74	39	-0.45	.66
Planning	19	21	38	0.79	.43	0.63	.43	35	0.32	.75	36	-0.45	.65
Switching	20	23	41	0.60	.55	0.97	.32	38	-0.5	.62	39	0.09	.93
Inhibition	15	22	35	0.05	.96	4.24	.04	32	0.27	.79	33	-0.09	.92

Participants had to be excluded from the analyses of individual tasks. The reasons for exclusion are described in Appendix Table 2.1. One hearing participant did not complete the behavioural session and their responses were coded as missing in the non-verbal reasoning assessment and the visuo-spatial working memory task.

2.2.2. Materials

Non-verbal reasoning assessment

The matrix reasoning subset of the Wechsler Abbreviated Scale of Intelligence (WASI; Wechsler, 1999) was used as a control measure for matching the groups. It is an assessment of non-verbal fluid ability. The task requires participants to complete the pattern with a missing section by choosing one of the five available options. The task increases in difficulty, and the starting and ending points vary depending on the participant's age. The test is terminated if the participant provided four consecutive incorrect answers.

Visuo-spatial working memory task

A computerised version of the Corsi block-tapping task (Corsi, 1972) – a visuo-spatial version of the standard digit span task – was used to access participants' working memory span. The task includes nine identical blue squares presented on the screen at irregular positions. The squares are lit up in a sequence, and the order must be reproduced by the participant by clicking on the squares with a computer mouse.

English Grammaticality Judgement Task (EGJT)

The task was constructed based on the examples of sentences from Linebarger et al. (1983). The participants were asked to decide whether the presented sentence is grammatical or ungrammatical as quickly as possible. 89 sentences in total were presented to participants. The following sentence is an example of an ungrammatical stimuli sentence: *'He came my house at six o'clock'*.

British Sign Language Grammaticality Judgement Task (BSLGJT)

The task (BSLGJT; Cormier et al., 2012) consisted of 14 pairs of grammatical and ungrammatical sentences. The ungrammatical sentences had a constituent moved into an incorrect position in the sentence. The following pair is an example of a correct and incorrect sentence pair:

A grammatical BSL sentence:
FIFTY YEAR AGO MOST MAN SMOKE
'Fifty years ago, most men were smokers.'

An ungrammatical BSL sentence:
*FIFTY SMOKE YEAR AGO MOST MAN
'Fifty smoke years ago, most men.'

Degree of deafness

Audiogram assessment was conducted with an R17 portable audiometer (Resonance, http://www.resonance-audiology.com/en/r17a-screening-audiometer/). Some deaf participants were able to provide recent results from similar screenings from a clinic; in this case, the hearing screening step of the session was skipped. The limit was set at 70 dB. Participants with the best ear PTA lower than 70 dB, suggesting that their hearing loss was not severe, were excluded.

Executive function tasks

Working memory, planning, switching, and inhibition were measured during the scanning sessions with the following tasks:

Working memory

A typical visuo-spatial working memory task (Fedorenko et al., 2011, 2013) was used. Participants were asked to keep sets of spatially-distributed elements (black squares) presented in sequences in memory for a brief period of time. The control task was a simple perceptual task of deciding whether a blue square appeared among the stimuli at any point during the trial (Figure 2.1). The trials in both tasks started with a visual cue (1500 ms) that indicated the type of task the participant was asked to perform. The cue was followed by identical 3 x 3 grids with black squares presented at randomly generated grid locations for 1000 ms. A total of eight squares were presented two at a time in each trial. In the control task, a blue square appeared on one of the grids during some trials. In the working memory task, the response screen included two grids with the combination of eight black squares, and the correct response was choosing the grid that corresponded to all eight locations of the black squares presented during the trial. In the control task, the response screen looked identical to the ones in the working memory condition, but the words 'YES' and 'NO' were presented under the grids, and the participants were asked to ignore the positions of the squares and respond 'YES' if they had seen a blue square and 'NO' if a blue square had not been present in the trial. The response screen was displayed for 3750 ms or until the participant pressed a response button. The total duration of each trial was 8000-10000 ms, with an inter-trial interval (ITI) jittered between 2000-3500 ms. Each run included 30 working memory trials and 30 control task trials.

Planning

A computerised 'beads and rods' version of the classic Tower of London task (Kaller et al., 2011; Shallice, 1982; O. A. van den Heuvel et al., 2003) was used as the planning task (Figure 2.1). In each trial, two configurations of coloured beads placed on rods of different heights were presented on a grey screen. Participants had to determine the minimum number of moves required to arrive from the starting (top) configuration to the target (bottom) configuration. They were asked to follow two rules:

1. One can move only one bead at a time;
2. A bead cannot be moved underneath another bead.

The Tower of London task was divided into four levels of complexity, depending on the correct answer, by the minimum number of moves required (2, 3, 4, or 5). In the control task, the visual configuration was identical, and the participants were asked to count the number of yellow and blue beads in both configurations on the screen. The response options were displayed from the beginning of each trial: one number indicating the correct response and one number corresponding to the incorrect response (+-1 from the correct response value). The maximum duration of a trial was 30 000 ms (30 seconds). The ITI was jittered between 2000-3500 ms. Each run included 30 planning task trials and 30 easy mathematical problem-solving (control) trials.

Switching

A typical switching task paradigm with geometric shapes (a rectangle and a triangle) was used (Liston et al., 2006; Rushworth et al., 2002) (Figure 2.1). At the beginning of each run, the button responses (left and right) were assigned to a certain shape. The instruction stating the rule was as follows: 'Press the right key if you see a triangle, press the left key if you see a square'. The task was designed in blocks, with each block starting with a cue indicating the kind of task participants were asked to perform. The trials of the control condition ('stay') started with the cue '=' and indicated that the rule should be kept as in the previous block, and the task ('switch') condition trials started with the cue 'x' and indicated a switch of the keys for the response (i.e., the left key for the triangle and the right key for the square). Each trial was followed by visual feedback (green for correct and red for incorrect). Each block included the presentation of the cue (200 ms), the fixation cross (500 ms), two to five trials of one type of task, and feedback (500 ms). The maximum duration of the trials in each block was 1500 ms. The duration of a block was 2500-4000 ms. Each run included 230 trials divided into 80 blocks of either stay (40) or switch (40) conditions.

Inhibition

A version of the classic Simon task (X. Liu et al., 2004) from (A. Kelly & Milham, 2016) was adopted. The instructions asked the participants to use the left key to respond to the presentation of a green square and use the right key when a red square appeared on the screen. The squares always appeared on the left or the right side of the fixation cross. The position of the stimuli was not relevant to the task and was supposed to be ignored. In the control condition – or the congruent condition – the key response was spatially congruent with the location of the stimulus (e.g., the right key response for a red square appearing on the right side of the screen) (Figure 2.1). In the challenging condition – or the incongruent condition – the correct response was in the opposite location (e.g., the right key response for a red square appearing on the left side of the screen). Each square was displayed for 700 ms. The response window was 1500 ms and started with the onset of the stimulus and was signalled by a change of colour of the fixation cross (from black to white). The ITI was 2500 ms for most trials, but there were 20 blank intervals of 7500 ms (7.5 seconds), two black intervals of 12500 ms (12.5 seconds), and one interval of 30 000 ms (30 seconds). Each run consisted of a maximum of 200 trials, half of each kind of task. Participants completed 1 or 2 runs of the inhibition task, depending on their scanning time availability.

The order of the tasks during both sessions was counterbalanced across participants. Laptop keys (left and right) were used for responses during the behavioural session when participants received training in the tasks, and the buttons on the response pads that participants held in their left and right hands were used during the neuroimaging session.

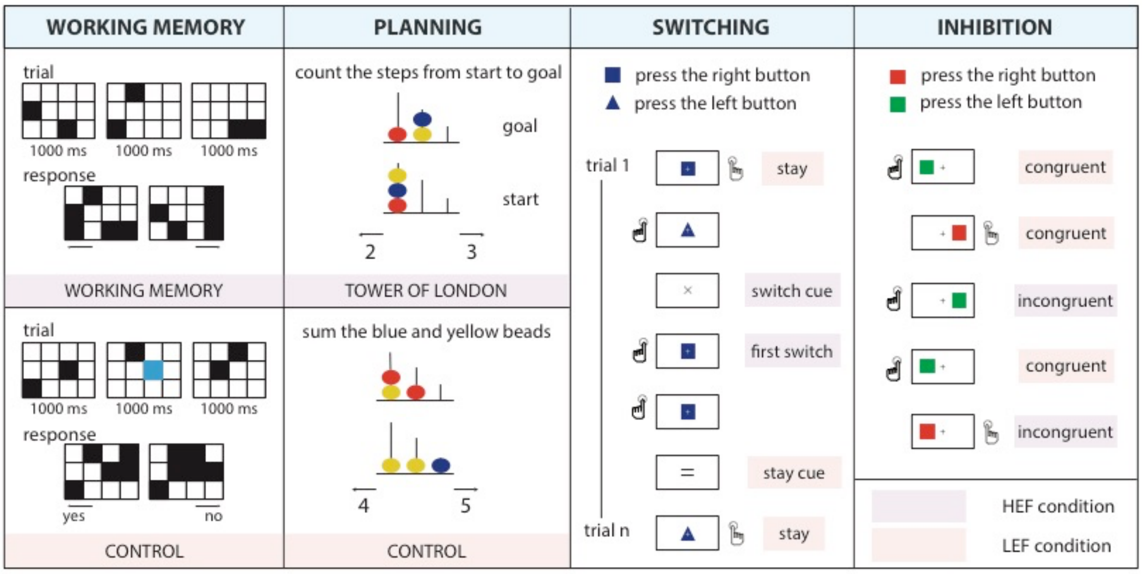

Figure 2.1. The design of the executive function tasks. The working memory and planning tasks consisted of two distinct tasks (labelled 'working memory' and 'Tower of London'), one of which was tapping into the executive function (working memory, planning), and the other acted as an easier control task that did not require challenging executive processing (control tasks). The switching and inhibition tasks had two conditions, with the easier conditions (stay and congruent respectively) acting as the control measure.

2.2.3. Procedure

Neuroimaging sessions took place at the Norfolk and Norwich University Hospital in Norwich, UK. A 3 Tesla wide-bore GE 750w MRI scanner was used with a 64-channel head coil. A web camera was used to communicate in BSL with deaf participants while they were inside the scanner. If the deaf participants preferred English, the text was typed on the laptop and displayed on the screen. An intercom was used to communicate with hearing participants. All volunteers were given earplugs. The tasks were presented using PsychoPy (http://psychopy.org) installed on a laptop (MacBook Pro, Retina, 15-inch, mid-2015). The tasks were projected by an AVOTEC silent vision projector (https://www.avotecinc.com/high-resolution-projector) on the screen reflected in a mirror mounted on the head coil. Button responses were collected via FORP fiber optic boxes (https://www.crsltd.com/tools-for-functional-imaging/mr-safe-response-devices/forp/).

The training part of the behavioural session always preceded the neuroimaging session so that participants could familiarise themselves with the tasks. The training required participants to respond to the tasks with an accuracy score of more than 80% to make sure that they understood the tasks.

2.2.4. Image acquisition

Functional images of the whole brain were acquired using a gradient-echo, echo-planar-imaging sequence (EPI) on a 3 Tesla (3T) GE750w wide bore MRI scanner using a 64-channel head coil, with the following parameters: 50 slices, repetition time (TR) = 3000 ms, echo time (TE) = 50 ms, field of view (FOV) = 192x192 mm, slice thickness = 2 mm, distance factor = 50% with an in-plane resolution of 3 x 3 x 3 mm.

High-resolution T1-weighted anatomical images for each participant (IR-FSPGR, TI = 400 ms, TE = minimum full, slice thickness = 1 mm) with an in-plane resolution of 1 x 1 x 1 mm were acquired at the start of the session.

Raw B_0 fieldmap data were acquired using a 2D multi-echo gradient echo sequence (GRE) with the following parameters: TR = 700 ms, TE = 4.4 and 6.9ms, flip angle = 50°, matrix size = 128 x 128, FOV = 240 mm x 240 mm, number of slices = 59, thickness = 2.5 mm, and gap = 2.5 mm. Real and imaginary images were reconstructed for each TE to permit the calculation of B_0 fieldmaps in Hz (Fessler et al., 2005; Funai et al., 2008; Jezzard & Balaban, 1995).

The session included six runs: one resting-state run (see Chapter 3 and Chapter 4) and five task scanning runs (working memory: 10.5 minutes, 210 volumes; planning: 11.5 minutes, 230 volumes; switching: 10.5 minutes, 210 volumes; inhibition: two runs of 10 minutes, 200 volumes each).

2.2.5. fMRI data preprocessing

Disclaimer. The preprocessing and initial analysis of the neuroimaging data (with the exclusion of the skull-stripping procedure performed by me) that were used in some of the analyses presented here, as well as the between-group analysis of the neuroimaging data discussed briefly in this chapter, were conducted by Dr Barbara Manini. Section *2.3. Results* only reports analyses performed by me.

Data were analysed using MATLAB 2018a (MathWorks Inc., Natick, MA, USA) and Statistical Parametric Mapping software (SPM12; Wellcome Trust Centre for Neuroimaging, London, UK). Anatomical images were segmented into different tissue files: grey matter, white matter, and cerebrospinal fluid. Using the Image Calculator function in SPM (ImCalc, http://tools.robjellis.net), skull-stripped anatomical images were created by combining the tissue files resulting from segmentation, with the expression set to [i1.*(i2+i3+i4) > threshold], where i1 corresponded to the bias-corrected anatomical scan and i2, i3, and i4 were the tissue images (grey matter, white matter, and cerebrospinal fluid). The threshold varied between 0.5 and 0.9, depending on each scan, to reach adequate brain extraction for each participant.

Each skull-stripped image was normalised to the standard MNI (Montreal Neurological Institute) space. Deformation field files resulting from this stage were then used for the normalisation of all functional scans. Susceptibility distortions in the EPI images were estimated using a fieldmap that was co-registered to the BOLD reference (Fessler et al., 2005; Funai et al., 2008). Finally, functional images underwent a standard preprocessing procedure, i.e. realignment with the use of the pre-calculated phase maps, co-registration, slice-time correction, normalisation, and smoothing (with an FWHM 8mm Gaussian kernel).

All functional scans were checked for motion and artifacts using the ART toolbox (https://www.nitrc.org/projects/artifact_detect) (see Appendix Table 2.1. for the runs excluded due to motion artifacts).

2.2.6. fMRI analysis

The first-level analysis was conducted by fitting a general linear model (GLM) with regressors of interest for each task (described below). All events were modelled as a boxcar and convolved with SPM's canonical hemodynamic response function. The motion parameters, derived from the realignment of the images, were added as regressors of no interest in the model. Regressors were entered into a multiple regression analysis to generate parameter estimates for each regressor at every voxel.

Working memory

The regressors of interest were working memory and control conditions. The onset was set at the start of the presentation of the first stimulus, and the duration was set to 3.5 seconds (i.e., the stimuli presentation duration plus the delay of 500 ms). Button responses were included separately for each hand and condition as regressors of no interest.

Planning

Planning (Tower of London) and the control tasks were included in the model as regressors of interest, with the onset set at the start of each trial and the duration set to the trial-specific reaction time (RT). Button responses were included separately for each hand as regressors of no interest.

Switching

The first switch ('x' cue) trial of each switch block and all stay ('=' cue) trials (the control condition) were included, separately for the hand of the button response, as regressors of interest. The cues and the remaining switch trials were included as regressors of no interest.

Inhibition

Four regressors of interest were entered into the first-level analysis. They were constructed by combining the visual hemifield where the stimulus appeared with the hand of the button response. We modelled the right visual hemifield-left hand and left visual hemifield-right hand separately as the incongruent condition trials; the right visual hemifield-right hand and left visual hemifield-left hand were modelled as the congruent (control) conditions trials.

2.2.7. Region-of-interest analyses: temporal regions

Region-of-interest (ROI) analyses were conducted in the temporal regions that typically perform auditory functions in hearing individuals (e.g., Hall et al., 2000): Heschl's gyrus (HG), the planum temporale (PT) and the posterior superior temporal cortex (pSTC). The posterior superior temporal cortex, including the planum temporale, reliably shows cross-modal recruitment in visual tasks in deaf individuals (Finney et al., 2001, 2003; Fine et al., 2005; Sadato et al., 2005; Cardin et al., 2013; Shiell et al., 2015; Petitto et al., 2000; Karns et al., 2012; Twomey et al., 2017). Heschl's gyrus was chosen specifically as the site containing the human primary auditory cortex (Liegeois-Chauvel et al., 1991; Abdul-Kareem et al., 2008; Morosan et al., 2001). It has previously shown cross-modal recruitment for visual tasks in deaf individuals (Finney et al., 2001; Lambertz et al., 2005; Karns et al., 2012) but not in every study (Sadato et al., 2005; Cardin et al., 2013). The choice of ROIs represents areas of both primary and secondary auditory cortices that have demonstrated cross-modal recruitment in deafness.

Heschl's gyrus and the planum temporale were defined anatomically for each participant. The participant's bias-corrected anatomical scan was parcellated and segmented using FreeSurfer software package (https://surfer.nmr.mgh.harvard.edu) (Dale et al., 1999; Fischl et al., 2001, 2002, 2004; Fischl & Dale, 2000; Han et al., 2006; Jovicich et al., 2006; Ségonne et al., 2004). Voxels within the Heschl's gyrus label and the planum temporale label were exported using ImCalc (http://robjellis.net/tools/imcalc_documentation.pdf). Participant-specific regions of interest were then normalised to the MNI space using the deformation fields from the normalisation step of the preprocessing step of the fMRI analysis.

The posterior superior temporal cortex was defined as in a study that found cross-modal working memory activations in deaf individuals (Cardin et al., 2018), [left: -59 -37 10; right: 56 -28 -1]; similar posterior superior temporal areas have been activated in visual working memory tasks in deaf individuals in other studies (Andin et al., 2021; Ding et al., 2015). There was a partial overlap between one of the anatomical regions of interest (the left planum temporale) and one of the functional regions of interest (the left posterior superior temporal cortex) in 39 of the 45 participants. The average overlap between regions of interest was 8.2 voxels (SD = 6.86), with no significant difference between the groups (deaf: mean = 9.92, SD = 7.02; hearing: mean = 6.05, SD = 6.17). To obtain two independent ROIs, common voxels were removed from the left planum temporale in a subject-specific manner. Removing the overlapping voxels did not significantly change the results of interest (effect of the group and interactions involving the group).

2.2.8. Region-of-interest analyses: fronto-parietal regions

Fronto-parietal ROIs were defined by extracting uniformity clusters from a meta-analysis map of 128 studies associated with the combination *'executive function'* using the http://neurosynth.org website (Yarkoni et al., 2011). From the uniformity clusters, we created spherical, symmetrical, and bilateral ROIs using Marsbar (MARSeille Boîte À Région d'Intérêt, http://marsbar.sourceforge.net) (Brett et al., 2002). The areas of interest were the dorsolateral prefrontal cortexes (DLPFC), the frontal eye field (FEF), the pre-supplementary motor area (pre-SMA), the superior parietal lobule (SPL), and the insulas. A 10-mm radius was set for the dorsolateral prefrontal cortexes, frontal eye field, and superior parietal lobule. The radius was set to 8 mm for the insula and 7 mm for the pre-SMA to exclude voxels in the neighbouring gyri.

2.2.9. Extraction of contrast values

Parameter estimates were extracted from each ROI using Marsbar 0.44 (http://marsbar.sourceforge.net) (Brett et al., 2002).

2.2.10. Statistical data analyses

All the statistical analyses presented in the results section were conducted using JASP (https://jasp-stats.org) and all data visualisation was done in R. Before conducting any analysis on the behavioural data, single outlier points were removed from the reaction time data based on the following criterion: each participant's interquartile range was calculated separately and values exceeding 1.5 interquartile ranges below the first quartile or above the third quartile were removed. If accuracy in one of the conditions of the tasks was below 55%, the data from that participant was removed from all analyses (the conditions considered were: 1) working memory: working memory, control; 2) planning: planning (Tower of London), control; 3) switching: all switch trials, all stay trials; 4) inhibition: all incongruent trials, all congruent trials). The threshold was set at 55% to exclude performance that might reflect guessing. The datasets with the excluded data points are displayed in Appendix Figure 2.1.

Behavioural and neuroimaging data were entered into repeated-measures analyses of variance (ANOVAs) or analyses of covariance (ANCOVAs). The initial neuroimaging analysis that investigated between-group effects in the temporal regions of interest is reported in Manini et al. (2022).

The ANOVAs investigating group differences in behavioural performance included between-subjects factor group (deaf, hearing) and within-subjects factor condition. Significant interactions and effects including group were explored by conducting post-hoc t-tests, and a Holm correction was applied to control the number of false positives (Holm, 1979). Language proficiency effects in behavioural performance were investigated with analyses of covariance (ANCOVAs) with a within-subjects factor condition and language proficiency score as a covariate on the data from the deaf group only. Language proficiency effects in neural activity were investigated with ANCOVAs with within-subjects factors condition, ROI (PT, HG, pSTC) and hemisphere (left, right), and language proficiency score as a covariate on the data from the deaf group only. Significant interactions and effects including language proficiency score were explored by conducting Pearson's correlation coefficient analyses.

Bayesian repeated-measures ANOVAs were also conducted to evaluate the effects of language proficiency on the neural activity in our regions of interest. Only the best five performing models are reported in the thesis. The analysis output includes the Bayes Factors (BF), the prior model probabilities (P(M), held uniform across all the models), and the posterior model probabilities (P(M|data)) for each model. BF_{10} in the tables shows all other models compared with respect to the best performing model. The BF_{10} of less than 1 suggests evidence in favour of the null hypothesis ranging from 'anecdotal' (1 to 0.33), 'moderate' (0.33 to 0.1) to 'strong' (0.1 to 0.033) and 'very strong' (0.033 to 0.01). The BF_{M} shows how much the model has improved after seeing the data. The analysis was conducted using the default prior options (r = 0.5 for fixed effects).

The 'Analysis of Effects' shows the Bayes factors for the inclusion of each effect that appears in at least one model. For each effect, the BF_{incl} reflects how well the effect predicts the data by comparing the performance of all models that include the effect to the performance of all the models that do not include the effect (van Doorn et al., 2021).

2.3. Results

2.3.1. Between-group differences in behavioural performance in executive function tasks

Behavioural results from all conditions of each task are shown in Table 2.4 and Figure 2.2. To explore the differences in performance in the executive function tasks between the hearing and the deaf participants, two separate 2x2 repeated-measures ANOVAs were conducted. One ANOVA for each task was conducted with accuracy (percent correct) as a dependent variable, and the other used reaction time (RT) in the correct trials. Both ANOVAs had group as the between-subjects factor (deaf, hearing) and condition as the within-subjects factor (hard, easy). The results of the ANOVAs are shown in Appendix Table 2.2 and Figure 2.2.

There was a significant main effect of condition for both accuracy (working memory: $F(1,41) = 91.59$, $p < .001$; planning: $F(1,38) = 46.88$, $p < .001$; switching: $F(1,41) = 28.27$, p

< .001; inhibition: *F*(1,35) = 17.57, *p* < .001) and RT (working memory: *F*(1,41) = 199.22, *p* < .001; planning: *F*(1,38) = 211.64, *p* < .001; switching: *F*(1,41) = 21.60, *p* < .001; inhibition: *F*(1,35) = 79.20, *p* < .001) in all tasks, indicating that the more demanding executive function condition was always more challenging and resulted in lower accuracy and slower RT.

There were no significant between-group differences in accuracy in working memory, planning, and inhibition tasks (all *p* > .05). There was a main effect of group, *F*(1,41) = 4.32, *p* = .04 and a condition x group interaction in the switching task, *F*(1,41) = 4.98, *p* = .03: the deaf participants were significantly less accurate in the switch condition of the switching task according to a post-hoc test with a Holm correction, *t* = -2.87, *p* = .02 (Appendix Table 2.2).

There was a significant main effect of group on RT in all tasks (working memory: *F*(1,41) = 8.11, *p* = .007; planning: *F*(1,38) = 10.96, *p* = .002; switching: *F*(1,41) = 4.50, *p* = .04; inhibition: *F*(1,35) = 4.91, *p* = .03). The post-hoc tests with a Holm correction applied confirmed that the deaf group was overall significantly slower in the working memory (*t* = 2.85, *p* = .007), planning (*t* = 3.31, *p* = .002), switching (*t* = 2.12, *p* = .04), and inhibition tasks (*t* = 2.22, *p* = .03).

The switch cost in the switching task and the interference effect in the inhibition task were calculated for the switching and the inhibition tasks respectively as the difference in accuracy and RT between the executive function (first switch trials of the switch blocks, incongruent trials) and the control (stay, congruent trials) conditions (accuracy/RT in the switch/incongruent condition – accuracy/RT in the control (stay, congruent) condition). The accuracy switch cost was different between the groups on the independent-samples t-test, *t*(41) = -2.23, *p* = .03, with the deaf group exhibiting a larger switch cost (*M* = -10.24, *SD* = 9.89) than the hearing group (*M* = -4.18, *SD* = 7.51), while the RT switch cost did not (*p* > .05). The accuracy and RT inhibition effect was not different between the groups (*p* > .05).

Table 2.4. Descriptive statistics on behavioural performance in the executive function tasks

	Working Memory				**Planning**				**Switching**				**Inhibition**			
	deaf *N* = 24				deaf *N* = 21				deaf *N* = 23				deaf *N* = 22			
	hearing *N* = 19				hearing *N* = 19				hearing *N* = 20				hearing *N* = 15			
	WM		**Control**		**ToL**		**Control**		**First switch**		**Stay**		**Incongruent**		**Congruent**	
	Accuracy (percent correct)															
	M	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*
deaf	83.45	9.79	97.40	3.27	76.46	9.97	94.08	11.26	83.12	14.14	93.35	5.94	94.21	4.36	96.98	2.59
hearing	82.30	9.65	97.95	4.02	74.45	11.47	91.54	11.92	91.56	10.10	95.74	4.89	94.66	2.42	97.40	3.20
	RT (correct responses, seconds)															
	M	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*
deaf	1.70	0.38	0.92	0.31	8.21	1.84	3.97	1.48	0.62	0.14	0.57	0.08	0.54	0.08	0.51	0.08
hearing	1.46	0.40	0.68	0.13	6.99	1.91	2.60	0.52	0.56	0.10	0.51	0.07	0.49	0.08	0.45	0.07

Note. ToL = Tower of London.

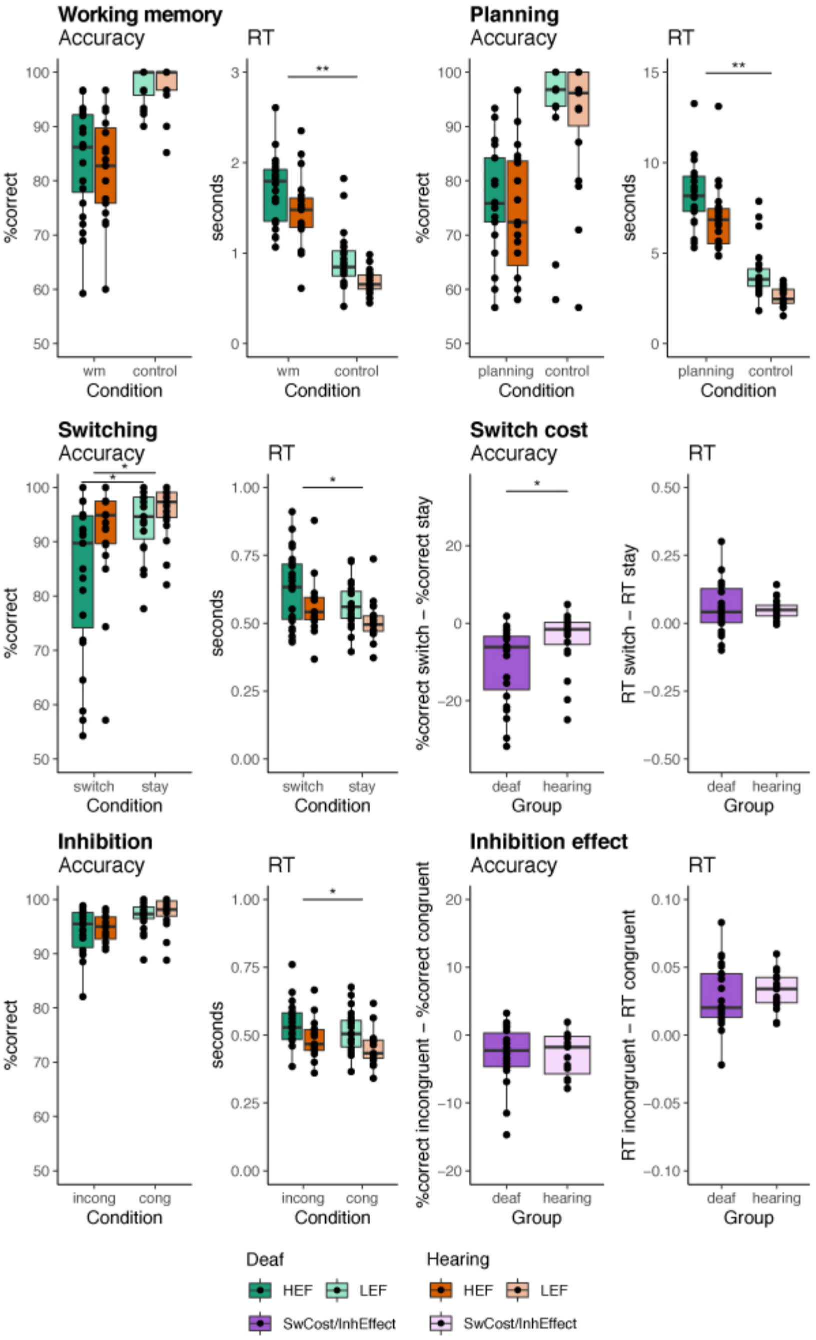

Figure 2.2. Behavioural performance in executive function tasks. The figure displays average accuracy (%correct) and reaction time (seconds) in each task and condition in both groups. The average switch costs and inhibition effects for both accuracy and reaction time are plotted for each group. Only the first trial of the switch block was included in the analysis and the plotting of the data of the switching condition. Bold lines in the box plots indicate the median for each group. The lower and upper hinges correspond to the first and third quartiles (the 25th and 75th percentiles). The upper and lower whiskers extend to the largest and smallest value no further than 1.5*IQR (inter-quartile range) from the hinge. Differences between conditions were statistically significant ($p < 0.05$) for all tasks in both groups (not shown). Values for all behavioural results can be found in Table 2.4. **$p < 0.01$; *$p < 0.05$. The executive function working memory, Tower of London tasks, and the switching and incongruent conditions are grouped by colour as the 'higher executive function/load/task' (HEF) type and the control, stay, and congruent conditions are grouped as the 'lower executive function/load/control' (LEF) type.

2.3.2. Performance in the grammaticality judgement tasks and a modality-independent language proficiency measure

To address the research aims of this thesis, it was necessary to develop a measure that could capture the language proficiency of deaf participants without modality constraints. The grammaticality judgement tasks are designed in a similar manner and tap into the same aspects of language proficiency by implementing a certain paradigm (grammatical vs ungrammatical sets of stimuli sentences). As these tasks use a common method of assessing grammaticality judgements, this allowed us to combine them into a single, modality-independent measure of language proficiency.

Accuracy (percent correct) scores in the EGJ (%correct: *M* = 83.51; *SD* = 11.4) and BSLGJ (%correct: *M* = 77.88; *SD* = 13.09) tasks (Table 2.5) were transformed into z-scores separately for each task in the deaf group. The highest score of the two (EGJT or BSLGJT) was chosen as the one single score of the participant's general language ability. As some of the participants were monolingual English speakers, their z-score in the EGJT was used. The outliers were excluded at two standard deviations from the mean (two participants were excluded at this stage). The z-scores for the EGJ and BSLGJ tasks are plotted in Figure 2.3.

From here on, only the deaf group is included in the analyses presented in this chapter, as the hearing group, being native English speakers, would lack variability in their performance on the English Grammaticality Judgement task, and their language abilities were not the focus of the language analyses or our research questions.

Table 2.5. Language proficiency measures for the sample of deaf participants for the analysis of executive function tasks

	EGJT	**BSLGJT**	**Language score**
Valid	25	21	25
Missing	0	4	0
Mean	83.51	77.88	0.51
Std. Deviation	11.40	13.09	0.69
Minimum	53.93	52.50	-1.56
Maximum	96.63	95.00	1.31

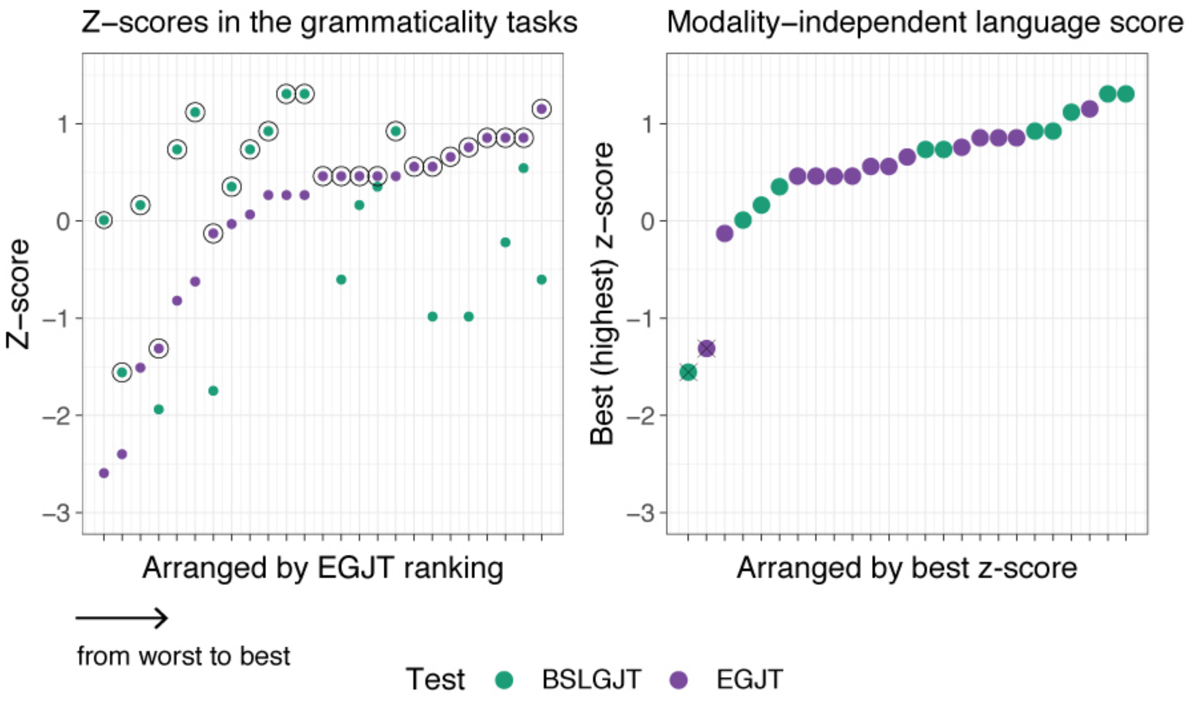

Figure 2.3. The creation of the modality-independent language score based on performance in the grammaticality judgement tasks. The left figure displays language z-scores in the EGJ and BSLGJ tasks in the deaf group, ranked on the x-axis by the performance in the EGJ task. The right figure displays the final language scores (from worst to best). Two participants with the lowest z-scores were removed from all language-related analyses.

2.3.3. The effects of language proficiency on performance in executive function tasks

Repeated-measures ANCOVAs with accuracy or RT as the dependent variable, condition (task/higher executive load, control/lower executive load) as the within-subjects factor, and language score as a covariate were performed on each executive function task. Two additional ANCOVAs with the switch cost in the switching task and the incongruence effect in the inhibition task as dependent variables and language score as a covariate were conducted. All significant and non-significant results are displayed in Appendix Table 2.3. The significant and close-to-significant language-related effects are reported below.

Working memory

There were no significant language-related effects in the ANOVAs on accuracy or RT in the working memory task.

Planning

There was a significant condition x language score interaction on the ANOVA on RT in the planning task, $F(1,17) = 5.87$, $p = .03$. The post-hoc correlational analysis showed a significant negative correlation between RT in the control condition and language score, $r(17) = -0.560$, $p = .01$. The correlation suggests that in the control condition of the planning task, participants with higher language proficiency scores were faster (Figure 2.4).

There was also a trend towards significance for the condition x language score interaction on the ANOVA on accuracy in this task, $F(1,17) = 4.23$, $p = .06$. There was a significant correlation between the accuracy in the control condition and language score, $r(17) = 0.56$, $p = .01$. Plotting the data revealed two outliers that could be driving the results. Removing the outliers made the correlation more significant, $r(17) = 0.71$, $p = .001$. The results suggest that participants with higher language proficiency scores also had higher scores in this condition (Figure 2.4).

Switching

There was a significant main effect of language score, *F*(1,19) = 4.93, *p* = .04 and a significant condition x language score interaction, *F*(1,19) = 4.96, *p* = .04 in the analysis on accuracy in the switching task. The post-hoc analysis showed that there was a significant positive correlation between accuracy in the switch condition and language scores, *r(19)* = 0.47, *p* = .03, but not in the stay condition, *p* > .05. The correlation suggests that participants with lower language proficiency scores were less accurate in their responses in the switch condition, while participants with higher language proficiency scores were more accurate (Figure 2.4).

Inhibition

There were no significant language-related effects in the ANOVAs on accuracy or RT in this task.

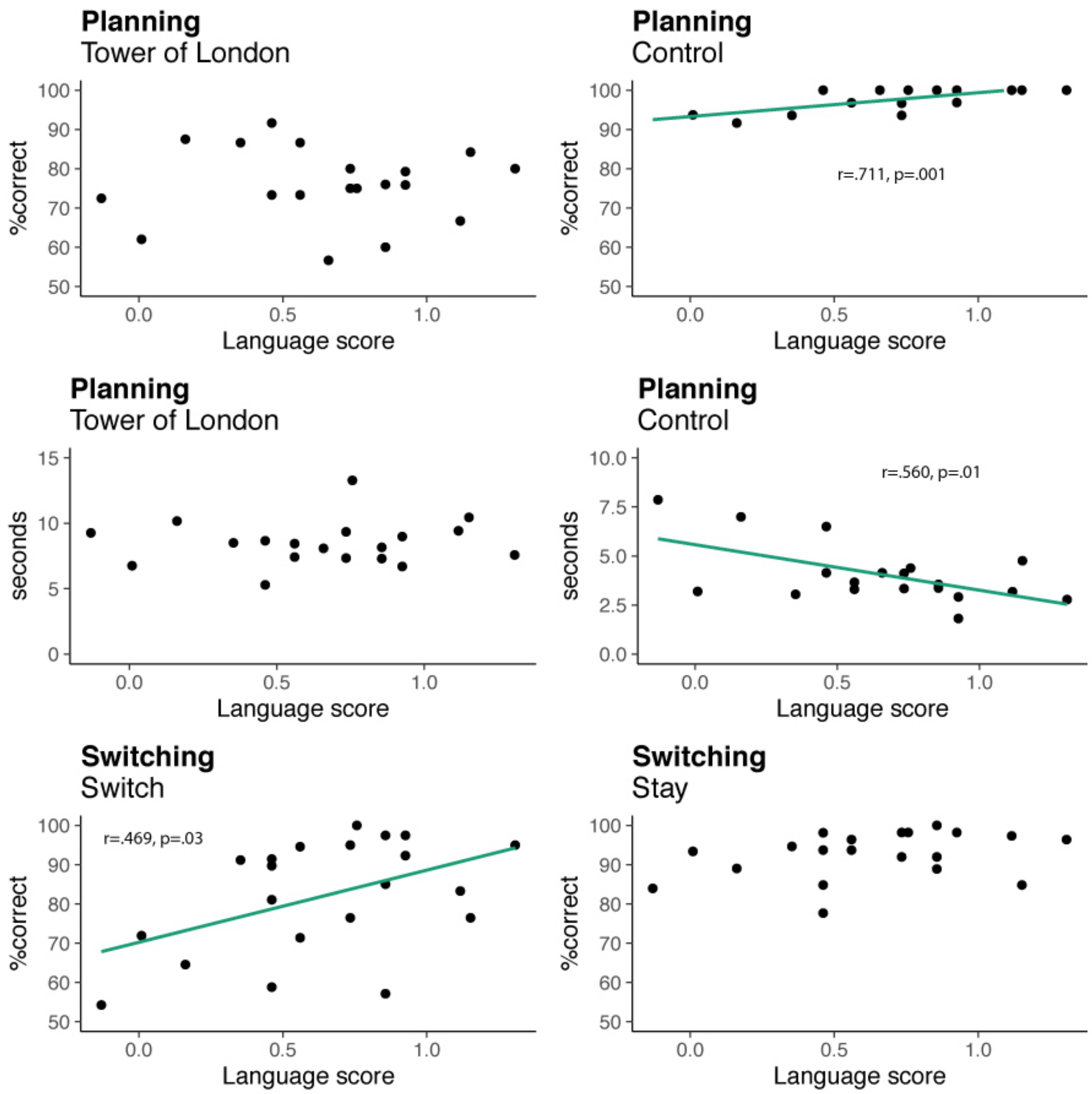

Figure 2.4. Associations between behavioural performance and language proficiency score in executive function tasks in the deaf group. Scatterplots display the associations between language proficiency and behavioural performance (accuracy and RT). Scatterplots for the non-significant condition of the task are included for comparison. In scatterplots representing significant associations, a linear regression line is included. Two outliers were removed from the display and the calculation for the association between accuracy and language score in the control condition of the planning task. The correlation remained significant at p = .001.

2.3.4. The effects of language proficiency on neural activity in executive function tasks

Background information

All executive function tasks recruited typical fronto-parietal regions (see Manini et al., 2022), such as dorsolateral prefrontal cortex (DLPFC), pre-supplementary motor area (pre-SMA), frontal eye field (FEF) and intraparietal sulcus (IPS). There were significantly different activations in these areas in the task/higher executive load and control/lower executive load conditions in the working memory, planning, and switching tasks but no significant differences between conditions in the inhibition task, apart from IPS and left FEF.

In the temporal regions of interest, there was a significant main effect of group in the planning task, with the hearing group significantly deactivating the temporal regions, rather than the deaf group recruiting them more. The cross-modal plasticity effect was found in the switching task across all three regions of interest. Moreover, there was a positive correlation between the behavioural switch cost and the neural switch cost (the neural activity in the switch condition – the neural activity in the stay condition) in the right pSTC in the deaf group. The opposite correlation was found in the hearing group. In the working memory and the inhibition task, there were some significant interactions involving group but the post-hoc analyses did not reveal significant between-group differences in recruitment of the temporal areas for the executive function conditions of these tasks.

In the fronto-parietal ROIs, there were no significant differences between the groups.

2.3.4.1. Language effects on the neural activity in temporal areas during executive function tasks

To investigate the effect of language proficiency on the neural activity in the temporal ROIs in the deaf group, we conducted a 3 x 2 x 2 repeated-measures ANOVA with ROI (PT, HG, pSTC), hemisphere (left, right) and condition (task/higher executive load, control/lower executive load) as factors and language score as a covariate for each of the tasks.

There were no significant language-related effects in the working memory task (Appendix Table 2.4).

There was a significant ROI x language score interaction in the planning task, $F(2, 34) = 8.57$, $p < .001$. All other effects and interactions were not significant (Appendix Table 2.5).

There were no significant language-related effects in the switching (Appendix Table 2.6) and inhibition tasks (Appendix Table 2.7). There was a trend towards significance for the hemisphere x language interaction in the inhibition task, $F(1,18) = 3.45$, $p = .08$. There were no significant correlations between language proficiency and averaged activity in the left or right hemisphere in this task.

2.3.4.2. *The effect of language on the neural activity in temporal regions in the planning task*

To evaluate further the effect of language on the neural activity in the temporal ROIs during the execution of the planning task described in the previous section, we conducted a Bayesian repeated-measures ANOVA with ROI (PT, HG, pSTC), hemisphere (left, right) and condition (task/higher executive load, control/lower executive load) as factors and language score as a covariate for each of the tasks. Language score was set to interact with all factors in the ANOVAs.

Each table lists, for the best five performing models, the Bayes Factors (BF), the prior model probabilities (P(M), held uniform across all the models), and the posterior model probabilities (P(M|data)). BF_{10} in the tables shows all other models compared with respect to the best performing model.

The best performing model was the model which included the main effect of condition, the main effect of ROI, the main effect of language score, and the interactions between ROI and language (BF_M = 81.14) (Table 2.6a). There is evidence in favour of the inclusion of the language score (B_{incl} = 1455.41) and the ROI x language score interaction into the model (B_{incl} = 5583.43) (Table 2.6b).

Table 2.6a. Model comparison for the ten best performing models in repeated-measures Bayesian ANOVA on the neural activity in the planning task in the temporal regions of interest

Models	**P(M)**	**P(M|data)**	**BF_M**	**BF_{10}**	**error %**
Condition + ROI + Language + ROI x Language	0.01	0.33	81.14	1.00	
Condition + Language	0.01	0.18	36.32	0.55	9.43
Null model (incl. subject)	0.01	0.11	20.76	0.34	10.38
Language	0.01	0.10	18.64	0.31	9.80
Condition + ROI	0.01	0.07	12.55	0.21	10.00
Condition + ROI + Language	0.01	0.03	5.01	0.09	10.49
Condition + Hemisphere	0.01	0.03	4.80	0.09	9.86
ROI	0.01	0.02	3.91	0.07	10.71
Condition + Hemisphere + Language	0.01	0.02	2.71	0.05	14.36
ROI + Language	0.01	0.02	2.65	0.05	10.43

Note. All models include subject.

Table 2.6b. Bayesian analysis of effects for the analysis on the neural activity in the planning task in the temporal regions of interest

Effects	**P(incl)**	**P(excl)**	**P(incl|data)**	**P(excl|data)**	**BF_{incl}**
Condition	0.89	0.11	0.78	0.23	0.44
ROI	0.89	0.11	1.00	1.385e-4	933.42
Condition x ROI	0.50	0.50	0.18	0.82	0.22
Hemisphere	0.89	0.11	0.25	0.75	0.04
Condition x Hemisphere	0.50	0.50	0.04	0.96	0.04
ROI x Hemisphere	0.50	0.50	0.02	0.98	0.03
Condition x ROI x Hemisphere	0.11	0.89	9.700e-5	1.00	7.505e-4
Language	0.89	0.11	1.00	8.880e-5	1455.41
Condition x Language	0.50	0.50	0.16	0.84	0.20
ROI x Language	0.50	0.50	1.00	1.791e-4	5583.43
Hemisphere x Language	0.50	0.50	0.08	0.92	0.08
Condition x ROI x Language	0.11	0.88	0.00	1.00	0.02
Condition x Hemisphere x Language	0.11	0.88	4.767e-4	1.00	0.00
ROI x Hemisphere x Language	0.11	0.88	7.252e-4	1.00	0.01

To explore the ROI x language score interaction, I performed Bayesian repeated-measures ANOVAs with condition (Tower of London, control) and hemisphere (left, right) as within-subjects factors and language score as a covariate on the neural activity in each temporal ROI separately. The best performing model for the PT included condition and language ($BF_M = 6.18$) (Table 2.7a). The best performing model for pSTC included only language ($BF_M = 9.15$) (Table 2.8a). The best model for HG included only condition (Appendix Table 2.8).

Table 2.7a. Model comparison for the ten best performing models in repeated-measures Bayesian ANOVA on the neural activity in the planning task in the planum temporale

Models	**P(M)**	**P(M I data)**	**BF_M**	**BF_{10}**	**error %**
Condition + Language	0.05	0.27	6.58	1.00	
Condition	0.05	0.17	3.71	0.64	3.57
Language	0.05	0.10	1.92	0.36	3.83
Condition + Hemisphere + Language	0.05	0.08	1.53	0.29	4.30
Null model (incl. subject)	0.05	0.06	1.24	0.24	3.48
Condition + Language + Condition x Language	0.05	0.06	1.20	0.23	4.08
Condition + Hemisphere	0.05	0.05	0.99	0.20	3.72
Condition + Hem. + Language + Hem. x Language	0.05	0.04	0.76	0.15	4.29
Hemisphere + Language	0.05	0.03	0.60	0.12	11.22
Condition + Hem. + Language + Condition x Hem.	0.05	0.03	0.49	0.10	4.49

Note. All models include subject.

Table 2.7b. Bayesian analysis of effects for the analysis on the neural activity in the planning task in the planum temporale

Effects	**P(incl)**	**P(excl)**	**P(incl I data)**	**P(excl I data)**	**BF_{incl}**
Condition	0.74	0.26	0.77	0.23	1.22
Hemisphere	0.74	0.26	0.34	0.66	0.18
Condition x Hemisphere	0.32	0.68	0.07	0.93	0.16
Language	0.74	0.26	0.68	0.33	0.74
Hemisphere x Language	0.32	0.68	0.09	0.92	0.20
Condition x Language	0.32	0.68	0.11	0.89	0.26
Condition x Hemisphere x Language	0.05	0.95	0.00	1.00	0.03

Table 2.8a. Model comparison for the ten best performing models in repeated-measures Bayesian ANOVA on the neural activity in the planning task in the posterior superior temporal cortex

Models	**P(M)**	**P(M I data)**	**BF_{M}**	**BF_{10}**	**error %**
Language	0.05	0.34	9.44	1.00	
Null model (incl. subject)	0.05	0.25	5.93	0.72	1.54
Hemisphere + Language	0.05	0.09	1.68	0.25	4.91
Condition + Language	0.05	0.08	1.60	0.24	2.29
Condition	0.05	0.06	1.19	0.18	1.86
Hemisphere	0.05	0.06	1.13	0.17	2.13
Hemisphere + Language + Hemisphere x Language	0.05	0.03	0.58	0.09	2.74
Condition + Language + Condition x Language	0.05	0.02	0.41	0.07	2.77
Condition + Hemisphere + Language	0.05	0.02	0.36	0.06	4.43
Condition + Hemisphere	0.05	0.02	0.27	0.04	2.95

Note. All models include subject.

Table 2.8b. Bayesian analysis of effects for the analysis on the neural activity in the planning task in the posterior superior temporal cortex

Effects	**P(incl)**	**P(excl)**	**P(incl I data)**	**P(excl I data)**	**BF_{incl}**
Condition	0.74	0.26	0.23	0.77	0.11
Hemisphere	0.74	0.26	0.24	0.76	0.11
Condition x Hemisphere	0.32	0.68	0.02	0.98	0.04
Language	0.74	0.26	0.61	0.39	0.56
Hemisphere x Language	0.32	0.68	0.05	0.96	0.10
Condition x Language	0.32	0.68	0.03	0.97	0.08
Condition x Hemisphere x Language	0.05	0.95	3.722e-4	1.00	0.01

To further explore these relationships, we calculated the correlation between language score and the neural activity for each combination of hemisphere and condition for each temporal ROI (left PT — control and Tower of London conditions, right PT — control and Tower of London conditions, etc.) (Table 2.9). There was a significant correlation between language z-score and the neural activity in the left PT in the Tower of London condition (*r(17)* = 0.56, *p* = .01) and the control condition (*r(17)* = 0.46, *p* = .05) (Figure 2.5). There was a trend towards significance for the correlation between language score and the neural activity in the right pSTC in the Tower of London condition (*r(17)* = 0.44, *p* = .06) (Figure 2.5). The correlations with the neural activity in the HG were not significant (Figure 2.5). None of the correlations remained significant when a Holm correction was applied.

Table 2.9. Correlation coefficients for the relationship between language score and neural activity in the temporal ROis during the planning task

Region		**Planum temporale**				**Posterior superior temporal cortex**				**Heschl's gyrus**			
Condition		Tower of London		Control		Tower of London		Control		Tower of London		Control	
Hemisphere		Left	Right	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right
Language	*r*	**0.56**	0.30	**0.46**	0.28	0.36	0.44	0.33	0.40	-0.13	-0.03	-0.04	-0.06
	p	**.01**	.22	**.05**	.25	.13	.06	.16	.09	.60	.91	.87	.81

Note. Pearson's correlations. Significant correlations are highlited in bold.

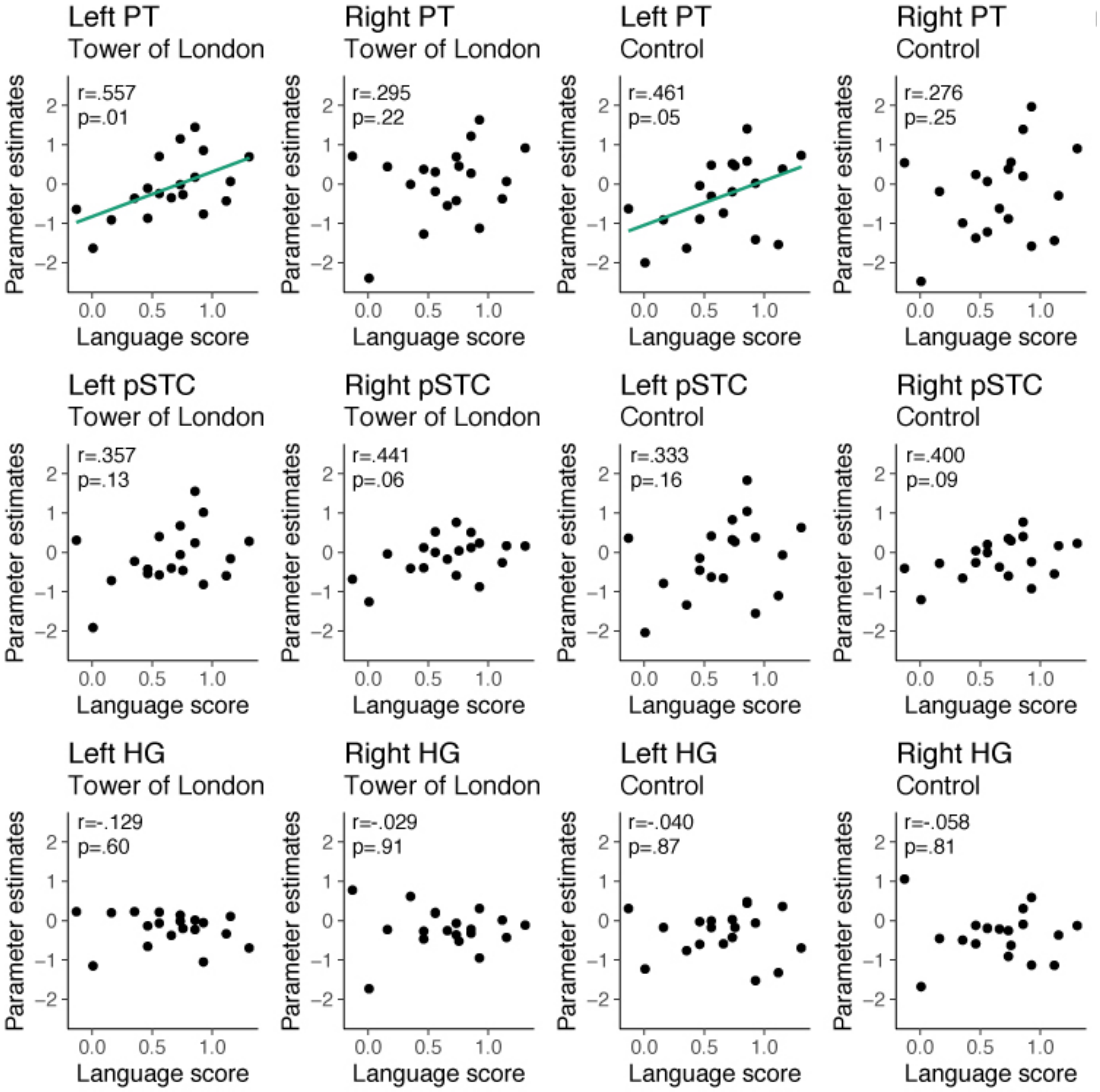

Figure 2.5. Associations between language proficiency and neural activity in the temporal regions of interest during the execution of both conditions of the planning task. Scatterplot representing significant relationships are plotted with a linear regression line.

2.3.4.3. The effects of language proficiency on neural activity in fronto-parietal areas in executive function tasks

To investigate the effect of language on the neural activity in the fronto-parietal ROIs, we conducted a 5 x 2 x 2 repeated-measures ANOVA with ROI (DLPF, FEF, SPL, insula, pre-SMA), hemisphere (left, right) and condition (task, control) as factors and language score as a covariate for each of the tasks. There were no significant effects or interactions involving language in this analysis for any of the tasks (Appendix Table 2.9, Appendix Table 2.10, Appendix Table 2.11, Appendix Table 2.12).

There was a trend towards significance for the ROI x language score interaction in the planning task, $F(4,68) = 2.36$, $p = .06$ but the exploration of the effect through correlations between the averaged neural activity and language in each ROI did not lead to any results (all $p > .05$).

There was a trend towards significance for the condition x ROI x language score interaction in the switching task but with the correction applied due to Mauchly's test of sphericity indicating that the assumption of sphericity was violated ($p < .05$), the trend of $p = .069$ became less significant, $p = .093$. None of the correlations were significant.

There was a significant hemisphere x ROI x language interaction in the inhibition task, $F(4,72) = 3.02$, $p = .02$ but none of the correlations were significant (all $p > .05$).

2.4. Discussion

Four tasks tapping into different aspects of executive function (working memory, planning, switching, and inhibition) were used here to investigate effects of language proficiency in cognition and brain reorganisation in this study. In a different manuscript, my colleagues and I present the data from the same tasks and describe the evidence of neural reorganisation in the temporal cortices in deaf individuals (Manini et al., 2022), with the deaf group recruiting the temporal areas significantly more than the hearing group during switching. This suggests a functional shift towards aspects of cognition in the temporal cortices of congenitally and early deaf individuals. These findings are partially in agreement with other evidence of the functional shift towards cognition in the temporal cortices in this population (Cardin et al., 2018; Ding et al., 2015). The fact that the only task that showed significant reorganisation of function was switching, and other tasks did not recruit temporal cortices significantly more in the deaf group suggests that the aspects of cognition that drive the reorganisation may be different from what had been suggested before. Neural activity in the reorganised regions also predicts RT performance in the deaf group, which emphasises the functional role of the shift towards cognition observed in temporal regions in the deaf group (Manini et al., 2022).

Reorganisation of the temporal cortices for switching is the central finding presented in Manini et al. (2022). To aid the interpretation of the findings from the study presented in this chapter it is important to note, in addition to the recruitment of temporal cortices for switching in the deaf group, high degree of variability in neural activity in the deaf group in the planning task, where deaf participants also did not deactivate the temporal cortices, unlike the hearing group (see Appendix Figure 2.2 and Appendix Figure 2.3). In this chapter, I demonstrate a relationship between a different aspect of performance in the switching task (accuracy) and language proficiency, and an association between language proficiency and neural activity during the execution of the planning task.

2.4.1. The association between behavioural performance in executive function tasks and language proficiency in deaf individuals

Switching between tasks may lead to costs in both speed and accuracy (Monsell, 2003), and we observed group differences in both in our study. It was also the only task out of four that showed differences in performance on accuracy between the groups, with the deaf group having lower accuracy scores. The fact that accuracy showed a positive association with language proficiency emphasises the importance of language development for the correct execution of the task.

Language experience has been linked to switching before. Advantages in set-shifting have been found in bilingual children with autism spectrum disorder in comparison to monolingual children on a computerised Dimensional Change Card Sort (DCCS) task while working memory was not different (Gonzalez-Barrero & Nadig, 2017). In bilingual adults, code-switching habits are related to verbal switching and non-verbal cognitive shifting, with frequent bilingual switchers having higher efficiency in these tasks (Han et al., 2022). In a different study, lower mixing costs in a non-verbal switching task were associated with an earlier active bilingualism onset (Khodos et al., 2021). These findings suggest that set-shifting may be one of the specific aspects of executive function that is related to, and may benefit from, bilingualism. Further research comparing monolingual and bilingual deaf children and adults on shifting tasks could shed light on the degree to which switching is related to bilingualism.

Bilingualism is not the only language-related factor that can influence switching abilities. Cognitive flexibility has been found to be impaired in children with developmental language disorder (Kapa et al., 2017). Deaf children with varying language backgrounds had lower scores in cognitive flexibility than hearing controls but these differences were eliminated when language scores were taken into account (Figueras et al., 2008). Here we demonstrate that these differences are also present and detectable in a group of deaf adults with varying language experiences, and can be explained by their degree of language proficiency.

Literature on the development and mechanisms underlying switching may explain the relationship between switching and language proficiency found in our study. Performance on a cognitive flexibility task is impaired by articulatory suppression (Fatzer & Roebers, 2012), and verbal self-instructions have been shown to be beneficial for performance in task switching (Kray et al., 2008). The role of inner speech in development has been emphasised since Vygotsky's work which considered inner speech to be a powerful tool for cognitive self-direction (Vygotsky, 1962). The Cognitive Complexity and Control theory (Zelazo, 2004; Zelazo & Frye, 1998) suggests that rules of the 'if-if-then' type that have to be used for the successful completion of the Dimensional Change Card Sort (DCCS) task cannot be successfully integrated in younger children. Language is proposed to have a critical role in this process of internalising the rules by supporting the representations of conflicting rules during switching (Doebel & Zelazo, 2016; Zelazo & Frye, 1998).

The disruption of inner speech leads to increases in switch costs (Emerson & Miyake, 2003). In tasks specifically designed to test what aspects of switching rely more on inner speech (Miyake et al., 2004), the switch cost was larger for the articulatory suppression condition when the task used a letter cue ('C' for the colour task and 'S' for the shape task), while in a condition that used whole words as cues ('COLOR' and 'SHAPE') performance did not differ between the articulatory suppression condition and the control condition. Our task used non-linguistic cues ('x' for switching and '='

for keeping the rule). It is possible that in the absence of linguistic prompts, our participants were using inner speech as a tool for accessing the relevant task goal, as proposed by Miyake et al. (2004) in their study. Their findings suggest that there is an increasing demand on inner speech when the cue is not transparent, like in our task. The authors suggest that it places a higher retrieval demand that is reflected by the switch cost. It is possible that a different task design, with linguistic prompts in different languages, depending on the preferred language of the participants, could lead to smaller retrieval demands. Further comparison of performance in switching studies with different types of cues (words, signs, letters, and symbols) in deaf and hearing participants could test this suggestion.

Taken together, our finding and evidence from studies on switching from different populations and with varying task design support the idea that successful acquisition of the hierarchical language rules of the 'if-if-then' type and their implementation through inner speech mechanisms can support non-verbal switching in deaf individuals. Further research can evaluate the contributions of specific aspects of language development in different switching paradigms in this population.

Our findings differ from the findings of the studies of executive function, particularly working memory, in deaf adults (Andin et al., 2021; Cardin et al., 2018; Ding et al., 2015). The results presented in this chapter show that deaf adults can have lower accuracy and/or slower reaction time in executive function tasks, including working memory. These results are more in line with the studies of deaf children, where lower performance has been detected across different executive function tasks, including planning, shifting, inhibition (Botting et al., 2017; Figueras et al., 2008; Merchán et al., 2022), and visuo-spatial working memory (Botting et al., 2017). Critically, performance in executive function tasks has been linked to language in these studies (Botting et al., 2017; Figueras et al., 2008; Merchán et al., 2022). Moreover, native signers, who have full access to natural language from birth in the same way as hearing children but through a different modality, do not show difficulties in executive function (Marshall et al., 2015). Taken together, this evidence suggests that it is a lack of language access that leads to disadvantages in components of executive function, rather than auditory deprivation, in agreement with the language scaffolding hypothesis, as opposed to the auditory scaffolding hypothesis (see Hall et al., 2018 for a discussion).

The language scaffolding hypothesis suggests that language provides the foundation for the development of other cognitive skills (Hall et al., 2017), including executive function. Here I described an association with accuracy in the switching task in a sample of deaf adults that reflects the heterogeneous language experiences in this population rather than in a controlled sample of native or early signers. I suggest that the fact that deaf individuals in our study were significantly slower in each of the four tasks and less accurate during switching is related to group composition and specifically the language background of the participants. The finding of such an association is highly relevant and can lead to implications for education and policy on a large scale, as our group composition was aimed at reflecting the heterogeneity found among deaf adults, rather than focusing on a smaller subgroup of native or early and proficient signers.

In addition to strengthening the evidence for the role of language in the development of other cognitive skills that can inform educational and language policies, this study addresses a fundamental question about the association between language and executive function. This association has been a subject of a large number of studies, especially in children, and interactions between these abilities and their developmental trajectories have been actively discussed in the literature (Henry et al., 2012; Im-Bolter et al., 2006; Ye & Zhou, 2009). It is not clear how strong this association is and how it manifests in relation to different aspects of executive function (Gooch et al., 2016). Children with developmental language disorders often show disadvantages in executive function (Henry et al., 2012; Roello et al., 2015). For instance, children with developmental language disorders with better language ability spend less time planning than children with developmental language disorders who have poorer language ability (Larson et al., 2019). This relationship has also been suggested by a smaller number of studies in typically developing children (Lambeth & Liesen, 2011; Trainor, 2012). Research on language and cognition through the prism of investigating the effects of insecure language acquisition in a population of individuals who often experience delayed language acquisition due to environmental, rather than neurological, reasons, can provide valuable insights into this relationship that can extend the knowledge on this topic that can be then generalised to different situations and populations, emphasising the importance of early language development.

In our study, higher language proficiency correlated with reaction time and accuracy in a simple operation of counting objects of the same colours. This relationship was not the primary focus of this investigation, as this thesis focuses on executive function. Nevertheless, it suggests important implications about the role of language development in numerical cognition, considering that deaf participants with higher language scores were more accurate and faster in counting how many blue and yellow beads were on the screen.

Deaf children showed similar performance to hearing children in object-counting and creating sets of given cardinality (Leybaert & van Cutsem, 2002). It should be noted that the majority of the children in that study had early exposure to a form of sign language or visual communication supported by signs at home. The authors hypothesised that sign language provides an advantage to deaf children by allowing mapping abstract linguistic counting onto the pre-existing representations of numbers (Leybaert & van Cutsem, 2002). The relationship between sign language and arithmetical and mathematical abilities has been suggested in later literature. Deaf signers and hearing controls did not differ in performance on subtraction, but the deaf group performed worse in multiplication (Andin et al., 2014). Critically, alphabetical and phonological skills in deaf signers were associated with their multiplicative reasoning, suggesting that sign language phonology acquisition can be beneficial for multiplication skills (Andin et al., 2014). The findings are in agreement with the triple code model of numerical cognition (Dehaene, 1992) that suggests that subtraction involves the magnitude processing code, and previous research showed that basic numerical knowledge for such functions as magnitude representation is intact in deaf individuals (Bull et al., 2005, 2006). Multiplication, on the other hand, relies on verbal competence and phonology, leading to the observed association to phonological skills. Our study did not test phonological abilities in deaf individuals in sign or spoken language but established that counting objects was associated with modality-independent language proficiency in deaf participants.

The groups in our study did not differ on accuracy in counting objects, similarly to children in the study by Laybaert & Cutsem (2002), but the deaf group was overall slower in both conditions of the planning task. The triple code model (Dehaene, 1992) states that the verbal module/code is used for counting, addition, and single-digit multiplication. Children with developmental language disorder perform below their typically-developing peers on a number of tasks of mathematical abilities that involve both verbal and non-verbal demands, including counting (Cross et al., 2019). Children with reading difficulties have been shown to have difficulties with verbal aspects of arithmetic, specifically counting, (Göbel & Snowling, 2010; Simmons & Singleton, 2006) and were slower in dot-counting. The latter finding suggests deficits in accessing the verbal code when counting dots (Moll et al., 2015). Speeded naming of small exact quantities (dots in groups of 1, 2, or 3 presented 8 times per page in four rows of six) predicts object counting abilities in young children (LeFevre et al., 2022), suggesting a link between retrieving words representing quantities and object-counting abilities. Our finding of the correlations between accuracy and response times for counting objects and language proficiency in the deaf group emphasises the role of verbal skills and strategies in counting, and the influence that language proficiency may have on counting performance, similarly to those described in children with reading difficulties (Moll et al., 2015).

2.4.2. The association between neural activity in the planning task and language proficiency in the deaf group

Studies of language, executive function, and deafness often focus on the language ability of the participants in a single modality. For instance, when the relationship between executive function and language was shown in deaf children (Botting et al., 2017), researchers assessed children's *preferred* language, which, for the majority of the children, was spoken English. While we had information about the preferred language of our participants, instead of assessing them in their preferred language, we created a measure of their *stronger* language. This allows us to make judgements about their general language ability, without the bias that the participants may have towards a language due to the demands of their daily interactions, for instance. This is crucial for understanding the relationship between general language ability and executive function in individuals with diverse language backgrounds, such as bilinguals, because of how different aspects of language use can vary from individual to individual and from timepoint to timepoint.

Typical group compositions for fMRI studies on deafness, including studies of executive function, often include native or early signers (Andin et al., 2021; Cardin et al., 2018) or, in cases with more diverse groups, they may only include a measure of language in a single modality in their analysis (Ding et al., 2015). Performance in executive function studies in native and early signers would not be affected by the effects of language delay, but other studies may misattribute the effects of language delay to deafness. Here we propose an alternative approach to studying language abilities in deafness that involves a continuous measure of modality-independent language proficiency that can add insights into the interpretation of behavioural and neuroimaging data.

Using our modality-independent approach, we found that the models with the best predictive adequacy for the neural activity in the planum temporale and pSTC included language proficiency. In the left planum temporale, language proficiency positively correlated (uncorrected) with the neural activity in both conditions of the planning task. There also was a trend toward a significant correlation between language score and neural activity in the right posterior superior temporal cortex in the planning (Tower of London) condition. The planum temporale and the posterior superior temporal cortex exhibited neural reorganisation in the deaf group during switching (Manini et al., 2022). In the planning task, the hearing group deactivated the auditory cortices, but the deaf group did not. The variability in neural activity in the deaf group was more spread, and the degree of neural activity in the left planum temporale in the deaf group was positively associated with language proficiency. Moreover, as described above, response time and accuracy in the object-counting condition were also correlated with language proficiency.

The left planum temporale overlaps with Wernicke's area and is involved in early auditory processing (Binder et al., 1996) and receptive language (Nakada et al., 2001) in hearing individuals. The right superior temporal cortex also has a role in hearing, speech, and language (Howard et al., 2000). In deaf individuals, the superior temporal cortex has also been shown to be activated in both linguistic and visual tasks (Cardin et al., 2018; Twomey et al., 2017).

Planning has been linked to verbal mediation (Al-Namlah et al., 2006; Fernyhough & Fradley, 2005; Larson et al., 2021). Internalised language, or private speech, has been suggested to be an important tool in promoting planning and problem-solving abilities in children (Vygotsky, 1962). Our findings of higher engagement of the temporal cortices during planning in participants with higher language proficiency could be in line with Vygotsky's framework and the Cognitive Complexity and Control theory (Zelazo, 2006; Zelazo et al., 2003). Zelazo and colleagues (Frye et al., 1995; Zelazo et al., 2003) suggest that language facilitates cognitive development as it acts as the basis for the higher-order if-if-then rule system implicated in executive function. We propose that developmental gains of successful language acquisition that are reflected in language proficiency later in life support the ability to formulate and internalise higher-order rules, which may be directly implicated in executive function not only during switching but also in planning. These processes may be reflected and supported by the brain reorganisation of the temporal cortices in deaf individuals with higher language scores. Activation in the right inferior parietal and superior temporal cortex is positively associated with performance during planning in hearing individuals (Unterrainer et al., 2004). Higher activation in the temporal areas in deaf participants with higher language scores may reflect more efficient use of rule-based systems during planning.

A higher tendency for reorganisation in the planum temporale during counting objects was associated with higher language proficiency scores, which, in turn, were associated with accuracy and reaction time in the control condition. The only study to date on the neural correlates of arithmetic processing in deaf individuals demonstrated that deaf signers may engage brain areas during arithmetic processing differently than hearing individuals (Andin et al., 2019), even when performance is not different between the groups. Our findings may suggest that deaf individuals may also differentially engage temporal cortices in counting objects, depending on individual differences in their language proficiency. The left angular gyrus, a region involved in the verbal code according to the triple code model (Dehaene et al., 2003), shows higher activation in solving multiplication problems in individuals with higher mathematical competence (Grabner et al., 2007). The recruitment of the left angular gyrus underlies individual differences in multiplication skills in hearing individuals, and the authors suggest that more competent individuals demonstrate stronger reliance on processes mediated by language. Our finding may indicate a similar relationship, but in the temporal areas, with a tendency towards reorganisation towards arithmetic processing in participants who are more competent in language and counting. These findings add an important piece of evidence for the discussion of the role of cross-modal plasticity in behaviour in deaf individuals, in agreement with the interpretation suggesting a compensatory role for the cross-modal reorganisation in sensory-deprived areas.

2.4.3. Conclusion

This chapter described differences in behavioural performance in executive function between hearing individuals and deaf individuals with varying language backgrounds. It also described an association between behavioural performance and general language proficiency in deaf participants. Lower scores in performance in executive function tasks have been reported for deaf children with varying language backgrounds (Botting et al., 2017; Figueras et al., 2008; Merchán et al., 2022). Here we demonstrate that these differences in performance between deaf and hearing individuals can remain significant in adulthood. Taken together with the existing literature on language and executive function development in deafness, our findings confirm that executive function abilities are closely associated with and supported by language development and describe this association in an adult population.

Capturing these effects may not have been possible without recruiting a group of deaf participants with varying language backgrounds. Studying groups of participants with high variability in language proficiency can reveal language-related effects in behavioural and neural functioning. Here we demonstrated that neural activity in the planum temporale during planning and counting objects is positively associated with language proficiency in deaf individuals, and the latter association is also reflected in behaviour. These patterns suggest a beneficial role of reorganisation of the temporal cortices in deaf individuals, considering that deaf participants with higher language scores show larger neural activity in the auditory cortex for counting objects and have faster response times in this task.

Finally, our study demonstrated that these effects in the brain and behaviour are related to general, modality-independent language proficiency. This highlights that higher language proficiency resulting from successful language development in any language modality is beneficial for cognitive processing on the level of behavioural performance and neural reorganisation.

3 The effects of sensory experience and language proficiency on resting-state functional connectivity in deaf individuals

3.1. Introduction

The current study aims to investigate the role of sensory experience and language proficiency in resting-state functional connectivity in deaf individuals. Resting-state functional connectivity has been shown to be associated with sensory experience (deafness: Andin & Holmer, 2022; Bonna et al., 2021; Dell Ducas et al., 2021; blindness: Guerreiro et al., 2021; Heine et al., 2015; Y. Liu et al., 2007; D. Wang et al., 2014; Wen et al., 2018; C. Yu et al., 2008) and language experience (language experience in hearing bilinguals: Berken et al., 2016; Gullifer et al., 2018; modality-specific language proficiency in deaf individuals: Holmer et al., 2022; Y. Li et al., 2013) in different regions and networks across the brain. However, the effects of sensory experience and language proficiency, independently of the modality of the language, have not been explored in relation to functional connectivity across the brain in deaf individuals in a single study. This chapter focuses on research questions related to the associations of functional connectivity at rest with the sensory experience of deafness and modality-independent language proficiency in a group of deaf participants with varying language experiences.

3.1.1. The role of sensory experience in resting-state functional connectivity

The study of individuals with unique sensory experiences can shed light on the way different areas of the brain function and interact and reveal the pathways for changes that occur in response to different environmental experiences. Such changes can occur on multiple levels, including the intrinsic functional architecture of the brain that is reflected by resting-state functional connectivity (M. W. Cole et al., 2014). Resting-state functional connectivity reflects spontaneous neural activity by measuring temporal correlations of low-frequency physiological fluctuations (< 0.1 Hz) across distributed brain regions when the subject is not performing a task. This allows researchers to map spatially distributed but functionally connected networks in the brain (Biswal et al., 1995; M. P. van den Heuvel & Pol, 2010). The ongoing spontaneous neural activity during rest is not caused by the presence of inputs or producing outputs, and represents the intrinsic functional architecture of the brain (see Fox & Raichle, 2007 for a review; M. W. Cole et al., 2014). Changes in resting-state functional connectivity have been found in different populations, such as in patients with schizophrenia (Sheffield & Barch, 2016), Parkinson's disease (Disbrow et al., 2014), in autism spectrum disorders (Cherkassky et al., 2006; Hull et al., 2017), but also in such groups as endurance athletes (Raichlen et al., 2016), professional musicians (Zamorano et al., 2017) and bilinguals (Berken et al., 2016), suggesting its sensitivity to environmental experience and training. Resting-state functional connectivity also demonstrates age-dependent differences (Roski et al., 2013), and has been shown to be associated with performance in various memory, attention, and executive function tasks in cognitive aging (Cabral et al., 2017; Hausman et al., 2020). It can predict individual differences in aspects of executive function (Reineberg et al., 2015), as well as task-induced fMRI activity (Mennes et al., 2010). Taken together, this literature demonstrates that resting-state functional connectivity is highly sensitive to developmental and environmental experiences and training.

The intrinsic functional architecture of the brain is suggested to be highly similar across different states, with resting-state network connectivity organisation exhibiting large correspondences with task-related network organisation (M. W. Cole et al., 2014; Krienen et al., 2014) (but see Chapter 1 and Chapter 4 for discussions of task-related changes). Brain networks are characterised by correlations and a shared function, such as attention (Fox et al., 2006), cognition (D. M. Cole et al., 2010), or motor function (Biswal et al., 1995). Such networks are often called 'resting-state networks' but can also be referred to as 'intrinsic functional connectivity networks' (Seeley et al., 2009), with the latter term often deemed more appropriate due to the network-wise patterns of functional connectivity being similar across task and rest states (Duyn, 2011; van Someren et al., 2011). Intrinsic functional connectivity networks are also consistent across different subjects (Damoiseaux et al., 2006) but the organisation of large-scale brain networks can change in populations of individuals with unique sensory experiences (Andin & Holmer, 2022; Dell Ducas et al., 2021; D. Wang et al., 2014).

Altered sensory experience can lead to striking changes in brain organisation, when the sensory-deprived cortices start processing information in a different modality, as has been well-documented in the literature on deafness (Cardin et al., 2013; Cardin, Smittenaar, et al., 2016; Finney et al., 2001; Karns et al., 2012) and blindness (Amedi et al., 2003; Kujala et al., 1995; Sadato et al., 1996). Studies of blind individuals point to a tendency of reduced resting-state functional connectivity couplings between sensory-deprived areas and other sensory cortices (Y. Liu et al., 2007; Qin et al., 2013; C. Yu et al., 2008). In particular, reports have described decreased connectivity within visual cortices (Liu et al., 2007; but see Heine et al., 2015 for evidence of increased functional connectivity within and decreased connectivity between the ventral and the dorsal visual streams in blind participants), between visual and somatosensory regions (Burton et al., 2014), visual and somatosensory-motor areas (Bauer et al., 2017; Y. Liu et al., 2007; C. Yu et al., 2008), visual and auditory (Yu et al., 2008), and visual and temporal multisensory cortices (Y. Liu et al., 2007) (see Bock & Fine, 2014 for a discussion on blindness). Such changes in functional connectivity of the visual cortices have been suggested to reflect the relevance of these associations in cross-modal plasticity effects when the occipital cortex is involved in auditory and tactile processing in blind individuals (Pelland et al., 2017). Bock and Fine (2014) propose that decreased connectivity between sensory cortices in blind individuals can be explained by the areas competing for representing sensory tasks, with one of the areas becoming the 'expert' area for processing one type of task (e.g., the occipital cortex in Braille reading), while the other (e.g., the somatosensory cortex) has to shift away from it, leading to a decrease in correlations between them. More recently, Guerreiro et al. (2021) pointed out how reduced connectivity between the visual and other sensory networks in blind individuals could be related to typically reported increased connectivity during resting state with eyes closed versus eyes open in sighted individuals. Guerreiro et al. (2021) showed that these differences were present between sighted and blind groups only when the sighted individuals had their eyes closed during the resting-state scan. This finding suggests that group differences in the connectivity of the sensory networks may also be dependent on the resting-state condition. In a different study, the strength of connectivity between the sensory areas was modulated by the introduction of Braille and practice times (Y. Liu et al., 2007), emphasising the role of training and suggesting experience-based plasticity, rather than plasticity driven by the experience of sensory deprivation, in functional connectivity changes in sensory networks in early blind individuals. Finally, differences in functional connectivity of the sensory networks between blind and sighted individuals can also be dependent on the cognitive state (Pelland et al., 2017).

While the functional connectivity of the sensory networks is often reduced in populations with an altered sensory experience (see a discussion on deafness below), connectivity between the sensory-deprived cortices and other areas often exhibits a different pattern. In blind individuals, connectivity between occipital and frontal (exploratory analysis in Bauer et al., 2017; Burton et al., 2014), and occipital and parietal areas is increased (Burton et al., 2014). The enhanced connectivity of the occipital cortex to the frontal areas was reported to be associated with cognitive control, as most of the frontal areas with altered functional connectivity in blind individuals respond to working memory demands (Deen, Saxe, et al., 2015), but there is also evidence of enhanced connectivity between occipital and frontal and prefrontal language cortices (Bedny et al., 2011; Heine et al., 2015; Y. Liu et al., 2007). Taken together, the findings from the literature on blindness suggest that developmental, environmental, language- and training-related experiences, as well as the cognitive state, may affect functional connectivity at rest in blind individuals in the visual cortices and beyond.

Resting-state functional network composition and functional connectivity have been shown to significantly change in deaf individuals (Andin & Holmer, 2022; Bonna et al., 2021; Dell Ducas et al., 2021), with studies often focusing on functional connectivity changes arising from reorganised temporal cortices (Andin & Holmer, 2022; Cardin et al., 2018; Ding et al., 2016). Studies repeatedly reported differences in connectivity from the temporal areas to other regions in the brain (Andin & Holmer, 2022; Bonna et al., 2021; Cardin et al., 2018; Cardin et al., submitted; Ding et al., 2016; X. Wang et al., 2015), but also between areas outside of the auditory regions (Bonna et al., 2021; Cardin et al., submitted; Dell Ducas et al., 2021).

In deaf individuals, auditory and somatomotor areas consistently show reduced functional connectivity in deaf signers (Andin & Holmer, 2022; Bonna et al., 2021; Cardin et al., submitted), in agreement with the patterns observed in sensory cortices in blind individuals (Bauer et al., 2017; Y. Liu et al., 2007; C. Yu et al., 2008). The studies agree that even though the differences could arise due to the connections between the auditory and motor cortices involved in the auditory-motor integration for speech processing (Hickok et al., 2011; Hickok & Poeppel, 2007) being weaker in deaf individuals, there is a number of arguments against this point of view. For instance, there is a lack of evidence of stronger connectivity between visual and somatomotor areas in deaf signers that would be expected due to reliance on visual information in sign language (Cardin et al., submitted), and there is consistent evidence of the same connectivity pattern in visual and somatomotor cortices in blind individuals (Bauer et al., 2017; Y. Liu et al., 2007; C. Yu et al., 2008) that suggests a possible common mechanism for changes in functional connectivity of the sensory-deprived cortices (Cardin et al., submitted).

Other effects repeatedly observed in functional connectivity in deaf individuals is the increased resting-state connectivity between auditory regions and regions of the salience (Andin & Holmer, 2022; Ding et al., 2016; Cardin et al., submitted) and fronto-parietal (Cardin et al., 2018; Ding et al., 2016) networks. The fronto-parietal network has been also shown to have stronger connectivity in deaf individuals to other networks (memory, cingulo-opercular, somatomotor, subcortical, visual, default mode: Bonna et al., 2021; visual and default mode: Dell Ducas et al., 2021). The default mode network has been found to have stronger connectivity with the subcortical network (Bonna et al., 2021) and motor areas (Dell Ducas et al., 2021). Generally, non-sensory networks (salience, dorsal attentional, fronto-parietal, default mode) seem to exhibit stronger functional connectivity in deaf individuals (Bonna et al., 2021; Dell Ducas et al., 2021), with exceptions such as reduced connectivity between the salience and language networks (Dell Ducas et al., 2021). The findings of increased connectivity in non-sensory networks are often considered by the authors to reflect compensatory mechanisms in cognitive and/or visual processing in deaf individuals (Bonna et al., 2021). For instance, Bonna et al. (2021) propose that stronger connectivity of the default mode network highlights its integrative role in cognitive functioning (Vatansever et al., 2015). Increased connectivity between the nodes of the default mode network and medial temporal gyri in deaf signers (Malaia et al., 2014) was suggested to reflect sign language processing experience. However, this conclusion has not been tested with an explicit language measure or comparison between deaf individuals with different language experiences. Disentangling the sensory and language experience in deaf individuals is a challenge for research (Lyness et al., 2013), and it is unclear what exact role language experience in deaf individuals has on the functional connectivity of both sensory and non-sensory networks.

3.1.1. Language development and functional connectivity in hearing and deaf individuals

Sensory experience is one of many environmental factors influencing brain organisation. Deaf people, in addition to relying on input from the environment in the non-auditory modalities, grow up in a linguistic environment that is different from that of a typical hearing child (Meier, 1991). The linguistic environment deaf children grow up in has great implications for their language development. Deaf children of deaf parents acquire sign language from birth through the visual input provided by their parents and go through the same language acquisition milestones as their hearing peers (Morgan & Woll, 2002). Critically, this applies only to less than 10% of deaf children born to deaf parents (Mitchell & Karchmer, 2004). The rest of the deaf children are born to hearing parents and grow up with great variability in their linguistic experiences. For the majority of deaf children, language acquisition poses a challenge (Morgan & Woll, 2002) and leads to delays in language development. Deaf individuals who did not have early language exposure perform at a lower level in tasks in both spoken (Mayberry et al., 2002) and sign language (Mayberry & Eichen, 1991). Moreover, variable language experiences can influence other aspects of development, such as executive function (Botting et al., 2017; Figueras et al., 2008; Merchán et al., 2022).

Measured in infancy and toddlerhood, functional resting-state connectivity in language-related regions predicts language and preliteracy outcomes at school (X. Yu et al., 2021). In children with high-functioning autism spectrum disorder, local connectivity within the regions of the brain that showed differences between autistic children and typically developing children was related to oral language ability differently in the two populations (stronger local connectivity was associated with better performance in autistic children and worse performance in typically developing children) (H. Li et al., 2014). Language experience in bilinguals has been linked to functional connectivity in the regions involved in language processing and executive control (Gullifer et al., 2018; Sulpizio et al., 2020), as well as within and between attention networks (Dash et al., 2022). In bimodal bilinguals, the functional connectivity of regions involved in spoken language processing was different from the connectivity in the monolingual controls during the task and resting states (L. Li et al., 2015). Early and late bilingualism also influences connectivity patterns of the language-related regions, as well as regions involved in language control (Berken et al., 2016). Age of literacy acquisition has differential effects on functional connectivity of the visual word form area to left fronto-parietal and lateral visual networks (López-Barroso et al., 2020). These studies demonstrate a relationship between language experiences and functional connectivity in regions related to language processing and executive control in different populations and at different ages.

Few studies have attempted to describe language-related functional connectivity changes in deafness. Li and colleagues (2016) described changes in functional connectivity between the limbic system to visual and language-relation regions, with increased connectivity in deaf adolescents, and decreased connectivity between visual and language networks. The former finding was interpreted in relation to poorer reading or speaking skills of the deaf participants, but no analysis was conducted to test this suggestion (W. Li et al., 2016). Another study focused on the functional connectivity of the default mode network between native/near-native deaf signers and hearing non-signers (Malaia et al., 2014). The study described differences in functional connectivity during task and no-task (passive viewing) processing, in particular, connectivity between the right inferior parietal lobule and right middle temporal gyrus. The authors suggest that visual language experience leads to alterations in connectivity between these regions, with higher connectivity in deaf signers in comparison to hearing non-signers. However, the study did not use direct measures of language proficiency, nor did it have a control group of native hearing signers or oral deaf participants to contrast deaf native signers with, which could be an alternative way of addressing this research question. Nevertheless, this research provides considerations for the role of sign language experience in functional connectivity changes in the default mode network and suggests that increased connectivity of the areas of the default mode network that have also been shown to be involved in sign language processing may reflect the experience of processing visual language.

In a study by Y. Li et al. (2013), changes in functional connectivity were investigated in relation to both sensory and language experiences. Altered functional connectivity was found between congenitally deaf individuals, those with acquired deafness, and hearing controls. Weaker connectivity between parts of the superior temporal sulcus and middle temporal gyrus found in both groups of deaf participants in comparison to controls was positively associated with their language skills, as tested in written language. Weaker connectivity between these areas was suggested to be a marker of the lack of associations between word forms and their lexical/conceptual representations that rely on the ventral stream (Hickok & Poeppel, 2007). Critically, sign language proficiency was not considered in this study, even though for all deaf participants sign language was the primary language. While this study demonstrated that proficiency in a language can be directly related to functional connectivity changes in deaf individuals with different sensory experiences, more research is needed to understand the impact of other aspects of language proficiency and proficiency in the preferred language of deaf individuals on functional connectivity in deafness. Taking into account skills in the preferred language or the language that the participants are more proficient in can help researchers avoid misattributing the effects of language deprivation or lack of language access in one modality to functional connectivity changes in deaf individuals.

A recent study by Holmer and colleagues (2022) directly addressed the question of the influence of language proficiency in sign language on functional connectivity in deaf signers. In this study, functional connectivity of the left inferior frontal gyrus to sensorimotor regions in the left precentral gyrus was related to sign language proficiency, with stronger connectivity associated with lower sign language sentence reproduction skills. The authors suggest that could reflect the differences in language network integrity between participants with different proficiency levels, with those with weaker proficiency relying on non-linguistic motor representations instead of language representations, or relying more on language-control functions during sentence reproduction. Nevertheless, the study demonstrates that language proficiency, which arises from different developmental trajectories in a population with variable language experiences, is associated with functional connectivity changes in the language network.

The two latter studies (Holmer et al., 2022; Y. Li et al., 2013) demonstrated that language proficiency is associated with resting-state functional connectivity in deaf individuals. They focused on different aspects of language proficiency, and the results suggest that different relationships may form in individuals with varying language abilities, highlighting the role of language development in brain reorganisation. They also show that using performance-based language proficiency measures allows capturing the effects of language experience on functional connectivity in the brain. Ding and colleagues (2016) investigated whether the connectivity of the reorganised superior temporal gyrus was related to the age of onset of sign language use or the percentage of lifetime using sign language in deaf individuals. The study did not find significant associations. It is possible that the outcomes of these studies could be different if language experiences were measured with a different approach, considering the interactions between language proficiency, usage, and bilingual experience (Luk & Bialystok, 2013), with the latter being highly prominent in deaf populations.

Taken together, studies on functional connectivity and language demonstrate that various language experiences can influence functional connectivity in the brain in hearing and deaf individuals, especially in the language and control networks. Considering a very limited number of studies on functional connectivity and language in deaf individuals, it is unclear whether language experience influences functional connectivity of the regions outside of the language-related and sensorimotor areas in this population. Changes in connectivity between visual and language areas (W. Li et al., 2016) and connectivity of the default mode network (Malaia et al., 2014) have been associated with language experience and language proficiency in deaf individuals but no direct analyses have been carried out to test these suggestions. Language experience influences functional connectivity in networks involved in language, executive control, and attention in bilinguals (Dash et al., 2022; Gullifer et al., 2018; Sulpizio et al., 2020). Considering this evidence from studies on bilingualism, and the evidence of associations between language skills and executive function in deaf children (Botting et al., 2017; Figueras et al., 2008; Merchán et al., 2022) and adults (Chapter 2), language proficiency may also modulate changes in functional connectivity in this population in higher-association cortices, in addition to changes in the language, visual, and sensorimotor areas.

3.1.2. Research questions

In Chapter 2, we explored differences in performance in executive function tasks between deaf and hearing individuals and tested associations between language proficiency and performance in these tasks, as well as associations between language proficiency and neural activity during task execution. General, modality-independent language proficiency scores proved to be a measure that can reveal associations between language proficiency, behavioural performance, and neural activity in deaf individuals. This chapter investigates the effects of sensory experience on functional connectivity at rest by comparing deaf and hearing participants and uses the same general, modality-independent language proficiency measure to explore the following research questions:

- **How does the sensory experience of deafness influence resting-state functional connectivity in a group of deaf individuals with varying language backgrounds? How do changes in resting-state functional connectivity between the deaf and hearing participants manifest beyond the auditory cortices?** Here we expect to replicate previous findings of reduced connectivity between sensory areas in individuals with unique sensory experiences (e.g., auditory and somatomotor areas in deaf individuals, as in Andin & Holmer, 2002; Bonna et al., 2021; Cardin et al., submitted). The connectivity from the sensory areas to the areas in the higher-association cortices (Jung et al., 2017) is expected to be predominantly increased (based on the findings of enhanced connectivity between the visual network and the fronto-parietal network, the somatosensory and memory network from Bonna et al. (2021), from the sensorimotor and visual networks to the default mode network from Dell Ducas et al. (2021), and findings of increased connectivity between the auditory regions and regions of the salience (Andin & Holmer, 2022; Cardin et al., submitted; Ding et al., 2016) and fronto-parietal networks (Cardin et al., 2018)).

Finally, we expect that the areas of the large-scale cognitive and attentional brain networks will show increased connectivity to each other in the deaf group (as between the control/fronto-parietal network and the default mode (Bonna et al., 2021; Dell Ducas et al., 2021) and dorsal attention networks (Dell Ducas et al., 2021), between attention networks (Dell Ducas et al., 2021), and between the language network to attention networks (Dell Ducas et al., 2021)). However, regions from the language network may demonstrate a different pattern of connectivity to other cognitive networks in relation to both sensory and cognitive areas, considering the findings of reduced connectivity of the language network to the visual (W. Li et al., 2016) and salience (Dell Ducas et al., 2021) networks in deaf individuals. If we replicate the findings from other studies on functional connectivity in deafness that predominantly recruited participants who were native, early, or proficient signers (Andin & Holmer, 2022; Bonna et al., 2021; Cardin et al., submitted; Dell Ducas et al., 2021), then these effects can be confidently attributed to the sensory experience of deafness, rather than language experience of the participants.

- **What are the effects of modality-independent language proficiency on resting-state functional connectivity in deafness?** Considering that language skills in separate modalities are associated with functional connectivity in deafness (sign language: Holmer et al., 2022; written language: Y. Li et al., 2013), and that Braille usage and practice times are related to functional connectivity (Liu et al., 2007), we suggest that general, modality-independent language proficiency will also be significantly associated with functional connectivity in deaf individuals. We expect language proficiency to have a modulatory role on functional connectivity, with higher language proficiency leading to the emergence of compensatory connections between different brain areas, considering that language proficiency has a role in supporting executive function in deaf individuals behaviourally (Botting et al., 2017; Figueras et al., 2008; Merchán et al., 2022), and in the brain (Chapter 2). Following this and the evidence of associations between language experience and connectivity in language, cognitive and attention networks in bilingualism (Dash et al., 2022; Gullifer et al., 2018; Sulpizio et al., 2020), we expect to see an association between language proficiency and connectivity in regions from the networks involved in cognition and attention in deaf individuals. Moreover, interactions in connectivity between the regions of the control, attention, default mode, and language networks may be related to the experience of reliance on visual strategies for communication in deaf individuals, as has been suggested before for the nodes of the default mode network involved in language processing (Malaia et al., 2014), or to other aspects of language use and proficiency, as it has been shown in bilinguals (Dash et al., 2022; Gullifer et al., 2018; Sulpizio et al., 2020). Finally, connectivity between areas of the language network and sensory cortices may also be related to language experience, as has been suggested before for both sign language and spoken/written language use and proficiency (Holmer et al., 2022; W. Li et al., 2016).

To address these questions, we will analyse resting-state functional connectivity in deaf and hearing individuals using seed-based functional connectivity analysis. Then we will compare functional connectivity estimates at rest between the groups. Finally, we will investigate the associations between language proficiency and resting-state functional connectivity by including the modality-independent language proficiency score in the analysis of functional connectivity in the deaf group. We hypothesise that resting-state functional connectivity in the sensory, cognitive, and attention cortices will be different between the groups, in agreement with previous literature (Andin & Holmer, 2022; Bonna et al., 2021; Cardin et al., 2018; Cardin et al., submitted; Dell Ducas et al., 2021; Ding et al., 2016) and that general language proficiency score will be associated with functional connectivity between areas from sensory, cognitive (particularly language) and attention brain networks in deaf individuals, reflecting the associations between language proficiency and connectivity in regions that support cognition and attention, and in regions relevant for visual communication. As we can only make general, network-wise predictions based on a limited number of studies in this population, we consider the analyses reported in this chapter exploratory.

3.2. Method

3.2.1. Participants

3.2.1.1. Inclusion criteria and demographics

The inclusion criteria and recruitment process were described in detail in Chapter 2 *(2.1.1. Participants)*. One of the 29 deaf participants was excluded from all studies presented in the thesis due to their degree of deafness not meeting the inclusion criteria of severe or profound deafness *(2.1.1. Participants).* Datasets from three participants were excluded due to excessive motion: these participants had 10 or more outlier scans (approximately 5% of data) revealed during the outlier identification preprocessing step (see description below). The sample size for the group of deaf participants was 25 for the between-group analysis presented in this chapter.

25 deaf participants included in the sample (16 female, 9 male) and 20 hearing (15 female, 5 male) participants were matched on age, gender, non-verbal reasoning, and visuo-spatial working memory span (Table 3.1, Table 3.2).

Table 3.1. Resting-state sample: age, non-verbal reasoning and visuo-spatial memory span

	Age		WASI		Corsi	
	deaf	hearing	deaf	hearing	deaf	hearing
Valid	25	20	25	19	25	19
Missing	0	0	0	1	0	1
Mean	41.96	37.50	59.44	57.47	5.26	5.40
Std. Deviation	14.79	16.85	8.56	8.02	0.79	1.10
Minimum	19.00	18.00	39.00	34.00	3.50	4.00
Maximum	66.00	66.00	72.00	69.00	7.50	8.50

Note. Data from one hearing participant is missing as they did not attend the second study session.

Table 3.2. Resting-state sample: group comparisons for gender, non-verbal reasoning, and visuo-spatial working memory span

	t	*df*	*p*
Age	0.95	43	.35
WASI	0.78	42	.44
Corsi	-0.47	42	.64
	X^2	*df*	*p*
Gender	0.63	43	.43

Note. Student's t-test (WASI, Corsi), Chi-Squared test (gender).

Deaf participants included in the sample for the analysis performed in this chapter had a total mean pure-tone average (PTA) of 94.89 dB (*SD* = 8.11) across the speech frequencies of 500-1000-2000 Hz, with the range for the better ear being 66.67-105 dB and the range for the average of both ears being 78.33-106.67 dB. Note that the maximum values in the dataset were set to 105 dB for consistency, which was lower than the actual recorded values for a number of participants who could not hear tones at 120 dB. Audiogram recordings were missing from three participants but they were all congenitally severely or profoundly deaf, the cause of deafness for two of them was genetic (one unknown), and they all communicated with the researchers through British Sign Language (BSL) or lipreading (see *2.2. Methods* for more details).

As described in Chapter 2 *(2.1.1. Participants)*, all deaf participants were congenitally or early (before 3 years of age) old, severely-to-profoundly deaf, and their first language was either from the BSL family and/or English (see Table 3.3 below).

3.2.1.2. Language variability

Participants had variable language backgrounds: eight participants had deaf signing parents or a deaf signing older sibling (one participant), six participants had early sign language exposure, and six participants learned BSL as adults. One participant did not specify the age of exposure to BSL, but it was not from family. Four participants did not know sign language and used English to communicate throughout their life.

Table 3.3. Questionnaire data on the deafness and language background of the deaf participants included in the functional connectivity analysis of resting-state data

Deafness onset	**Cause of deafness**	**British Sign Language**	**Sign language acquisition**	**Preferred language**
Birth	Unknown	Yes	Native	BSL
Birth	Other	Yes	Early	BSL
Birth	Genetic	Yes	Native	BSL
Birth	Genetic	No	N/A	English
Birth	Genetic	Yes	Native	BSL
< 3 years	Meningitis	Yes	Early	BSL
Birth	Genetic	Yes	Early	English
Birth	Genetic	No	N/A	English
Birth	Unknown	Yes	Late	English
Birth	Genetic	Yes	Native	BSL
Birth	Unknown	Yes	Late	English
Birth	Mother had rubella	Yes	Late	English
Birth	Unknown	Yes	Late	BSL
Birth	Genetic	Yes	Native*	BSL
Birth	Mother had rubella	Yes	Early	English
Birth	Genetic	No	N/A	English
Birth	Genetic	Yes	Non-native**	BSL
Birth	Genetic	Yes	Native	Auslan
Birth	Genetic	Yes	Native	English
Birth	Genetic	Yes	Late	English
Birth	Mother had rubella	No	N/A	English
~ 3 years	Genetic	Yes	Native	BSL
< 3 years	Meningitis	Yes	Late	BSL
Birth	Genetic	Yes	Early	BSL
Birth	Mother had infection	Yes	Early	BSL

Note. *The participant learned BSL from an older sibling. Two participants learned BSL after they learned a different sign language from the same family: Australian Sign Language (Auslan) and South African Sign Language. **The participant did not provide specific age of acquisition for BSL.

3.2.1.3. *Language assessment*

The majority of deaf participants in our sample were bilingual, therefore their general language ability could not be reflected by performance in a single language task. The same measure of language proficiency was used here as in other chapters (see *2.1.2. Materials* for more details). One participant was excluded before transforming task scores into z-scores to avoid the effects of severe language deprivation because they performed at chance in both language proficiency tasks (50.56% in the English Grammaticality Judgement Task (EGJT) and 55% in British Sign Language Grammaticality Judgement Task (BSLGJT). The combined general language score was created from the z-transformed scores from the scores obtained in the EGJT (%correct: $M = 83.80$; $SD = 11.54$) and BSLGJT (%correct: $M = 77.15$; $SD = 12.99$) tasks for the sample of participants included in the resting-state analysis (Table 3.4). The higher z-score was chosen as the measure of the general, modality-independent language proficiency ability. For deaf monolinguals who only know English and have never learned a signed language, their EGJT score was chosen as their general proficiency score. Three participants were excluded from the language-related analyses as outliers (more than two standard deviations from the mean) but not from the general resting-state analysis.

Table 3.4. Language proficiency measures for the sample of deaf participants in resting-state functional connectivity analysis

	EGJT	BSLGJT	Language score
Valid	24	20	24
No test	0	4	0
Mean	83.80	77.15	0.49
Std. Deviation	11.54	12.99	0.69
Minimum	53.93	52.50	-1.51
Maximum	96.63	95.00	1.38

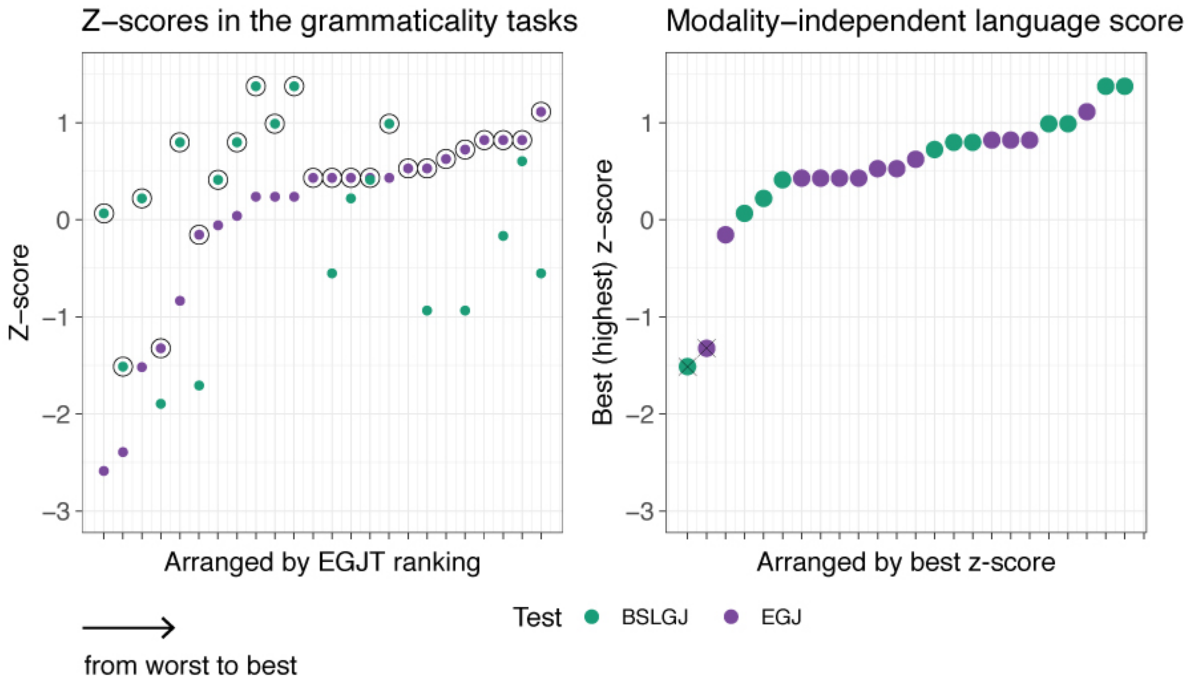

Figure 3.1. The modality-independent z-score in the sample of participants included in the functional connectivity analysis on resting-state functional connectivity. The left figure displays language z-scores in the EGJ and BSLGJ tasks in the deaf group, ranked on the x-axis by the performance in the EGJ task. The right figure displays the final language scores (from worst to best). Two participants with the lowest z-scores were removed from all language-related analyses.

3.2.2. Procedure

The procedure for data collection was the same as described in Chapter 2 *(2.1.3. Procedure)*. The standard duration of the resting-state scan was approximately 10 minutes for each participant. The participants were asked to relax and 'let their mind wander' with their eyes open for the duration of the resting-state scan.

3.2.3. Image acquisition and fMRI data preprocessing

Image acquisition parameters and fMRI data preprocessing were the same as described in Chapter 2 *(2.1.4. Image acquisition and 2.1.5. fMRI data preprocessing)*. The preprocessing was conducted using SPM12. All images were then input into the Functional Connectivity (CONN) 18b Toolbox (https://www.nitrc.org/projects/conn/) (Whitfield-Gabrieli & Nieto-Castanon, 2012) in Matlab R2019b. The Artefact Detection

Tools (ART, (https://www.nitrc.org/projects/artifact_detect) toolbox was used with the default parameters based on the differences in global signal intensity and composite motion to identify image artefacts and outlying volumes caused by movement (scrubbing). Regressor files were generated for outlier images for each participant to be regressed out during first-level analysis for each subject. The maximum number of outliers could not exceed 10 per participant, meaning that if approximately 5% or more of all volumes were identified as outliers, the dataset of this participant was excluded completely from the analysis at this stage.

The ART-based scrubbing and realignment (subject motion correction) regressors were incorporated into the analysis at the stage of denoising, in accordance with the default denoising pipeline (Whitfield-Gabrieli & Nieto-Castanon, 2012) using the component-based noise correction method (CompCor) (Behzadi et al., 2007) that also includes the segmented white matter, cerebrospinal fluid and the effect of rest as confounding effects into the linear regression model. The images were band-pass filtered ($0.008 < f < 0.09$ Hz). Denoising outputs were evaluated visually, and no changes were made to the number of components.

3.2.4. Atlas redistribution procedure

The Schaefer brain parcellation atlas with 400 cortical regions was used (Schaefer et al., 2018) for the analysis. Each parcellation in the version of the atlas that was used in this study is clustered into one of the 17 resting-state networks based on the procedure described in (Yeo et al., 2011) that uses a local gradient approach. Parcellations are based specifically on resting-state fMRI and cover the entire brain.

The networks included in the 17-network version of the atlas are: control (A, B and C), default mode (A, B, and C), dorsal attention (A and B), limbic (A and B), salience/ventral attention (A and B), somatomotor (A and B), temporo-parietal, and visual (A and B).

While we kept network assignments for most of the regions included in the atlas, the distribution of regions among networks was slightly adjusted to match the aims and research questions of this study. To investigate the effects of sensory and language experience specifically on temporo-parietal/auditory and language regions, corresponding networks were constructed from the pre-defined regions in the atlas. First, every seed from the original temporo-parietal network was included in either a temporo-parietal/auditory network or the language network. Secondly, the frontal and parietal seeds across the atlas were investigated to identify if they should be classified as language or auditory regions. This was done manually by using the meta-analysis maps and the 'associations' and 'studies' sections on the Neurosynth website. The 2-mm radius centroid coordinates for each region were input into the Neurosynth system to extract the list of terms associated with activation in this region according to the meta-analysis maps. If the region showed overlap with the maps of activations for words 'language' and 'auditory', it was included in one of these networks. Moreover, regions with high occurrences (among the top five terms) of language-related terms such as 'auditory', 'language', 'sentences', 'linguistic', and 'phonological' among the terms associated with the activations in these regions (according to the 'associations' tab on the Neurosynth website) were included in the corresponding networks. The final list did not include regions in Wernicke's area, so we added two seeds closest to Tomasi & Volkow's (2012) definition of Wernicke's area [-51 -51 30] (Tomasi & Volkow, 2012).

The full list of the seeds assigned to the temporo-parietal/auditory and language networks can be found in Table 3.5, and the visual representations are in Figure 3.2. The coordinates for the remaining seeds can be found online.

Table 3.5. Reassignment of the parcellations into the auditory and language networks

New network	**Original name and network**	**Hemisphere**	**MNI coordinates**
TP/auditory	TempPar_2	Left	[-60 -12 -2]
TP/auditory	TempPar_3	Left	[-62 -32 6]
TP/auditory	SomMotB_Aud_1	Left	[-50 -10 0]
TP/auditory	SomMotB_Aud_2	Left	[-56 -22 8]
TP/auditory	SomMotB_Aud_3	Left	[-58 -36 16]
TP/auditory	SomMotB_Aud_4	Left	[-40 -36 14]
TP/auditory	SomMotB_Aud_1	Right	[52 4 -6]
TP/auditory	SomMotB_Aud_2	Right	[54 -4 6]
TP/auditory	SomMotB_Aud_3	Right	[60 -24 10]
TP/auditory	TempPar_1	Right	[48 16 -20]
TP/auditory	TempPar_2	Right	[54 -4 -20]
TP/auditory	TempPar_3	Right	[48 -20 -8]
TP/auditory	TempPar_4	Right	[62 -18 0]
TP/auditory	TempPar_5	Right	[50 -34 2]
TP/auditory	TempPar_6*	Right	[60 -46 6]
TP/auditory	TempPar_7	Right	[52 -40 12]
TP/auditory	TempPar_8	Right	[64 -34 10]
TP/auditory	TempPar_9*	Right	[54 -46 20]
TP/auditory	TempPar_10*	Right	[62 -40 22]
Language	SalVentAttnA_FrOper_2	Left	[-52 8 14]
Language	ContA_PFClv_1	Left	[-48 36 10]
Language	ContA_PFCl_1	Left	[-50 6 26]
Language	ContA_PFCl_2	Left	[-44 20 26]
Language	DefaultB_Temp_4	Left	[-56 -8 -14]
Language	DefaultB_Temp_5	Left	[-60 -34 -4]
Language	DefaultB_Temp_6	Left	[-52 -22 -6]
Language	DefaultB_PFCv_3	Left	[-46 32 -10]
Language	DefaultB_PFCv_4	Left	[-48 28 0]
Language	DefaultB_PFCv_5	Left	[-54 20 12]
Language	TempPar_1	Left	[-52 6 -12]
Language	TempPar_4	Left	[-52 -44 4]
Language	TempPar_5	Left	[-58 -54 10]
Language	TempPar_6	Left	[-58 -48 16]
Language	DefaultB_IPL_2	Left	[-56 -54 30]
Language	SalVentAttnA_ParOper_2	Left	[-58 -44 28]

*The seed was included to avoid reassignment to a different network.

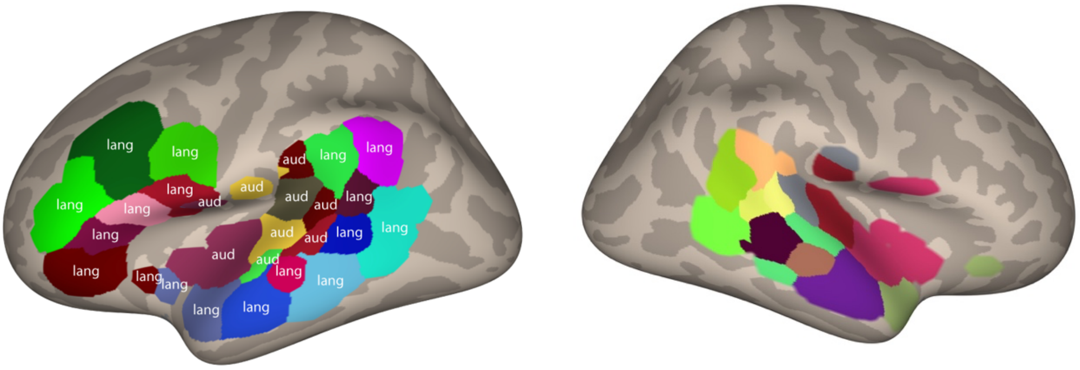

Figure 3.2. The language, temporo-parietal/auditory (left), and temporo-parietal/auditory (right) networks after reassignment.

3.2.5. Resting-state functional connectivity analysis

The CONN toolbox was used further to compute individual seed-to-seed functional connectivity maps. The first-level analysis computed a correlation map for each subject using residual BOLD time course from each seed and computing bivariate correlation coefficients between regions across the brain. The multiple-seed approach was chosen to avoid selection bias in definitions of networks because seed selection can lead to significant variability in the analysis and interpretations of resting-state data (D. M. Cole et al., 2010) and because sensory experience can significantly influence the spatial distribution of large-scale brain networks (Andin & Holmer, 2022; Dell Ducas et al., 2021; D. Wang et al., 2014).

Correlation coefficients were converted from r- to z-values using Fisher's transformation and were used for second-level General Linear Model (GLM) analyses.

3.2.6. Statistical analyses

Second-level analyses were conducted in the CONN toolbox. Independent samples t-tests were implemented for detecting between-group differences in seed-to-seed connectivity across the brain. Then, with only the deaf group selected for the analysis, the association between functional connectivity at rest and language proficiency was assessed by including the modality-independent language z-score as a covariate in the seed-to-seed analysis. For both analyses, CONN's default parametric seed-level multiple comparisons correction method was applied by setting the significance threshold at $p < .05$ (two-sided) with a false discovery rate (FDR) correction (Genovese et al., 2002) to correct across the multiple comparisons arising from having multiple target regions of interest and control for false positives. The FDR-correction method was chosen because the analyses performed in Chapter 3 and Chapter 4 involve a large number of tests (J. J. Chen et al., 2010; Zehetmayer et al., 2005), and because the correction method used in the previous chapter (Holm, 1979) assumes that each test is independent, while voxels are not independent in motion-corrected fMRI data (Kamitani & Sawahata, 2010), and such corrections can result in a high false negative rate (Streiner & Norman, 2011).

3.3. Results

3.3.1. The role of sensory experience in functional connectivity at rest: seed-to-seed between-group analysis

Our first research objective was to investigate differences in resting-state functional connectivity between the deaf and hearing groups, evaluating the effects of deafness on functional connectivity in the brain at rest. The results for each significant connection are displayed in Figure 3.3 and Table 3.6 and summarised below. There were 32 significant pairs of connections.

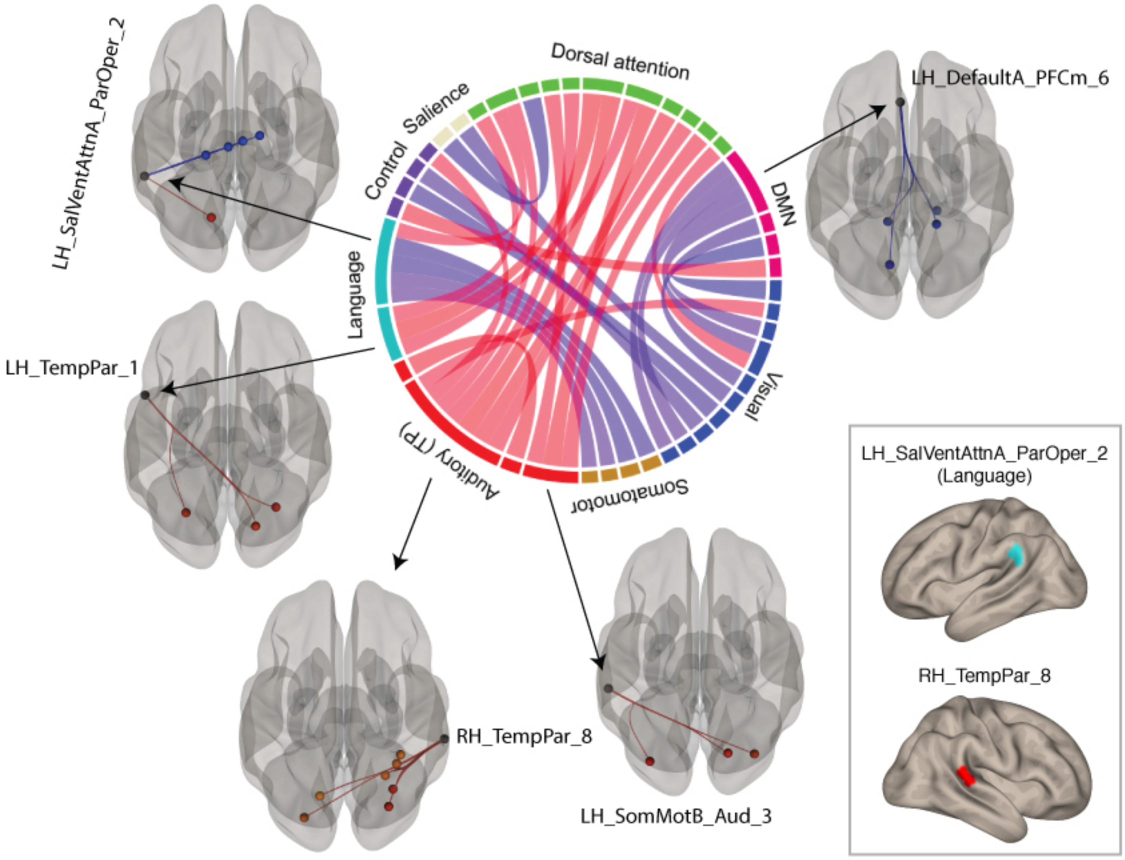

Figure 3.3. Between-group connectivity differences in resting-state functional connectivity. Only pairs of regions that showed significant differences between the deaf and hearing participants for the contrast [deaf > hearing] in the second-level analysis are included in the display. The regions are grouped by network. Red lines indicate increased connectivity between regions in the deaf group, while blue lines indicate increased connectivity in the hearing group. Uninterrupted sections on the wheel indicate that connections arise in the same region. DMN = default mode network; TP = temporo-parietal; salience = salience/ventral attention.

Table 3.6. Resting-state functional connectivity differences between the groups

Source network	**Source region name**	**Target network**	**Target region name**	***T*(df)**	***p*-FDR**
Default mode	LH_DefaultA_PFCm_6	Visual	LH_VisPeri_ExStrSup_3	-4.01(43)	.04
Default mode	LH_DefaultA_PFCm_6	Visual	LH_VisPeri_ExStrInf_4	-3.99(43)	.04
Default mode	LH_DefaultA_PFCm_6	Visual	RH_VisPeri_ExStrInf_2	-3.88(43)	.04
Default mode	LH_DefaultA_PFCm_6	Visual	RH_VisPeri_ExStrInf_5	-3.83(43)	.04
Default mode	LH_DefaultA_pCunPCC_7	Visual	LH_VisCent_ExStr_6	-4.81(43)	.008
Default mode	LH_DefaultA_pCunPCC_3	Visual	RH_VisCent_ExStr_1	-4.32(43)	.04
Default mode	RH_DefaultB_PFCv_3	Control	LH_ContB_IPL_3	4.49(43)	.02
Language	LH_SalVentAttnA_ParOper_2*	Somatomotor	LH_SomMotA_15	-4.47(43)	.01
Language	LH_SalVentAttnA_ParOper_2*	Somatomotor	LH_SomMotA_17	-4.52(43)	.01
Language	LH_SalVentAttnA_ParOper_2*	Somatomotor	RH_SomMotA_18	-3.88(43)	.04
Language	LH_SalVentAttnA_ParOper_2*	Somatomotor	RH_SomMotA_19	-3.81(43)	.04
Language	LH_TempPar_1*	Dorsal attention	LH_DorsAttnA_SPL_1	4.05(43)	.04
Language	LH_TempPar_1*	Dorsal attention	RH_DorsAttnA_SPL_2	4.83(43)	.007
Language	LH_TempPar_1*	Dorsal attention	RH_DorsAttnA_SPL_3	3.94(43)	.04
Language	LH_SalVentAttnA_ParOper_2*	Dorsal attention	LH_DorsAttnA_SPL_6	3.76(43)	.04
TP/auditory	LH_SomMotB_Aud_3*	Dorsal attention	LH_DorsAttnA_ParOcc_2	4.12(43)	.02
TP/auditory	LH_SomMotB_Aud_3*	Dorsal attention	RH_DorsAttnA_SPL_3	4.78(43)	.008
TP/auditory	LH_SomMotB_Aud_3*	Dorsal attention	RH_DorsAttnA_ParOcc_3	4.27(43)	.02
TP/auditory	RH_TempPar_8	Dorsal attention	RH_DorsAttnA_SPL_1	4.06(43)	.02
TP/auditory	RH_TempPar_8	Dorsal attention	RH_DorsAttnA_SPL_2	4.33(43)	.02
TP/auditory	RH_TempPar_8	Dorsal attention	RH_DorsAttnA_SPL_6	4.46(43)	.02
TP/auditory	RH_TempPar_8	Dorsal attention	RH_DorsAttnA_SPL_7	4.16(43)	.02
TP/auditory	RH_TempPar_8	Dorsal attention	LH_DorsAttnA_SPL_6	3.61(43)	.05
TP/auditory	LH_TempPar_3	TP/auditory	RH_TempPar_10	4.64(43)	.01
TP/auditory	RH_TempPar_8	Visual	LH_VisCent_ExStr_11	3.80(43)	.06
TP/auditory	RH_TempPar_8	Control	RH_ContA_IPS_4	3.92(43)	.03
Control	RH_ContA_PFCl_1	Visual	RH_VisCent_Striate_1	-4.53(43)	.02
Control	RH_ContB_PFCld_2	Visual	RH_VisCent_ExStr_7	-4.22(43)	.05
Dorsal attention	RH_DorsAttnA_SPL_3	Somatomotor	LH_SomMotB_S2_2	4.13(43)	.03
Visual	LH_VisPeri_ExStrSup_3	Dorsal attention	RH_DorsAttnB_PostC_3	4.00(43)	.05
Salience/ventral attention	RH_SalVentAttnA_PrC_1	Visual	RH_VisCent_ExStr_6	-4.33(43)	.04
Salience/ventral attention	RH_SalVentAttnB_PFCl_2	Dorsal attention	LH_DorsAttnA_ParOcc_1	-4.63(43)	.01

**Note*. The seeds were reassigned to this network during the atlas redistribution procedure. TP = temporo-parietal.

One of the most consistent patterns found in this analysis was decreased connectivity of the left-lateralised seeds in the default mode network, in particular, a region in the anterior cingulate cortex [-6 34 20] with the secondary central and peripheral visual cortices bilaterally in the deaf group (6 connections). One of the seeds from the default mode network also showed increased connectivity to a target region in the control network (1 connection).

The language network, specifically the left supramarginal gyrus [-58 -44 28], showed reduced connectivity with regions of the somatomotor network bilaterally (4 connections) and with a region in the salience/ventral attention network on the right (1 connection). The same language region in the left supramarginal gyrus and a region in the left superior cortex [-52 6 -12], and the left and right temporo-parietal/auditory regions, namely a seed region in the right superior temporal cortex [64 -34 10] and a somatomotor auditory seed in the left superior temporal cortex [-58 -34 16], consistently showed increased connectivity with the dorsal attention network (4 connections and 8 connections respectively). In addition, a region of the temporo-parietal network showed increased within-network connectivity across hemispheres (1 connection). The auditory seed region in the right superior temporal cortex that showed connectivity differences to the areas of the dorsal attention network (5 connections) also showed increased connectivity with a region in the visual network (1 connection) and the control network (1 connection).

The visual network overall showed differences in connectivity with cognitive and attention networks, namely decreased connectivity with regions of the default mode network (6 connections), as reported above, of the salience/ventral attention network (1 connection), and the control network (2 connections), and increased connectivity to a region in the dorsal attention network (1 connection).

Finally, one region in the salience/ventral attention network showed decreased connectivity to a region in the dorsal attention network in the deaf group (1 connection).

3.3.2. The associations between language proficiency and resting-state functional connectivity in deaf individuals

Our second research objective was to investigate the effect of language proficiency on the patterns of resting-state connectivity in the deaf group by using the language proficiency score as a covariate. The results for each significant connection are displayed in Table 3.7 and Figure 3.4. There were 70 connections significantly associated with language. The main findings are summarised below.

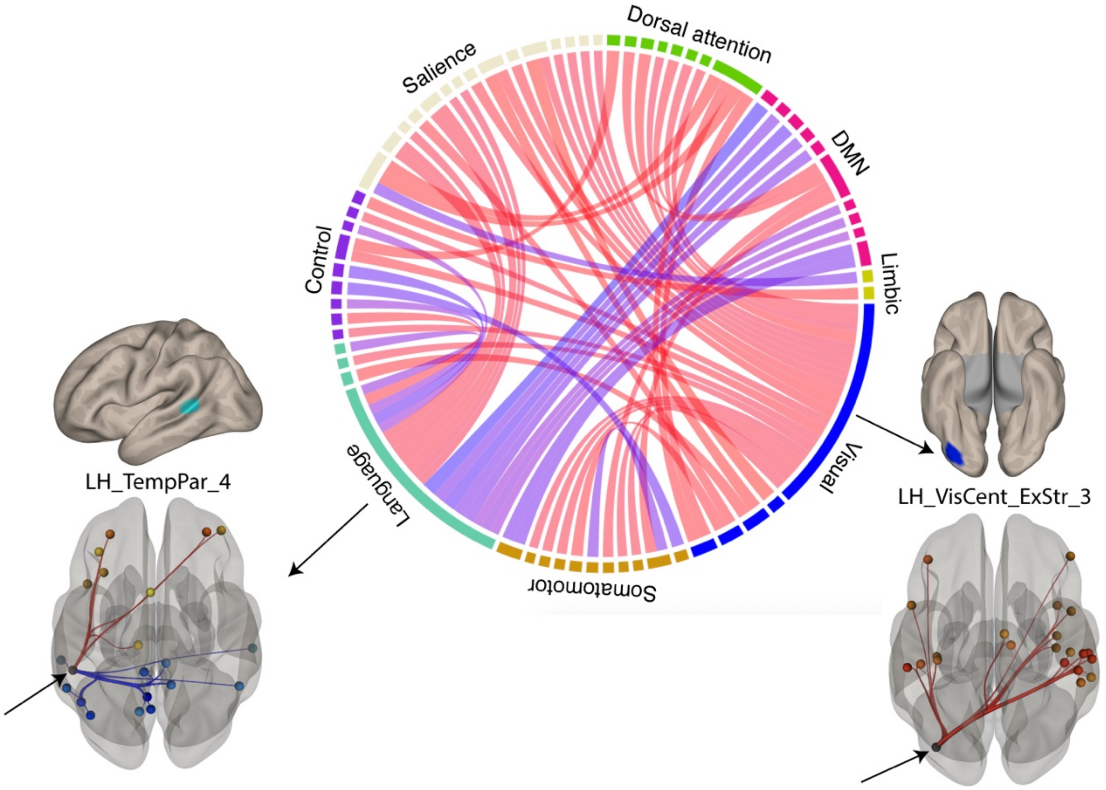

Figure 3.4. Associations between language proficiency and resting-state functional connectivity in the deaf group. The second-level analysis contrast was set as [deaf, language score] [0, 1]. Red lines indicate a positive relationship between connectivity values and language proficiency scores and blue lines indicate a negative relationship. Uninterrupted sections on the wheel indicate that connections arise in the same region.

Table 3.7. The effect of language proficiency on functional connectivity at rest in the deaf group

Source network	**Source region name**	**Target network**	**Target region name**	***T*(df)**	***p*-FDR**
Visual	LH_VisCent_ExStr_3	Somatomotor	RH_SomMotB_Ins_1	4.08(20)	.03
Visual	LH_VisCent_ExStr_3	Somatomotor	LH_SomMotB_S2_2	4.02(20)	.03
Visual	LH_VisCent_ExStr_3	Somatomotor	LH_SomMotB_Ins_1	3.82(20)	.03
Visual	LH_VisCent_ExStr_3	Somatomotor	RH_SomMotA_5	3.79(20)	.03
Visual	LH_VisCent_ExStr_3	Somatomotor	RH_SomMotB_S2_7	3.62(20)	.04
Visual	RH_VisPeri_ExStrSup_3	Somatomotor	RH_SomMotA_17	4.72(20)	.04
Visual	LH_VisCent_ExStr_3	Language	LH_SalVentAttnA_FrOper_2*	3.86(20)	.03
Visual	RH_VisCent_ExStr_9	Language	LH_ContA_PFCl_1*	4.90(20)	.02
Visual	LH_VisCent_ExStr_3	Control	RH_ContA_IPS_2	4.49(20)	.02
Visual	LH_VisCent_ExStr_3	Control	RH_ContB_IPL_3	3.91(20)	.03
Visual	LH_VisCent_ExStr_3	Control	LH_ContA_PFClv_2	3.69(20)	.04
Visual	LH_VisCent_ExStr_3	Dorsal attention	LH_DorsAttnB_PostC_3	4.86(20)	.02
Visual	LH_VisCent_ExStr_3	Dorsal attention	RH_DorsAttnB_PostC_2	4.04(20)	.03
Visual	LH_VisCent_ExStr_3	Dorsal attention	RH_DorsAttnB_PostC_4	3.79(20)	.03
Visual	LH_VisCent_ExStr_3	Dorsal attention	LH_DorsAttnB_PostC_4	3.45(20)	.05
Visual	RH_VisPeri_StriCal_1	Dorsal attention	RH_DorsAttnB_PostC_5	4.86(20)	.04
Visual	LH_VisCent_ExStr_3	Salience/ventral attention	RH_SalVentAttnA_ParOper_3	4.63(20)	.02
Visual	LH_VisCent_ExStr_3	Salience/ventral attention	RH_SalVentAttnA_ParOper_2	4.47(20)	.02
Visual	LH_VisCent_ExStr_3	Salience/ventral attention	RH_SalVentAttnA_Ins_2	4.37(20)	.02
Visual	LH_VisCent_ExStr_3	Salience/ventral attention	RH_SalVentAttnA_Ins_3	3.87(20)	.03
Visual	LH_VisCent_ExStr_3	Salience/ventral attention	RH_SalVentAttnA_FrOper_2	3.65(20)	.04
Visual	LH_VisCent_ExStr_3	Salience/ventral attention	RH_SalVentAttnB_IPL_1	3.58(20)	.05
Visual	LH_VisCent_ExStr_3	Salience/ventral attention	RH_SalVentAttnA_ParMed_1	3.62(20)	.04
Visual	LH_VisCent_ExStr_3	Salience/ventral attention	RH_SalVentAttnB_PFClv_1	3.47(20)	.05
Visual	RH_VisCent_ExStr_9	Salience/ventral attention	RH_SalVentAttnA_ParOper_3	5.15(20)	.02
Visual	RH_VisCent_ExStr_2	Salience/ventral attention	RH_SalVentAttnA_Ins_3	5.66(20)	.006
Visual	RH_VisPeri_ExStrSup_3	Salience/ventral attention	LH_SalVentAttnA_FrMed_3	4.56(20)	.04
Language	LH_TempPar_4*	Language	LH_DefaultB_IPL_2*	-3.97(20)	.03
Language	LH_ TempPar_4*	Default mode	LH_DefaultA_pCunPCC_2	-5.67(20)	.005
Language	LH_ TempPar_4*	Default mode	LH_DefaultA_pCunPCC_6	-5.25(20)	.005

Language	LH_ TempPar_4*	Default mode	LH_DefaultA_pCunPCC_3	-4.65(20)	.01
Language	LH_ TempPar_4*	Default mode	LH_DefaultA_IPL_2	-4.61(20)	.001
Language	LH_ TempPar_4*	Default mode	LH_DefaultA_IPL_1	-4.62(20)	.001
Language	LH_ TempPar_4*	Default mode	RH_DefaultA_pCunPCC_5	-4.02(20)	.03
Language	LH_ TempPar_4*	Default mode	RH_DefaultA_pCunPCC_3	-3.71(20)	.04
Language	LH_ TempPar_4*	Default mode	RH_DefaultA_IPL_1	-3.61(20)	.04
Language	LH_ TempPar_4*	Control	LH_ContC_pCun_1	-5.05(20)	.006
Language	LH_ TempPar_4*	Control	LH_ContA_Cingm_1	4.45(20)	.01
Language	LH_ TempPar_4*	Control	LH_ContB_Temp_1	-3.83(20)	.03
Language	LH_ TempPar_4*	Control	RH_ContB_Temp_1	-3.58(20)	.04
Language	LH_ TempPar_4*	Salience/ventral attention	LH_SalVentAttnB_PFCl_2	3.98(20)	.03
Language	LH_ TempPar_4*	Salience/ventral attention	LH_SalVentAttnA_Ins_3	3.88(20)	.03
Language	LH_ TempPar_4*	Salience/ventral attention	LH_SalVentAttnB_PFCl_2	3.98(20)	.03
Language	LH_ TempPar_4*	Salience/ventral attention	LH_SalVentAttnA_Ins_3	3.88(20)	.03
Language	LH_ TempPar_4*	Salience/ventral attention	LH_SalVentAttnA_ParMed_1	3.78(20)	.03
Language	LH_ TempPar_4*	Salience/ventral attention	LH_SalVentAttnB_Ins_3	3.47(20)	.05
Language	LH_ TempPar_4*	Salience/ventral attention	LH_SalVentAttnB_PFCl_3	3.46(20)	.05
Default mode	LH_DefaultC_PHC_3	Somatomotor	LH_SomMotA_18	4.46(20)	.04
Default mode	LH_DefaultC_PHC_3	Somatomotor	RH_SomMotA_12	4.24(20)	.04
Default mode	RH_DefaultA_IPL_2	Somatomotor	RH_SomMotB_Cent_1	-4.74(20)	.04
Default mode	LH_DefaultC_PHC_3	Dorsal attention	RH_DorsAttnA_SPL_7	4.27(20)	.04
Default mode	LH_DefaultC_PHC_3	Dorsal attention	LH_DorsAttnA_SPL_7	4.45(20)	.04
Control	LH_ContB_PFCd_1	Somatomotor	LH_SomMotA_11	-5.03(20)	.02
Control	RH_ContB_IPL_4	Limbic	RH_LimbicB_OFC_3	4.80(20)	.04
Dorsal attention	RH_DorsAttnB_PostC_5	Visual	RH_VisPeri_StriCal_1	4.86(20)	.02
Dorsal attention	LH_DorsAttnA_TempOcc_4	Control	RH_ContA_IPS_2	5.01(20)	.03
Dorsal attention	RH_DorsAttnB_PostC_5	Salience/ventral attention	LH_SalVentAttnA_Ins_1	5.21(20)	.02
Salience/ventral attention	LH_SalVentAttnA_Ins_1	Dorsal attention	RH_DorsAttnB_PostC_5	5.21(20)	.02
Salience/ventral attention	LH_SalVentAttnA_Ins_1	Limbic	RH_LimbicB_OFC_2	-4.63(20)	.03
Somatomotor	LH_SomMotA_18	Somatomotor	RH_SomMotA_13	-4.47(20)	.05

Note. *The seeds were reassigned to this network during the atlas redistribution procedure.

The majority of connections significantly associated with language score in the deaf group were in the regions of the visual network (28 connections out of 61 involved seed or target regions from that network), in the language network (22 connections), and in the salience/ventral attention network (18 connections).

Sensory networks

The visual network demonstrated multiple associations with language proficiency in connectivity with regions from several other networks: somatomotor, language, control, dorsal attention, and salience/ventral attention. Most of the significant results were revealed in relation to connections between regions from the visual and salience/ventral attention networks, with 11 connections significantly positively associated with language proficiency. Increased connectivity of the visual areas with the dorsal attention (6 connections), control (3 connections), somatomotor (6 connections), and language areas (2 connections) was also associated with higher language scores. Most of the connections involved a single region in the left fusiform gyrus [-36 -82 -16] (21 connection).

Regions of the somatomotor network, in addition to increased connectivity (6 connections) with the visual network in participants with higher language scores, also showed decreased connectivity within-network (1 connection), with a region in the control network (1 connection), and both decreased (1 connection) and increased connectivity with regions from the default mode network (2 connections) in participants with higher language proficiency scores.

The language network

Language areas showed a large number of significant associations with language scores. Higher language scores were associated with decreased connectivity to regions of the default mode network (8 connections) and increased connectivity to salience/ventral attention network (7 connections). Connectivity with regions of the control network showed both negative (3 connections) and positive (1 connection) associations to language scores. In relation to within-network connectivity, within-network connectivity between two regions showed a negative association with language scores. The majority of the results (20 connections) were found for a seed in the left posterior superior temporal sulcus [-52 -44 4] (with the exception of two connections with areas from the visual network).

The dorsal attention network

The associations between connectivity of the regions in the dorsal attention network to the salience/ventral attention, default mode, and control networks followed a similar pattern, with higher connectivity related to higher proficiency scores in every connection (2 connections with regions of the default mode network; 2 connections with regions of the salience/ventral attention network, and one connection with a region of the control network). These were also the only significant associations between two non-sensory networks, or associations not involving language regions, in this analysis.

3.4. Discussion

This chapter investigated the effects of sensory and language experience on resting-state functional connectivity across the whole brain in deaf individuals. In agreement with our expectations, differences in connectivity between deaf and hearing individuals were found across regions from sensory (auditory, visual, somatomotor), cognitive (default mode, language, control), and attention (salience/ventral attention, dorsal attention) networks. Specific predictions regarding connectivity differences between the groups have been partially met. While connectivity between areas from the sensory networks in the deaf group was not found to be reduced, unlike in several other studies (Andin & Holmer, 2022; Bonna et al., 2021; Cardin et al., submitted) (but see the *3.4.3. The connectivity of the language and attention networks*), connectivity between the regions of the temporo-parietal/auditory network and higher-order associations cortices in the dorsal attention and control network was increased. Moreover, connectivity between regions from the networks involved in attention and cognition was stronger in the deaf group: between regions of the default mode and control networks, and between regions of the language and dorsal attention networks. The findings described in this chapter highlight the influence of sensory experience on the connectivity of the visual and temporo-parietal/auditory networks to the areas in the brain related to cognition and attention, considering that the majority of differences between the groups are found in connectivity of the regions from the temporo-parietal/auditory and visual networks to regions in the dorsal attention and default mode networks respectively. Temporo-parietal/auditory regions revealed a larger number of altered connections in the deaf group, in agreement with a suggestion that the temporal cortex is a central node of plasticity in deaf individuals based on functional connectivity findings (Andin & Holmer, 2022). Interestingly, while temporo-parietal/auditory regions showed significant differences in connectivity between the groups, the connectivity of these regions was not modulated by language experience in deaf individuals, suggesting a dissociation between plasticity effects driven by sensory experience and language-related effects on functional connectivity. The majority of the findings presented in this chapter are related to the modulation of functional connectivity by language proficiency in deaf individuals. These results highlight the importance of language experience for the functional organisation of visual and language networks, as well as those involved in cognitive and attentional processes.

3.4.1. The connectivity of the visual network

Contrary to our predictions, visual areas showed decreased connectivity in the deaf group to regions from cognitive and attention networks, especially in the default mode network. The only instances when the visual areas showed increased connectivity were single connections to a region in the dorsal attention network and a region in the temporo-parietal/auditory network.

The latter finding may be related to the reports of increased connectivity between the auditory cortex and areas processing visual information in deaf individuals during visual task execution (working memory: Andin et al., 2021; rhythm discrimination: Bola et al., 2017) and rest (Andin & Holmer, 2022). Bola and colleagues (2017) suggested that this enhanced coupling during visual task execution reflects the contribution of the visual dorsal stream areas to communication between visual and auditory cortices in a task that showed cross-modal reorganisation in the auditory cortex for visual motion processing in deaf individuals. Andin and Holmer (2022) propose that the dorsal visual stream in deaf signers may contribute to carrying information about linguistic elements in a visual language, extending the processes occurring in the temporal regions. The enhanced connection revealed in our analysis in the deaf group is between a region in the right superior temporal gyrus [64 -34 10] and a region in the left middle occipital gyrus [-26 -84 22], a region of the dorsal occipital stream that is involved in visuo-spatial and motion processing (Collignon et al., 2011; L. A. Renier et al., 2010). Taken together, this evidence could suggest that the enhanced connectivity between a visual and an auditory area at rest in deaf participants in our sample reflects optimal functional organisation for visual processing of motion in this population and therefore may be related to compensatory mechanisms described in deaf individuals, such as enhanced visual motion processing (see Bavelier et al., 2006 for a review).

The connectivity between several visual areas, mostly in the higher-order visual cortex, and several higher-order association cortices (Jung et al., 2017), namely three regions in the default mode network, an area in the salience/ventral attention network, and two regions in the control network, was decreased in the deaf group. The functional interaction between visual areas and higher-order frontal and posterior areas has been emphasised before in relation to behaviour, with resting-state functional connectivity between visual regions and the control network being negatively correlated with task fitness in a visual perceptual task (Baldassarre et al., 2012). The decreased connectivity in the deaf group, in comparison to hearing controls, between areas in these networks may also be related to compensatory effects in visual perception in deaf individuals that may lead to enhanced performance in visual perceptual tasks (Bavelier et al., 2006).

The visual network had a large number of decreased connections in the deaf group to regions in the default mode network. No connections between these areas or other areas from these networks were modulated by language, which may suggest that the reduced connectivity between these areas observed in the deaf group is a consequence of the sensory experience of deafness, rather than general language proficiency. On the other hand, connectivity between a region in the default mode and a visual region was higher in a group of proficient signers than in hearing controls in a different study (Dell Ducas et al., 2021), which may indicate that these changes may be related to sign language use, considering the differences in group composition and findings in our study and the study by Dell Ducas and colleagues (2021). In hearing individuals, visual regions that process relevant task information are connected with the control network, while those that process irrelevant information are coupled with the default mode network during a visually demanding task, suggesting that the connectivity of the sensory regions is 'differentially and dynamically coupled' with other networks depending on the goal of the task (Chadick & Gazzaley, 2011). The differences in connectivity between visual cortices and areas of the default mode network, and visual cortices and regions in the control network between deaf and hearing individuals during rest may reflect important compensatory mechanisms relevant for visual processing and task execution. Further analysis of the task-related data could shed light on the functional importance of these differences (Chapter 4).

Connectivity between visual areas, especially a region of the left fusiform gyrus [-36 -82 -16] (Lockhofen et al., 2014), and areas from the salience/ventral attention, dorsal attention, and control networks was associated with an increase in language proficiency scores. Connectivity between visual and somatomotor areas, and visual and language areas – regions from networks where differences in connectivity between the groups were not observed – also was positively associated with language proficiency scores. The left fusiform gyrus responds to social gaze and is involved in the processing of social information (Lockhofen et al., 2014) and face processing (V. P. Clark et al., 1996; Haxby et al., 2000; Pageler et al., 2003). The connectivity of that region to somatomotor areas in the left and right insular cortices, the left and right secondary somatosensory cortices, and the right supplementary motor area (J. Zhang et al., 2018) was associated with higher language proficiency in deaf individuals. Deaf individuals have been shown to have larger grey matter volume in the insular cortex, which was proposed to reflect the dependence on lipreading and articulatory-based representations of speech in deaf individuals (Allen et al., 2008). A meta-analysis suggested a role of the left insular cortex and the right supplementary motor area in phonological code retrieval (Indefrey & Levelt, 2004), and the left insular cortex was recruited for both signed and spoken narrative production (Emmorey et al., 2007). Our findings may reflect a connection between language observation and production in both modalities. When using phonological code retrieval in language production, participants with higher language proficiency scores may benefit from mappings established between observation of the visual forms of visual language (e.g., lipreading and/or mouthings and facial expressions in sign language) and language production.

Overall, positive associations between language proficiency and the degree of connectivity of the visual network to a large number of areas involved in motor control, attention, and cognition may reflect the efficient use of visual communicative strategies and successful reliance on visual modality during communication in both sign and spoken language in deaf participants with higher language scores. For example, the increased connectivity between the left fusiform gyrus and the postcentral gyrus, located in the dorsal attention network involved in top-down control of visual attention processes (Corbetta and Shulman, 2002), in deaf participants with higher language proficiency scores can reflect the efficiency of coordination of this visual area and the dorsal attention system in the top-down selection of visual stimuli during visual communication.

One of the strongest patterns revealed by the analysis presented in this chapter was the increased connectivity between the visual and salience/ventral attention network in participants with higher language proficiency scores. The salience/ventral attention network is involved in shifting attention to salient stimuli (Menon & Uddin, 2010) and does not differ in composition between deaf and hearing individuals (Andin & Holmer, 2022). The increased connectivity between the visual areas and the salience network may be related to the increased involvement of the visual areas in the detection of salient stimuli that could be supported by life-long reliance on visual cues. The salience network has shown decreased connectivity during narrative comprehension in children with reading difficulties (Twait et al., 2018). Our findings may reflect similar processes on the level of intrinsic organisations of networks in the resting state. More research on functional connectivity during language task execution, such as narrative comprehension and production, in deaf individuals can shed light on the functional relevance of these associations between connectivity patterns and language proficiency.

3.4.2. The connectivity of the temporo-parietal network

Two regions of the temporo-parietal/auditory network showed increased connectivity in the deaf group within the network (one connection) and with regions from other networks, predominantly from the dorsal attention network, but also single connections to areas from the control and visual areas. There were no significant connections with the somatomotor network, contrary to previous reports on resting-state functional connectivity in deaf individuals (Andin & Holmer, 2022; Bonna et al., 2021; Cardin et al., submitted). There were also no enhanced connections between the temporo-parietal/auditory areas and areas of the salience network described in deaf participants previously (Andin & Holmer, 2022; Cardin et al., 2018; Ding et al., 2016). Nevertheless, other significant connections corroborate previous studies: the increased connectivity between the auditory regions and the control/fronto-parietal network at rest has been reported in both Cardin et al. (2018) and Ding et al. (2016) (but not by Andin & Holmer, 2022). The increased connectivity of the auditory areas with the control network has been previously discussed as a sign of incorporation of the reorganised regions into the fronto-parietal module. In this study, we showed that temporal regions in deaf individuals have a role in cognitive switching (Manini et al., 2022). The increased connectivity in the deaf group between the temporo-parietal and control network, as well as between the temporo-parietal and visual network, and temporo-parietal and dorsal attention network may reflect the involvement of the temporal regions in cognition and visual attention in this population and be related to cross-modal plasticity effects, similar to what was suggested by Ding et al. (2016) and Cardin et al. (2018) in their studies where reorganised portions of the auditory cortex had stronger coupling with fronto-parietal areas involved in cognitive tasks that showed reorganisation in deaf participants.

3.4.3. The connectivity of the language and attention networks

In the deaf group, one seed of the language network in the left supramarginal gyrus [-58 -44 28] consistently showed reduced connectivity with regions of the somatomotor network in the paracentral lobule in comparison to hearing controls bilaterally. The supramarginal gyrus has been associated with rapid motor reprogramming (Hartwigsen et al., 2012) and is involved in sign language processing, namely phonological assembly and encoding (Emmorey et al., 2007), and in speech processing (Hickok, 2012). It is suggested that it is associated with speech production to a lesser extent than with sign production, as demonstrated by direct comparisons between sign and speech (Emmorey et al., 2007). The reduced connectivity between the left supramarginal gyrus and somatomotor area in deaf individuals found in our study could point to either a modality-specific or modality-independent language effect. Holmer and colleagues (2022) showed that connectivity between a language-related area in the left inferior frontal gyrus and sensorimotor regions in deaf early signers was related to sign language proficiency, namely sign language sentence reproduction skills. Stronger connectivity was associated with lower sign language sentence reproduction scores. This could be interpreted as the reflection of the use of non-linguistic motor representations when language representations are not accessible in individuals with lower sign language skills, or the effortful access to linguistic motor representations by these individuals (Holmer et al., 2022). It is possible that this is an effect that could be generalised to other modalities, or it could be specific to sign language. In relation to our finding, we do not see an association with the general, modality-independent language score based on performance in grammaticality judgement tasks. This could be due to the nature of the task that is not testing phonological assembly and encoding directly, or due to the effect being associated with language modality, considering that higher activation in the paracentral lobule was suggested to be associated with the active visuomotor encoding of unfamiliar movements in a sign language comprehension study of deaf and hearing individuals (Levänen et al., 2001), and the evidence of higher involvement of the supramarginal gyrus in sign production compared to speech production (Emmorey et al., 2007). Further research with the use of other tasks, similar to the ones used by Holmer and colleagues (2022) and Emmorey and colleagues (2007), could determine whether reduced connectivity between somatomotor and language areas in deaf individuals is related to language abilities, or whether it is a consequence of the sensory experience of deafness. It should also be noted that the evidence of reduced connectivity between auditory and somatomotor areas in deaf individuals described in other studies (Andin & Holmer, 2022; Bonna et al., 2021; Cardin et al., submitted) could also be at least partially related to language experience, considering that often studies of functional connectivity do not define a separate language network, and some language-related areas may be included into the auditory network.

The left supramarginal gyrus and the left superior temporal cortex also showed increased connectivity with the superior parietal lobule in the dorsal attention network in the deaf group. This increased connectivity may be reflecting an increased demand on the visual attention system in communicative processes in the deaf group that arises from perceptual demand and is not related to the degree of language proficiency, considering the lack of connections in the language-related analysis between these areas. Linguistic and non-linguistic demand has been shown to differentially modulate regions from the language and dorsal attention network (Quillen et al., 2021), and further studies of connectivity during linguistic and non-linguistic tasks could shed light on this relationship.

The left posterior superior temporal sulcus [-52 -44 4] showed a large number of connections associated with language proficiency, with consistently decreased connectivity to areas in the default mode network and increased connectivity to areas from the salience/ventral attention areas in participants with higher language proficiency scores. The left posterior superior temporal sulcus is a classic posterior perisylvian language area involved in language processing, independently of the modality (Neville et al., 1998; S. M. Wilson et al., 2018), with studies emphasising its role in sign and spoken language comprehension and phonetic processing (Emmorey et al., 2011; Moreno et al., 2018). It is also sensitive to communicative intent through language and gesture (Redcay et al., 2016). Moreover, posterior sections of the superior temporal sulcus can respond to faces and voices, highlighting its role in social perception and cognition (Deen, Koldewyn, et al., 2015). The left posterior superior temporal was proposed to have a role in representing phonetic sequences irrespectively of whether they are perceived or generated internally, which is critical speech production (Wise et al., 2001). Finally, there is evidence of the posterior superior temporal sulcus responding to visual biological motion (Grossman et al., 2005), and in deaf individuals, it responds to velocity changes (Bavelier et al., 2001) (see Malaia & Wilbur, 2010 for a discussion of linguistic and non-linguistic effects in the posterior superior temporal sulcus in deaf individuals). Our findings suggest that connectivity of the left posterior superior temporal sulcus to higher-association cortices (Jung et al., 2017) in the regions of the default mode network and the salience network is differentially sensitive to language proficiency. The default mode network has been shown to have decreased connectivity to language regions during a semantic processing task (DeSalvo et al., 2014), and it is possible that decreased connectivity at rest in participants with higher language proficiency score reflects the optimal organisation for successful language processing. Moreover, children with autism spectrum disorder show increased connectivity between the posterior cingulate cortex of the default mode network and language regions at rest and between the posterior cingulate cortex and visual areas, with the latter being associated with their language skills (Y. Gao et al., 2019). Taken together, these findings suggest that decoupling between the default mode network and language network regions during active language processing may be beneficial for language processing, and this association in deaf individuals may be also reflected in the resting state. The salience network has been linked to several language processing aspects (Hertrich et al., 2020), such as narrative comprehension (Twait et al., 2018) or atypical prosody understanding in case of a foreign accent (Hernández et al., 2019). The finding of increased connectivity of the posterior superior temporal sulcus to areas from the salience network suggests potential benefits the participants with higher language scores may have in narrative comprehension and understanding oral speech that for many of the deaf participants could be similar to 'foreign' if their preferred language is sign language or understanding sign language if it is not their stronger language.

Regions from the salience/ventral attention network and the dorsal attention network showed decreased connectivity with each other in the deaf group compared to the hearing. The connectivity between other regions in these networks was positively associated with language scores. The attention networks are necessary for goal-directed executive control and salience evaluations, which are crucial for the control of spatial attention and the orientation of attention to a specific area of interest (Gratton, Sun, et al., 2018), thus stronger coupling between them can be argued to be beneficial. In this study, we show that in deaf individuals this coupling can be supported by successful language development, independently of the modality of the language.

3.4.4. Conclusion

This chapter described the effects of sensory and language experience on resting-state functional connectivity across the brain in deaf individuals. The findings presented in this chapter show that functional connectivity in deaf individuals is associated with both sensory experience and language proficiency, independently of the language modality. Significant connections related to both sensory and language experience can be found beyond auditory and language cortices: regions from every network included in the analysis showed altered connectivity associated with either sensory or language experience, or both. The temporo-parietal/auditory network showed differences in connectivity between the groups but did not include connections significantly modulated by language proficiency in the deaf group. This emphasises that language proficiency in deaf individuals, independently of the modality, is associated predominantly with areas from the visual, attention, and cognitive networks, such as the default mode and language networks, while the sensory experience of deafness influences the auditory areas more.

Increased connectivity of the visual areas, mostly a specific area in the fusiform gyrus involved in socially relevant gaze and face processing, to areas from the somatomotor, attention (dorsal attention and salience/ventral attention), language, and control networks, as well as increased connectivity between regions of the language and salience/ventral attention networks were positively associated with language proficiency. These findings may indicate that enhanced connectivity between areas involved in visual perception of social and language-related information in deaf individuals and language processing areas to regions from the networks that may be involved in different forms of visual communication through somatomotor, cognitive, and attentional processes may have functional relevance, leading to benefits in general language competence in participants with higher language proficiency scores.

4 The role of sensory experience and language proficiency in state-related functional connectivity changes in deafness

4.1. Introduction

The research presented in this chapter explores the influence of the sensory experience of deafness and language proficiency on state-dependent differences in functional connectivity, while carefully disentangling these effects. Functional connectivity can efficiently reshape during switching between cognitive states, such as resting state and task execution (Gonzalez-Castillo & Bandettini, 2018). The sensory experience of deafness has been shown to lead to changes in task-related functional connectivity (Andin et al., 2021; Bola et al., 2017). However, it is unclear how deafness affects switching between different types of cognitive states from and between brain regions outside of the sensory-reorganised auditory areas. Considering the associations between language skills and executive function in the brain (Chapter 2) and/or behaviour (Chapter 2) (Botting et al., 2017; Figueras et al., 2008; Merchán et al., 2022), and the associations between language skills and functional connectivity at rest (Holmer et al., 2022; Y. Li et al., 2013; Chapter 3), language proficiency may also be associated to differences in functional connectivity between cognitive states in executive function tasks. This chapter aims to explore the role that sensory and language experiences play in state-dependent differences in functional connectivity between deaf and hearing individuals.

4.1.1. Functional connectivity during rest and task states

Introduced in Chapter 1 and investigated in Chapter 3, the functional connectivity architecture of the brain has been primarily investigated by studying hemodynamic fluctuations in functionally-coupled brain regions in the state of rest (Biswal et al., 1995; Fox & Raichle, 2007) (resting-state functional connectivity is discussed in detail in Chapter 1 and Chapter 3). When it comes to functional connectivity during task execution, some studies have suggested that functional architectures during rest and task states are highly similar. For instance, researchers have found high correspondence between resting-state functional connectivity and task-related residual timecourses (Fair, Schlaggar, et al., 2007), close correspondence between independent analyses of resting-state and task-activation brain dynamics (S. M. Smith et al., 2009), high correlation (0.75) between rest-based and task-based functional connectivity MRI (Krienen et al., 2014) and the dominance of common organisational principles and stable individuals features in functional network organisation, with 'substantially more modest' contributions from being in a state of task (Gratton, Laumann, et al., 2018). These observations agree with a hypothesis that resting-state functional connectivity reflects an 'intrinsic' standard functional brain architecture that shapes the functional network configuration during task performance. Other researchers have noted differences in functional connectivity during task and rest and advocated for differential task and rest architectures (see Cole et al., 2014 for a discussion). The latter view is supported by the evidence from differences in connectivity between states, for example, variations in the topography of brain networks due to exogenous processing demands in periods of language comprehension (Hasson et al., 2009), distinct task states leading to differences in functional coupling in response to varied demands in a wide range of task paradigms (Krienen et al., 2014) and moderate state-based modulations in functional networks configuration (Gratton, Laumann, et al., 2018).

Cole and colleagues (2014) aimed at bridging the gap between the two approaches by using large-scale graphs built from functional connectivity in hundreds of brain regions and across dozens of task states. They have found that while functional connectivity during task is largely composed of the 'intrinsic' resting-state architecture, task-evoked differences are also present and consist of task-general and task-specific changes from the resting state (M. W. Cole et al., 2014).

The similarities between task and resting-state functional connectivity can be explained by the fact that blood flow associated with task execution often accounts for no more than a 5% increase in energy consumption over rest (Raichle, 2010). Nevertheless, studies have repeatedly observed significantly different connections between rest and task states (M. W. Cole et al., 2014; Hasson et al., 2009; Krienen et al., 2014). The differences in functional connectivity are marginally explained by task-evoked functional connectivity and are mostly attributed to changes in emerging spontaneous networks driven by ongoing activity during the execution of the task (Lynch et al., 2018).

To date, task-related changes in functional connectivity and their functional importance remain a less investigated topic in functional connectivity studies. Task-related changes (Büchel & Friston, 1997; M. W. Cole et al., 2014; Hasson et al., 2009; Krienen et al., 2014), although often considered by many to be 'small' (M. W. Cole et al., 2021), may be crucial for successful adaptation to task demands. Indeed, functional connectivity task-general patterns improve predictions on fMRI activations from different task conditions over resting-state functional connectivity (M. W. Cole et al., 2021). Moreover, task-evoked functional connectivity has been found to be related to individual differences in behaviour and traits (Barch et al., 2013; Greene et al., 2018), further emphasising its functional relevance. Studying task-related changes in functional connectivity can be critical for understanding brain functions supporting cognitive processing: the networks can dynamically adapt to task demands to facilitate information processing in agreement with the idea of the economy of brain network organisation (Bullmore & Sporns, 2012).

Some common differences observed between functional connectivity at rest and during task execution have been systemically described by Gonzalez-Castillo & Bandettini (2018). For instance, the following patterns have been observed:

- *Within-network connectivity decreases during task execution.* For example, this appears in the somatosensory network during motion (Gonzalez-Castillo et al., 2012); in the visual network during visual attention (Spadone et al., 2015) or natural scenes viewing (Betti et al., 2013). It is also possible for higher-order networks to reduce their within-network connectivity during task execution (Betti et al., 2013; M. W. Cole et al., 2014), for example, in the dorsal attention network (Betti et al., 2013).
- *Across-network connectivity changes during task execution.* The common observation is that networks recruited by the task increase their connectivity (Gonzalez-Castillo & Bandettini, 2018): attention to visual stimuli increased connectivity between the default mode, dorsal attention, and visual networks (Kwon et al., 2017); the connectivity between visual and language networks was increased during video watching (Betti et al., 2013). The default mode network in particular has demonstrated flexible coupling with task-relevant brain regions, such as increased connectivity between the default mode network and language networks during movie watching (Betti et al., 2013) and between the default mode network and task-promoting regions across six different tasks (Elton & Gao, 2015b). Moreover, the changes in connectivity were related to individual differences in task performance (Elton & Gao, 2015b). In addition to the changes described by Gonzalez-Castillo & Bandettini (2018) in the default mode network, higher variability of dynamic functional connectivity between the default mode network and the fronto-parietal network during task execution was associated with increased cognitive flexibility outside of the scanner, while higher variability in the dynamics of

connectivity between these networks in comparison to the rest of the brain during resting state was associated with poorer performance (Douw et al., 2016). Increased cooperation between the default mode network and a component of the external attention system was associated with faster memory recollection (Fornito et al., 2012). Finally, greater interaction between the default mode network and regions of the fronto-parietal network has also been described at the phase of retrieval in working memory (Piccoli et al., 2015). Generally, current literature emphasises the role of interactions between the default mode and control networks (Hearne et al., 2015), default mode and attention networks (Elton & Gao, 2015a), and between the default mode network and regions involved in task execution (Betti et al., 2013), during task execution and in cognition.

4.1.2. Functional connectivity changes during rest and task states in deafness and blindness

One of the fundamental questions is how the functional connectivity organisation of the brain is modified during task execution to support flexibility in behaviour and task performance. Functional connectivity during task execution is expected to be related to the function of the areas involved, with functionally related areas exhibiting increased connectivity during tasks (Bartels & Zeki, 2005; Kwon et al., 2017; Nir et al., 2006). Investigating the functional connectivity relationships between brain areas during rest and task in individuals with unique sensory experiences can be a valuable contribution to the field of cross-modal plasticity, but it can also expand our understanding of the way the human brain reorganises to support task-related processing.

Resting-state functional connectivity studies of early blind individuals have been reliably demonstrating increased connectivity between the visual areas and areas supporting cognitive control of attention (Burton et al., 2014) and language (Y. Liu et al., 2007; Striem-Amit et al., 2015) in comparison to sighted individuals. Such findings can be explained by the involvement of the occipital cortex of early blind individuals in higher-level cognitive functions (Burton et al., 2014), such as language (Amedi et al., 2003; Bedny et al., 2011). One of the hypotheses is that the sensory-deprived cortex becomes incorporated into other functional systems (Burton et al., 2014).

Reduced connectivity between the visual and other sensory cortices at rest has also been well-documented in blind individuals (Bedny et al., 2011; Burton et al., 2014; Y. Liu et al., 2007; Striem-Amit et al., 2015; C. Yu et al., 2008) (see Bock & Fine, 2014 for a review). However, the visual regions have been repeatedly found to be activated during the processing of auditory (Collignon & de Volder, 2009; Poirier et al., 2006; Röder et al., 2002; Sadato et al., 1996; Saenz et al., 2008) and tactile (Amedi et al., 2001; Ricciardi et al., 2007; Sadato et al., 1996) tasks in blind individuals, suggesting a functional relationship between the visual and non-visual sensory regions, which is not seemingly supported by the resting-state studies. The lack of enhanced connectivity between the non-deprived and sensory-deprived cortices in blind individuals in the resting state (Y. Liu et al., 2007; D. Wang et al., 2014; Watkins et al., 2012; C. Yu et al., 2008), the evidence of reduced connectivity between visual and somatomotor, auditory and multisensory cortices in the blind (Y. Liu et al., 2007) and reduced connectivity between primary visual cortex and the rest of the brain (C. Yu et al., 2008) can support the suggestion that the visual cortex is re-programmed for 'metamodal' purposes (Pascual-Leone et al., 2005; Pascual-Leone & Hamilton, 2001), as supported by evidence of the visual cortex involvement in cognitive tasks (Amedi et al., 2003; Bedny et al., 2011; Burton et al., 2014; Röder et al., 2002).

The discrepancy between the evidence of reduced connectivity of the visual and other sensory networks in blind individuals and studies where the visual and auditory regions have been consistently activated for the same auditory processing tasks in the same population and have also been demonstrating enhanced connectivity during auditory processing has led researchers to focus on the differences in functional connectivity between the states (Pelland et al., 2017). The early blind group of participants demonstrated higher connectivity between occipital and temporal areas during task than at rest, and the sighted controls exhibited an opposite pattern. Such evidence leads to a conclusion that functional connectivity differences in architecture between groups of individuals with different sensory experiences should be considered with caution when inferred from resting-state studies only (Pelland et al., 2017), as the groups can exhibit different, and even opposite, patterns of connectivity depending on the state.

In relation to functional connectivity in deaf individuals, as discussed previously in Chapter 1 and Chapter 3, some evidence suggests similar patterns for the sensory-deprived cortices in deafness as in the sensory-deprived visual cortices in blind individuals at rest, for instance, reduced connectivity between the sensory networks (auditory and somatomotor regions: Bonna et al., 2021; visual and somatomotor regions: Dell Ducas et al., 2021; auditory and visual regions: X. Wang et al., 2015) and enhanced connectivity of the reorganised auditory regions with the regions involved in cognition. In deaf individuals, cross-modal reorganisation has been observed in the auditory cortex of deaf individuals for cognitive tasks (Andin et al., 2021; Cardin et al., 2018; Ding et al., 2015; Manini et al., 2022). In a group of deaf participants that demonstrated such reorganisation during visual working memory in the superior temporal cortex, this region also showed increased connectivity with the fronto-parietal regions, such as the pre-supplementary motor area and the dorsolateral prefrontal cortex at rest (Cardin et al., 2018). The superior temporal gyrus demonstrated enhanced connectivity to the salience network, the bilateral anterior insula, and the dorsal anterior cingulated cortex during rest (Ding et al., 2016) in a group of participants who recruited the temporal area for a visual working memory task and also outperformed the hearing controls (Ding et al., 2015). Moreover, the functional connectivity of the superior temporal gyrus predicted the performance in the working memory task, emphasising the functional relevance of the functional connectivity of the region to behavioural performance (Ding et al., 2016).

In relation to task-related functional connectivity in deafness, the current evidence is very limited but shares similarities with the observations from studies on blindness. The cross-modal plasticity effects in the auditory cortex of deaf individuals have been long-established in visual tasks (Andin et al., 2021; Bottari et al., 2014; Cardin et al., 2013; Karns et al., 2012) and tactile processing (Karns et al., 2012). There has been evidence of functional connectivity changes complementing these effects. For example, deaf individuals demonstrated increased connectivity of the high-level auditory cortex to the dorsal visual stream, namely the V5/MT (area V5, or the middle temporal area) cortex during the execution of a task with dynamic visual stimuli (Bola et al., 2017). The coupling was only present in the deaf group and not in hearing controls and was discovered with the use of a psychophysiological interaction (PPI) analysis (Friston et al., 1997). The enhanced connectivity was only present during the task on visual rhythm discrimination, but not the control condition. Other recent studies also demonstrated increased task-based connectivity from the auditory cortex to regions of the visual cortex (during a visual working memory task) (Andin et al., 2021) and from the face-selective reorganised temporal area to visual areas during visual face processing (Benetti et al., 2017b) in deaf individuals.

Functional connectivity at rest has been shown to be altered in large-scale brain networks in deaf individuals beyond the sensory regions at rest (Andin & Holmer, 2022; Bonna et al., 2021; W. Li et al., 2016) and it has been suggested by the authors (Andin & Holmer, 2022; Bonna et al., 2021) that neural reorganisation in functional connectivity in deaf individuals can provide a mechanism for the superior behavioural performance of deaf individuals in visual and attentional tasks (Bavelier et al., 2006; Corbetta & Shulman, 2002; Hong Lore & Song, 1991; Neville & Lawson, 1987; C. Stevens & Neville, 2006).

There have been very few studies of functional connectivity during task performance in deafness, with one study focusing specifically on sensory networks during task performance (Bola et al., 2017). The findings of increased task-based connectivity between the temporal and visual cortices in deaf individuals (Andin et al., 2021; Bola et al., 2017) shed light on the reorganisation of the sensory cortices, but it remains unclear how functional connectivity changes in deafness across the whole brain in different states. Notably, in the study by Andin and colleagues (Andin et al., 2021), the auditory cortex in the deaf group also showed stronger connectivity to the left insula, complementing the evidence of the same pattern from a study by Ding et al. (2016), with the insula acting as a hub for identification of relevant stimuli and forwarding it to executive networks (Andin et al., 2021). These findings may also support the notion of the ‘intrinsic’ functional architecture at rest acting as the architectural foundation for task-related connectivity (M. W. Cole et al., 2014). Most notably, these findings suggest that functional connectivity changes during task performance in deafness are not limited to connections between the sensory networks but also extend to other, non-sensory brain networks, namely the salience network (Andin et al., 2021). More research on this topic could answer the question of whether connectivity changes during task execution are present in the non-sensory large-scale networks, as they do at rest (Andin & Holmer, 2022; Bonna et al., 2021).

It is unclear whether functional connectivity differences between deaf and hearing individuals during task execution (Andin et al., 2021; Bola et al., 2017) are driven exclusively by the sensory experience of deaf individuals, or linguistic factors can also contribute to changes in functional connectivity in this population. There is evidence of significant effects of linguistic experience on functional connectivity in groups with different language experiences, with some of this evidence also related to executive functioning: for instance, children with reading difficulties demonstrated greater functional connectivity between the executive functions network and visual, language, and cognitive control regions during the Stroop task, compared to typical readers (Levinson et al., 2018); greater language diversity was related to higher brain network specialization and segregation in default mode and executive control networks defined by performance during executive control tasks in hearing bilinguals (X. Li et al., 2021); long-term Cantonese-Mandarin bilinguals had stronger functional connectivity underlying inhibitory control in the cingulo-opercular network at rest (Cai et al., 2021).

Overall, there are very few studies on functional connectivity during task execution in deaf individuals and on functional connectivity in deafness in general, and some of the previous studies of functional connectivity in deafness have not explicitly included the measures representing the unique language experiences in this population into the functional connectivity analysis and considered it a limitation (e.g. W. Li et al., 2016), even if they may aim at explaining the effects of linguistic experience in deaf individuals (Malaia et al., 2014). Nevertheless, to our knowledge, there are two studies that have directly investigated the effects of language proficiency on functional connectivity in deaf individuals (sign language: Holmer et al., 2022; written language: Y. Li et al., 2013) and one study that used the age of onset of sign language use in their analysis instead of a direct proficiency measure (Ding et al., 2016) and did not find effects associated to the age of sign language use onset. Previous relevant studies on deafness have either looked at the effect of language deprivation on structural connectivity in deaf individuals (Cheng et al., 2019) or the effects of language experience on functional connectivity at rest (Ding et al., 2016; Holmer et al., 2022; Y. Li et al., 2013). Therefore, functional connectivity studies have looked at language experience in either of the two language modalities and only in the state of rest. As far as we know, there have been no studies investigating the effects of modality-independent language proficiency on functional connectivity during task execution in deaf individuals. While resting-state functional connectivity can be used to infer information about the organisation of language networks in the brain (Tomasi & Volkow, 2012), it has been established that task-fMRI predicted language measures better than resting-state fMRI (Greene et al., 2018; R. Jiang et al., 2020; Tomasi & Volkow, 2020). Investigating task-related functional connectivity MRI in relation to language proficiency in a population with variable language backgrounds and executive function abilities (Chapter 2) can help in identifying functional changes directly involved in cognitive task performance and how they may relate to language skills shaped by early developmental experience.

4.1.3. Research questions

In Chapter 2, the main objective of the analysis was to investigate how specific components of executive function may be influenced by the degree of language proficiency in deaf individuals in relation to both behaviour and neural activity. We have established that general language proficiency scores are significantly related to behavioural performance during switching. We also found that in the planning task, language proficiency correlated with neural activity during both conditions of the task (higher executive load: Tower of London and lower executive load: counting beads). In this chapter, we aim to address two broad research questions in relation to these two tasks:

- **How do patterns of state-dependent functional connectivity differ between deaf and hearing individuals?** Here we will focus on changes in connectivity between task execution and resting state (using the data from the higher executive load condition (Tower of London) and resting-state data) and between different task states (higher and lower executive load conditions in switching) caused by the sensory experience of deafness. We expect that changes in connectivity in deaf individuals will extend beyond the sensory cortices, similarly to what has been observed at rest (Andin & Holmer, 2022; Bonna et al., 2021; Cardin et al., submitted; Dell Ducas et al., 2021; Chapter 3). Considering extensive plasticity effects in resting-state functional connectivity, the differences between the groups in executive function processing (Chapter 2) and the role of dynamic reconfiguration between sensory, cognitive, and attention networks for task execution and cognition (Betti et al., 2013; Douw et al., 2016; Elton & Gao, 2014, 2015a; Fornito et al., 2012; Hearne et al., 2015; Piccoli et al., 2015) (see Gonzales-Castillo & Bandettini, 2018 for a review), we expect to see significant between-group differences in state-dependent connectivity between higher-association cortices, especially between the regions of the default mode network, the control network and, broadly, regions involved in task execution. In the study described in Chapter 3, the areas from the visual and control networks showed connectivity differences at rest, and the default mode network areas showed differences in connectivity to both visual and control regions. We suggest that these changes may reflect important compensatory mechanisms relevant to task execution. Here we expect that the coupling of the regions from the default mode network and control networks to other task-relevant networks may be affected by the cognitive state. We will also investigate whether differences in connectivity between executive function task execution and resting state can also be observed on the level of whole brain networks rather than individual regions.

- **Is it the sensory experience of deafness that drives state-dependent changes in functional connectivity in the deaf group, or can specific changes between the states be related to language proficiency in deaf individuals?** Here we will investigate if state-dependent changes in functional connectivity in executive processing found between deaf and hearing individuals are associated with the degree of language proficiency in the deaf group. Considering that language proficiency may support components of executive function and contribute to the execution of executive function tasks (Botting et al., 2017; Figueras et al., 2008; Merchán et al., 2022), also on the level of neural activity (Chapter 2), we suggest that some of the changes observed between the groups may be driven by the language experience of the deaf participants. The associations between language experience and functional connectivity have been discussed before in resting-state studies (Holmer et al., 2022; Y. Li et al., 2013; Malaia et al., 2014), but the association between dynamic reconfiguration between different cognitive states and language experience has not yet been investigated, to the best of our knowledge.

To address these questions, we will first describe between-group differences in functional connectivity for each of the tasks of interest (planning and switching). Then, we will investigate whether the detected differences in connectivity between the groups can be explained by the unique language experience of deaf individuals, or whether they are likely to arise from the sensory experience of deafness. We hypothesise that there will be between-state changes in functional connectivity between the group of deaf individuals and hearing controls in regions from sensory, cognitive, and attention networks, as has been demonstrated at rest (Andin & Holmer, 2022; Bonna et al., 2021; W. Li et al., 2016; Chapter 3), and that some of these changes will be related to the unique language experience of deaf individuals, as we have found effects of the degree of language proficiency on the neural activity and/or performance in these two executive functions tasks (Chapter 2) and on functional connectivity at rest (Chapter 3), and other studies have discussed associations between functional connectivity and language experience in deaf individuals (Holmer et al., 2022; W. Li et al., 2016). However, since there have been no studies investigating task-related effects in functional connectivity in deafness across the whole brain, we suggest that the exploratory analyses reported in this chapter should be used to gain initial insights into little-understood effects of deafness and language proficiency on functional connectivity changes between cognitive states across different brain areas.

4.2. Methods

4.2.1. Participants

4.2.1.1. Inclusion criteria and demographics

Planning

The sample consisted of 19 hearing (14 female, 5 male) participants (one hearing participant was excluded due to low accuracy, see *2.2. Method* in Chapter 2) and 20 deaf (12 female, 8 male) participants (one participant was excluded due to motion artefacts from the resting-state analyses (see *3.2. Method* in Chapter 3), and six participants were excluded from all analyses of the planning task due to excessive motion or low accuracy, as described in *2.2. Method* in Chapter 2). The groups were matched on age, gender, non-verbal reasoning, and visuo-spatial working memory span (Table 4.1, Table 4.2).

Table 4.1. Planning: age, non-verbal reasoning, and visuo-spatial working memory span

	Age		**WASI**		**Corsi**	
	deaf	hearing	deaf	hearing	deaf	hearing
Valid	20	19	20	18	20	18
Missing	0	0	0	1	0	1
Mean	39.90	36.95	59.60	57.56	5.25	5.44
Std. Deviation	13.34	17.13	9.43	8.25	0.84	1.11
Minimum	19	18	39	34	3.50	4.00
Maximum	63	66	72	69	7.50	8.50

Table 4.2. Planning: group comparisons for gender, non-verbal intelligence, and visuo-spatial working memory span

	t	***df***	***p***
Age	0.60	37	.55
WASI	0.71	36	.48
Corsi	-0.61	36	.54
	X^2	***df***	***p***
Gender	0.82	39	.37

Note. Student's t-tests (WASI, Corsi), Chi-Squared test (gender).

Switching

The sample consisted of 20 hearing (15 female, 5 male) and 23 deaf (14 female, 9 male) participants. As the analysis did not involve resting-state data (see *4.2.5. Functional connectivity analysis* below), all 23 deaf participants included in the analysis of the switching task data in Chapter 2 were included here (two participants were excluded due to low accuracy and not completing the scanning session). The groups were matched on age, gender, non-verbal reasoning, and visuo-spatial working memory span (Table 4.3, Table 4.4).

Table 4.3. Switching: age, non-verbal reasoning, and visuo-spatial memory span

	Age		**WASI**		**Corsi**	
	deaf	hearing	deaf	hearing	deaf	hearing
Valid	23	20	23	19	23	19
Missing	2	0	2	1	2	1
Mean	40.30	37.50	59.87	57.47	5.39	5.40
Std. Deviation	13.93	16.85	8.76	8.02	0.71	1.10
Minimum	19	18	39	34	4.50	4.00
Maximum	63	66	72	69	7.50	8.50

Table 4.4. Switching: group comparisons for gender, non-verbal reasoning, and visuo-spatial working memory span

	t	*df*	*p*
Age	0.60	41	.55
WASI	0.92	40	.37
Corsi	-0.01	40	.99
	X^2	*df*	*p*
Gender	0.97	43	.32

Note. Student's t-tests (WASI, Corsi), Chi-Squared test (gender).

4.2.1.2. *Language variability*

Planning

The group of participants had highly variable language backgrounds (Table 4.5), with six out of 20 participants having deaf parents or at least a deaf sibling (one participant), six participants having early sign language exposure (before the age of 8), four participants learning sign language later in life (between 12 and 20 years old), one participant learning sign language after the age of 20 and three participants having no exposure to sign language and using spoken English to communicate.

Table 4.5. Questionnaire data on the deafness and language background of the deaf participants included in the functional connectivity analysis of the planning task

Deafness onset	**Cause of deafness**	**British Sign Language**	**Sign language acquisition**	**Preferred language**
Birth	Unknown	Yes	Native	BSL
Birth	Genetic	Yes	Early	BSL
Birth	Genetic	Yes	Native	BSL
< 3 years old	Meningitis	Yes	Early	BSL
Birth	Genetic	Yes	Early	English
Birth	Genetic	No	N/A	English
Birth	Genetic	Yes	Native	BSL
Birth	Unknown	Yes	Late	English
Birth	Mother had rubella	Yes	Late	English
Birth	Unknown	Yes	Late	BSL
Birth	Genetic	Yes	Native*	BSL
Birth	Mother had rubella	Yes	Early	English
Birth	Genetic	No	N/A	English
Birth	Genetic	Yes	Native	Auslan
Birth	Genetic	Yes	Late	English
Birth	Mother had rubella	No	N/A	English

Deafness onset	Cause of deafness	British Sign Language	Sign language acquisition	Preferred language
3 years old	Genetic	Yes	Native	BSL
< 3 years old	Meningitis	Yes	Late	BSL
Birth	Genetic	Yes	Early	BSL
Birth	Mother had infection or virus	Yes	Early	BSL

Note. *The participants learned BSL from an older sibling. Two participants learned British Sign Language after they learned a different sign language from the same family: Australian Sign Language (Auslan) and South African Sign Language.

Switching

Eight out of 23 deaf participants were native signers who had deaf signing parents or at least a deaf sibling (one participant), six participants had early sign language exposure (before the age of 8), five participants learned sign language later in life (between 12 and 20 years old), one participant learned sign language after the age of 20 and three participants had no exposure to sign language and used spoken English to communicate (Table 4.6).

Table 4.6. Questionnaire data on the deafness and language background of the deaf participants included in the functional connectivity analysis of the switching task

Deafness onset	Cause of deafness	British Sign Language	Sign language acquisition	Preferred language
Birth	Unknown	Yes	Native	BSL
Birth	Genetic	Yes	Early	BSL
Birth	Genetic	No	N/A	English
Birth	Genetic	Yes	Native	BSL
Birth	Genetic	Yes	Native	BSL
< 3 years old	Meningitis	Yes	Early	BSL
Birth	Genetic	Yes	Early	English
Birth	Unknown	Yes	Late	English
Birth	Genetic	Yes	Native	BSL
Birth	Unknown	Yes	Late	English
Birth	Mother had rubella	Yes	Late	English
Birth	Unknown	Yes	Late	BSL
Birth	Genetic	Yes	Native*	BSL
Birth	Mother had rubella	Yes	Early	English
Birth	Genetic	No	N/A	English
Birth	Genetic	Yes	Native	Auslan
Birth	Genetic	Yes	Native	English
Birth	Genetic	Yes	Late	English
Birth	Mother had rubella	No	N/A	English

Deafness onset	Cause of deafness	British Sign Language	Sign language acquisition	Preferred language
~ 3 years old	Genetic	Yes	Native	BSL
< 3 years old	Meningitis	Yes	Late	BSL
Birth	Genetic	Yes	Early	BSL
Birth	Mother had infection	Yes	Early	BSL

Note. *The participants learned BSL from an older sibling. Two participants learned British Sign Language after they learned a different sign language from the same family: Australian Sign Language (Auslan) and South African Sign Language.

4.2.1.3. Language assessment

The language proficiency measure was analogous to the one used in the previous chapters (see *2.1.2. Materials* and *2.2.2. Performance in the grammaticality judgement tasks and a modality-independent language proficiency measure* in Chapter 2 for more details). The combined language measures were obtained by transforming the scores in the English Grammaticality Judgement Task and British Sign Language Grammaticality Judgement Task (Cormier et al., 2012) tasks (Table 4.7) for each specific sample of deaf participants included in each analysis. Then the higher z-score of the two was chosen as a measure of the participant's general language proficiency (Figure 4.1). Z-scores of two participants in each sample were excluded as outliers (more than 2 standard deviations from the mean) from the language-related analyses, but not from the state-related analyses.

Table 4.7. Language proficiency measures for the sample of deaf participants in the task-dependent functional connectivity analysis

	EGJT		**BSLGJT**		**Language score**	
	Planning	Switching	Planning	Switching	Planning	Switching
Valid	20	23	17	20	20	23
No test	0	0	3	3	0	0
Mean	82.70	83.05	76.65	77.03	0.48	0.51
Std. Deviation	12.34	11.77	13.29	12.82	0.70	0.70
Minimum	53.93	53.93	52.50	52.50	-1.44	-1.52
Maximum	96.63	96.63	95.00	95.00	1.38	1.40

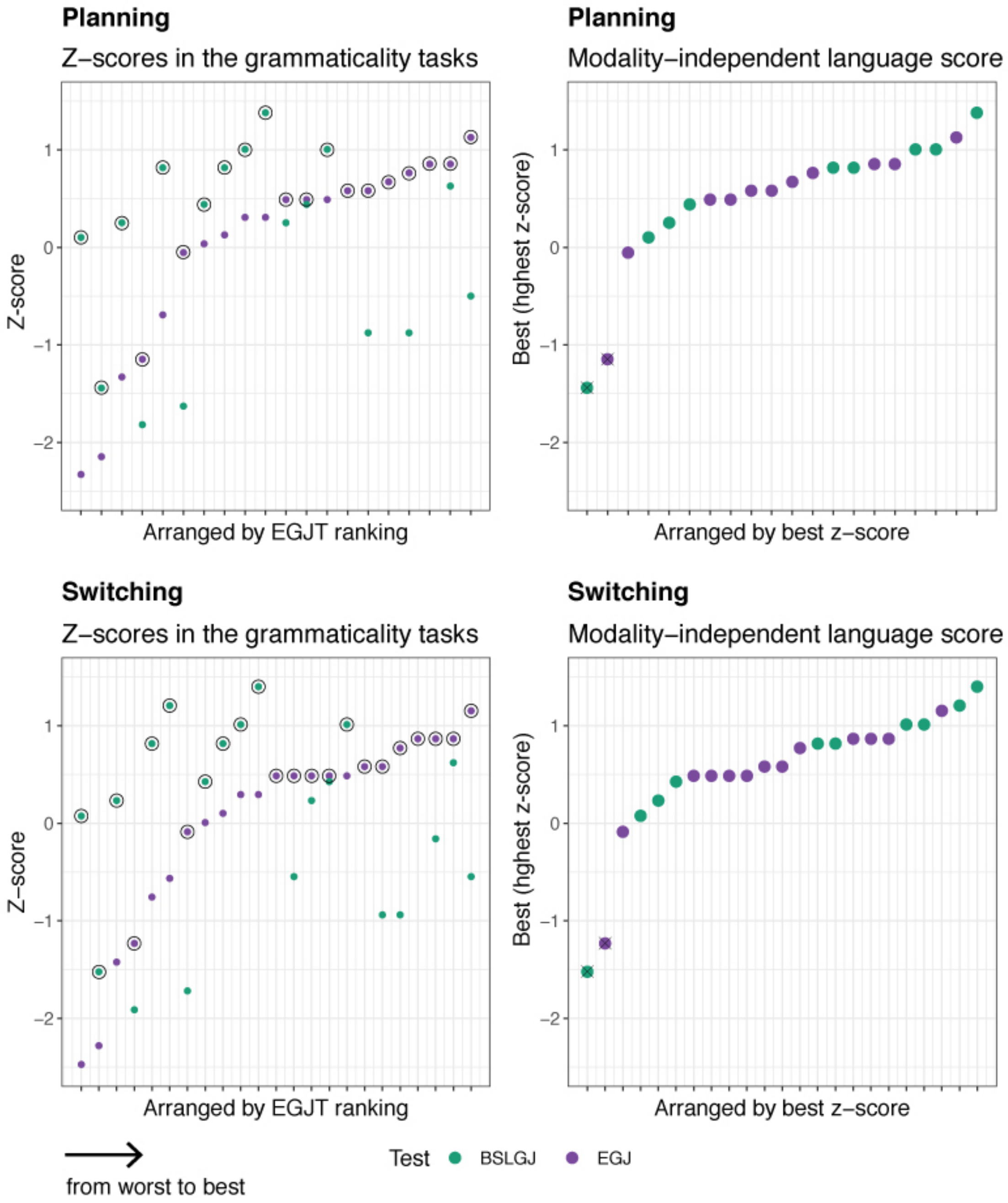

Figure 4.1. Modality-independent z-score in the sample of participants included in the analysis of task-related functional connectivity changes. The left figures display language z-scores in the EGJ and BSLGJ tasks for the specific samples for the planning and switching analysis separately, ranked on the x-axis by the performance in the EGJ task. The right figures display the final language scores (from worst to best) for each analysis. Two participants with the lowest z-scores were removed from all language-related analyses.

4.2.2. Materials and procedure

The design, stimuli, and procedure are described in detail in *2.2. Method* in Chapter 2 for the data on planning and switching and in *3.2. Method* in Chapter 3 for the acquisition of the resting-state data.

4.2.3. Image acquisition and fMRI data preprocessing

The image acquisition parameters, the preprocessing, and denoising steps were identical to the procedures described in Chapter 2 *(2.1.4. Image acquisition and 2.1.5. fMRI data preprocessing)* and Chapter 3 *(3.2.3. Image acquisition and fMRI data preprocessing)*, unless specified below.

The onset times and durations for each trial for each subject were input in the *Setup (Experimental conditions: within-subjects effects)* tab in CONN toolbox for both tasks for each condition: planning (higher executive load: Tower of London and lower executive load: counting beads conditions) and switching (first switch, stay, remaining switch). The durations for the dynamic switching task were set at 0. The onset times and durations were included in the list of confounding effects during the denoising step to remove the main task effects (i.e., the convolution of each condition's timeseries with the hemodynamic response function) from the BOLD signal before computing connectivity measures. The list of confounds, in addition to the scrubbing, realignment, white matter, and cerebrospinal fluid, also included the effect of rest, the effect of planning (higher executive load: Tower of London), the effect of the control condition in planning (lower executive load: counting beads), the effect of the first switch, the effect of stay trials and the remaining switch trials. Resting-state data was re-added to the analysis with a different band-pass filter [0.008 inf] than in the resting-state analysis to keep the same band-pass filter across the analyses.

4.2.4. Atlas redistribution procedure

The atlas redistribution procedure is described in detail in *3.2.4. Atlas redistribution procedure* in Chapter 3. The Schaefer-Yeo brain parcellation atlas was used (Schaefer et al., 2018; Yeo et al., 2011). The regions in the parcellation belonged to one of the following networks (after redistribution): control (Ctr) (A, B, and C), default mode (DMN) (A, B, and C), dorsal attention (DorsAttn) (A and B), language (Lang) (added), limbic (Limb) (A and B), salience/ventral attention (Sal) (A and B), somatomotor (SomMot/SM) (A and B), temporo-parietal/auditory (TP) (redefined) and visual (Vis) (A and B). ROIs from networks under different letters (e.g., somatomotor A and B) were treated as belonging to the same network (somatomotor) in this chapter.

4.2.5. Functional connectivity analyses

For the planning task and the resting-state data, functional connectivity analysis was performed using the standard pipeline for a seed-based functional connectivity analysis in the CONN toolbox. Only the higher executive load (Tower of London) condition was used in the analysis to focus on the differences in connectivity between executive functions task execution and resting state.

For the switching task, a seed-to-seed task-modulation effects (gPPI: generalised psycho-physiological interactions; McLaren et al., 2012) analysis was performed, as a preferred analysis for investigating task-related modulation of functional connectivity patterns in event-related designs (Nieto-Castanon, 2020). PPI analysis identifies regions of interest where the BOLD response time courses are related in a given psychological context and has been found to improve the model fit for event-related fMRI tasks (McLaren et al., 2012). The PPI terms were created for each type of trial: ‘first switch’ (or ‘switch’), ‘stay’, and ‘remaining switch’.

4.2.6. Statistical analyses

Second-level analyses were performed on the measures of connectivity obtained in the first-level analysis step: bivariate correlation coefficients (Fisher-transformed into standardised z-values) representing absolute connectivity values in each condition in the planning task and the bivariate regression measures representing relative measures of connectivity in each condition to the implicit baseline in the switching task. All 400 seeds from the atlas were chosen to be seeds and targets to perform an analysis on the data across the brain and in every network (see *3.2.5. Resting-state functional connectivity analysis*).

The second-level analyses included the between-subject effects [deaf, hearing] and two conditions for the analysis of each task: 'planning' and 'rest' for the analysis between different states during planning and rest, and 'first switch' and 'stay' for the analysis on differences between conditions in switching.

The interactions between the group and condition were investigated with the between-subject contrast [1 -1] (deaf, hearing) and the between-condition contrast [1 -1] (planning, rest; first switch, stay). Significantly different connections are reported in this chapter after seed-level FDR-correction was applied at $p < .05$ (see *3.2.6. Statistical analyses* for details).

To investigate if the changes in connectivity between the groups were driven by the sensory or language experience of the deaf participants, Pearson's r correlation coefficients were calculated between the differences in connectivity between conditions in the pairs of regions that showed significantly different connections between the groups and the general language proficiency score in the deaf group.

4.2.7. Network-level analysis

To investigate the difference between network-level dynamics during task execution and at rest, the whole-brain network-level analysis was performed on the data from the high executive load condition of the planning task (Tower of London) and the resting-state data. The implementation of a similar analysis on the data from the switching task could not be done in a similar way: being a fast-paced event-related design, the analysis of the switching task requires conducting a gPPI analysis that should not be used to measure absolute connectivity in a specific condition (Di et al., 2021).

Absolute condition-specific connectivity measures obtained during the first-level step of data analysis on the planning task were extracted from the CONN toolbox for each participant as Fisher-transformed correlation coefficients for the connectivity between all seeds in the atlas, resulting in a 400 x 400 connectivity matrix for each participant for each condition (conditions: planning, resting state with a band-pass filter of [0.008 inf]). The values were averaged between all seeds in each pair of networks, resulting in a 9 x 9 connectivity matrix for each participant. The connectivity values for each pair of networks in the resting-state condition were subtracted from the connectivity values for the same pair of networks in the planning condition for every participant to be used in statistical analyses.

For the purpose of data visualisation and exploration, the following network pairs were plotted and included in the dataset: Ctr-DMN, Ctr-DorsAttn, Ctr-Limb, Ctr-SalVentAttn, Ctr-SomMot, Ctr-TP, Ctr-Vis, DMN-DorsAttn, DMN-Lang, DMN-Limb, DMN-SalVentAttn, DMN-SomMot, DMN-TP, DMN-Vis, DorsAttn-Lang, DorsAttn-Limb, DorsAttn-SalVentAttn, DorsAttn-SomMot, DorsAttn-TP, DorsAttn-Vis, Lang-Limb, Lang-SalVentAttn, Lang-SomMot, Lang-TP, Lang-Vis, Limb-SalVentAttn, Limb-SomMot, Limb-TP, Limb-Vis, SalVentAttn-SomMot, SalVentAttn-TP, SalVentAttn-Vis, TP-Vis[1] (33 connections).

Independent-samples t-tests were conducted on connectivity difference measures [$\text{conn}_{\text{planning}}$ – $\text{conn}_{\text{rest}}$] between pairs of networks to investigate the between-group differences. Only connections involving task-related networks (default mode, dorsal attention, salience/ventral attention, and language) and sensory networks (auditory/temporo-parietal, visual, and somatomotor) were included in the analysis, resulting in 28 connections and t-tests.

To investigate the role of language proficiency in the deaf group on the connectivity differences between network pairs between the two groups, correlational analysis was performed on the differences in connectivity between significantly different network pairs and the general language proficiency score in the deaf group.

4.3. Results

4.3.1. Planning

4.3.1.1. Seed-to-seed between-group analysis

The results for the analysis of the contrast planning > rest [1; -1] for the between-group analysis (deaf > hearing [1; -1]) are displayed in the figure below (Figure 4.2, Table 4.8). There were 17 significantly different connections.

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[1] Abbreviations. Ctr: control, DMN: default mode network, DorsAttn: dorsal attention, Limb: limbic, SalVentAttn: salience/ventral attention, SomMot: somatomotor, TP: temporo-parietal/auditory, Vis: visual, Lang: language.

Table 4.8. Between-group differences in connectivity between planning and resting state

Source network	**Source region name**	**Target network**	**Target region name**	**T(*df*)**	***p-FDR***
Default mode	LH_DefaultB_PFCd_3	Default mode	RH_DefaultA_pCunPCC_1	4.25*(37)*	.05
Default mode	LH_DefaultB_PFCd_3	Control	RH_ContB_PFCld_3	-3.85*(37)*	.05
Default mode	LH_DefaultB_PFCd_3	Control	RH_ContC_Cingp_1	3.77*(37)*	.05
Default mode	RH_DefaultB_PFCd_4	TP/auditory	LH_SomMotB_Aud_2*	4.90*(37)*	.008
Default mode	RH_DefaultB_PFCd_4	TP/auditory	RH_SomMotB_Aud_2*	4.64*(37)*	.009
Default mode	RH_DefaultB_PFCd_4	TP/auditory	RH_SomMotB_Aud_3*	4.11*(37)*	.03
Default mode	RH_DefaultA_PFCm_3	Visual	RH_VisCent_ExStr_3	3.32(37)	.04
Default mode	LH_DefaultB_PFCd_3	Visual	LH_VisPeri_ExStrSup_2	4.06*(37)*	.05
Default mode	LH_DefaultB_PFCd_3	Visual	RH_VisPeri_ExStrSup_2	3.79*(37)*	.05
Default mode	LH_DefaultA_pCunPCC_7	Somatomotor	LH_SomMotA_15	-4.27*(37)*	.03
Default mode	LH_DefaultA_pCunPCC_7	Somatomotor	RH_SomMotA_18	-4.26*(37)*	.03
Salience/ventral attention	RH_SalVentAttnA_FrMed_2	Salience/ventral attention	LH_SalVentAttnB_PFCl_3	-4.24*(37)*	.04
Salience/ventral attention	RH_SalVentAttnA_FrMed_2	Control	RH_ContB_PFCld_1	-4.12*(37)*	.04
Salience/ventral attention	RH_SalVentAttnB_PFCmp_2	Limbic	LH_LimbicA_TempPole_2	4.13*(37)*	.04
Salience/ventral attention	RH_SalVentAttnB_PFCmp_2	Somatomotor	LH_SomMotA_17	4.13*(37)*	.04
TP/auditory	RH_SomMotB_Aud_2*	Somatomotor	LH_SomMotB_Cent_3	4.08*(37)*	.02
Limbic	LH_LimbicA_TempPole_2	Somatomotor	RH_SomMotA_2	4.24*(37)*	.04

Note. Between-group [1 -1] (deaf; hearing) differences in connectivity between the higher executive load (Tower of London) condition of the planning task and resting state [1 -1] (planning, rest).

*The seeds were reassigned to this network during the atlas redistribution procedure.

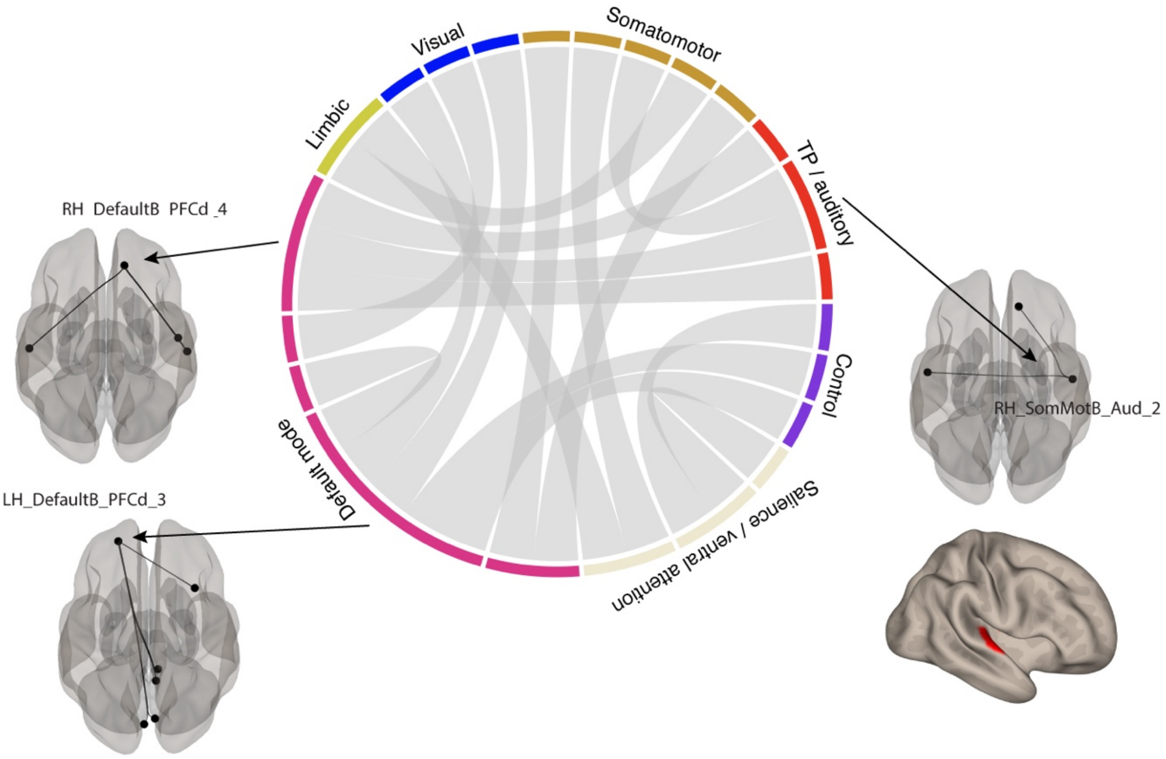


Figure 4.2. Between-group differences in state-dependent connectivity during planning and resting state. Between-group [1 -1] (deaf, hearing) differences in connectivity between the higher executive load (Tower of London) condition of the planning task and resting state [1 -1] (planning, rest). Significant connections are plotted in a single colour because the sign of the statistic is not meaningful for the interpretation of the direction of the differences.

Out of 17 significantly different connections, most of them (10 connections) involved the default mode network. The default mode network showed differences in connectivity between groups with the task-involved control network and with all sensory networks: the visual and somatomotor networks, as well as the somatomotor seeds of the temporo-parietal/auditory network.

The salience network was another task-related network that showed differences in connectivity between the groups. The differences were within-network and intra-network: with the seeds from the control, limbic and somatomotor networks.

To interpret the between-state differences in connectivity between the groups, connectivity values for the between-condition difference for each pair of regions that were significantly different between the groups were extracted for each participant for each of the two analyses. The values for the difference in connectivity between conditions were then plotted for each group to represent the direction of the effects.

The group-average differences in connectivity between planning and resting state are plotted in the figures below (Figure 4.3, Figure 4.4, Figure 4.5, Figure 4.6).

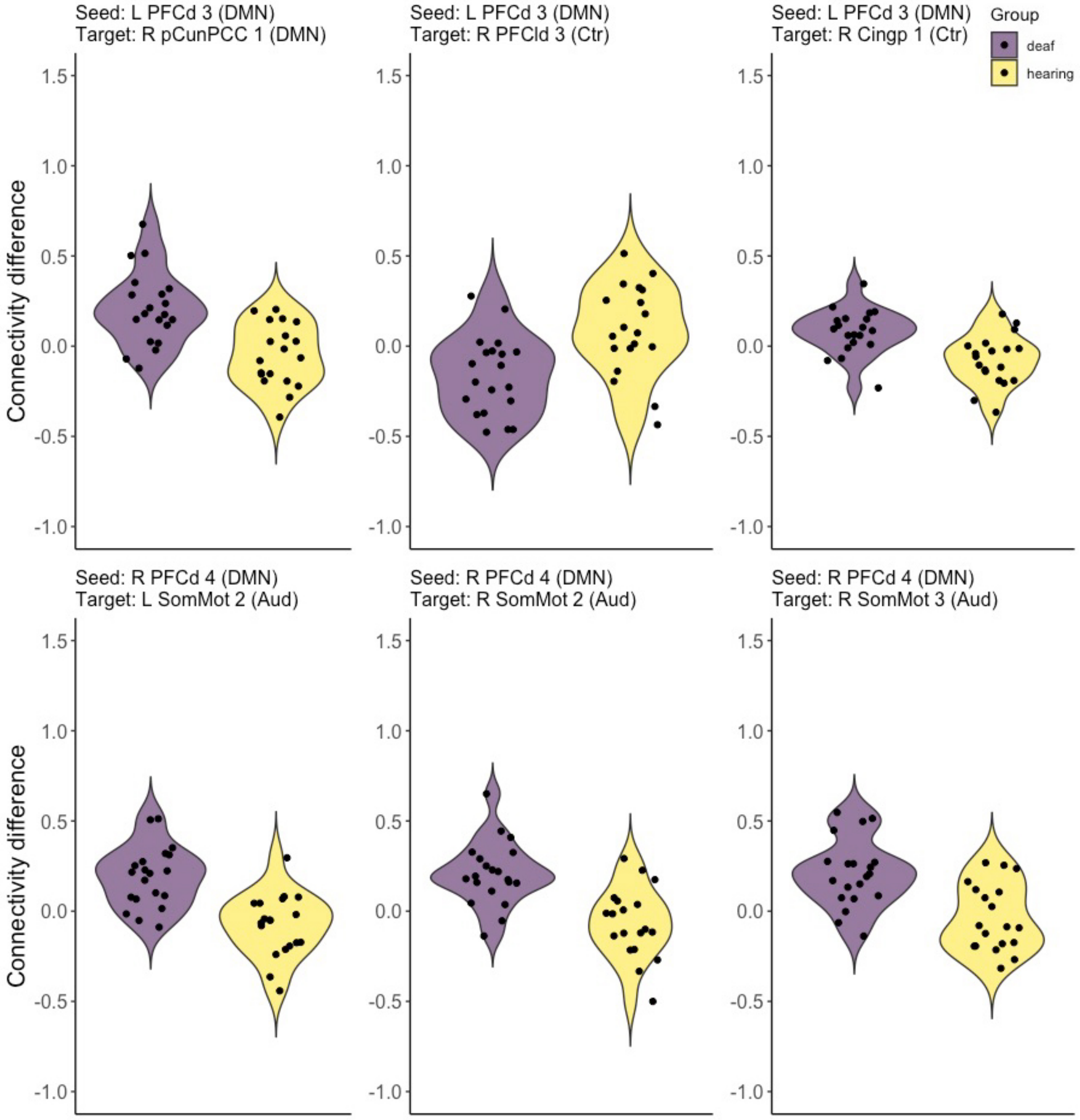


Figure 4.3. State-dependent differences in connectivity between planning and resting state in the deaf and hearing groups in the default mode network (part 1). Mean differences between seed-to-target (ROI-to-ROI) correlation coefficients (Fisher z-transformed) associated with connectivity during planning and resting state in each group. The contrast was defined as [1 -1] (planning, resting state). Positive values indicate an increase in connectivity during planning in comparison to rest. The figure contains connectivity differences in pairs where one of the regions is from the default mode network.

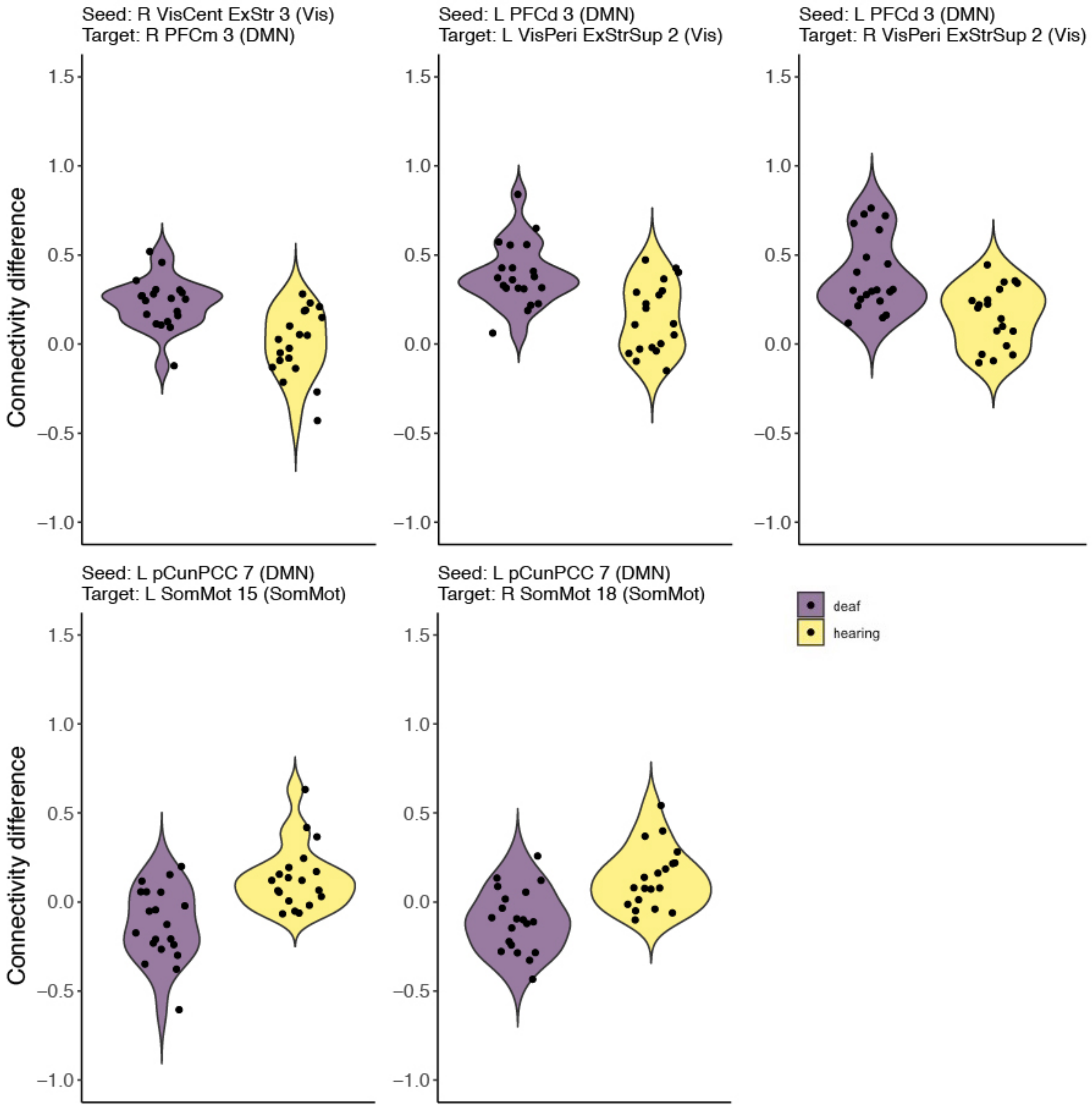


Figure 4.4. State-dependent differences in connectivity between planning and resting state in the deaf and hearing groups in the default mode network (part 2). Mean differences between seed-to-target (ROI-to-ROI) correlation coefficients (Fisher z-transformed) associated with connectivity during planning and resting state in each group. The contrast was defined as [1 -1] (planning, resting state). The figure contains connectivity differences in pairs where one of the regions is from the default mode network.

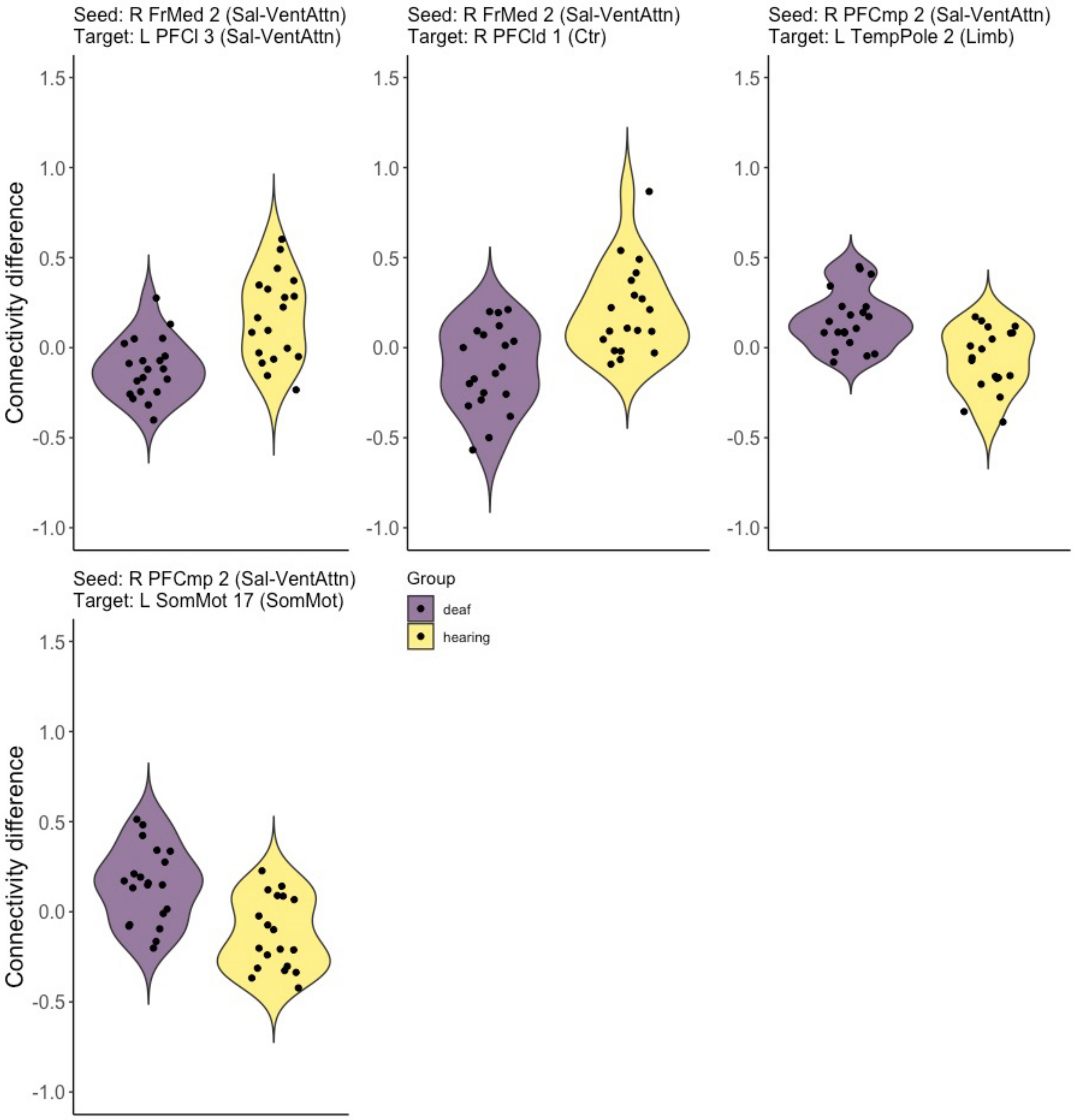


Figure 4.5. State-dependent differences in connectivity between planning and resting state in the deaf and hearing groups in the salience/ventral attention network. Mean differences between seed-to-target (ROI-to-ROI) correlation coefficients (Fisher z-transformed) associated with connectivity during planning and resting state in each group. The contrast was defined as [1 -1] (planning, resting state). The figure contains connectivity differences in pairs where all the seeds are from the salience/ventral attention network.

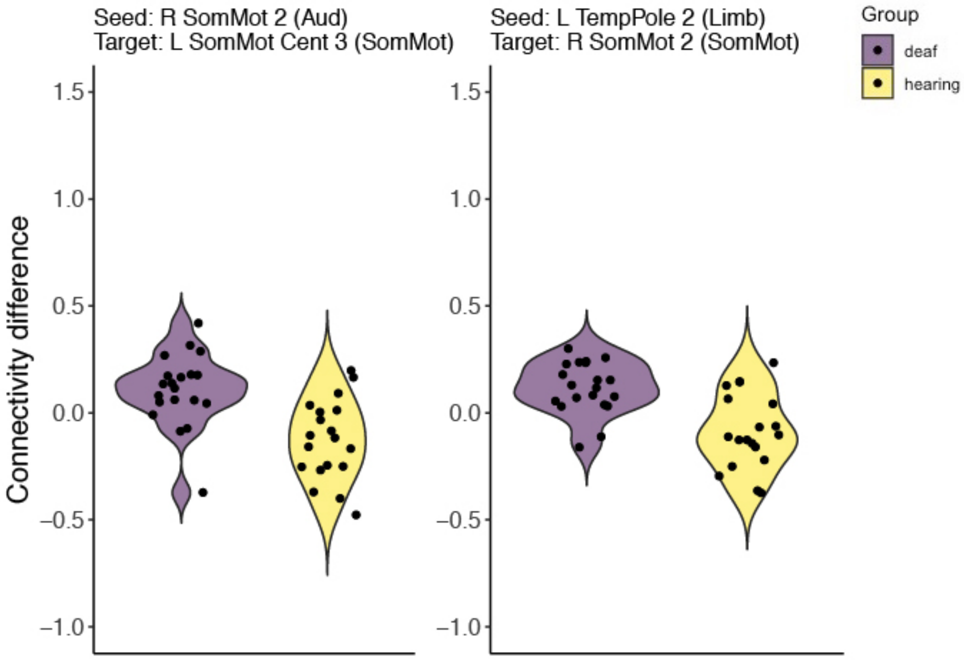


Figure 4.6. The remaining state-dependent differences in connectivity between planning and resting state in the deaf and hearing groups. Mean differences between seed-to-target (ROI-to-ROI) correlation coefficients (Fisher z-transformed) associated with connectivity during planning and resting state in each group. The contrast was defined as [1 -1] (planning, resting state).

Default mode network

One of the left dorsal prefrontal cortex (PFCd) seeds in the default mode network [-22 20 52] was the region that showed the most differences in connectivity between the planning and resting state between the groups. The groups showed differences in between-state connectivity to the following target regions:

1. the right precuneus posterior cingulate cortex (pCunPCC) (another region of the default mode network) [16 -64 28] (deaf: *M* = 0.21, *SD* = 0.20, hearing: *M* = -0.05, *SD* = 0.17),
2. the left [-2 -84 24] (deaf: *M* = 0.39, *SD*=0.18, hearing: *M* = 0.15, *SD* = 0.19) and the right [4 -80 24] (deaf: *M* = 0.39, *SD*=0.21, hearing: *M* = 0.16, *SD* = 0.17) visual peripheral, extrastriate superior cortex regions,
3. the right lateral dorsal prefrontal cortex (PFCld) in the control network [42 6 50] (deaf: *M* = -0.16, *SD* = 0.22, hearing: *M* = 0.09, *SD* = 0.25),

4. the right posterior cingulate cortex (Cingp) in the control network [8 -44 20] (deaf: *M* = 0.08, *SD* = 0.12, hearing: *M* = -0.08, *SD* = 0.14).

The connectivity difference between the states in the connectivity of a seed in the right medial prefrontal cortex (PFCm) area [8 42 4] and a right visual central extrastriate cortex region [24 -74 -10] was also different (deaf: *M* = 0.23, *SD* = 0.14, hearing: *M* = 0.00, *SD* = 0.19).

Another PFCd seed from the default mode network, in the right hemisphere [14 38 52], showed differences in connectivity between the states between the groups with one somatomotor region of the auditory network in the left hemisphere [-56 -22 8] (deaf: *M* = 0.19, *SD* = 0.17, hearing: *M* = -0.08, *SD* = 0.18) and two somatomotor auditory regions in the right hemisphere [54 -14 6] (deaf: *M* = 0.21, *SD* = 0.18, hearing: *M* = -0.07, *SD* = 0.20); [60 -24 10] (deaf: *M* = 0.21, *SD* = 0.19, hearing: *M* = -0.04, *SD* = 0.19].

One of the left pCunPCC [-6 -50 41] seeds of the default mode network showed differences between the states between the groups in connectivity with the somatomotor regions on the left [-4 -26 68] (deaf: *M* = -0.13, *SD* = 0.21, hearing: *M* = 0.14, *SD* = 0.18) and on the right [6 -22 72] (deaf: *M* = -0.11, *SD* = 0.18, hearing: *M* = 0.14, *SD* = 0.17).

The salience/ventral attention network

The right medial frontal cortex (FrMed) seed of the salience/ventral attention network [6 10 58] showed connectivity differences between the states between the groups with the targets in the left lateral prefrontal cortex in the same network [-38 50 10] (deaf: *M* = -0.11, *SD* = 0.16, hearing: *M* = 0.17, *SD* = 0.24) and in the PFCld in the control network in the right hemisphere [38 34 38] (deaf: *M* = -0.11, *SD* = 0.23, hearing: *M* = 0.21, *SD* = 0.25). Another seed of the salience/ventral attention network, in the right PFCmp [8 18

36], also showed a connectivity difference with a somatomotor region on the left [-18 -32 68] (deaf: *M* = 0.15, *SD* = 0.21, hearing: *M* = -0.13, *SD* = 0.20), as described above, and the temporal pole (in the limbic network) on the left [-24 6 -40] (deaf: *M* = 0.15, *SD* = 0.16, hearing: *M* = -0.07, *SD* = 0.17) (the same region that showed connectivity differences with a region of the somatomotor network, as reported above).

The somatomotor network

In addition to the connectivity differences described in the paragraphs above in relation to the default mode network, the connectivity difference between the states was significantly different between the groups between a left central somatomotor region [-54 -8 30] and a somatomotor region of the auditory network [54 -14 6] (deaf: *M* = 0.11, *SD* = 0.17, hearing: *M* = -0.13, *SD* = 0.19), as well as between a left somatomotor region [-18 -32 68] and the right medial posterior prefrontal cortex (PFCmp) in the salience/ventral attention network [8 18 36] (deaf: *M* = 0.15, *SD* = 0.21, hearing: *M* = -0.13, *SD* = 0.20) and the left temporal pole in the limbic network [-24 6 -30] (deaf: *M* = 0.12, *SD* = 0.12, hearing: *M* = -0.09, *SD* = 0.18).

4.3.1.2. Correlational analysis on seed-to-seed connectivity differences between the states in the deaf group: can language proficiency explain connectivity differences between the groups?

To investigate whether the observed between-group differences are modulated by the language experience of the deaf participants, we have conducted a correlational analysis on the 17 significantly different connections between the groups discussed above. No correlations were significant in this analysis (all p > .05).

4.3.1.3. Between-group network analysis

Connectivity matrices were plotted to visualise between-networks connectivity in each group in the resting state and planning (Tower of London) conditions (Figure 4.7) and to visualise the difference in connectivity between the groups (Figure 4.8) in each condition.

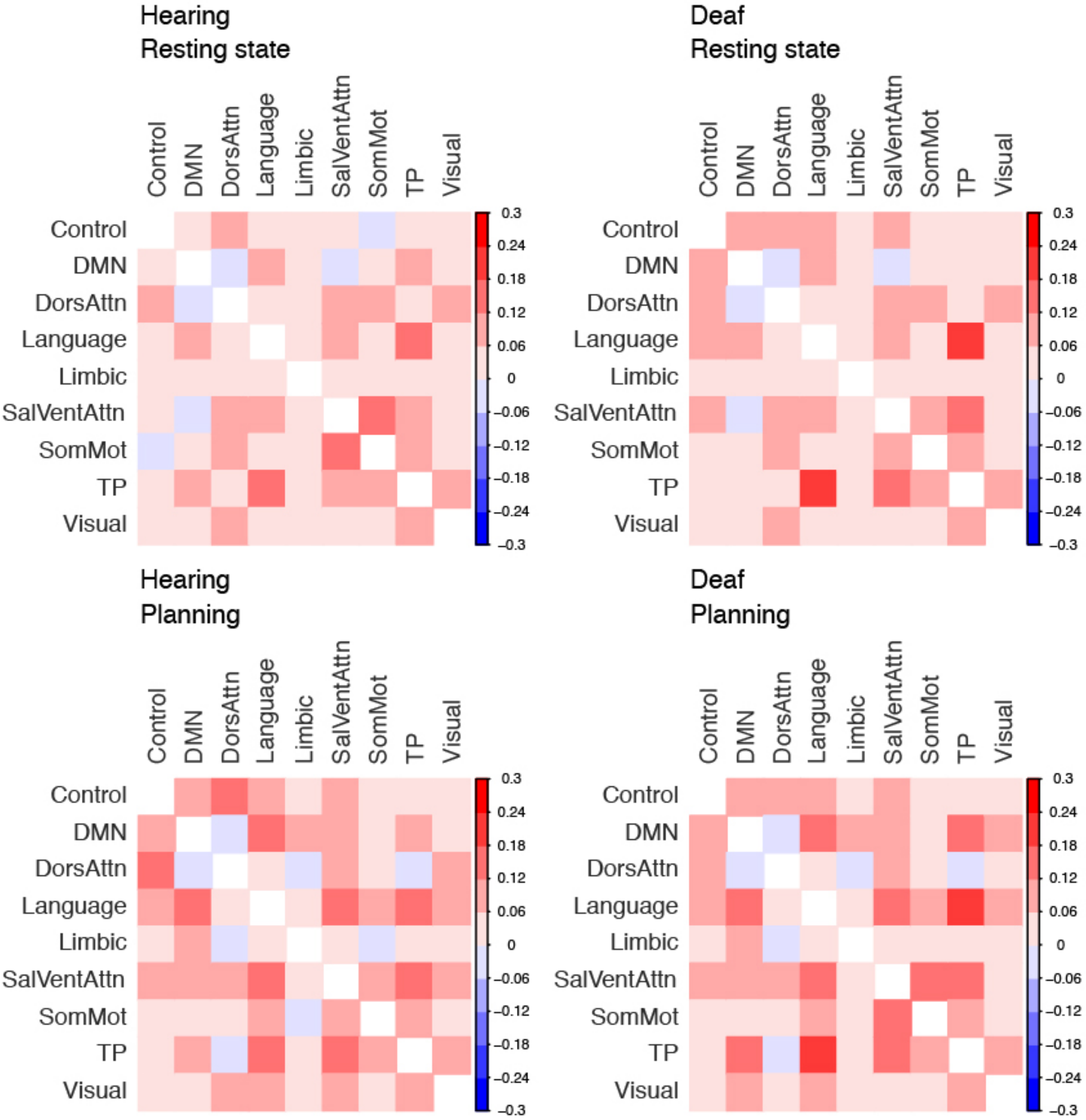
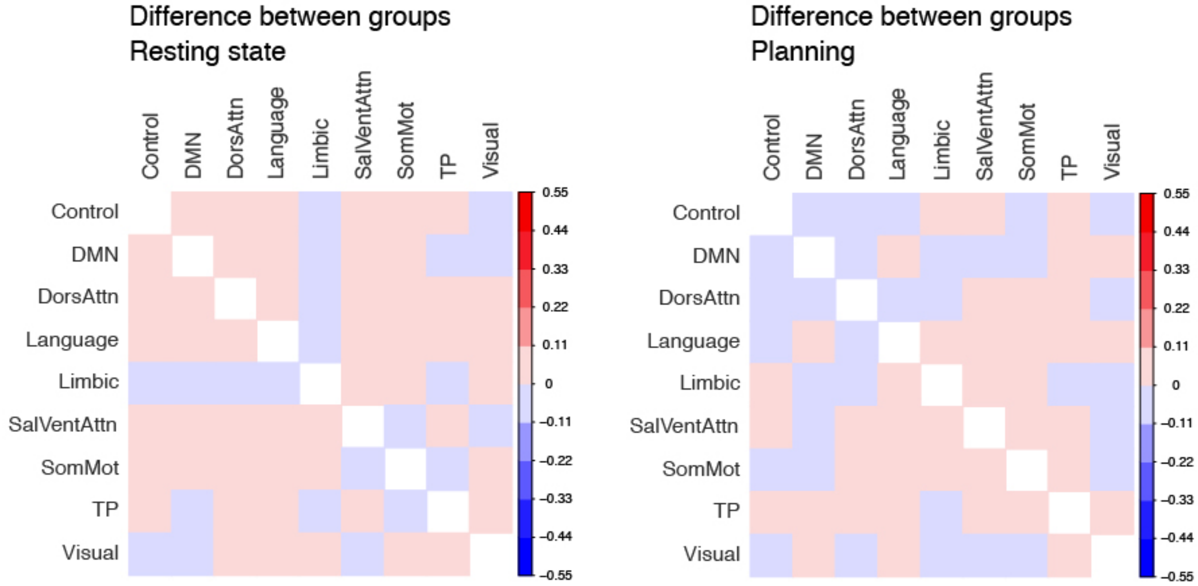


Figure 4.7. Network connectivity during resting state and planning in the deaf and hearing groups. Condition-specific connectivity measures extracted from the first-level analysis and transformed so that each element in the matrix is defined as a value resulting from averaging Fisher-transformed bivariate correlation coefficients of the connectivity between all the seeds in the corresponding networks (e.g., the second element in the first row in each matrix is the averaged connectivity value between all seeds in the control network and all seeds in the default mode network).


Difference between groups
Resting state

Difference between groups
Planning

Figure 4.8. Between-group differences in network connectivity during resting state and planning. The difference in condition-specific connectivity measures between the groups during resting state and planning, calculated as [$\text{conn}_{\text{deaf}}$ – $\text{conn}_{\text{hear}}$] for each network pair. Blue elements indicate a negative difference in connectivity between the groups, with the connectivity being higher in the hearing group than in the deaf group.

Overall, the deaf and hearing groups demonstrated similar connectivity profiles, especially during planning. Independent-samples t-tests on connectivity between the pairs of networks involving task-related networks and sensory-deprived and non-deprived sensory networks showed one significantly different connection between the groups in connectivity between the language network and the salience/ventral attention network, $t(37) = -2.19$, $p = .04$ (but it does not survive corrections for multiple comparisons) (Table 4.9).

Table 4.9. Independent samples t-tests on network connectivity differences between the deaf and hearing groups

Network pair	*t*	*df*	*p*
Ctr-DMN	-1.12	37	.27
Ctr-DorsAttn	-0.67	37	.51
Ctr-Lang	-1.74	37	.09
Ctr-Sal	-0.91	37	.37
Ctr-SomMot	-0.45	37	.66
Ctr-TP	0.10	37	.92
Ctr-Vis	0.24	37	.82
DMN-DorsAttn	-1.04	37	.31
DMN-Lang	0.29	37	.78
DMN-Sal	-0.24	37	.81
DMN-SomMot	-0.85	37	.40
DMN-TP	1.47	37	.15
DMN-Vis	1.45	37	.16
DorsAttn-Lang	-1.37	37	.18
DorsAttn-Sal	-0.66	37	.51
DorsAttn-SomMot	-1.55	37	.13[a]
DorsAttn-TP	-1.42	37	.17
DorsAttn-Vis	-1.58	37	.12
Lang-Sal	-2.19	37	.04*
Lang-SomMot	-0.39	37	.70
Lang-TP	-0.15	37	.88
Lang-Vis	0.11	37	.91
Sal-SomMot	0.29	37	.78
Sal-TP	0.28	37	.78
Sal-Vis	0.23	37	.82
SomMot-TP	0.81	37	.42
SomMot-Vis	-0.92	37	.36
TP-Vis	-1.00	37	.32

Note. Student's t-test.

[a] Levene's test is significant ($p < .05$), suggesting a violation of the equal variance assumption. Welch t-test did not show significant differences between the groups for this connection either, $t(30.20) = -1.57$, $p = .13$.

*Significance level: < .05.

The connectivity difference between the conditions between the salience/ventral attention and the language network was higher in the hearing group (*M* = 0.06, *SD* = 0.07) than in the deaf group (*M* = 0.01, *SD* = 0.07). The connectivity difference between the groups was significant because the difference in resting-state connectivity was significantly different between the groups, $t(37) = 3.48$, $p = .001$, with the deaf group exhibiting higher connectivity (*M* = 0.12, *SD* = 0.04) than the hearing group (*M* = 0.07, *SD* = 0.05) (Table 4.10), while connectivity between the language and salience/ventral attention networks was not significantly different during planning between the groups (*p* > .05), according to independent-samples t-tests.

Table 4.10. Connectivity between the language and salience/ventral attention networks in the deaf and hearing groups during rest and planning

	Language-Salience Resting state		**Language-Salience Planning**		**Language-Salience [Planning-Rest]**	
	deaf	hearing	deaf	hearing	deaf	hearing
Valid	20	19	20	19	20	19
Mean	0.12	0.07	0.13	0.13	0.01	0.06
Std. Deviation	0.04	0.05	0.06	0.07	0.07	0.07
Minimum	0.04	-0.01	0.05	0.04	-0.12	-0.03
Maximum	0.18	0.16	0.29	0.29	0.15	0.22

4.3.1.4. *Can language proficiency explain connectivity differences in connectivity between the groups?*

To investigate whether the observed between-group differences in connectivity between the salience and language network are modulated by the language proficiency of the deaf participants, we have conducted a correlational analysis on the difference between connectivity in these networks between conditions in the deaf group and general language proficiency score. The correlation was not significant, *r(37)* = 0.16, *p* = .52.

4.3.2. Switching

4.3.2.1. *Seed-to-seed between-group analysis*

The results for the analysis of the contrast switch > stay [1 -1] for the between-group comparison (deaf > hearing [1 -1]) are displayed in the table below (Table 4.11) (Figure 4.9). There were 20 significantly different connections.

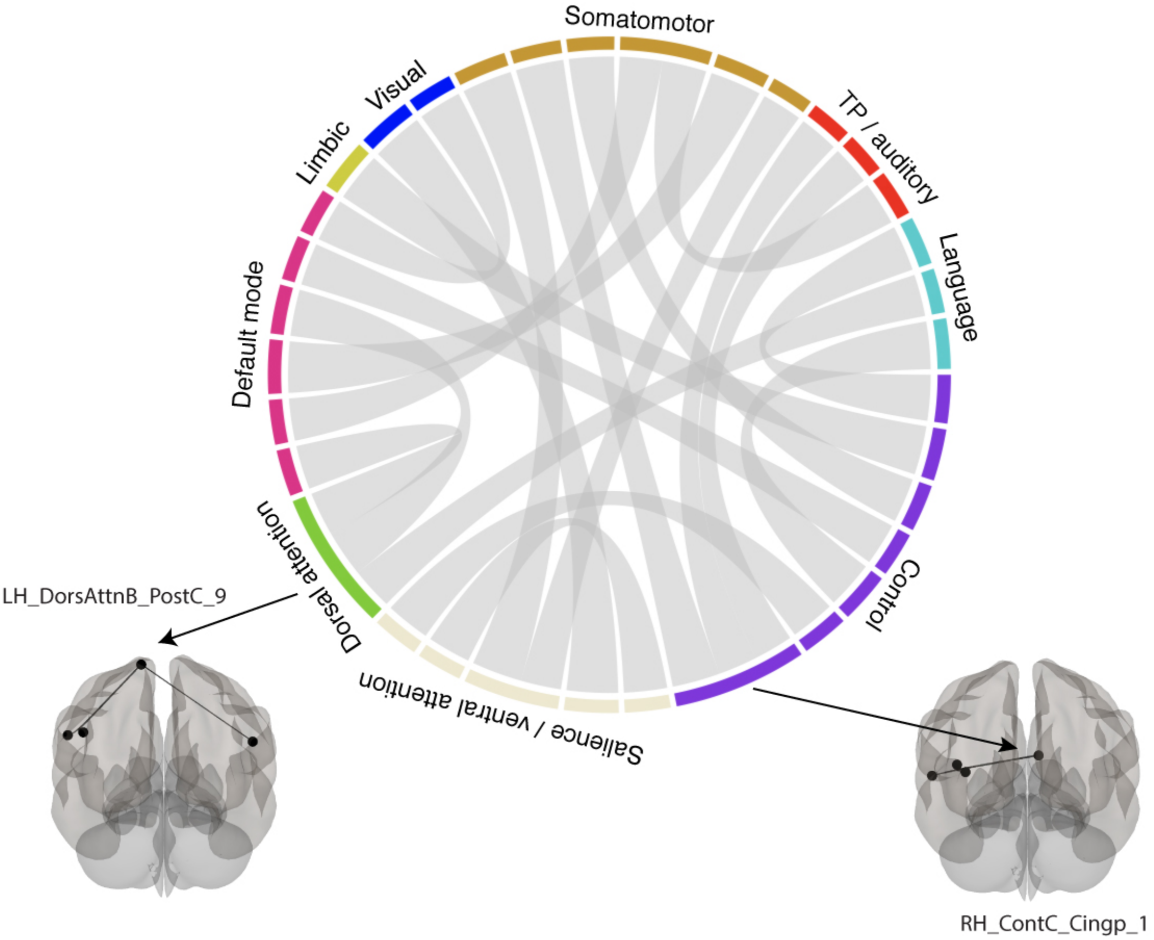


Figure 4.9. Between-group differences in condition-dependent functional connectivity during switching. Between-group [1 -1] (deaf, hearing) differences in connectivity between two conditions of the switching task [1 -1] (switch, stay). Significant connections are plotted in a single colour because the sign of the statistic is not meaningful for the interpretation of the direction of the difference.

Table 4.11. Condition-dependent connectivity differences between the groups in the switching task

Source network	**Source region name**	**Target network**	**Target region name**	***T(df)***	***p-FDR***
Control	RH_ContC_Cingp_1	Somatomotor	LH_SomMotB_Ins_1	-4.81*(41)*	.008
Control	RH_ContC_Cingp_1	TP/auditory	LH_SomMotB_Aud_2*	-3.97*(41)*	.04
Control	RH_ContC_Cingp_1	TP/auditory	LH_SomMotB_Aud_4*	-3.93*(41)*	.04
Control	RH_ContA_IPS_2	Somatomotor	LH_SomMotB_S2_5	-4.51*(41)*	.02
Control	RH_ContB_PFCld_4	Salience	RH_SalVentAttnB_PFCl_1	4.47*(41)*	.02
Control	LH_ContB_PFClv_3	Limbic	LH_LimbicB_OFC_5	-4.95*(41)*	.005
Language	LH_ContA_PFClv_1*	Control	LH_ContB_PFClv_2	-4.63*(41)*	.02
Control	RH_ContB_PFCld_1	Language	LH_TempPar_4*	-4.81*(41)*	.008
Dorsal attention	LH_DorsAttnB_PostC_9	Language	LH_DefaultB_IPL_2*	4.25*(41)*	.02
Dorsal attention	LH_DorsAttnB_PostC_9	Default mode	RH_DefaultA_IPL_1	4.70*(41)*	.01
Default mode	LH_DefaultA_IPL_1	Dorsal attention	LH_DorsAttnB_PostC_9	4.45*(41)*	.03
Default mode	RH_DefaultA_PFCm_6	Control	RH_ContA_PFCl_4	-4.29*(41)*	.04
Default mode	RH_DefaultB_PFCd_1	Visual	LH_VisCent_ExStr_7	4.34*(41)*	.04
Default mode	LH_DefaultC_PHC_3	Somatomotor	RH_SomMotA_15	5.18*(41)*	.003
Default mode	LH_DefaultA_PFCm_5	Somatomotor	RH_SomMotA_1	-4.28*(41)*	.04
Salience	LH_SalVentAttnA_Ins_1	Salience	RH_SalVentAttnA_FrMed_4	-4.34*(41)*	.04
Salience	LH_SalVentAttnA_FrMed_3	Visual	LH_VisCent_Striate_1	-5.16*(41)*	.003
Salience	RH_SalVentAttnA_Ins_3	Somatomotor	LH_SomMotA_19	5.05*(41)*	.004
Salience	RH_SalVentAttnA_Ins_3	Somatomotor	RH_SomMotA_19	4.06*(41)*	.04
TP/auditory	RH_SomMotB_Aud_3*	Somatomotor	RH_SomMotA_1	4.45*(41)*	.03

Note. *The seeds were reassigned to this network during the atlas redistribution procedure.

9 out of 20 significantly different connections involved the control network, with three involving the cingulate cortex and others coming from the areas in the prefrontal cortex. The control network showed differences in connectivity with two somatomotor regions and two auditory somatomotor regions, two regions from the language network, and single regions in the default mode, salience, and limbic networks.

7 significantly different connections involved somatomotor regions, and three more regions belonged to the somatomotor network before being reclassified into the temporo-parietal/auditory network. They showed differences in connectivity between themselves (a connection between an auditory somatomotor seed and a somatomotor region), and to the default mode (2 connections with somatomotor regions) and control networks (2 connections with somatomotor regions and 2 connections with somatomotor auditory regions).

The default mode network showed differences in connectivity with two somatomotor regions and single regions in the dorsal attention, control, and visual networks.

For the first time, we observed between-group state-related differences in regions belonging to the language network, with significantly different connections to regions in the control network and a region in the dorsal attention network.

To allow the interpretation of the results, differences in connectivity between the switch and stay conditions are plotted for each group in the figures below (Figure 4.10, Figure 4.11, Figure 4.12, Figure 4.13).

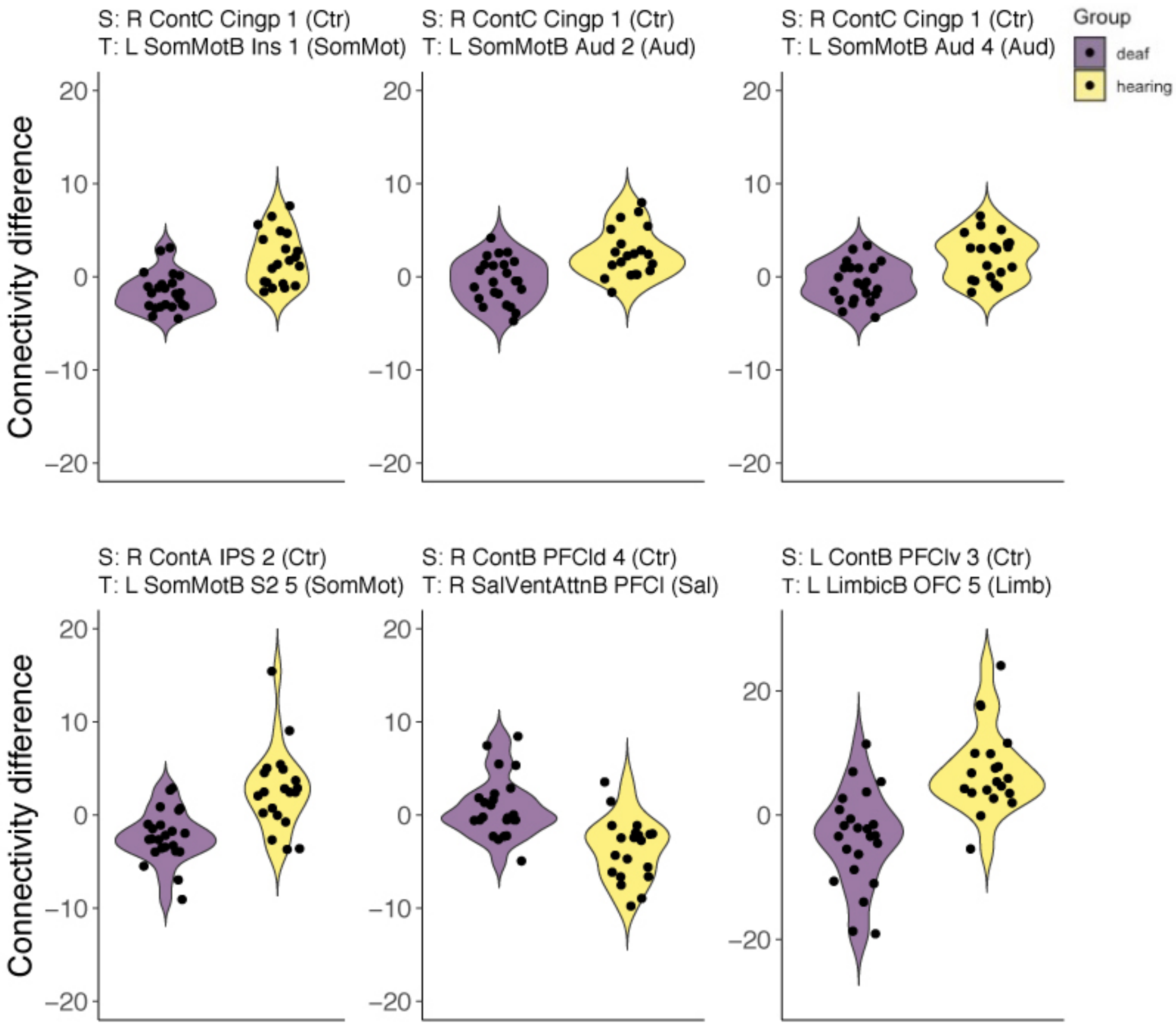


Figure 4.10. Between-condition differences in the deaf and hearing groups in the switching task in the control network. Connectivity differences are represented as seed-to-target (ROI-to-ROI) group-level differences in gPPI interaction beta estimates (connectivity change in each condition) for the between-condition contrast [1 -1] (switch, stay). The figure contains connectivity differences in pairs where the seeds are from the control network.

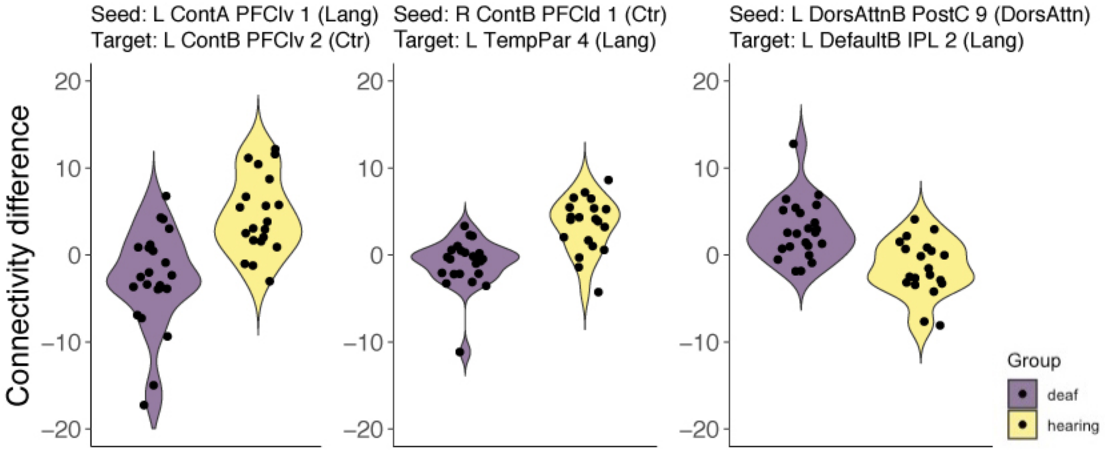


Figure 4.11. Between-condition differences in connectivity in the deaf and hearing groups in the switching task in the language network. Connectivity differences are represented as seed-to-target (ROI-to-ROI) group-level differences in gPPI interaction beta estimates for the between-condition contrast [1 -1] (switch, stay). The figure contains connectivity differences in pairs where seeds or targets are from the language network.

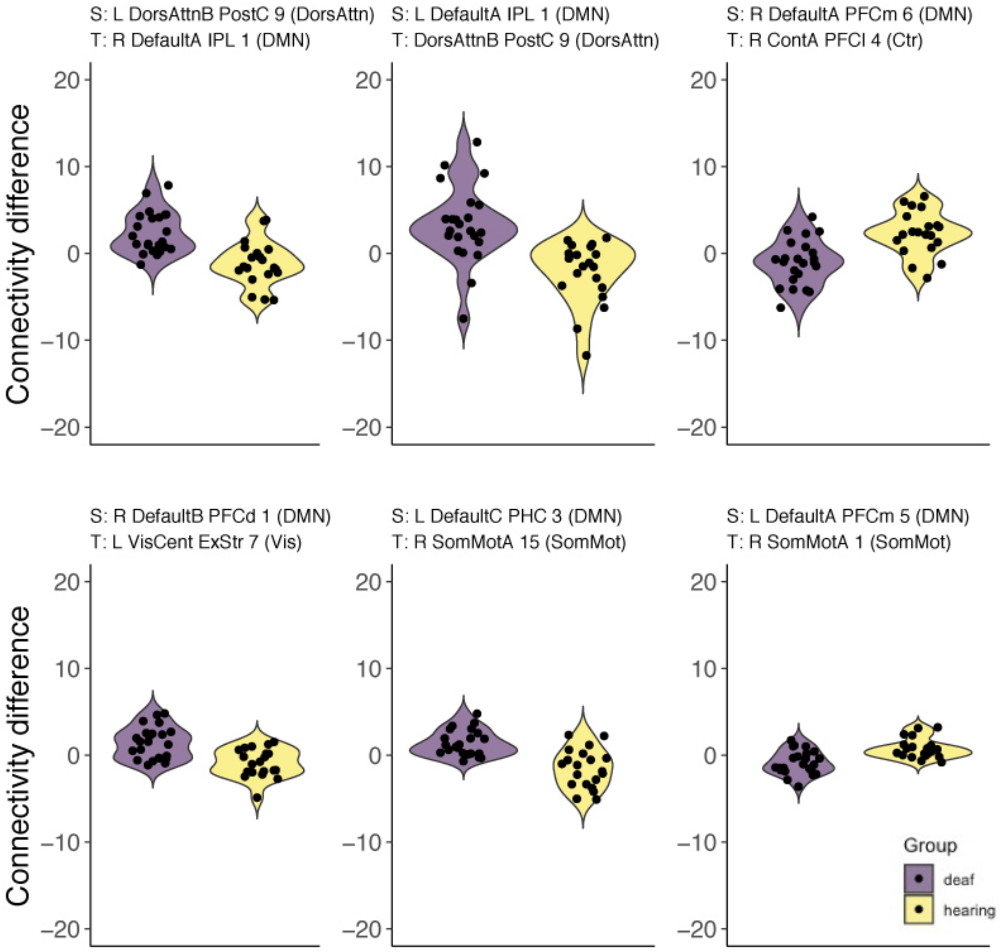


Figure 4.12. Between-condition differences in connectivity in the deaf and hearing groups in the switching task in the default mode network. Connectivity differences are represented as seed-to-target (ROI-to-ROI) group-level differences in gPPI interaction beta estimates for the between-condition contrast [1 -1] (switch, stay). The figure contains connectivity differences in pairs where one of the regions is from the default mode network.

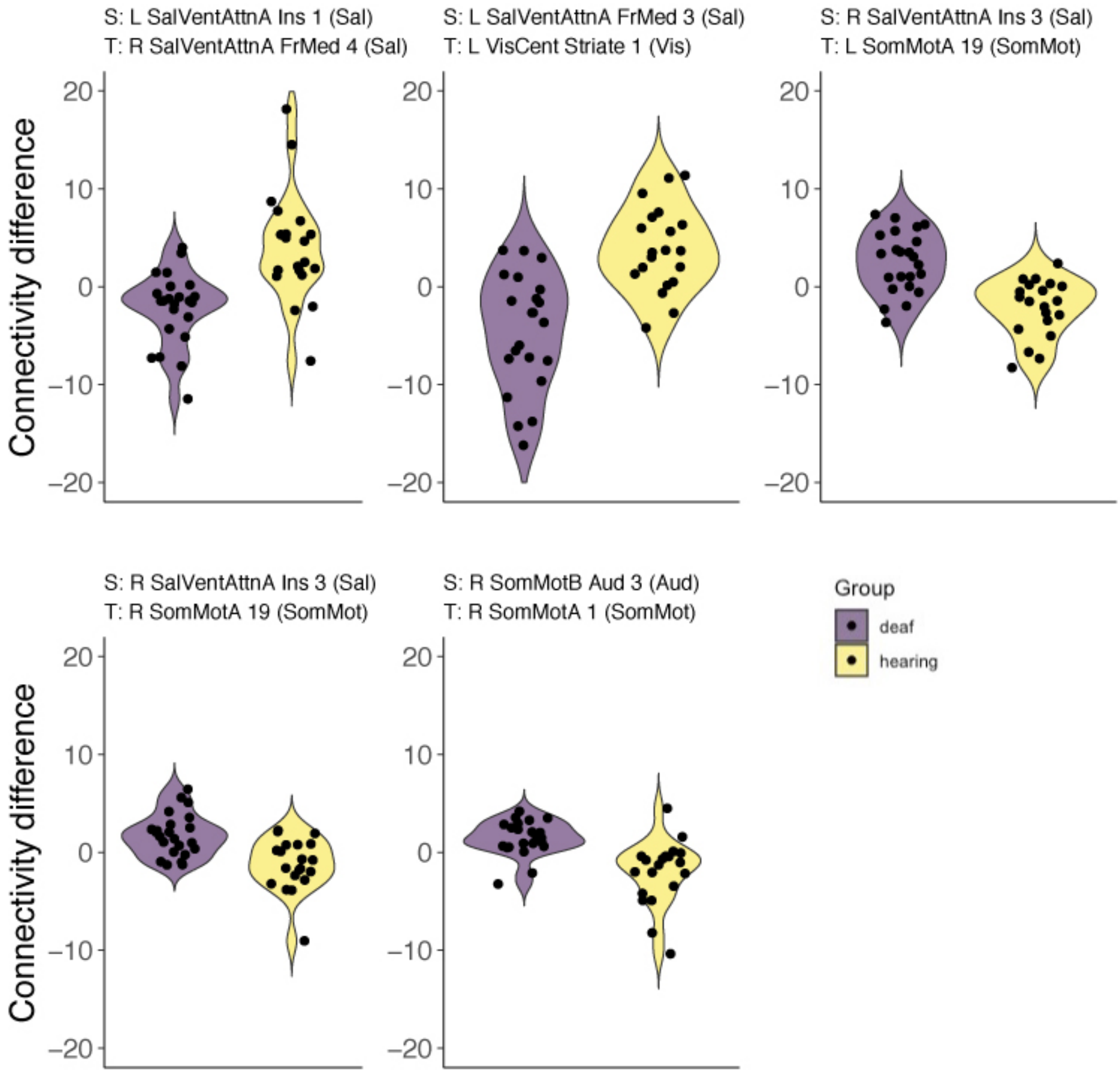


Figure 4.13. The remaining between-condition differences in connectivity in the deaf and hearing groups in the switching task. Connectivity differences are represented as seed-to-target (ROI-to-ROI) group-level differences in gPPI interaction beta estimates for the between-condition contrast [1 -1] (switch, stay). The figure groups connections from the salience/ventral attention and somatomotor network.

The control network

In the switching task, the control network was the one demonstrating the most differences in connectivity with other networks (9 connections). The groups demonstrated differences in functional connectivity between the states between the left ventral prefrontal cortex (PFClv) regions of the language [-48 36 10] and control network [-28 58 0] (deaf: *M* = -2.78, *SD* = 5.74, hearing: *M* = 4.55, *SD* = 4.47), and between a left temporo-parietal seed of the language network [-52 -44 4] (the same region that showed a large number of significantly different connections in resting-state analysis) and the right dorsal lateral prefrontal cortex (PFCld) in the control network [38 34 38] (deaf: *M* = -0.98, *SD* = 2.84, hearing: *M* = 3.42, *SD* = 3.16).

A seed in the default mode network in the right medial prefrontal cortex (PFCm) [6 26 18] had different connectivity patterns between the groups to the right lateral prefrontal cortex (PFCl) [48 8 24] (deaf: *M* = -1.03, *SD* = 2.61, hearing: *M* = 2.33, *SD* = 2.52).

A seed in the right PFCld [34 16 56] showed differences in connectivity between the states between the groups to a target in the right PFCl in the salience/ventral attention network [42 46 14] (deaf: *M* = 0.89, *SD* = 3.29, hearing: *M* = -3.66, *SD* = 3.56).

A seed region in the control network in the right posterior cingulate cortex (Cingp) [8 -44 20] showed significant condition-dependent differences between the groups in connectivity to a somatomotor region in the insular cortex [-36 -24 10] (deaf: *M*=-1.59, *SD*=2.00, hearing: *M*=1.96, *SD*=2.83) and two auditory somatomotor regions: region 2 [-56 -22 8] and region 4 [-40 -36 14] (region 2, deaf: *M* = -0.43, *SD* = 2.37, hearing: *M* = 2.58, *SD* = 2.60; region 4, deaf: *M* = -0.57, *SD* = 2.09, hearing: *M* = 2.13, *SD* = 2.42). Connectivity between another seed of the control network in the right intraparietal sulcus (IPS) [54 -32 52] was also different to another somatomotor region in the secondary somatosensory cortex (S2) [50 -10 14] (deaf: *M* = -2.30, *SD* = 2.80, hearing: *M* = 2.69, *SD* = 4.38).

Finally, connectivity differences between the conditions were also different between the groups between the left PFClv in the control network [-28 56 12] and the left orbitofrontal cortex (OFC) of the limbic network [-16 64 08] (deaf: *M* = -3.73, *SD* = 7.61, hearing: *M* = 7.19, *SD* = 6.71).

The default mode network

The default mode network again showed several significant differences between the groups in connectivity between the states. In relation to task-related networks, in addition to the significant difference in connectivity between a PFCm region with a region in the control network described above, the inferior parietal lobe (IPL) in both hemispheres [left: -48 -64 32] [right: 54 -54 26] showed differences in connectivity between the states with a region in the left postcentral gyrus (PostC) of the dorsal attention network [-14 -50 72] (left IPL: deaf: *M* = 3.30, *SD* = 4.37, hearing: *M* = -2.16, *SD* = 3.56; right IPL: deaf: *M* = 2.83, *SD* = 3.35, hearing: *M* = -1.44, *SD* = 3.21).

Two seeds in the default mode network (the left PFCm [-16 68 8] and the left parahippocampal cortex (PHC) [-18 -38 -12]) showed across-hemisphere differences in connectivity between the states between the groups to regions in the somatosensory network [54 -16 40] [22 -28 68] (deaf: *M* = -0.86, *SD* = 1.37, hearing: *M* = 0.81, *SD* = 1.16 for the right PFCm connection and deaf: *M* = 1.41, *SD* = 1.45, hearing: *M* = -1.52, *SD* = 2.23 for the left PHC connection).

A seed in the right dorsal prefrontal cortex (PFCd) [-24 28 44] showed differences in connectivity to the left visual central extrastriate cortex region of the visual network [-46 -74 6] (deaf: *M* = 1.43, *SD* = 1.83, hearing: *M* = -0.88, *SD* = 1.64).

The language network

In addition to the differences in connectivity with the control network described above between two regions in the PFClv and the left temporo-parietal seed of the language network and the right PFCld, the language network showed differences between the groups in a seed region in IPL [-42 -72 44] with a seed in the left postcentral gyrus in the dorsal attention network [-14 -50 72] (that also showed differences in connectivity between the groups with the default mode network, as described above) (deaf: *M* = 2.83, *SD* = 3.35, hearing: *M* = -1.44, *SD* = 3.21).

The salience/ventral attention network

The salience/ventral attention network, in addition to the connection to the control network described above, showed a within-network difference between the left insula [-38 2 -4] and the right medial frontal cortex (FrMed) [16 6 70] (deaf: *M* = -2.18, *SD* = 3.70, hearing: *M* = 4.08, *SD* = 3.21). It also showed differences in connectivity with two regions of the somatomotor network (the salience/ventral attention seed in the right insula: [40 -10 4]; the left somatomotor target: [-12 -26 74] (deaf: *M* = 2.50, *SD* = 3.11, hearing: *M* = -2.16, *SD* = 2.92), the right somatomotor target [16 -18 74] (deaf: *M* = 1.75, *SD* = 2.18, hearing: *M* = -1.23, *SD* = 2.65). The FrMed seed [-8 -2 70] showed differences in connectivity to a region in the visual network in the left striate cortex [-8 -98 -8] (deaf: *M* = -5.40, *SD* = 6.95, hearing: *M* = 3.85, *SD* = 3.85).

The somatomotor network

All differences in connectivity found in regions of the somatomotor network have been described above: 2 connections to regions in the control network, 2 connections to regions of the default mode network, and 2 connections to regions in the salience network. In addition, a somatomotor seed of the auditory network [60 -24 10] showed differences in connectivity with a target in the somatomotor network [54 -16 40] (both in the right hemisphere) (deaf: *M* = 1.46, *SD* = 1.74, hearing: *M* = -2.06, *SD* = 3.31).

4.3.2.1. Correlational analysis on seed-to-seed differences between the conditions in the deaf group: can language proficiency explain connectivity differences between the groups?

To investigate whether the observed between-group differences are modulated by the language experience of the deaf participants, we have conducted a correlational analysis on the 20 significantly different connections between the groups discussed above in the deaf group. The correlation between language proficiency score and the between-condition differences in connectivity between a region in the default mode network in the right medial prefrontal cortex (PFCm) [right PFCm_6: 6 26 18] and a region in the right lateral prefrontal cortex (PFCl) [right PFCl_4: 48 8 24] in the control network was significant (Table 4.7, Figure 4.14), *r(41)* = 0.53, *p* = .01. The correlation did not survive the Holm correction for multiple comparisons. All other correlations had a p-value > .05.

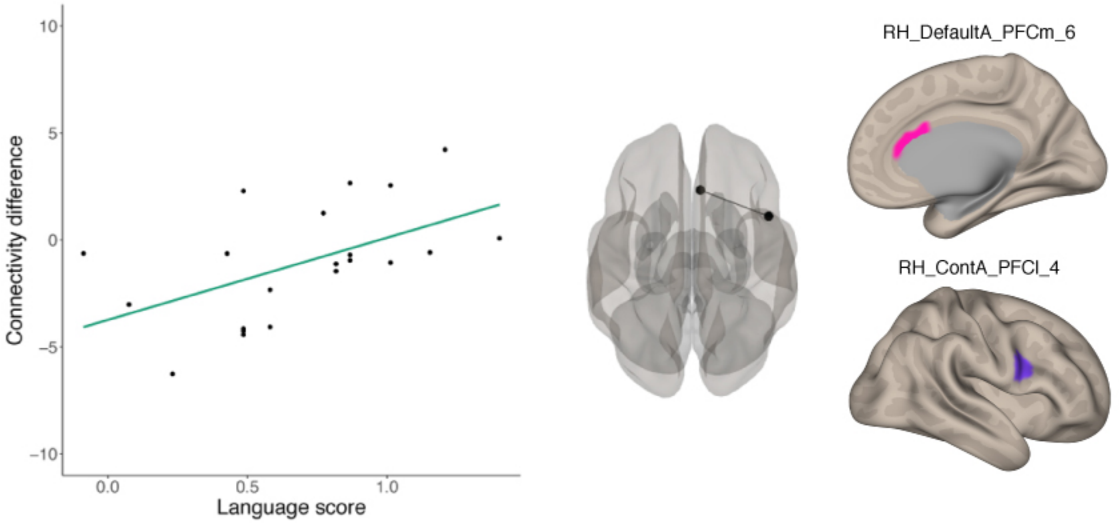


Figure 4.14. The relationship between the modality-independent language proficiency score and between-condition connectivity change in the right medial prefrontal cortex (PFCm) and the right lateral prefrontal cortex (PFCl). The scatterplot represents the association between the modality-independent proficiency score and the connectivity change between the right PFCm in the default mode network and the right PFCl in the control network, represented as differences in gPPI beta estimates between the switch and stay [1 -1] conditions. Positive values mean that connectivity between these regions of the PFCm and the PFCl increases during switching in comparison to the stay condition.

4.4. Discussion

In this chapter, we investigated between-state functional connectivity differences between deaf and hearing individuals during the execution of two executive function tasks and the role of modality-independent language proficiency in functional connectivity changes found between the groups. The results of these analyses highlight the role of sensory experience in shaping brain development and function and shed light on the reconfiguration of the brain networks between different cognitive states and task conditions.

The fundamental question of the extent of functional connectivity differences between resting state and task execution has been debated in the literature, as some studies have shown that resting-state patterns correlate highly with task-related connectivity (e.g., Krienen et al., 2014). Nevertheless, there has been substantial evidence of changes in functional connectivity patterns in task execution (M. W. Cole et al., 2014; Gonzalez-Castillo & Bandettini, 2018; Krienen et al., 2014). Such changes align with the economic theory of brain network organisation, with the resting state being the 'energy saving mode' and the brain adapting to task demands by changing network configuration (Bullmore & Sporns, 2012; Di et al., 2013). In this chapter, we observed significant between-state changes in functional connectivity between our groups of participants. Such interactions suggest that functional connectivity reconfigurations between the states that subserve executive function task demands differ in deaf and hearing individuals. Functional connectivity differences in state-dependent functional connectivity can arise from the unique sensory experience of deafness and our findings propose that some of these changes may be driven by unique and heterogeneous language experiences in this population.

Changes in functional connectivity between different states and conditions were found in sensory-deprived auditory regions, as could be expected considering the role of the temporal cortex as a central node of plasticity in deaf individuals (Andin & Holmer, 2022) but also in multiple regions in networks responsible for higher-order cognitive processing (the control network) and attending to stimuli and switching between stimuli and cognitive states (the default mode network, the attention networks). These changes confirm that brain reorganisation in deaf individuals goes beyond the auditory system, as between-state differences in connectivity were detected between regions of different sensory, attention, and cognitive networks. These findings contribute to the more established evidence of large-scale changes in functional connectivity in deaf individuals at rest (Andin & Holmer, 2022; Bonna et al., 2021; Cardin et al., submitted).

This chapter introduces considerations for the role of early sensory experience and language proficiency in executive function by describing state-dependent functional connectivity changes between areas involved in sensory, cognitive, and attention processing in deaf and hearing individuals.

4.4.1. Between-state functional connectivity changes in the temporo-parietal/auditory network

Changes in functional connectivity of the auditory regions have been highlighted in several studies investigating functional connectivity changes in deafness at rest (Andin & Holmer, 2022; Bonna et al., 2021; Cardin et al., 2018; Ding et al., 2016; X. Wang et al., 2015) and during task execution (Andin et al., 2021; Bola et al., 2017).

Here we found between-state functional connectivity changes in three auditory regions in the deaf group between planning and resting state and in three auditory regions between different conditions during switching. Differences in connectivity between an auditory region and a somatomotor region were present in both analyses. Altered connectivity between the auditory and somatomotor networks in deaf individuals has been found before (Andin & Holmer, 2022; Bonna et al., 2021; Cardin et al., submitted). In these previous studies, deaf individuals showed decreased connectivity between auditory and somatomotor regions at rest. Such changes could be explained by 'not using the fast feedback language-speech mechanisms in early development' (Bonna et al., 2021), or by a common mechanism for sensory-deprived areas, considering similar findings in blind individuals, as suggested by Bonna et al. (2021) and Cardin et al. (submitted). In our sample, auditory and somatomotor regions did not show reduced connectivity at rest between the groups (Chapter 3). The proposal that circuits between auditory and somatomotor regions may not be fully established in deaf individuals for spoken language usage (Bonna et al., 2021) does not seem to apply to our group of deaf participants: this may be explained by the fact that some of them use spoken English as their preferred method of communication, unlike proficient deaf signers in other studies that discovered these effects (Bonna et al., 2021; Cardin et al., submitted). In our study, the right planum temporale [60 -24 10] showed significant differences in connectivity to the postcentral gyrus during switching. Connectivity between auditory cortices and the postcentral gyri, specifically, has been shown to be reduced in deaf adults at rest (Andin & Holmer, 2022), and in deaf children (Shi et al., 2016). In our analysis, deaf participants had higher and more positive connectivity difference values in these regions, indicating a larger increase in connectivity between these regions during task execution in the deaf group. This may be explained by these areas arriving to an optimal functional state for demanding task execution. The planum temporale has shown cross-modal plasticity effects during the execution of the switching task (Manini et al., 2022; Chapter 2), suggesting that this connectivity pattern can also be a reflection of the involvement of the auditory cortex in demanding task execution, resulting in higher connectivity to other brain areas relevant for switching. The postcentral gyrus has been shown to be activated for cognitive switching, with its involvement being suggested to be related to motor components of switching (A. B. Smith et al., 2004). The reorganised auditory and somatomotor regions may interact to contribute to efficient task execution, and in deaf participants, whether they have reduced connectivity during rest between these areas or not, these reconfigurations may aid the motor responses during the task execution in response to cognitive decisions. Future research on tasks related to spoken language production, compared to cognitive tasks, and in samples with different language experiences can shed light on the relationship between auditory and somatomotor areas in deaf individuals.

There were three significantly different connections between auditory regions and a region in the right dorsolateral prefrontal cortex in the default mode network in the planning/resting state analysis and two significantly different connections between auditory seeds and a region in the posterior cingulate cortex in the control network in the switching analysis. These findings may reflect the role of the auditory regions in cognition in deaf individuals. The differences in connectivity were more positive with the regions of the default mode network, suggesting higher connectivity during task execution in planning as compared to rest, and negative with the regions of the control network during switching. The former results seem to be in agreement with the general trend of increased connectivity in the default mode network during task execution, specifically as compared to rest, in the deaf group (see discussion below: *4.4.3. Between-state functional connectivity changes in the default mode network*), as they do not arise in the analysis of the switching task.

The latter finding can be connected to increased connectivity between reorganised auditory regions and the fronto-parietal/control network that has been described in deaf individuals during rest (Cardin et al., 2018; Ding et al., 2016: Chapter 3) and task execution (Andin et al., 2021) in deaf individuals. We observe a pattern where connectivity between the control and auditory regions decreased during task execution in comparison to the resting state in the deaf group. It may be that our group of participants could have an at least a partially different functional connectivity profile to the groups of native (Cardin et al., 2018), early (Andin et al., 2021), and proficient (Bonna et al., 2021) signers due to variable developmental language experiences and language delay leading to differences in performance between the groups, especially in the switching task that was the only task significantly recruiting auditory cortices in deaf individuals in our sample (Chapter 2). Decreased connectivity between auditory regions and regions of the control network during the execution of the more demanding condition of the switching task in our sample may be related to lower performance in this task by the deaf participants. This would suggest that a coupling between these regions may have stronger functional relevance in deaf participants who do not show lower performance in cognitive tasks caused by language delay. This highlights that the language experiences of deaf individuals should be considered when interpreting data on brain reorganisation, as the functional relevance of changes observed in the brain of deaf individuals may be different for groups with different language backgrounds.

4.4.2. Between-state functional connectivity changes in other sensory networks

There were no more significant connections between two sensory networks in the analysis: other results involved a sensory network and a cognitive or attention network. Regions of the somatomotor network showed between-condition differences in connectivity between two groups with three networks (the default mode, control network, and the salience network) in the switching task and with the default mode and salience networks in the analysis on planning and resting states. Differences in connectivity between the somatomotor network and the control network have been observed in deaf individuals before (Bonna et al., 2021). The difference in between-condition connectivity between the somatomotor regions and the default mode network is a novel finding, although this connection has been highlighted in single-sided deafness (Zhu et al., 2021). Executive function has been linked to more positive connectivity between the somatomotor and default network at rest, leading to a suggestion that executive functions may rely on functional connectivity across many brain systems, including those that are not typically discussed in relation to inter-individual variation in executive functions tasks, such as the sensory/somatomotor network (Reineberg et al., 2018). Here the deaf group demonstrated an increase in connectivity during switching between the somatomotor and default mode network, in agreement with the argument that the connectivity between somatomotor and the default mode networks can support executive processing, suggesting that this may occur at a group-level in individuals with a unique sensory experience.

In relation to visual cortices, there were single altered connections to task-related networks (default mode in the planning/resting state analysis and default mode and salience during switching), some of the pairings matching with those described in literature at rest (visual to salience and DMN: Dell Ducas et al., 2021).

4.4.3. Between-state functional connectivity changes in the default mode network

Most differences in between-state connectivity changes between the two groups in the analysis on planning and resting state were related to the default mode network, with the changes in connectivity both within-network and between the default mode network regions and other regions from the control, visual, dorsal attention, somatomotor networks and temporaparietal/auditory networks. There were 11 altered connections in the planning and resting state analysis and 6 altered connections in the switching task in this network. During switching, the default mode network showed differences in between-state connectivity between the groups to regions from the three of the four networks that showed differences in planning: the control, visual and somatomotor, but not to the temporo-parietal/auditory network. In addition to these changes, between-state connectivity was different between the groups between the inferior parietal lobule in the default mode network and the postcentral gyrus in the dorsal attention network in switching, with deaf participants showing a larger increase in connectivity between these networks in switching. The relationship between the default mode network and the dorsal attention network has been described as one of the main mechanisms supporting executive functions (C. Grady, 2012). The dynamic network coupling between these two networks may help to facilitate goal-directed control (Spreng et al., 2013) in this cognitively demanding task.

It has been well-established that the default mode network is deactivated during externally focused tasks (Arsalidou et al., 2013; McKiernan et al., 2003; Raichle et al., 2001; Raichle & Snyder, 2007), although there is also contradictory evidence for its involvement in demanding cognitive control in switching (Crittenden et al., 2015). In relation to functional connectivity, it shows strong within-network connectivity and anticorrelates with the dorsal attention network at rest (Fox & Raichle, 2007), highlighting its relevance for externally-oriented attention. In relation to the functional connectivity of the default mode and cognitive control networks, stronger negative correlation between the default mode and the working memory network during resting state was related to better behavioural performance (Sala-Llonch et al., 2012). Generally, deactivations in the default mode network during task execution have been considered to be evidence of the default mode network 'competing' with other task-related networks. The strength of anticorrelations in functional connectivity between task-positive networks and the default mode network has been suggested to be related to cognitive function (Hampson et al., 2010). In relation to task-related functional connectivity, there is evidence of flexible coupling with task-relevant brain regions in internal and external goal-directed tasks (Elton & Gao, 2015a). The default mode network has been shown to significantly increase its connectivity with task-promoting regions across different tasks, and the task-related connectivity changes were associated with individual differences in task performance (Elton & Gao, 2015a), highlighting its functional relevance.

The default mode network has been repeatedly shown to have altered functional connectivity in deaf individuals compared to hearing individuals (Andin & Holmer, 2022; Bonna et al., 2021; Cardin et al., 2022 (under review); Dell Ducas et al., 2021; Malaia et al., 2014). It has been suggested that altered functional connectivity of the default mode network in deafness may be related to its role in the network integration 'that is necessary to compensate for sensory deficits in the deaf' (Bonna et al., 2021), or that in deaf signers there may be a link with visual language processing (Malaia et al., 2014). Andin and Holmer (2022) noted that another possibility for changes in the default mode network, as well as in the somatomotor network, is the influence of the noise inside the scanner that has been shown to contribute to the suppression of the default mode network in hearing individuals. In relation to our sample, the explanation focusing on the role of sign language processing is unlikely, as our group of deaf participants included those with no experience of signing and, as in the Andin and Holmer's study (2022), we also minimised the scanner noise by providing all participants with ear protection. This leads us to the conclusion that the default mode network connectivity has a highly significant role in reconfiguration between the states in deaf individuals in tasks related to executive control.

In our study, the deaf group showed predominantly increased connectivity of the default mode network during the execution of the task in comparison to the resting state. There is evidence of flexible coupling of the default mode network with task-relevant brain regions during task execution and its functional relevance (Elton & Gao, 2015a). Changes in functional connectivity and network composition of the default mode network in deaf individuals have been observed in several studies (Andin & Holmer, 2022; Bonna et al., 2021; Cardin et al., submitted; Dell Ducas et al., 2021; Malaia et al., 2014). Given this, our findings of higher functional connectivity of the default mode network to other brain areas during task execution in deaf individuals may point to the integrative role of the default mode network in deaf individuals in supporting cognition, which has been suggested before in this population (Bonna et al., 2021). The differences in connectivity between the default mode network and other networks, including the salience/ventral attention network, have been repeatedly highlighted in functional connectivity studies in deafness (Andin & Holmer, 2022; Bonna et al., 2021; Ding et al., 2016), with the default mode network and salience networks showing altered connectivity to the control network (Bonna et al., 2021). The authors highlighted that these task-related networks may cooperate during the execution of demanding cognitive control tasks (Sridharan et al., 2008) and hypothesised that, as deaf individuals have demonstrated superior performance in attention (Bavelier et al., 2000) and visuo-spatial working memory (Ding et al., 2015), the altered connectivity patterns between these networks at rest may explain their enhanced performance (Bonna et al., 2021). Here we observe that functional connectivity between the states in both analyses is also different in deaf individuals between these networks (default mode network – control; salience – control), with the default mode network exhibiting the majority of altered connections, even in a group of deaf participants that did not demonstrate superior performance during task execution.

4.4.4. Between-state functional connectivity changes in the salience/ventral attention network

The salience network also showed within- and between-network connectivity differences, with the control, limbic, and somatomotor regions in the analysis on planning and resting state and with the control, visual, and somatomotor regions in switching. In the switching task, connectivity patterns were compared between the two visually identical conditions of the task, allowing us to analyse the effects arising purely from cognitive demand, rather than reflecting a change between cognitive states and reconfiguration supporting directing attention to external visual stimuli. In previous studies, while data-driven independent component analysis conducted by Andin and Holmer (2022) demonstrated that the salience network did not differ between the groups in terms of its organisation, the connectivity in the salience network has been found to be increased during rest in deaf individuals to the temporo-parietal/auditory (Andin & Holmer, 2022; Cardin et al., submitted; Ding et al., 2016) and visual areas (Dell Ducas et al., 2021). The increased connectivity to the auditory areas in the salience network has been suggested to facilitate the identification of salient stimuli from the deprived sensory areas (Andin & Holmer, 2022), highlight the role of the superior temporal cortices in multisensory or higher-order processes in deaf individuals (Cardin et al., submitted) and contribute to enhanced abilities in attention and working memory (Ding et al., 2016) in this population. In our data, the deaf participants did not exhibit such differences neither at rest (see Chapter 3) nor in the between-state analyses, which could be explained by the effects related to language modality, or language delay (and/or subsequent cognitive performance differences in switching) in our sample, as compared to other studies that recruited proficient signers (Ding et al., 2016; Cardin et al., submitted).

Nevertheless, the salience/ventral attention network connectivity showed other significant differences in connectivity in our analysis. These are likely to be related to the involvement of the salience network in integrating relevant sensory and cognitive information to guide behaviour (Seeley et al., 2007). This network may precede cognitive control in mediating sensory and cognitive information to arrive at visual perceptual decisions (Chand & Dhamala, 2016). Therefore, the differences in connectivity between the salience/ventral attention and visual, somatomotory, and control regions may reflect this and the differences in detecting and filtering relevant stimuli and in the way the salience network assists in recruiting other relevant networks, particularly the control network (Menon & Uddin, 2010) for planning or switching. Associations between performance in executive function tasks and resting-state connectivity between deaf and hearing individuals have been found in the salience network before, emphasising its relevance for cognition and how network organisation for executive processing is modulated by environmental experience (Cardin et al., submitted).

The salience/ventral attention network also showed a significant difference between the groups in between-state (planning and resting state) connectivity on the whole-network level to the language network. The difference was driven by the differences in connectivity in resting state, with the deaf group showing higher connectivity between the salience/ventral attention and language networks during rest, while during planning the difference was not significant. This could indicate that the 'intrinsic' functional connectivity profile of these networks already reflects the optimal connectivity configuration for demanding executive functions task performance in deaf individuals, suggesting a compensatory reorganisation of resting-state connectivity patterns for efficient execution of the task in this population.

4.4.5. Between-state functional connectivity changes in the control network

The control network exhibited the largest number of altered connections between the states in the switching task in the deaf group, with altered between-condition connections to default mode, salience, language, somatomotor, and limbic networks. Previous studies on functional connectivity in deafness at rest also noted differences in connectivity between the control/fronto-parietal network and some of these networks. For instance, Bonna and colleagues (2021) described increased connectivity between the fronto-parietal and visual network, as well as default mode, and that regions of the fronto-parietal network were coupled with the salience network. Dell Ducas and colleagues (2021) noted increased connectivity between a region in the left fronto-parietal network and a sensorimotor region, while also describing increased connectivity of the fronto-parietal network to the visual network and to the default mode network. The fronto-parietal network has been consistently showing stronger coupling to other networks in deaf individuals in resting-state studies (Bonna et al., 2021). Here we show that in deaf participants the differences in connectivity of the control network in comparison to hearing controls are also present in between-state analyses of cognitive states, especially in a comparison of two conditions with different cognitive demands in the switching task. This suggests that the dynamic reconfigurations in this network contribute not only to the processing of visual stimuli in tasks requiring visual attention, as has been suggested before (Bonna et al., 2021; Dell Ducas et al., 2021), but also to varying degrees of cognitive load. Notably, in this study, the deaf group shows altered connectivity between the control and salience/ventral attention networks, with a connectivity increase during the switching condition where deaf participants were less accurate than the hearing group, while the hearing group showed a decrease in connectivity between these networks in this condition. Lesser connectivity between the control and salience network during task state, in comparison to rest, leads to better selective attention task accuracy in hearing individuals, suggesting a functional dissociation between these networks (Elton & Gao, 2014). The authors believe that the dissociation may allow each network to perform its role more efficiently. Here, following the argument from Elton & Gao (2014), we suggest that, while the salience network is detecting salient stimuli regardless of the task, the control network attends to stimuli that match with task goals (Corbetta & Shulman, 2002), therefore the observed uncoupling serves to reduce interference from the task-irrelevant attentional processing in the hearing group, potentially aiding the more successful task execution. Another possible mechanism explaining the connectivity difference between the salience/ventral attention and the control network is related to the evidence that functional and effective connectivity between the salience and central executive networks at rest is positively correlated with performance in a working memory task (Fang et al., 2016). This evidence suggests that the integration of these networks at rest is important for working memory, and it is possible that the intrinsic organisation between them supports other aspects of executive processing, such as switching.

The connectivity differences between two regions in the control network and two regions in the language network have only been observed in this analysis between two different task conditions in switching that had a varying cognitive load. This is a particularly valuable finding for this task, as we have observed the effect of language proficiency on performance in switching (Chapter 2). It can be suggested that the connectivity reconfiguration between the language network and the control network can be related to performance in the higher executive load condition of the switching task. Taken together with the behavioural findings from Chapter 2, this relationship emphasises the relevance of the developmental language experience in cognitive performance and can suggest that language experience also has a role in functional connectivity during executive processing.

4.4.6. Between-state functional connectivity changes in the language network and the role of language proficiency in connectivity between the default mode and control networks

Three regions of the language network showed changes in connectivity to regions in the control network and a region in the dorsal attention network in switching between different conditions of the switching task. Enhanced functional connectivity has been reported between the superior temporal cortex and fronto-temporal areas in language-related tasks in deaf individuals (Que et al., 2018). The authors have also described strong associations of activity in the superior temporal cortex with experience of sign language learning. In our study, for both connections involving regions from the language and control networks, deaf participants showed a decrease in connectivity during the more demanding switching condition, while hearing participants showed an opposite pattern. Considering lower performance in the switching condition by the deaf group and the relationship to language proficiency (Chapter 2), it could be that hearing participants show a pattern of connectivity that reflects a beneficial coupling of the language and control regions during switching. This could be a reflection of the efficient internalisation and retrieval of the hierarchical rules that are supported by language and verbal mediation during switching in hearing participants, in agreement with the Cognitive Complexity and Control theory (Zelazo & Frye, 1997), as discussed in Chapter 2.

Dell Ducas et al. (2021) described enhanced functional connectivity between the language network with dorsal attention and salience networks in deaf native and early signers at rest. Here, the language network and the salience network showed significant connectivity differences between the states in deaf individuals at the network level, being the only two networks revealing such a relationship in this analysis (see *4.4.4. Between-state functional connectivity changes in the salience/ventral* *attention network*). Taken together, our findings suggest that the language network in deaf individuals has a role in switching between cognitive states, showing interactions with attention networks. It is possible that in this highly-demanding executive functions task, where our group of deaf participants was less accurate than the hearing controls, the interactions between the language, control, and attention networks reflect the high cognitive demand and emphasise the relationship between language experience and non-linguistic switching on the level of neural processing, which has been highlighted before in bilinguals (Rodríguez-Pujadas et al., 2013).

Switching has been discussed in relation to language experience in bilingual cohorts in multiple behavioural studies, with a link between language-switching and bilingual advantages in task-switching (Prior & Gollan, 2011), language switching training improving switching abilities in the non-linguistic domain (Timmer et al., 2019) and better abilities in bilinguals in reconfiguring stimulus-response associations (Wiseheart et al., 2016). High-frequency language switchers responded more quickly in the task on cognitive flexibility but not in inhibition or alerting (Barbu et al., 2018). Neuroimaging evidence has shown that in the Stroop task, a paradigm that engages both inhibition and switching (Stroop, 1935), children with reading difficulties showed greater functional connectivity between the executive functions network and the visual, language, and cognitive control regions during the Stroop task (Levinson et al., 2018). Bilinguals recruited a common shared language and cognitive network for verbal and non-verbal switching, while monolinguals recruited distinct networks (J. A. E. Anderson et al., 2018).

We suggest that functional connectivity changes between the states in the switching task between the groups may reflect effects related to bilingualism (see *4.4.7 Limitations* below) or different aspects of language proficiency, such as, for example, sentence processing and phonological processing skills in sign language were associated with distinct functional connectivity associations in deaf individuals (Holmer et al., 2022). Further analysis and studies comparing samples with different linguistic experiences, rather than a mixed sample of bilinguals and monolinguals, as in this study, and investigating different aspects of language proficiency, and not just grammaticality judgement, could provide insights into these effects. In addition, it can explain why the general modality-independent language proficiency scores were not associated with the between-group differences in connectivity described in this chapter in the deaf group, with the exception of one connection. We suggest that other aspects of language proficiency may be relevant here. On the other hand, it is possible that the effect of general, modality-independent, language proficiency in relation to significant between-group differences related specifically to executive functioning may be limited to behavioural performance and neural activity in the planning task (Chapter 2) and that specific between-state changes observed in functional connectivity between the deaf and the hearing individuals in our study are more likely driven by differences in sensory experiences during development. Nevertheless, one critical connection was associated (uncorrected) with the general language proficiency score in the deaf group: the difference in connectivity between a region in the default mode network and a region in the control network was associated with the language proficiency score. Connectivity between these networks has been found to be different in deaf individuals before, with increased connectivity between them at rest (Bonna et al., 2021; Dell Ducas et al., 2021). In the analysis of the resting-state data presented in Chapter 3, connectivity between a region in the default mode network and a region in the control network was higher in deaf participants, in agreement with the previous findings, but none of the connections between regions from these networks were modulated by language proficiency during rest. This suggests that the effects may be related to sensory experience, rather than language proficiency. Here we show that interaction in connectivity between regions of the default mode and control networks may be supported by language development. The default mode network has been shown to couple with the fronto-parietal control network and the regions involved in executive functions during task execution, facilitating goal-directed behavior (Spreng et al., 2010; Vatansever et al., 2015). Moreover, increased connectivity predicts faster reaction times (Vatansever et al., 2015). In our study, higher language proficiency scores were associated with an increase in connectivity between the regions of the default mode and control network during switching, suggesting that language proficiency may contribute to the coupling of networks associated with the facilitation of goal-directed behavior. Considering that language proficiency is also related to behavioural performance during the challenging condition of the switching task (Chapter 2), this functional connectivity interaction may be related to behavioural performance. This result highlights the importance of considering different types of data and analyses when conducting research and interpreting the effects related to sensory and language experiences.

Taken together, language-related results presented in this chapter demonstrate the involvement of the language network in reconfiguration between different task states and its interaction with the control network, complementing the findings of an association between language proficiency and behavioural performance from Chapter 2. Moreover, language proficiency is associated with both behavioural performance (Chapter 2) and functional connectivity changes during switching in deaf individuals, with increased connectivity between the default mode and control networks during task execution supported by more successful language development.

4.4.7. Limitations

The analysis presented in this chapter focused on the effects of sensory experience and modality-independent language proficiency on functional connectivity changes between different states in a group of participants with varying language backgrounds. The majority, but not all, participants were bilingual in a signed and spoken language. There is evidence of differences in resting-state functional connectivity between bilinguals and monolinguals in the language and control networks (Berken et al., 2016; Sulpizio et al., 2020), as well as differences in task-dependent connectivity (different language tasks: Dodel et al., 2005; task vs fixation: C. L. Grady et al., 2015). Functional connectivity at rest and during task execution has been investigated in bimodal bilinguals during language production (L. Li et al., 2015, 2016). The dynamic nature of bilingual experience makes studies of both resting-state and task-related functional networks in bilinguals and monolinguals particularly valuable (Pliatsikas & Luk, 2016). The experience of bilingualism has been shown to influence neural activity in non-linguistic switching tasks (Rodríguez-Pujadas et al., 2013), and language proficiency in bilinguals with different proficiency levels has been shown to be related to resting-state functional connectivity of the regions involved in switching (X. Sun et al., 2019). Studies that compare cohorts with different sensory and linguistic experiences (e.g., native signers, bilingual signers, monolingual deaf individuals who only use spoken language, and bimodal bilinguals) can help investigate the effects of bilingualism and language modality in non-linguistic cognitive control. In our sample, the degree of bilingualism was variable and the bilingualism status itself was not consistent across the participants, so we refrained from investigating bilingualism-related effects.

Language modality is another significant factor that can influence functional connectivity. There have been studies investigating the relationship between spoken language skills (Y. Li et al., 2013) or sign language skills (Holmer et al., 2022) and resting-state functional connectivity in deafness but no studies that investigated modality-specific effects in connectivity during task execution. Here we focused on the effects of general, modality-independent, language proficiency on functional connectivity during cognitive and resting states to focus on one of the overarching questions of the thesis, namely, how language delay may affect cognition and functional brain organisation. Further research on functional connectivity during different cognitive states with the use of measures of proficiency in a single language modality can expand our understanding of connectivity changes related to the use of spoken and sign language in deaf individuals.

Another possible limitation concerns the choice of network definitions. We used the same pre-defined network distributions of brain regions across all functional connectivity analyses. The brain parcellation used (Schaefer et al., 2018; Yeo et al., 2011) was based on data from hearing populations. It has been noted in the literature on functional connectivity in deafness (Andin & Holmer, 2022) that using pre-defined network nodes based on data from hearing individuals to investigate differences in connectivity between deaf and hearing participants may lead to bias and confound interpretations, since the evidence from the independent component analysis that the control, default mode, ventral somatomotor, and attention networks differ in composition between deaf and hearing individuals (Andin & Holmer, 2022). Throughout the thesis, we largely avoided network measures and used them only in one analysis presented in this chapter which complemented other analyses that investigated the effects in distinct seeds.

Finally, there have been very few studies of functional connectivity in deaf individuals, with most studies recruiting proficient deaf signers (e.g., Andin & Holmer, 2022; Cardin et al., submitted). The studies presented in this chapter and in the previous chapter on resting-state functional connectivity attempt at uncovering possible relationships between areas from different networks that are influenced by the sensory experience of deafness and language proficiency and do not define precise hypotheses for individual connections. The results reported in these chapters can lay the groundwork for more specific, in-depth investigations of changes in functional connectivity that will target specific regions of interest and connections.

4.4.8. Conclusion

In this chapter, we described reorganisation in functional connectivity across multiple regions from nine networks in deaf individuals during different cognitive states: 1. the execution of the planning task and resting state; 2. different conditions of the switching task. Each network included in the analysis demonstrated at least one altered between-state or between-condition connection between the groups of deaf individuals and hearing controls. These findings, in agreement with the evidence from previous functional connectivity studies on deafness, emphasise the role of the sensory experience of deafness in changes in functional connectivity. Critically, some changes in connectivity are related to language experience: the difference in connectivity between the default mode and control networks is related to language proficiency in deaf individuals, independently of the modality of their best language.

5 General discussion

This thesis evaluated the effects of language proficiency on components of executive function (working memory, switching, planning, and inhibition) in behaviour and in the brain. Further, the effects of language proficiency and the sensory experience of deafness were investigated in functional connectivity at different states. The main prediction was that language proficiency would be associated with components of executive function, following the evidence of language mediating executive function skills in deaf children. The other predictions concerned differences in connectivity between regions from sensory, cognitive, and attention networks and their associations to sensory experience and language proficiency. The analysis presented in Chapter 2 revealed a positive association between switching and language proficiency, and positive associations between language proficiency and neural activity during the execution of the planning task. Chapter 3 described the effects of sensory experience and language proficiency on functional connectivity at rest and demonstrated significant differences in connectivity between deaf and hearing individuals across regions from sensory, cognitive, and attention networks. The results presented in Chapter 3 emphasise the role of the sensory experience of deafness in connectivity of the auditory areas and the role of language proficiency in the connectivity of the visual, attention, and cognitive networks. Finally, Chapter 4 described state-related differences in connectivity between deaf and hearing individuals and demonstrated that language experience can explain changes in connectivity during the execution of an executive function task in regions from the default mode and control networks in deaf individuals.

Language proficiency and cognition

The first study presented in this thesis compared executive function skills in deaf and hearing adults and explored whether performance in executive function tasks was associated with language proficiency in deaf individuals in behaviour and in the brain. Research on executive function in deaf children often describes differences in performance between groups of deaf children and their hearing peers (Botting et al., 2017; Figueras et al., 2008; Jones et al., 2020; Merchán et al., 2022), but there is a high degree of variability in performance that has shown to be associated with language abilities: vocabulary scores predict outcomes in executive function two years later (Jones et al., 2020), language ability is positively associated with executive function in hearing and deaf children (Figueras et al., 2008), and language skills mediate the non-verbal executive function in composite analyses (Botting et al., 2017) and analyses on specific components (Merchán et al., 2022) (see Hall et al., 2017; Morgan & Dye, 2020 for reviews on the topic). Moreover, children who are native signers do not show differences in working memory performance to hearing controls (Marshall et al., 2015).

Taken together, findings from developmental research on deafness suggest that language may shape aspects of cognition. Results from the present work allow us to build on the idea that language development positively influences cognition and contribute to the existing literature on the topic by describing similar associations in an adult population. The present study, to the best of our knowledge, was the first one to examine the relationship between different components of executive function and language proficiency in deaf adults. Critically, in our study, the only difference in performance between the groups in the accuracy of responses was observed during switching, and switching scores were positively associated with language proficiency in the deaf group. This finding demonstrates that differences in switching ability may be detected in deaf adults with varying language backgrounds, suggesting that they are carried over through adolescence in this population from childhood (Figueras et al., 2008). Moreover, the relationship between switching ability and language ability is also detectable in adulthood. Switching (or shifting) abilities in particular have been suggested to be supported by linguistic structures of the ‘if-if-then’ type by the Cognitive Complexity and Control (CCC) theory (Zelazo & Frye, 1998). Similarly to what has been demonstrated for intergroup differences between deaf and hearing children (Figueras et al., 2008), we believe that language abilities may underpin switching difficulties observed in the deaf group. Following the argument by Morgan and Dye (Morgan & Dye, 2020), early interaction and communication with parents is a precursor to language and executive function development. Successful early interaction is critical for language development, and the linguistic environment of deaf children with some language backgrounds may lead to a delay in vocabulary development and other aspects of language abilities that in turn support aspects of executive function (Zelazo & Frye, 1998). Children and adults who experienced successful language development in childhood are able to use metacognitive strategies, such as private speech, when solving cognitive tasks (Morgan & Dye, 2020).

General language proficiency in this study was also associated with reaction time in the control condition of the planning task (counting objects) and neural activity in the planum temporale in both conditions of this task. This suggests the relevance of language proficiency in other cognitive processes, such as counting objects, in deaf individuals. The role of language, particularly phonological skills, has been suggested for aspects of arithmetic processing in deaf signers (Andin et al., 2014; Bull et al., 2005). Here we show that modality-independent language proficiency is positively associated with the speed of counting in deaf individuals with varying language backgrounds. The verbal code is suggested to underlie counting (Cohen & Dehaene, 1996), considering that counting relies on verbal labels, and phonological skills in deaf signers have been proposed to lead to a successful development of multiplicative reasoning that is supported by the verbal code (Andin et al., 2014). Taken together, the association between language proficiency and reaction time and the association between language proficiency and neural activity during counting suggests the contribution of language mechanisms to faster mapping retrieval for counting in deaf participants with higher language scores. This may be supported by the involvement of the planum temporale in language processing (Binder et al., 1996; Nakada et al., 2001) or the observed variability in its activation during planning in the deaf group (Manini et al., 2022).

Neural activity in the planum temporale during planning was also positively correlated to language proficiency. Language abilities have been proposed to affect the strategies used for solving planning tasks in children with specific language impairment and in typically developing children (Al-Namlah et al., 2006; Fernyhough & Fradley, 2005; Henry et al., 2012; Larson et al., 2019). Deaf individuals with higher language proficiency scores may benefit from employing strategies supported by language in both counting (through the verbal code) and planning (through verbal mediation) (Marcovitch & Zelazo, 2009). Private speech has been suggested to support planning during development (Fernyhough & Fradley, 2005; Larson et al., 2019; Vygotsky, 1962), and the lack of private speech in deaf children has been proposed to be the underlying factor of deficits in executive function in deaf children. (Vissers & Hermans, 2018). The present study proposes that successful early language development is beneficial for the development of executive function abilities, such as planning and switching, and continues to support these components of executive function later in life. It may also indicate that a higher degree of reorganisation of the temporal cortices is beneficial for cognition, considering the positive association with language proficiency scores during planning and counting objects, and the association between language proficiency and reaction time during counting, but more research is needed to investigate the specific mechanisms underlying this association.

The research presented in this thesis evaluated the effects of general language proficiency, rather than performance in language tests of one modality, on cognition and brain reorganisation. It is possible that sign language skills, in co-occurrence with deafness (Bavelier et al., 2006), may support the execution of visual tasks, considering that sign language is a language that relies on the visual modality. There has also been evidence of enhanced visual cognitive task performance in a group of deaf signers in working memory (Ding et al., 2015). Our sample composition was chosen to specifically investigate modality-general effects in cognition and brain reorganisation. Exploring the effects of sign language proficiency would be better suited for other studies of native or proficient deaf signers that seek to evaluate the effects of visual language use, rather than the effects of varying language experiences during development.

Deafness, language, and functional connectivity

Studies of functional connectivity in deafness consistently reveal significant differences in resting-state connectivity between areas from the auditory network between deaf and hearing individuals, but also in regions from other networks (Andin & Holmer, 2022; Bonna et al., 2021; Cardin et al., 2018; Cardin et al., submitted; Dell Ducas et al., 2021; Ding et al., 2016). The findings of this thesis confirm that changes in functional connectivity driven by the sensory experience of deafness are widespread and are not limited to the auditory cortices. They may also arise between regions from cognitive (e.g., default mode, control, language) and attention (e.g., salience, dorsal attention) networks. Moreover, such changes are also present when state-dependent functional connectivity is investigated.

Other literature on functional connectivity in deaf individuals also showed that functional connectivity may be associated with language skills in signed and spoken/written language in this population (Holmer et al., 2022; Y. Li et al., 2013). In a study that used the age of sign language exposure as a measure, there were no significant findings in relation to the functional connectivity of the reorganised auditory regions (Ding et al., 2016). Studies by Holmer et al. (2022) and Li et al. (2013) and our study suggest that performance-based measures of language proficiency may be a better tool for investigating such effects.

Our study is the first study to examine the effects of modality-independent, general language proficiency on functional connectivity across the brain in deaf individuals. The analysis of the resting-state data presented in Chapter 3 revealed significant associations between functional connectivity at rest and language proficiency in the deaf group. Chapter 4 employed a different approach and investigated whether differences found in between-state functional connectivity between deaf and hearing individuals could be directly explained by the degree of language proficiency of the deaf participant. Modality-independent language proficiency was found to be associated with connectivity differences between regions from the default mode and control networks. These findings confirm the commonly emphasised argument that the effects of sensory and language experience in changes in brain function in deaf individuals should be disentangled.

Sensory experience

Analyses of resting-state functional connectivity and state-dependent functional connectivity revealed a high number of significant differences between deaf and hearing individuals that could be attributed to the sensory experience of deafness. The temporal lobe is known to show altered functional connectivity to other areas in the brain in deafness (Andin & Holmer, 2022; Bonna et al., 2021; Cardin et al., 2018; Dell Ducas et al., 2021; Ding et al., 2016; Shiell et al., 2015). Taken together, evidence from functional connectivity studies suggests that the auditory cortex acts as a central node of plasticity in the brain of deaf individuals (Andin & Holmer, 2022). The differences in functional connectivity between deaf and hearing individuals at rest described in

Chapter 3 confirm that connectivity of the areas from the temporo-parietal/auditory network, particularly the superior temporal cortex, is particularly influenced by deafness. Enhanced connectivity between the superior temporal cortex and the superior parietal lobule in the dorsal attention network in the deaf group suggests a role of sensory experience in interactions between the reorganised auditory cortex and areas of the dorsal attention network responsible for the top-down allocation of attention to sensory stimuli (Corbetta et al., 2008). These regions in deaf individuals may exhibit increased coordination in response to the reallocation of sensory processing resources to the temporal cortex (Benetti et al., 2021; Finney et al., 2001; M. Simon et al., 2020).

The current study also described a distinct role of the sensory experience of deafness in interactions between sensory and cognitive areas, particularly between areas of the visual network and the medial prefrontal cortex in the default mode network. This finding replicates the results from Bonna et al. (2021), suggesting that this is an effect of the sensory experience of deafness, considering the different language background profiles of participants in the study by Bonna and colleagues (2021) and this thesis. Changes in connectivity between the visual and the default mode network have been attributed to compensatory mechanisms in deafness (Bonna et al., 2021), considering the dynamic reconfigurations in the interaction between the default mode network and other networks that contribute to cognition (Vatansever et al., 2015).

The analysis of the associations between language proficiency and functional connectivity at rest in the deaf group did not reveal any significant connections in the temporo-parietal/auditory network, or changes between the visual and the default mode network. This may suggest that these changes largely depend on the sensory experience of deafness rather than the language experience.

The role of sensory experience manifested very differently in the analyses of functional connectivity changes between different cognitive states described in Chapter 4. Few temporo-parietal/auditory areas showed significant differences between the groups but, as in the resting-state analysis, their connectivity was mostly altered to cognitive (e.g., default mode, control) networks rather than other sensory areas. This is expected in the switching task specifically, where two conditions of interest in our analysis did not differ visually, meaning that all the changes we described are associated with the change in cognitive load.

Language experience

Increased resting-state connectivity between the language and the salience/ventral attention networks during resting state in the deaf group in comparison to the hearing group was detected at the level of whole networks. During task execution, connectivity between these networks was similar in both groups, which could suggest a compensatory mechanism in the deaf group who show optimal connectivity configuration between these networks for task execution during rest. On the other hand, considering that the salience network is involved in detecting and filtering salient stimuli from different modalities (Menon & Uddin, 2010), deaf participants may rely on it more in their communication when detecting linguistically relevant stimuli in the environment. Resting-state connectivity between the language and the salience networks predicts lexico-semantic learning success and is positively associated with it (Schlaffke et al., 2017). There was no association with language proficiency in our data, but it is possible that a different language measure would shed light on whether enhanced connectivity between these networks in the deaf group at rest is associated with advantages in communication. Research comparing populations of deaf individuals with different language backgrounds could explore this difference further.

While not all deaf participants in our sample use signed language, they all share the experience of relying on visual means for communication, such as lipreading or sign language. Higher language proficiency scores were associated with an increase of connectivity between regions in the visual network and areas in the sensory, cognitive, and attention networks at rest. Increased connectivity of the visual network may reflect the successful use of visual communication means and strategies in deaf participants with higher language scores. In particular, connectivity to regions of the somatomotor and salience/ventral attention networks showed a larger number of associations with language proficiency. The association between language skills and coordination between the visual and the somatomotor area can be explained by the role of body, face, and hand movements in sign language perception and production and visual communication, such as lipreading and gesture perception. Stronger connectivity between the visual network and the salience/ventral attention network in participants with higher language scores may be attributed to the increased involvement in the salience/ventral attention regions during the successful detection of communicatively relevant visual stimuli in deaf individuals. Taken together, these findings highlight the relevance of the visual system for successful communication strategies that support language proficiency in deaf individuals, independently of the modality of the language.

One of the main findings of this thesis is the association between the differences in connectivity in areas of the default mode network and the control network during switching and language proficiency in the deaf group. The connection between these two regions, in the right medial prefrontal cortex in the default mode network and the right lateral prefrontal cortex in the control network, was the only connection that was significantly different between the groups and was also associated with language proficiency. This finding highlights the role of language experience in interactions between regions involved in cognition during a cognitively demanding executive function task. Connectivity difference was positively associated with the language proficiency score, suggesting that increased connectivity during switching in comparison to the less cognitively demanding condition was related to better general language proficiency. Considering the evidence of coupling between the default mode and fronto-parietal networks during task execution (Spreng et al., 2010; Vatansever et al., 2015), this finding has great implications for our understanding of the role of language proficiency in the coordination of networks relevant for higher-order cognitive processing, and the way it manifests in deaf individuals in particular. This finding also complements the results from the analysis of the behavioural data, highlighting the functional importance of successful language development for the execution of the executively-demanding condition of the switching task, the only task where the group of deaf participants demonstrated lower performance scores in comparison to hearing controls.

Throughout the thesis, a combined measure of language proficiency in signed and spoken modalities was used, an approach that has not yet been employed in studies of brain plasticity in deaf adults, to the best of my knowledge. However, even though we have observed several modality-independent language effects, language-specific effects have been reported before in functional connectivity in deafness (Holmer et al., 2022; Y. Li et al., 2013). This thesis specifically aimed at exploring the effects of general language proficiency to highlight the importance of successful early language acquisition in cognitive and brain development, independently of the modality of the language. Further research using different measures of language proficiency and different group compositions can extend our understanding of the associations between deafness, cognition, language, and functional connectivity in the brain.

Conclusion

This thesis provides evidence for a relationship between components of executive function and language in deaf adults and describes associations between sensory and language experience and functional connectivity in deafness.

Studies on the role of the sensory experience of deafness in cognition and brain function have contributed to our understanding of brain plasticity and the way the sensory environment can shape brain organisation. Language is another factor that can influence the development of cognitive functions. Early language deprivation in deaf individuals has drastic consequences for language development, while successful language acquisition can support cognition. The findings reported in this thesis emphasise the importance of explicitly addressing the role of language experience in deaf participants when examining and interpreting the effects that may be initially assigned to the sensory experience of deafness.

Humans are born with the ability to acquire language independently of its modality. Language skills then contribute to the development of cognitive abilities, specifically those that may rely on language-related strategies. This thesis suggests that variability in language experiences in childhood that leads to varying levels of language proficiency in deaf individuals results in differences in aspects of cognition and brain development. The findings presented in this thesis highlight the role of successful early language development in cognition, and language proficiency should be considered when discussing cognitive and brain development in deaf individuals.

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Appendix

Appendix Table 2.1. Participants with runs excluded from the analyses of behavioural and neuroimaging data in executive function tasks

Group	Working memory	Planning	Switching	Inhibition
Hearing	Low accuracy			x
Hearing				x
Hearing				x
Hearing				1 run
Hearing				Low accuracy
Hearing				x
Hearing		Low accuracy		
Deaf		x	x	1 run
Deaf				x
Deaf		Low accuracy		x
Deaf	Low accuracy		Low accuracy	Not recorded
Deaf		Movement		
Deaf				1 run
Deaf		Misunderstood		1 run
Deaf				1 run

Note. 'Low accuracy', 'x', and 'movement' mean that data for this task for this participant was excluded from the analysis; 'x' means that the participant did not perform the task due to a technical problem occurring in the first weeks of data collection; '1 run' means that the participant performed one run of the inhibition task instead of two runs due to insufficient scanning time or fatigue. 'Low accuracy' means the participant had <55% correct answers for that task (in one of the following types of trials: 1) working memory, control; 2) Tower of London, control; 3) all switch trials, all stay trials; 4) all incongruent trials, all congruent trials), or was an extreme outlier. One participant reported that they may have misunderstood the task ('misunderstood').

Appendix Table 2.2. Repeated-measures ANOVAs on behavioural performance in executive function tasks

	Working memory		**Planning**		**Switching**		**Inhibition**	
	Accuracy							
	F(df)	*p*	*F(df)*	*p*	*F(df)*	*p*	*F(df)*	*p*
Condition	**91.59 (1,41)**	**<.001**	**46.88 (1,38)**	**<.001**	**28.27 (1,41)**	**<.001**	**17.57 (1,35)**	**<.001**
Group	0.03 (1,41)	.86	0.86 (1,38)	.36	**4.32 (1,41)**	**.04**	0.24 (1,35)	.63
Condition × Group	0.3 (1,41)	.59	0.01 (1,38)	.92	**4.98 (1,41)**	**.03**	0.00 (1,35)	.98
	Reaction time							
	F(df)	*p*	*F(df)*	*p*	*F(df)*	*p*	*F(df)*	*p*
Condition	**199.22 (1,41)**	**<.001**	**211.64 (1,38)**	**<.001**	**21.6 (1,41)**	**<.001**	**79.2 (1,35)**	**<.001**
Group	**8.11 (1,41)**	**.007**	**10.96 (1,38)**	**.002**	**4.5 (1,41)**	**.04**	**4.91 (1,35)**	**.03**
Condition × Group	0.0 (1,41)	.97	0.06 (1,38)	.80	0.03 (1,41)	.87	0.35 (1,35)	.56

Note. Repeated-measures ANOVAs on behavioural performance in executive function tasks. Factors in the analysis were: condition (task/higher executive load, control/lower executive load) and group (deaf, hearing). Significant effects are shown in bold.

Appendix Table 2.3. Repeated-measures ANOVAs on behavioural performance in the deaf group with language score as a covariate

	Accuracy	*df*	*F*	*p*
Working memory	Condition	1, 20	3.30	.08
	Condition x language score	1, 20	2.80	.11
	Language score	1, 20	0.21	.65
Planning	Condition	1, 17	1.00	.33
	Condition x language score	1, 17	4.23	.06
	Language score	1, 17	3.68	.07
Switching	Condition	1, 19	20.25	<.001
	Condition x language score	**1, 19**	**4.96**	**.04**
	Language score	**1, 19**	**4.93**	**.04**
Inhibition	Condition	1, 18	0.69	.42
	Condition x language score	1, 18	0.29	.60
	Language score	1, 18	2.60	.12
	Reaction time	*df*	*F*	*p*
Working memory	Condition	1, 20	12.84	.002
	Condition x language score	1, 20	1.83	.19
	Language score	1, 20	3.69	.07
Planning	Condition	1, 17	10.04	.006
	Condition x language score	**1, 17**	**5.87**	**.03**
	Language score	1, 17	1.54	.23
Switching	Condition	1, 19	2.83	.11
	Condition x language score	1, 19	0.41	.53
	Language score	1, 19	3.80	.06
Inhibition	Condition	1, 18	3.8	.07
	Condition x language score	1, 18	0.43	.52
	Language score	1, 18	0.15	.70

Note. Repeated-measures ANOVAs with condition (task/higher executive load, control/lower executive load) as a within-subjects factor and language score as a covariate. Bold letters indicate significant language effects.

Appendix Table 2.4. Repeated-measures ANOVA on the neural activity in the temporal regions of interest in the working memory task in the deaf group with language score as a covariate

Within-Subjects Effects

Cases	**Sum of Squares**	***df***	**Mean Square**	***F***	***p***
Condition	1.65	1	1.65	0.87	.36
Condition x Language	0.01	1	0.01	0.01	.94
Residuals	37.95	20	1.9		
ROI	14.45	2	7.23	2.16	.13
ROI x Language	3.94	2	1.97	0.59	.56
Residuals	133.74	40	3.34		
Hemisphere	3.21	1	3.21	3.43	.08
Hemisphere x Language	1.60	1	1.60	1.71	.21
Residuals	18.72	20	0.94		
Condition x ROI	0.02	2	0.01	0.03	.97
Condition x ROI x Language	1.11	2	0.56	1.70	.20
Residuals	13.11	40	0.33		
Condition x Hemisphere	0.49	1	0.49	1.24	.28
Condition x Hemisphere x Language	0.75	1	0.75	1.92	.18
Residuals	7.81	20	0.39		
ROI x Hemisphere	5.28	2	2.64	1.29	.29
ROI x Hemisphere x Language	0.06	2	0.03	0.01	.99
Residuals	81.97	40	2.05		
Condition x ROI x Hemisphere	0.09	2	0.05	0.30	.74
Condition x ROI x Hemisphere x Language	0.71	2	0.36	2.28	.12
Residuals	6.22	40	0.16		

Note. Type III Sum of Squares.

Between-Subjects Effects

Cases	**Sum of Squares**	***df***	**Mean Square**	***F***	***p***
Language	0.68	1	0.68	0.03	.87
Residuals	489.38	20	24.47		

Note. Type III Sum of Squares.

Appendix Table 2.5. Repeated-measures ANOVA on the neural activity in the temporal regions of interest in the planning task in the deaf group with language score as a covariate

Within-Subjects Effects

Cases	Sum of Squares	*df*	Mean Square	*F*	*p*
Condition	0.36	1	0.36	0.92	.35
Condition x Language	0.01	1	0.01	0.02	.89
Residuals	6.64	17	0.39		
ROI	2.97	2	1.48	4.23	.02
ROI x Language	6.01	2	3.00	8.57	< .001
Residuals	11.92	34	0.35		
Hemisphere	0.29	1	0.29	1.00	.33
Hemisphere x Language	0.27	1	0.27	0.93	.35
Residuals	4.90	17	0.29		
Condition x ROI	0.12	2	0.06	1.78	.19
Condition x ROI x Language	0.00	2	5.910e-4	0.02	.98
Residuals	1.12	34	0.03		
Condition x Hemisphere	3.066e-4	1	3.066e-4	0.00	.95
Condition x Hemisphere x Language	0.01	1	0.01	0.19	.67
Residuals	1.17	17	0.07		
ROI x Hemisphere	0.29	2	0.15	0.47	.63
ROI x Hemisphere x Language	0.21	2	0.11	0.34	.71
Residuals	10.53	34	0.31		
Condition x ROI x Hemisphere	0.03	2	0.02	0.80	.46
Condition x ROI x Hemisphere x Language	0.03	2	0.02	0.73	.49
Residuals	0.69	34	0.02		

Note. Type III Sum of Squares.

Between-Subjects Effects

Cases	Sum of Squares	*df*	Mean Square	*F*	*p*
Language	8.20	1	8.20	1.94	.18
Residuals	71.85	17	4.23		

Note. Type III Sum of Squares.

Appendix Table 2.6. Repeated-measures ANOVA on the neural activity in the temporal regions of interest in the switching task in the deaf group with language score as a covariate

Within-Subjects Effects

Cases	Sum of Squares	*df*	Mean Square	*F*	*p*
Condition	80.04	1	80.04	4.00	.06
Condition x Language	1.96	1	1.96	0.10	.76
Residuals	380.61	19	20.03		
ROI	23.54	2	11.77	2.67	.08
ROI x Language	19.33	2	9.67	2.20	.13
Residuals	167.32	38	4.40		
Hemisphere	5.66	1	5.66	0.95	.34
Hemisphere x Language	0.13	1	0.13	0.02	.89
Residuals	113.17	19	5.96		
Condition x ROI	1.47	2	0.74	0.74	.49
Condition x ROI x Language	1.17	2	0.59	0.59	.56
Residuals	38.05	38	1.00		
Condition x Hemisphere	1.49	1	1.49	1.07	.31
Condition x Hemisphere x Language	2.57	1	2.57	1.84	.19
Residuals	26.49	19	1.39		
ROI x Hemisphere	51.90	2	25.95	5.53	.01
ROI x Hemisphere x Language	9.17	2	4.58	0.98	.39
Residuals	178.35	38	4.69		
Condition x ROI x Hemisphere	9.20	2	4.60	3.39	.04
Condition x ROI x Hemisphere x Language	2.13	2	1.07	0.79	.46
Residuals	51.56	38	1.36		

Note. Type III Sum of Squares.

Between-Subjects Effects

Cases	Sum of Squares	*df*	Mean Square	*F*	*p*
Language	12.96	1	12.96	0.25	.62
Residuals	977.54	19	51.45		

Note. Type III Sum of Squares.

Appendix Table 2.7. *Repeated-measures ANOVA on the neural activity in the temporal regions of interest in the inhibition task in the deaf group with language score as a covariate*

Within-Subjects Effects

Cases	Sum of Squares	*df*	Mean Square	*F*	*p*
Condition	1.10	1	1.10	0.11	.75
Condition x Language	4.93	1	4.93	0.49	.50
Residuals	182.95	18	10.16		
ROI	26.45	2	13.23	3.46	.04
ROI x Language	2.80	2	1.40	0.37	.70
Residuals	137.64	36	3.82		
Hemisphere	8.37	1	8.37	1.34	.26
Hemisphere x Language	21.48	1	21.48	3.45	.08
Residuals	112.24	18	6.24		
Condition x ROI	0.63	2	0.32	0.54	.59
Condition x ROI x Language	1.48	2	0.74	1.26	.30
Residuals	21.20	36	0.59		
Condition x Hemisphere	0.10	1	0.10	0.30	.59
Condition x Hemisphere x Language	0.05	1	0.05	0.16	.69
Residuals	5.89	18	0.33		
ROI x Hemisphere	17.21	2	8.60	2.67	.08
ROI x Hemisphere x Language	5.65	2	2.83	0.88	.43
Residuals	116.19	36	3.23		
Condition x ROI x Hemisphere	0.74	2	0.37	1.90	.16
Condition x ROI x Hemisphere x Language	0.72	2	0.36	1.85	.17
Residuals	6.97	36	0.19		

Note. Type III Sum of Squares.

Between-Subjects Effects

Cases	Sum of Squares	*df*	Mean Square	*F*	*p*
Language	12.14	1	12.14	0.28	.60
Residuals	774.10	18	43.01		

Note. Type III Sum of Squares.

Appendix Table 2.8. Ten best performing models in repeated-measures Bayesian ANOVA on the neural activity in the planning task in Heshl's gyrus

Model Comparison

Models	P(M)	P(M|data)	BF_M	BF_{10}	error %
Null model (incl. subject)	0.05	0.25	5.97	1.00	
Condition	0.05	0.23	5.32	0.92	1.15
Language	0.05	0.13	2.63	0.51	1.62
Condition + Language	0.05	0.12	2.44	0.48	1.95
Hemisphere	0.05	0.06	1.13	0.24	1.18
Condition + Hemisphere	0.05	0.05	1.01	0.21	1.58
Condition + Language + Condition x Language	0.05	0.04	0.72	0.15	2.46
Hemisphere + Language	0.05	0.03	0.57	0.12	2.10
Condition + Hemisphere + Language	0.05	0.03	0.54	0.12	2.54
Condition + Hemisphere + Condition x Hemisphere	0.05	0.02	0.34	0.08	10.47

Note. All models include subject.

Analysis of Effects

Effects	P(incl)	P(excl)	P(incl|data)	P(excl|data)	BF_{incl}
Condition	0.74	0.26	0.52	0.48	0.40
Hemisphere	0.74	0.26	0.24	0.76	0.11
Condition x Hemisphere	0.32	0.68	0.04	0.97	0.08
Language	0.74	0.26	0.39	0.61	0.23
Hemisphere x Language	0.32	0.68	0.03	0.97	0.06
Condition x Language	0.32	0.68	0.06	0.95	0.13
Condition x Hemisphere x Language	0.05	0.95	4.940e-4	1.00	0.01

Appendix Table 2.9. Repeated-measures ANOVA on the neural activity in the fronto-parietal regions of interest in the working memory task in the deaf group with language score as a covariate

Within-Subjects Effects

Cases	Sum of Squares	*df*	Mean Square	*F*	*p*
Condition	9.17	1	9.17	1.24	.28
Condition x Language	16.92	1	16.92	2.30	.15
Residuals	147.43	20	7.37		
Hemisphere	0.13	1	0.13	0.06	.82
Hemisphere x Language	0.12	1	0.12	0.05	.83
Residuals	46.58	20	2.33		
ROI	51.35	4	12.84	2.77	.03
ROI x Language	8.88	4	2.22	0.48	.75
Residuals	370.17	80	4.63		
Condition x Hemisphere	0.19	1	0.19	0.57	.46
Condition x Hemisphere x Language	0.22	1	0.22	0.65	.43
Residuals	6.78	20	0.34		
Condition x ROI	4.20	4	1.05	1.26	.29
Condition x ROI x Language	4.86	4	1.21	1.46	.22
Residuals	66.52	80	0.83		
Hemisphere x ROI	4.55	4	1.14	0.95	.44
Hemisphere x ROI x Language	1.89	4	0.47	0.39	.81
Residuals	96.13	80	1.20		
Condition x Hemisphere x ROI	0.40	4	0.10	0.46	.77
Condition x Hemisphere x ROI x Language	0.21	4	0.05	0.25	.91
Residuals	17.41	80	0.22		

Note. Type III Sum of Squares.

Between-Subjects Effects

Cases	Sum of Squares	*df*	Mean Square	*F*	*p*
Language	193.24	1	193.24	2.37	.14
Residuals	1630.22	20	81.51		

Note. Type III Sum of Squares.

Appendix Table 2.10. Repeated-measures ANOVA on the neural activity in the fronto-parietal regions of interest in the planning task in the deaf group with language score as a covariate

Within-Subjects Effects

Cases	Sum of Squares	*df*	Mean Square	*F*	*p*
Condition	0.34	1	0.34	0.92	.35
Condition x Language	0.02	1	0.02	0.04	.84
Residuals	6.31	17	0.37		
Hemisphere	0.10	1	0.10	0.31	.59
Hemisphere x Language	0.02	1	0.02	0.07	.80
Residuals	5.59	17	0.33		
ROI	7.94	4	1.99	2.11	.09
ROI x Language	8.89	4	2.22	2.36	.06
Residuals	63.90	68	0.94		
Condition x Hemisphere	0.01	1	0.01	0.57	.46
Condition x Hemisphere x Language	0.01	1	0.01	0.30	.59
Residuals	0.26	17	0.02		
Condition x ROI	0.22[a]	4[a]	0.06[a]	0.64[a]	.63[a]
Condition x ROI (corrected)	0.22	2.63	0.08	0.64	.57
Condition x ROI x Language	0.53[a]	4[a]	0.13[a]	1.55[a]	.20[a]
Condition x ROI x Language (corrected)	0.53	2.63	0.20	1.55	.21
Residuals	5.78	68	0.09		
Hemisphere x ROI	0.75	4	0.19	1.01	.41
Hemisphere x ROI x Language	0.85	4	0.21	1.15	.34
Residuals	12.62	68	0.19		
Condition x Hemisphere x ROI	0.03	4	0.01	0.22	.93
Condition x Hemisphere x ROI x Language	0.20	4	0.05	1.70	.16
Residuals	2.00	68	0.03		

Note. Type III Sum of Squares.

[a] Mauchly's test of sphericity indicates that the assumption of sphericity is violated (p < .05), so the Holm correction was applied.

Between-Subjects Effects

Cases	Sum of Squares	*df*	Mean Square	*F*	*p*
Language	3.78	1	3.78	0.32	.58
Residuals	199.36	17	11.73		

Note. Type III Sum of Squares.

Table 2.11. Repeated-measures ANOVA on the neural activity in the fronto-parietal regions of interest in the switching task in the deaf group with language score as a covariate

Within-Subjects Effects

Cases	Sum of Squares	*df*	Mean Square	*F*	*p*
Condition	28.03	1	28.03	3.62	.07
Condition x Language	0.13	1	0.13	0.02	.90
Residuals	146.94	19	7.73		
Hemisphere	12.50	1	12.50	13.87	.001
Hemisphere x Language	0.04	1	0.04	0.05	.83
Residuals	17.13	19	0.90		
ROI	25.09[a]	4[a]	6.27[a]	2.31[a]	.07[a]
ROI (corrected)					
ROI x Language	17.41[a]	4[a]	4.35[a]	1.60[a]	.18[a]
ROI x Language (corrected)					
Residuals	206.58	76	2.72		
Condition x Hemisphere	2.20	1	2.20	6.10	.02
Condition x Hemisphere x Language	0.02	1	0.02	0.06	.81
Residuals	6.85	19	0.36		
Condition x ROI	7.65[a]	4[a]	1.91[a]	2.28[a]	.07[a]
Condition x ROI (corrected)	7.65	2.57	3.0	2.28	.10
Condition x ROI x Language	7.90[a]	4[a]	1.98[a]	2.35[a]	.06[a]
Condition x ROI x Language (corrected)	7.90	2.57	3.07	2.35	.09
Residuals	63.92	76	0.84		
Hemisphere x ROI	1.50[a]	4[a]	0.38[a]	0.37[a]	.83[a]
Hemisphere x ROI with correction	1.50	2.86	0.53	0.37	.77
Hemisphere x ROI x Language	1.94[a]	4[a]	0.49[a]	0.47[a]	.76[a]
Hemisphere x ROI x Language (corrected)	1.94	2.86	0.68	0.47	.69
Residuals	78.20	76	1.03		
Condition x Hemisphere x ROI	0.92	4	0.23	1.03	.40
Condition x Hemisphere x ROI x Language	0.73	4	0.18	0.82	.52
Residuals	16.86	76	0.22		

Note. Type III Sum of Squares.

[a] Mauchly's test of sphericity indicates that the assumption of sphericity is violated ($p < .05$), so the Holm correction was applied.

Between-Subjects Effects

Cases	Sum of Squares	*df*	Mean Square	*F*	*p*
Language	3.42	1	3.42	0.12	.74
Residuals	554.87	19	29.20		

Note. Type III Sum of Squares.

Appendix Table 2.12. Repeated-measures ANOVA on the neural activity in the fronto-parietal regions of interest in the inhibition task in the deaf group, with language score as a covariate

Within-Subjects Effects

Cases	Sum of Squares	*df*	Mean Square	*F*	*p*
Condition	6.12	1	6.12	0.70	.41
Condition x Language	0.04	1	0.04	0.00	.95
Residuals	157.05	18	8.73		
Hemisphere	11.25	1	11.25	2.14	.16
Hemisphere x Language	1.02	1	1.02	0.19	.67
Residuals	94.78	18	5.27		
ROI	147.74[a]	4[a]	36.94[a]	6.12[a]	< .001[a]
ROI (corrected)	147.74	2.35	62.80	6.12	.003
ROI x Language	18.26[a]	4[a]	4.56[a]	0.76[a]	.56[a]
ROI x Language (corrected)	18.26	2.35	7.76	0.76	.50
Residuals	434.76	72	6.04		
Condition x Hemisphere	0.90	1	0.90	2.78	.11
Condition x Hemisphere x Language	0.01	1	0.01	0.04	.85
Residuals	5.83	18	0.32		
Condition x ROI	1.51[a]	4[a]	0.38[a]	0.56[a]	.69[a]
Condition x ROI (corrected)	1.51	2.28	0.66	0.56	.60
Condition x ROI x Language	1.11[a]	4[a]	0.28[a]	0.41[a]	.80
Condition x ROI x Language (corrected)	1.11	2.28	0.49	0.41	.69
Residuals	48.11	72	0.67		
Hemisphere x ROI	22.86	4	5.71	3.72	.008
Hemisphere x ROI x Language	18.51	4	4.63	3.01	.02
Residuals	110.49	72	1.54		
Condition x Hemisphere x ROI	0.56	4	0.14	0.98	.42
Condition x Hemisphere x ROI x Language	0.34	4	0.09	0.60	.66
Residuals	10.31	72	0.14		

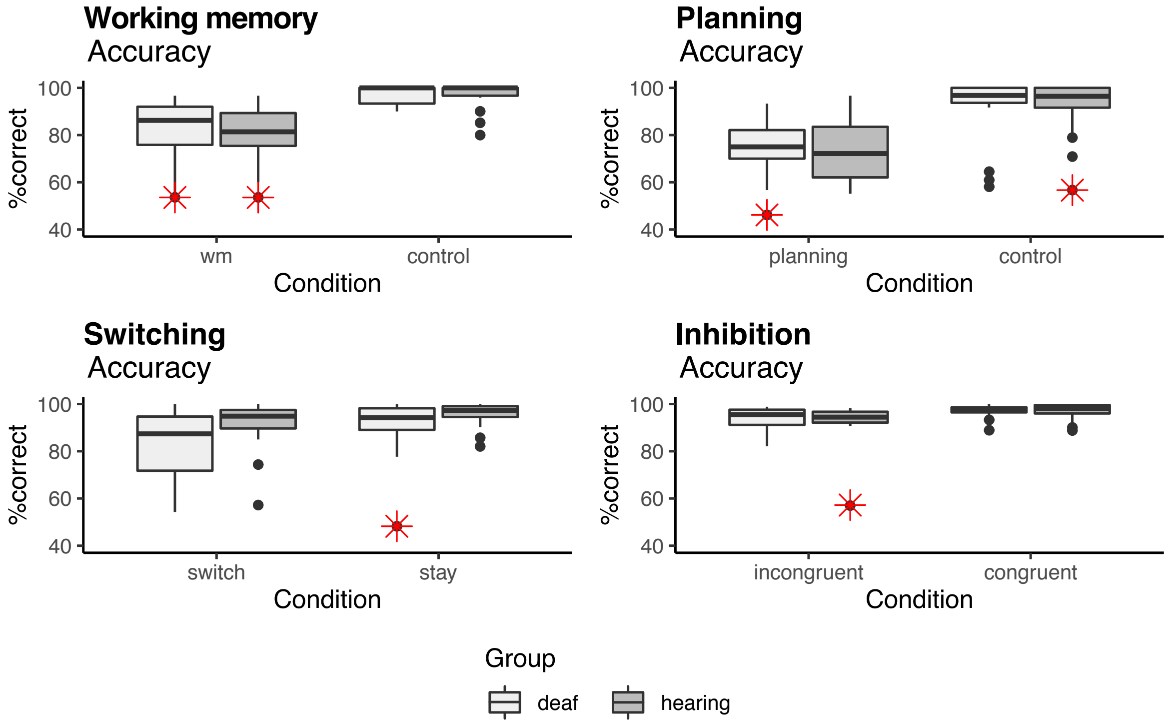
Note. Type III Sum of Squares.

[a] Mauchly's test of sphericity indicates that the assumption of sphericity is violated (p < .05), so the Holm correction was applied.

Between-Subjects Effects

Cases	Sum of Squares	*df*	Mean Square	*F*	*p*
Language	12.24	1	12.24	0.17	.68
Residuals	1291.32	18	71.74		

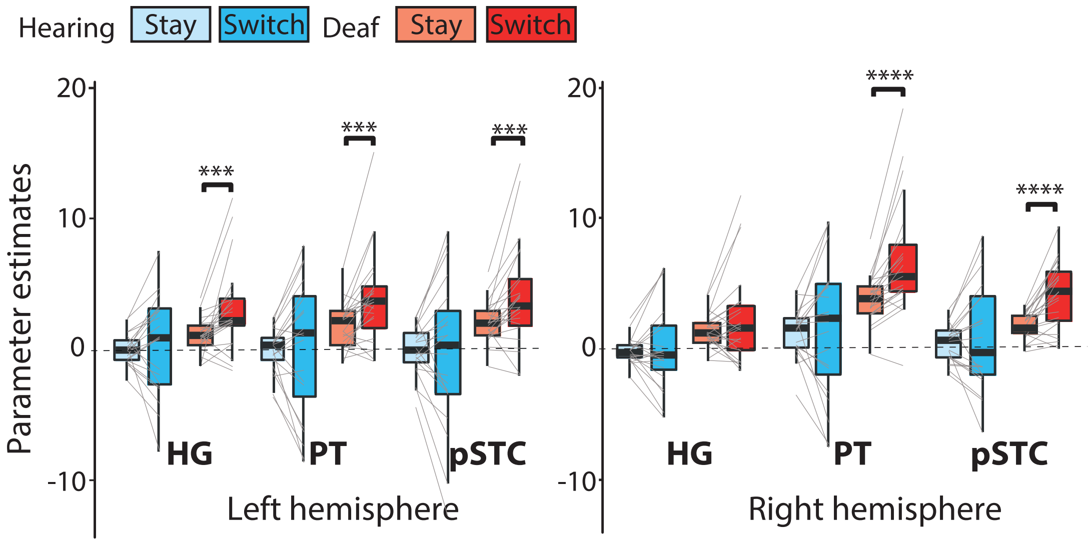
Note. Type III Sum of Squares.



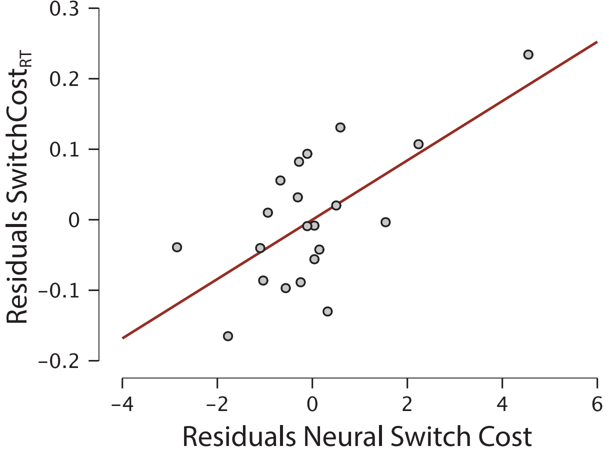
Appendix Figure 2.1. Behavioural performance in executive function tasks with the data points excluded from the analysis as outliers. The figure displays average accuracy (%correct) in each task and condition in both groups. Bold lines indicate the median. The lower and upper hinges correspond to the first and third quartiles (the 25th and 75th percentiles). The upper and lower whiskers extend to the largest and smallest value no further than 1.5*IQR (inter-quartile range) from the hinge. Data points excluded from the analyses are marked with red stars.

Switching

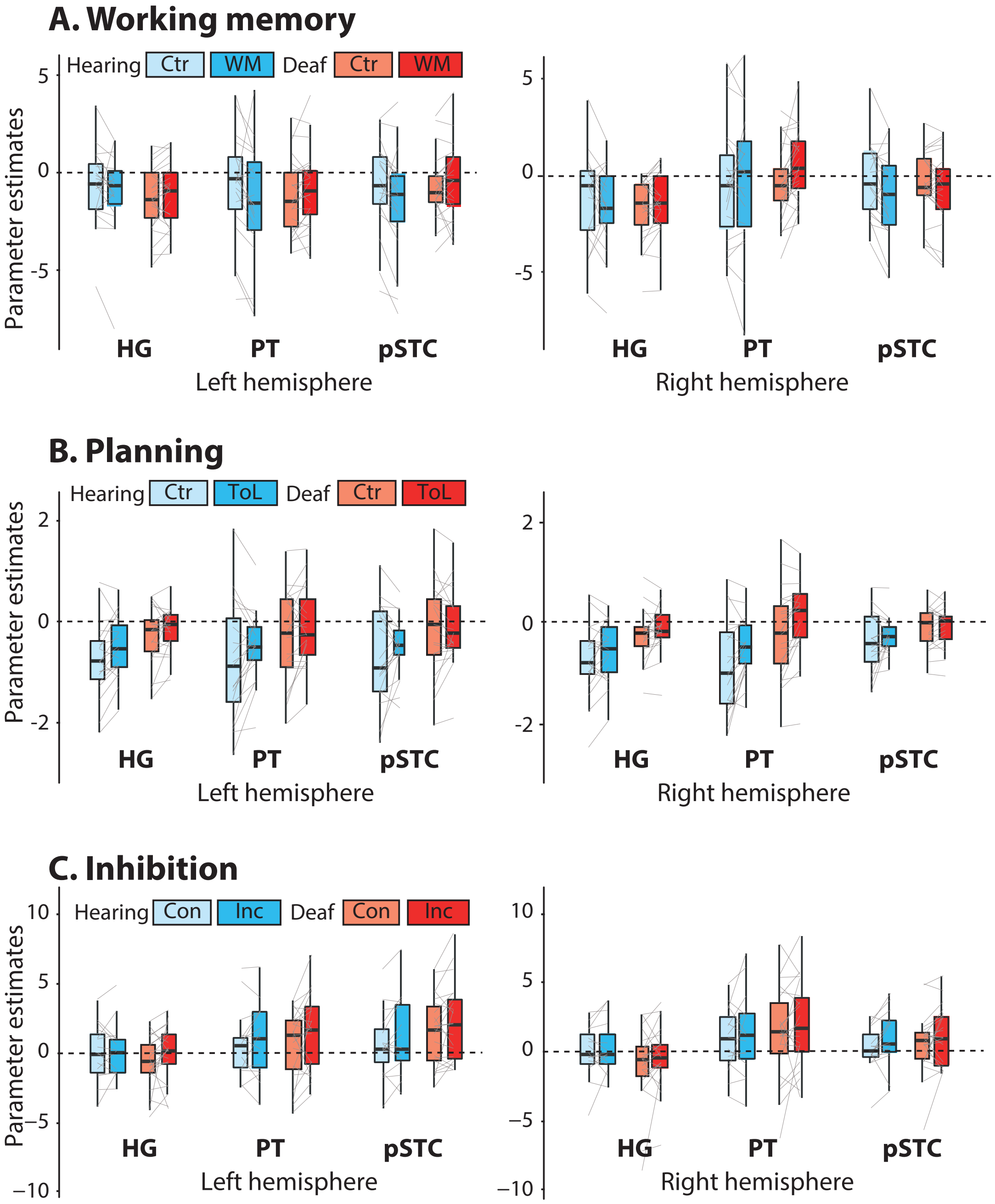
A. Neural activity in the temporal regions



B. Relantionship between neural switch cost and SwitchCost$_{RT}$ in right temporal ROIs in the deaf group



Appendix Figure 2.2. Neural activity in the deaf and hearing groups and the relationship between neural activity and behaviour in the switching task in the deaf group. Figure A: Neural activity in temporal regions of interests. ***$p < 0.005$; ****$p < 0.001$. Figure B: Partial correlation plot between SwitchCost$_{RT}$ (RT$_{\text{first switch trial}}$ – RT$_{\text{all stay trials}}$) and neural switch cost (BOLD$_{\text{switch}}$ – BOLD$_{\text{stay}}$) in right temporal regions on interest in the group of deaf individuals. Partial correlation from a multiple linear model with RT switch cost as dependent variable and the following covariates: right hemisphere neural switch cost, left hemisphere neural switch cost, and language score. No changes were made to the illustration. Open Access under Creative Commons (CC) BY license (https://creativecommons.org/licenses/by/3.0/). From 'Sensory experience modulates the reorganization of auditory regions for executive processing', by Manini et al. (2022): https://doi.org/10.1093/brain/awac205.



Appendix Figure 2.3. Neural activity in the deaf and hearing groups in the working memory, planning and inhibition tasks. Ctr=control, WM=working memory, ToL=Tower of London, Con=congruent, Inc=incongruent. HG=Heschl's gyrus, PT=planum temporale, pSTC=posterior superior temporal cortex. No changes were made to the illustration. Open Access under Creative Commons (CC) BY license (https://creativecommons.org/licenses/by/3.0/). From 'Sensory experience modulates the reorganization of auditory regions for executive processing' by Manini et al. (2022): https://doi.org/10.1093/brain/awac205.