Perception and Action: Behavioural, Neuroimaging and Neuropsychological Studies

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A thesis submitted in partial fulfilment of the requirements of the University of East Anglia for the degree of Doctor of Philosophy.

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Student ID: 100292119

Date of submission: April 2024

Word count: 67,724

Abstract

Traditional models of vision highlight the existence of two neural pathways: the dorsal pathway, subserving vision for action, and the ventral stream for vision for perception. While these streams are responsible for separate outputs, it is argued that they are not entirely independent. This thesis aimed to further explore the link between perception and action using behavioural (Chapter 2), neuroimaging (Chapter 3) and neuropsychological investigations (Chapter 4). The first experiment was a registered report using an influential stimulus-response compatibility paradigm with images of handled objects to investigate affordances. We failed to replicate a common finding that reaction times are faster when objects' handles are oriented to the same side as the hand used to respond to an irrelevant task. However, we did observe this handle compatibility effect when objects were presented in the lower, but not upper, visual field, suggesting affordances may be dependent on the suitability for action. In our second experiment, we used MVPA to examine what properties ventral and dorsal visual stream regions represent. Specifically, whether they code how to use a tool (rotate or squeeze), and if this representation is task or modality specific. Here we found that regions in the ventral and dorsal stream represent tool use actions both when viewing and pantomiming. Thirdly, we investigated how visuomotor performance is affected by Alzheimer's disease and mild cognitive impairment. Participants in the clinical group were slower initiating and executing reaches, and correcting their movements in response to a jump in target position, a task thought to be mediated by the dorsal visual stream. Allocentric reaching, thought to be mediated by the ventral visual stream, was associated with cognitive decline. Put together, this thesis highlights a tight link between perception and action which subserves our ability to carry out skilled movements with objects such as tools.

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Acknowledgements

First and foremost, I would like to thank my supervisor, Dr. Stéphanie Rossit, for being an excellent mentor for the past four and half years, for pushing me out of my comfort zone at times and fuelling my passion for research. Thanks also to my secondary supervisor, Dr. Fraser Smith, for all his practical support, particularly in my fMRI project.

I would also like to thank my collaborators, Dr. George Malcolm and Dr. Allan Clark for their contributions to my affordance project, and Max Havekost, for picking up eye-tracking so quickly and for being an enthusiastic and thorough fellow data collector. Thanks also to Emma Harris and Niamh Parkinson for their excellent support on my dementia project.

A massive thank you to all those who participated in my studies, without whom this research would not be possible. In particular, I would like to thank my patient participants and their carers who travelled to UEA to contribute to my studies not long after labs opened after lockdown. I really appreciate the dedication.

Although it took a while for us to meet in person, I'm so grateful for all the friendships I've made with colleagues in the psychology department. Thank you Dr. Alice Bush, Dr. Courtney Mansfield and Dr. Jon Brooks for all of the break time pep talks, Ling Bai for salvaging my knitting on numerous occasions, Bea Serman for always being up for lunch, and Hannah Browning for all the important and enlightening chats about tools and life. Thanks also to Richard Carey-Knight and Malcolm Rae for addressing all my tech issues with patience and humour. I am also incredibly grateful for my best friends outside of UEA, thanks especially to Sophie, Ellen, Lois, Jack, Kaine, and Brett for sticking with me for over ten years, and for being there through the highs and lows of this PhD, I love you all.

I would like to thank Nathan, for the love and good food he's provided me with during this write up period and for putting a smile on my face every day. Looking forward to doing the same for you as you write up your PhD now!

Finally, thank you Mum, Dad and Joe for keeping me going and always supporting me. And to Cubby, Grayson and Kaya for being the best feline remote working companions, especially helping me code and type up this thesis.

This research would not have been possible without the funding from the UEA studentship. Thank you Prof. Andrew Bayliss and Prof. Patric Bach for taking the time to read and examine this thesis.

Author’s Declaration

I declare that the work contained in this thesis has not been submitted for any other award and that it is all my own work. I also confirm that this work fully acknowledges opinions, ideas and contributions from the work of others.

Parts of this work have been presented at conferences and published in an academic journal.

Oral Presentations

Warman, A., Havekost, M., Clark, A., Malcolm, G. L., & Rossit, S. (2023). Is there a lower visual field advantage in object affordances? A registered report. **School of Psychology Postgraduate Conference Day, University of East Anglia, UK.**

Poster Presentations

Warman, A., & Rossit, S. (2021). Research Plan: Is there a lower visual field preference for object affordances? A series of online reaction time studies. **Experimental Psychology Society (EPS) - Virtual**

Warman, A., Mitchell, A. G., Kenning, E., Williamson, L., Shapland, R., Harris, E., Parkinson, N., Hornberger, M., McIntosh, R., Smith, F. W., Pal, S., & Rossit, S. (2022). Allocentric visuomotor processing is particularly sensitive to cognitive decline: evidence from the iReach app in prodromal and clinical Alzheimer’s Disease. **EPS - University of Stirling, UK.**

Warman, A., Tonin, D., Smith, F. W., & Rossit, S. (2022). Decoding structural and functional manipulation knowledge of tools from viewing and pantomiming. **British Academy of Cognitive Neuroscience annual meeting (BACN) – University of Birmingham, UK.**

Warman, A., Tonin, D., Knights, E., Smith, F. W., & Rossit, S. (2023). Human see, human do? Viewing tool pictures evokes action-specific activity in visual hand-selective occipitotemporal cortex. **Vision Sciences Society annual meeting – Florida, USA.**

Publications related to this thesis

Warman, A., Clark, A., Malcolm, G. L, Havekost, M., & Rossit, S. (2024). Is there a lower visual field advantage for object affordances? A registered report. *Quarterly Journal of Experimental Psychology.* DOI: https://doi.org/10.1177/17470218241230812

Publications unrelated to this thesis

Mitchell, A. G., Rossit, S., Pal, S., Hornberger, M., **Warman, A.,** Kenning, E., Williamson, L., Shapland, R., & McIntosh, R. D. (2022). Peripheral reaching in Alzheimer's disease and mild cognitive impairment. *Cortex*, *149*, 29-43. DOI: https://doi.org/10.1016/j.cortex.2022.01.003

1. Chapter 1 - Introduction

Everyday, we encounter thousands of objects that we can interact with. While writing this thesis, I have been vigorously typing away at my keyboard, using my computer mouse to point to sections on my screen, picking up and drinking from my coffee mug, and often unfortunately succumbing to the temptation to pick up and scroll through my phone. These are just a few of the objects situated on my desk as I write away. While all these object interactions feel like a seamless process, my brain is undergoing a multitude of processes to achieve these goals. For instance, I first need to identify the keyboard and that the keyboard is for typing, my coffee mug is for drinking, and so on. Then, I need to locate where the objects are to allow me to guide my hands towards them and perform the sufficient skilled hand movements to type, adjust my grip aperture and the force of my grip to account for the weight of my coffee mug, and bring it to my mouth to sip on. Throughout these processes, my brain is also constantly updating the positioning of my hands with respect to these objects in space, and to any changes in these object locations.

1.1. Perception triggers action properties

In a highly influential ecological model of visual perception, Gibson (1979) coined the term ‘affordances’. Affordances, according to Gibson, are the action possibilities provided by objects in the environment. For example, a chair affords sitting, while a hammer affords hammering. Gibson’s theory highlighted the reciprocal relation between perceiving and acting as central to perception. The core philosophy here was how perception carries direct information, rather than stored representations, about afforded actions. This differs from traditional top-down views suggesting that perception involves building accurate representations of the world based on sensory inputs and prior knowledge (e.g. Gregory, 1972).Gibson (1966) also highlighted the possibility that affordances can be both innate and learned. For example, while the affordances of food may be detected without learning by infants, children learn which objects in the environment are manipulable or harmful indefinitely (Gibson, 1966). Indeed, later, Gibson (1979) highlighted that affordances depend on the capabilities of the observer, thus varying between species but also among them. Therefore, while a chair may afford sitting for adults, this would not be the same for infants.

The concept has been widely debated and developed over the past 40 years (see Borghi & Riggio, 2015; Buxbaum & Kalénine, 2010; Osiurak et al., 2017 for reviews). For example, while Gibson highlights that affordances are properties of the environment (see also Turvey, 1992), such that a chair will always afford sitting for a human even in the absence of a human, others argue that affordances are the relations between animals and features of the environment (Chemero, 2003). More representational accounts of affordances have suggested they are internal representations which allow for a fast mapping between two other representations: the environment, and how one might act (Vera & Simon, 1993). In this more computational view, affordances are seen as the mapping from perceptual representations to action representations (Chemero & Turvey, 2007). While the contribution of internal representations are debated, the fundamental concept underlying affordances reflect how our perception of the world can quickly, and maybe automatically, trigger action.

Early experimental work has demonstrated the perception of affordances for action is based on intrinsic information in the environment and relative to the information of observers. For example, Warren and Whang (1987) demonstrated that participants could correctly determine that they could walk through a doorlike aperture if the aperture was greater than 1.16 times their shoulder width. This proportion remained constant regardless of the size of participants. Moreover, when the researchers altered participants' eye height, the perception of pass-ability changed. Further research manipulating eye height, by adding blocks to participants' shoes also changed perceptions of objects' utility for sitting and climbing, showing that the perception of eye height is important for individuals' actions in the environment (Mark, 1987). Moreover, perceived pass-ability has been shown to be sensitive to the body constraints of the observer, for example when using a wheelchair to pass rather than walk (Higuchi et al., 2004). Therefore, in line with Gibson's view that perception is tightly linked to possibilities for action, these studies demonstrated that the possibility for action is relative to the observer, rather than the objective length of the gap in the environment.

Significant interest in the concept of affordances stemmed from an affordance effect reported in a stimulus-response compatibility (SRC) paradigm with graspable handled objects (Tucker & Ellis, 1998). In this highly influential experiment (cited over 1500 times), participants were shown images of objects with handles pointing leftwards or rightwards, thus affording a left- or right-handed grasp respectively. Participants judged whether the object was upright or inverted by making a left- or right-handed keypress. In compatible trials, the handle was oriented to the correct side of response (i.e., leftward pointing handle, and left-hand response), while in incompatible trials, the handle was oriented to the opposite side of response. Importantly, the orientation of the handle was irrelevant to task performance. Reaction times were significantly shorter when the objects' handles were compatible with the hand of response, i.e., reaction times were faster when the handle was pointed rightwards, and the correct response required a right-handed keypress. Interestingly, this 'handle compatibility effect' was not observed when participants were required to respond with the index and middle finger of the same hand. Therefore, the handle compatibility effect was attributed to an automatic potentiation of motor responses in response to the seen object, rather than simply abstract left or right spatial codes (Tucker & Ellis, 1998). Given the effect was observed without a subsequent action with the object, this was taken as evidence to suggest that affordances are automatically evoked even without the intent to act (Tucker & Ellis, 1998).

It is important to note that the definition of affordances here differs from that of Gibson's (1979) for the following reasons: rather than affordances being properties of objects in the environment, affordances in this context are properties of the observer's nervous system (Ellis & Tucker, 2000). Moreover, while Gibson's (1979) concept refers to actions in general, such as a grasp, or a sit, here the specific orientation of the object is of interest, i.e. a grasp with the right or left hand. The term 'micro-affordances' has sometimes been adopted to explain the handle compatibility effect observed in SRC paradigms (Ellis & Tucker, 2000).

Numerous researchers have demonstrated the triggering of action properties from the mere perception of manipulable objects. Behaviourally, the handle compatibility effect observed in keypress SRC paradigms has been replicated in response to 2D images of handled objects (e.g. Pappas, 2014; Saccone et al., 2016; Symes et al., 2005). While grip type compatibility effects have also been observed, such that presenting an object affording a power grip leads to faster reaction times to initiate and execute a power grip, compared to precision grip. response in an irrelevant task (Ellis & Tucker, 2000). Others, however, have questioned the automaticity of the effect by findings that the handle compatibility effect is enhanced in certain contexts. For instance, Tipper et al. (2006) used door handles facing leftwards or rightwards as stimuli. They found an enhanced compatibility effect when the door handles were in an 'active state' (pushed down as opposed to horizontal), which was interpreted as evidence that the affordance effect was only automatically evoked when action was implied by the stimulus. In line with this, others have found the effect is reduced when 3D images of objects are presented in extrapersonal compared to peripersonal space, and thus out of reach

(Ambrosini & Costantini, 2013; Costantini et al., 2010, 2011). This suggests that affordances may depend on the perceived reachability of objects, and thus the possibility for action, even when presented as images.

The activation of motor representations from simply viewing manipulable objects has also emerged in research combining transcranial magnetic stimulation (TMS) and electromyography (EMG). In these studies, TMS is applied to motor cortex and motor evoked potentials (MEPs) are recorded from EMG recordings in peripheral muscles which provides a measure of cortico-spinal excitability (Bestmann & Krakauer, 2015). Buccino et al. (2009) found higher MEPs in response to viewing handled mugs affording a grasp with the dominant hand (i.e., a mug handle oriented to the right for a right-handed person), compared to when the handle was oriented towards the non-dominant hand, and when the mug handle was broken and no longer afforded a grasp. This activation was suggested to reflect the recruitment of motor representations related to the use of familiar objects when the objects are graspable, but not when they are ungraspable (Buccino et al., 2009).

In line with this, Makris et al. (2011) found slight differences in MEPs between hand muscles responsible for power compared to precision grips when viewing objects associated with power or precision grasps. Moreover, MEPs were higher in response to passively viewing objects that afford a grasp compared to non-graspable ‘neutral’ objects (e.g., sofa, chair). Higher MEPs have also been observed when viewing objects presented in peripersonal space (within reach) compared to extrapersonal space (Cardellicchio et al., 2011). The converging evidence therefore suggests that upon viewing an object one can grasp, affordances are automatically generated, possibly to facilitate interaction with the object. Neuroimaging has corroborated this link between perception and action by findings that merely viewing images of manipulable objects activates brain regions associated with reaching, grasping and using objects (e.g. Beauchamp et al., 2002; Chao & Martin, 2000; Creem-Regehr & Lee, 2005; Ishibashi et al., 2016; Lewis, 2006). These studies will be reviewed later, however first it is important to explain models, and their associated neural pathways, contributing to perception and action.

1.2. Perception and Action Models

1.2.1. Two Visual Streams Hypothesis

In a seminal paper, Ungerleider and Mishkin (1982) proposed that visual processing occurs within two separate cortical systems originating in the primary visual cortex (V1): a ventral route, culminating in the inferior temporal cortex (IT), or a dorsal route, projecting to posterior parietal cortex (PPC). The ventral stream was proposed to process information about object properties, such as their shape, texture, and colour. This was corroborated by evidence that IT lesions in primates led to deficits in object identification and pattern discrimination (Gaffan et al., 1986; Iwai, 1985; Iwai & Mishkin, 1969), and subsequently referred to as the ventral 'what' stream. On the other hand, the dorsal stream was proposed to be responsible for object localisation, referred to as the dorsal 'where' pathway. In support of two distinct streams, research in primates revealed that lesions to IT resulted in impaired object discrimination but an intact ability to perceive object location, while the reverse was found following PPC lesions (Pohl, 1973).

Ungerleider and Mishkin's (1982) model was subsequently expanded on, and slightly reconceptualised, by Goodale and Milner (1992). Goodale and Milner's (1992) two visual streams hypothesis (TVSH) placed greater emphasis on the contributions of each pathway to their outputs and functions rather than informational perceptual inputs. Here, the ventral pathway, projecting from V1 to IT, was proposed to be responsible for the conscious experience of visual attributes and their meanings, 'perception'. The dorsal stream, on the other hand, projecting from V1 to PPC, was proposed to be responsible for the transformation of visuospatial information, such as object size and location, into coordinates for completing actions such as pointing, reaching, or grasping. It is important to note that Milner and Goodale (1992, 1995, 2006) stressed that the efficient programming and coordination of behaviour requires the contributions of both visual streams, therefore neither stream works in isolation.

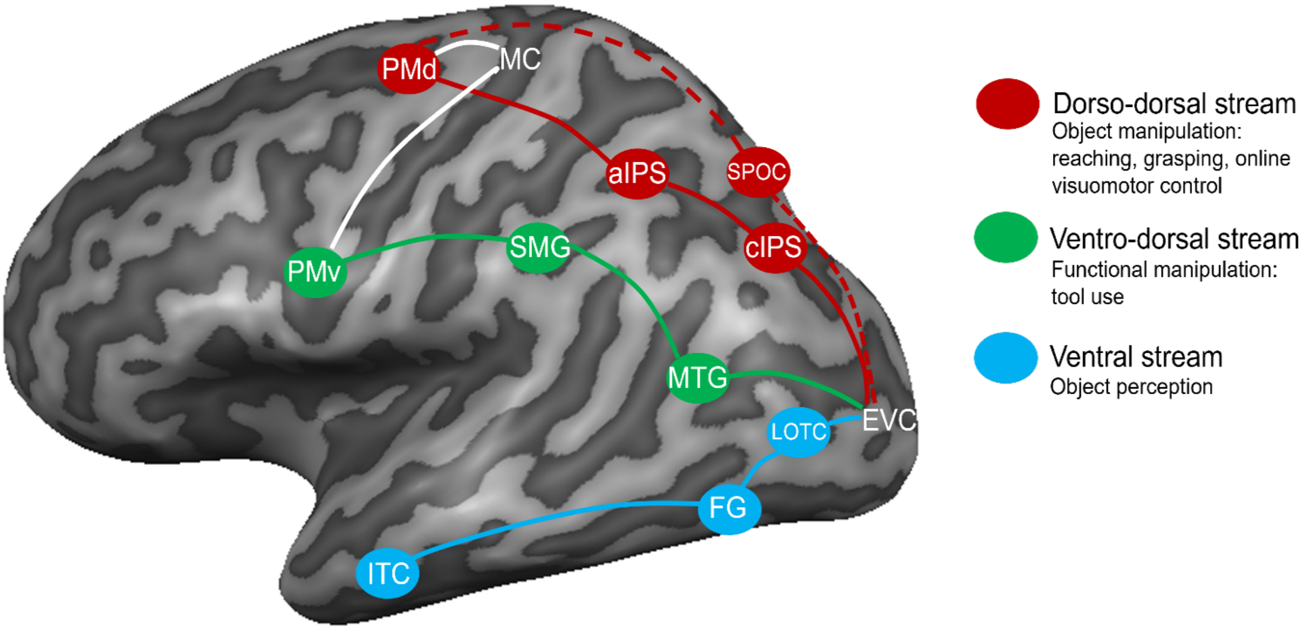
Anatomically, IT within the ventral stream is well positioned to receive low level visual input from V1 and also posterior to medial temporal regions known to subserve long-term memory storage and retrieval (Squire et al., 2004; Squire & Zola-Morgan, 1991). Therefore, IT in the ventral visual stream is well-placed to receive feedback and feedforward connections between early visual regions and medial temporal regions for the identification and recognition of objects (Kravitz et al., 2013). On the other hand the PPC, within the dorsal visual stream, is located anteriorly to V1 and posteriorly to somatosensory cortex and is therefore widely considered as the key associative area responsible for coordinating between sensory and motor information (Sakata et al., 1997). Dorsal visual stream regions are therefore well placed functionally for the visual guidance of action.

1.2.2. Two action streams

While Milner and Goodale’s (1992, 1995, 2006) TVSH provides a framework for the neural underpinnings of sensory guided movements, it has been argued that they fail to capture or explain humans’ ability to use complex tools based on acquired skills (Frey, 2007). The ability to build complex tools is considered a key milestone of brain development in humans (Peeters et al., 2009; Reynaud et al., 2016). Tools are unique as they are thought to form the intersection between object recognition, visuomotor control, and higher-level processing, such as knowing how to use a tool to achieve a goal. Thus, the functional specificity of tools distinguish them from other graspable objects (e.g. a ball) as tools have a semantic identity tightly linked to specific action routines (Creem-Regehr & Lee, 2005; Johnson-Frey et al., 2005). For example, when attempting to open a bottle of wine sealed with a cork, one would need to identify a corkscrew and rotate the tool until it is possible to remove the cork. Any other manner of manipulating a corkscrew, for example by performing a hammering movement would be useless in achieving the goal.

The dorsal visual stream has been further subdivided into two anatomically and functionally distinct subsystems based on the evidence of two separate pathways within the dorsal visual stream that appear separated by the intraparietal sulcus (IPS; Rizzolatti & Matelli, 2003). Rizzolatti and Matelli (2003) proposed that these parieto-premotor systems are therefore organised in a dorso-dorsal (DD) pathway, which projects from regions in the superior parietal lobe (SPL) to the dorsal premotor cortex (PMd), and a ventro-dorsal (VD) pathway running from middle temporal (area MT) regions to the ventral premotor cortex (PMv) via the inferior parietal lobe (IPL; Rizzolatti & Matelli, 2003). Binkofski and Buxbaum (2013) proposed that the DD pathway, including the superior parieto-occipital cortex (SPOC), SPL, and IPS, subserved a ‘Grasp’ system which is responsible for processing the structural features of objects (such as shape and size) to support prehensile actions towards currently viewed objects. This system is consistent with the description of the dorsal visual stream by Goodale and Milner (1992, 1995, 2006). On the other hand, the ’Use’ system, subserved by regions in the VD stream, including posterior middle temporal gyrus (pMTG) and IPL, was proposed to process stored representations of skilled, functional object-related actions, such as how we use tools (see Figure 1.1). These two action systems aimed to explain the apparent double dissociation between the types of actions impaired and preserved in optic ataxia (resulting from DD stream damage) and apraxia (resulting from VD stream damage).

Figure 1.1 *Key regions of the neural pathways described in the TVSH (red and blue) and the two-action streams model (green). Adapted from Rossit and McIntosh (2021).*



1.3. Neuropsychological Evidence for Perception and Action Models

Much of the theoretical implications for the TVSH and two action streams models have been derived from observations in neurological patients. Thus, the following section highlights key impairments associated with damage to the ventral, VD and DD streams, specifically visual agnosia, optic ataxia, and apraxia.

1.3.1. Visual Agnosia

The TVSH was based on observations of patient DF who sustained bilateral occipito-temporal lesions as a result of anoxia due to carbon monoxide intoxication (James et al., 2003). Milner et al. (1991) reported a case study on DF with tests from three months post-trauma. DF was found to be significantly impaired in identifying objects presented visually, for example misidentifying a cup as an ashtray. She was, however, able to describe the properties of objects, such as a pair of scissors being ‘long, thin, silver’, and sometimes make guesses based on these features, however this was a slow process. Interestingly, DF was easily able to identify objects based on tactile information. Moreover, while she was unable to perceive the orientation of a slot, she was able to match her reaching movement to the orientation of the slot (Goodale et al., 1991; Milner et al., 1991). However, when attempting to match more complex ‘T’ shaped objects to slots, DF made errors approximately half of the time (Goodale, Jakobson, Milner, et al., 1994). This suggested that DF may be unable to combine the orientation of more than one component to form a ‘visual shape’. DF’s deficits were therefore associated with ‘visual agnosia’, characterised by impairments in higher order visual processing for object recognition despite preserved low-level visual functioning (Baugh et al., 2017).

Further investigations in patient DF revealed that in the presence of two different sized blocks, DF was unable to judge whether the blocks were the same size or different, nor was she able to manually estimate the size of the blocks, using the finger and thumb to estimate the width of the blocks (Goodale, Meenan, et al., 1994). Despite this, when asked to reach and grasp the blocks, DF’s grip aperture was consistent with the block size and similar to healthy controls (Goodale, Meenan, et al., 1994). Put together, while DF’s ventral stream damage has resulted in deficits in vision-for-perception, her vision-for-action appears intact, due to her preserved dorsal visual stream. Further studies have indeed provided evidence that DF’s visuomotor abilities are intact, including when grasping tools and utensils (Carey et al., 1996), and during obstacle avoidance reaching tasks (Rice, McIntosh, et al., 2006). This suggests that the neural substrates underlying vision-for-perception may be distinct from those subserving vision-for-action (Goodale et al., 1991; Goodale, Jakobson, Milner, et al., 1994; Goodale, Meenan, et al., 1994; Goodale & Milner, 1992; Milner et al., 1991).

1.3.2. Optic Ataxia

On the other hand, lesions to the dorsal visual stream are associated with optic ataxia. The condition, first described as a feature of Balint’s syndrome (Balint, 1909), is characterised by an impairment in visually guided actions in the absence of any motor, somatosensory or purely visual deficits. Optic ataxia was first considered as an isolated deficit after an observation in a patient with a right PPC lesion which resulted in mis-reaching to objects presented in the left (contralesional) hemifield with both the left and right hands (Garcin et al., 1967). A highly influential study qualitatively examined video recordings of ten patients with unilateral optic ataxia conducting various reaching assessments, such as reaching for a pencil presented in differing locations of the visual field. Patients made significant, uncorrected, reaching errors towards objects presented in the peripheral, contralesional, visual hemifield (Perenin & Vighetto, 1988). In addition to field effects, some patients with left hemisphere lesions also presented with ‘hand effects’ which affected reaching with the contralesional hand in both hemifields. However, reaching towards objects presented in central vision, or to foveated objects, remained largely unimpaired. Therefore, the deficits appear most specific to visually guided reaching in the peripheral visual field (Perenin & Vighetto, 1988).

Despite this, some studies have identified reaching and grasping deficits in foveated vision, possibly as a result of bilateral lesions (Goodale, Meenan, et al., 1994; Jakobson et al., 1991). Early single case studies of optic ataxia associated deficits with lesions to the SPL (Auerbach & Alexander, 1981; Buxbaum & Coslett, 1998; Ferro, 1984). The development of lesion subtraction techniques allowed researchers to identify that the centre of lesion overlap in optic ataxia was at the junction between the IPL, the superior occipital cortex and extending medially to the precuneus around the parieto-occipital junction (Karnath & Perenin, 2005). This region encompassed the SPL and intraparietal sulcus (IPS), however the IPL remains spared (Karnath & Perenin, 2005). This suggests that optic ataxic deficits may arise from lesions to the DD stream responsible for the online visual guidance of actions.

The behaviours of those with visual agnosia have been argued to be dissociated from those with optic ataxia. For example, Goodale et al. (1994) contrasted DF’s performance at reaching and grasping irregular shaped wooden plaques with the performance of patient RV, who had optic ataxia as a result of bilateral parieto-occipital lesions. RV was unable to choose an appropriate grasp to pick up the blocks, although was reliably able to tell the objects apart and estimate their width. This provided evidence of a double dissociation between deficits associated with perception, due to ventral stream lesions, and action resulting from dorsal stream lesions.

1.3.3. Apraxia

Apraxia is a clinical manifestation of lesions to the VD stream, and is considered a deficit in skilled movement, in the absence of sensory or motor deficits (Rothi et al., 1997). The first theoretical framework for the classification of apraxia was described by Liepmann (1908). Here, types of apraxia were defined based on the aspect of praxis which was thought to be affected. Specifically, ideomotor apraxia was characterised as a deficit in performing and/or imitating pantomimed actions. These mostly affect the pantomime of tool-use actions (e.g. using a toothbrush without a toothbrush in the hand), but also sometimes lead to deficits in communicative gestures (e.g. waving), which can be considered as a disruption in transforming semantic knowledge into motor acts (Gross & Grossman, 2008; Petreska et al., 2007; Wheaton & Hallett, 2007). Ideational apraxia, on the other hand, is characterised by a conceptual deficit leading the inappropriate use of tools (e.g. eating with a toothbrush), despite an intact ability to name tools (Petreska et al., 2007). There have been over thirty subtypes of apraxia identified in the literature (Baumard & Le Gall, 2021), thus it is beyond the scope of this thesis to evaluate each subtype and their associated deficits. However, the accounts of ideomotor and ideational apraxia have been the subject of much debate in clinical and research settings, and it has therefore been suggested that the focus on apraxia research should be on the symptoms and anatomy rather than attempting to label subtypes purely from behavioural observations (Buxbaum & Randerath, 2018).

Some specific manifestations of apraxia, however, may include impairments in manipulation knowledge and technical reasoning, particularly when handling tools. Types of errors observed in patients with apraxia have been sometimes classed as ‘action errors’, where there is an impairment in the demonstration of how to use a tool to perform an action. For example, continuously rubbing a nail with a hammer rather than hammering it, or lighting a candle and bringing it to the mouth to smoke (Goldenberg & Hagmann, 1998; Osiurak et al., 2013). The second type of error has been classed as a ‘hand posture error’, where patients demonstrate the incorrect handgrip when pantomiming tool use or grasping tools (Buxbaum, Kyle, et al., 2005). Interestingly, while hand posture errors are observed in pantomime tasks, they are rarely observed when patients engage in real tool use tasks (Randerath et al., 2009, 2010). Although, often grasping tools correctly to use them (for example, so that the thumb is pointing towards the functional end of the tool) can followed by inappropriate subsequent tool use (Randerath et al., 2010).

Apraxia is commonly observed following left hemisphere lesions (Niessen et al., 2014), while right hemisphere lesioned patients exhibit almost no apraxic deficits (Randerath et al., 2009). People with apraxia have been noted to have deficits imitating meaningless gestures and in mechanical problem solving tasks which has been linked to lesions in the left IPL in the VD stream (Goldenberg, 2009; Goldenberg & Spatt, 2009). Despite this, there is often a preserved ability to handle tools based on their perceptual properties (Dovern et al., 2012; Goldenberg & Hagmann, 1998), and evidence of spared semantic knowledge related to tools, such as naming tools and their functions (Buxbaum & Saffran, 2002). Randerath et al. (2010) found that tool use action errors were associated with lesions to the supramarginal gyrus (SMG) in the IPL, while hand posture errors were associated with the angular gyrus (AG) and the inferior frontal gyrus (IFG). This suggests that there are separate mechanisms involved in grasping tools with respect to their structure and other visual properties, and manipulation knowledge associated with tools' use. Randerath et al. (2010) proposed that the SMG is therefore responsible for integrating visual and learned information into an action plan, while the AG processes grasp related information about action goals. This finding is in line with Binkofski and Buxbaum's (2013; see also Buxbaum, 2017) model which suggests that SMG in the VD stream is responsible for storing learned manipulation knowledge related to tools, such as how we move a tool for its functional use.

1.4. Primate and neuroimaging evidence for perception and action models

1.4.1. Vision for perception in the ventral stream

Single cell recordings in primates have provided a wealth of evidence for the separate streams of visual processing. In evidence for a ventral 'what' pathway, single cell recordings have identified cells within IT, and posteriorly in V4, which respond selectively to the size, orientation, colour and texture of objects of varying complex shapes (Desimone et al., 1984; Kobatake & Tanaka, 1994; Tanaka et al., 1991). Moreover, IT neurons show similar patterns of responses to animate objects of the same categories, such as bodies, hands and faces (Kiani et al., 2007). fMRI in humans has corroborated these findings, for instance, the fusiform face area is preferentially activated from viewing faces (compared to scrambled images of faces, and other object categories such as houses; Kanwisher et al., 1997); the extrastriate body area preferentially responds to human bodies (Downing et al., 2001), and the parahippocampal place area responds preferentially to images of scenes and buildings (Epstein & Kanwisher, 1998). Put together, these studies highlight a key role of the ventral stream in the recognition of visual input. In line with this, fMRI studies in humans have found that bilateral lateral occipitotemporal complex (LO) in the ventral stream is activated by the presentation of intact objects and shapes compared to scrambled objects or textures (Grill-Spector et al., 2001; Kanwisher et al., 1996; Malach et al., 1995).

In support of a perception-action distinction between the ventral and dorsal visual streams, Culham et al. (2003) conducted a study where participants performed reach-to-grasp movements, reaches without preshaping the hand, or simply viewed 2D objects. Area LO was activated in response to object presentation, however no difference in activation was observed between reaching and grasping. Higher activation was found in the anterior intraparietal sulcus (aIPS) in grasping compared to reaching. This was interpreted as evidence that the ventral stream does not process object properties for the purposes of action, and that aIPS may be more suited for computing object properties necessary to preshape the hand for grasping (Culham et al., 2003).

1.4.2. Vision for action in the dorsal stream

On the other hand, a substantial body of research has examined how the PPC in the dorsal stream controls visually guided reaching and grasping. Electrophysiological investigations in non-human primates provided the first evidence that PPC was responsible for the visual guidance of hand movements. Specifically, single cell recordings in the monkey PPC identified ‘hand manipulation’ neurons in the IPL which discharged specifically in response to movements carried out to obtain a desired object with the hand (Mountcastle et al., 1975). These same neurons did not respond to other movements using the same muscles, or random movements of the hand, suggesting they are specific to object directed movements (Hyvärinen & Poranen, 1974; Mountcastle et al., 1975).

Further research highlighted that hand manipulation neurons appeared concentrated in the anterior intraparietal (AIP) area, which lies on the lateral bank of the IPS (Sakata et al., 1995). Specifically, single cell recordings have shown that some hand manipulation neurons in AIP respond during grasping in both light and dark (with no visual feedback), others responds solely during grasping in the light, and others respond when the primates fixate presented objects (Sakata et al., 1995; Taira et al., 1990). Interestingly, further research in monkey AIP has shown that these visually responsive neurons represent 3D object shape, orientation and size (Murata et al., 2000). This shows that AIP neurons respond to visual stimuli and sensorimotor processing but also contain a specific subset of neurons responsible for the visual control of hand movements.

Area AIP has been shown to be strongly connected to area F5 within the PMv (Luppino et al., 1999; Matelli et al., 1986; Rizzolatti et al., 1998) which has been shown to contain neurons which code specific goal-related hand actions, rather than merely the single movements that form them (e.g. grasping; Rizzolatti et al., 1988). This finding was extended on with a larger set of object and grip type stimuli, and it was also discovered that F5 contains neurons that are selective to object shapes when simply viewing them, and a grasp was not required (Raos et al., 2006; Theys et al., 2012). Interestingly, the objects evoking the strongest activity from visual presentation also evoked strongest activity for the grasp of the same object. These findings have been taken as evidence that F5 is involved in visuomotor transformations for grasping, and that the selectivity is determined by the grip type required to grasp the object rather than the object shape. In line with this, inactivation of F5 disrupts monkeys' ability to preshape the hand based on visual information about the shape and size of objects, however this was not considered a motor deficit as monkeys retained the ability to grasp the objects based on haptic information (Fogassi et al., 2001). Similar findings have also been observed following inactivation of area AIP (Gallese et al., 1994), which suggests that the PPC plays a crucial role in the visuomotor transformations required for visually guided grasping.

The response properties of neurons in F5 are similar to those in AIP, in that they show selectivity for particular objects, firing both during grasping particular objects and during visual presentation, however there are also key differences. Firstly, F5 contains no neurons that are homologous to the visual-dominant neurons in AIP, there are more motor neurons in F5 than AIP, and less visually responsive neurons in F5 compared to AIP (Raos et al., 2006). Raos et al. (2006) also argued that object related visual responses in AIP reflected the geometric shapes of objects, whereas the responses in F5 reflected the grip required. Given that there are numerous possible ways one could interact with an object, for example to grasp and use a pair of scissors, or to grasp them to pass to another person, it has been proposed that area AIP provides multiple descriptions of an object and thus the grasping possibilities to F5. F5 is then thought to select the most appropriate grip based on contextual information such as the goal of the movement (Rizzolatti et al., 1997).

In line with AIP being a crucial region for grasping, fMRI studies in humans have found that aIPS, considered the human homologue of AIP, is more strongly activated when grasping, compared to reaching without preshaping the hand and pointing movements (Binkofski et al., 1998; Culham et al., 2003; Frey et al., 2005). Hamilton and Grafton (2006) conducted an fMRI repetition suppression study where participants watched a series videos of hand actions towards objects. Specifically, movies showed a hand reaching to pick up and move one of two objects to a different location. Subsequent movies repeated the trajectory and goal of the previous video (i.e. a reach to the left to pick up a cookie), repeated the goal but to a novel trajectory (i.e. a reach to the right to pick up a cookie), had a novel goal with a novel trajectory (i.e. a reach to the left to pick up a floppy disk), and had a novel goal with a repeated trajectory (i.e. a reach to the left to pick up a cookie). Repetition suppression was observed in aIPS when the action goal was repeated (i.e. all videos involving reaching to the cookie regardless of trajectory). That is, BOLD signal in aIPS decreased in response to trials with repeated goals (but not for repeated trajectories). This was taken as evidence that aIPS represents observed immediate action goals, such as taking a cookie (Hamilton & Grafton, 2006). Similar findings have been observed in IPL in the macaque (Fogassi et al., 2005).

Another important region identified in primates for visuomotor coordination is within the parieto-occipital sulcus. Area PO has been identified as a region which facilitates visual input from V1 to the SPL and has been further subdivided into two different areas: V6, which is a retinotopically organised visual motion area (Galletti, Fattori, Gamberini, et al., 1999), and V6A, which is not retinotopically organised and appears to overrepresent the lower VF (Galletti et al., 1996; Galletti, Fattori, Kutz, et al., 1999). Area V6 is reciprocally connected to areas V1, V2, V3A and MT+, as well as V6A and AIP (Galletti et al., 2001) and is thus thought to represent a key component of the dorsal stream in distributing visual information from visual areas into sensorimotor areas in the parietal lobe.

As well as visual neurons which have been shown to encode the spatial location of objects (Galletti & Fattori, 2002), area V6A also contains neurons which are discharged by arm movements, and somatosensory stimulation, specifically from the upper limbs (Bosco et al., 2010; Breveglieri et al., 2002; Galletti et al., 1997, 2022; Gamberini et al., 2011). These reach related neurons in V6A have been shown to code reach direction, even in the absence of visual feedback (Fattori et al., 2005), which appears to occur before the onset of movement (Fattori et al., 2005; Galletti et al., 1997). This provides evidence that area V6A may be responsible for reaching movements in terms of feedback control, and possibly the online control of such actions. V6A has connections with areas F2 and F7, thought to be the homologue of PMd in humans (Gamberini et al., 2009). This region has been shown to encode grip/wrist orientation (Raos et al., 2004). V6 and V6A are thought to correspond to SPOC in humans which has also been implicated in reaching (e.g. de Jong et al., 2001; Rossit et al., 2013). Overall, evidence from primate and human studies has shown that the PPC and its connections with premotor regions is crucial for performing visually guided movements, in line with the TVSH.

1.4.3. Reach and Grasp Systems

It has been suggested that there are two subnetworks in the dorsal stream, with a dorsomedial circuit (SPOC, medial intraparietal, PMd) specialised for reaching (Caminiti et al., 1996, 1998; Jeannerod, 1997), and a dorsolateral circuit (aIPS, PMv) specialised for grasping (Jeannerod et al., 1994; Luppino et al., 1999). In line with this, Tanné-Gariépy et al. (2002) provided evidence that PMd/F2 and PMv/F5 receive inputs from separate regions of the PPC. Specifically, the PMd receives inputs predominantly from SPL within the PPC whereas PMv is connected to the IPL (Rizzolatti & Matelli, 2003; Tanné-Gariépy et al., 2002). Human fMRI research has also provided support for a dorsomedial 'reach' pathway and a dorsolateral 'grasp' pathway. For example, aIPS activity has been shown to be higher for grasping compared to reaching movements (Cavina-Pratesi et al., 2010; Culham et al., 2003).

More recent studies have employed multivariate pattern analysis (MVPA), which extracts information from fine-grained voxel activity patterns within a region of interest and passes them through a classification-based machine learning algorithm to test whether an experimental condition can be decoded from patterns of activity in a given ROI. In contrast to univariate fMRI studies, which can specify which areas are involved in a given condition (e.g. reach vs grasp), decoding in MVPA allows researchers to infer an ROI's representational content (i.e. a neural representation of action type; Haxby, 2012; Mur et al., 2009). In a study employing MVPA, participants performed reach-to-grasp movements, and reach-to-touch movements (thus no preshaping of the hand). Dorsomedial regions (SPOC, Precuneus and IPS) coded grasp versus reach movements during the planning phase, while aIPS additionally discriminated between grasps with differing sized grips (Gallivan, McLean, Valyear, et al., 2011). This suggests that regions in the SPL contain representations of reach direction but cannot discriminate between types of grips which instead is represented in aIPS in the dorsolateral stream.

Virtual lesions in healthy participants using TMS have also provided evidence for separate reach and grasp streams. In particular, TMS to SPOC has been shown to disrupt reach movements to targets presented in the periphery (Ciavarro et al., 2013; Vesia et al., 2010). Other studies have provided causal evidence of the contribution of the PPC for grasping. For example, TMS to aIPS in the dorsal stream (but not other areas of the IPS) has been shown to disrupt grasping with the contralateral limb, increasing both movement time and time to peak grip aperture, particularly when the grasp target was perturbed during the movement (Rice, Tunik, et al., 2006; Tunik et al., 2005). Moreover, TMS at the error correction stage of the movement (when the target was perturbed), was shown to increase peak grip aperture, suggesting a causal role of the aIPS in the online control of grasping (Rice, Tunik, et al., 2006). In line with this, TMS to IPS also disrupts grasping in response to a change in object size when applied at the perturbation stage (Glover et al., 2005). Overall, it appears that SPOC in the dorsolateral stream is responsible for the online control of reach movements, whereas the aIPS is responsible for preshaping the hand to grasp objects.

Despite this, more recent primate research has shown that area V6A neurons are sensitive to wrist orientation (Fattori et al., 2009) and grip formation (Breveglieri et al., 2016, 2018; Fattori et al., 2010), which suggests that dorsomedial region V6A is not simply responsible for reaching. V6A neurons also encode the shape of graspable objects, which suggests it is a critical region for all phases of prehension, such as encoding action relevant visual properties of objects (Fattori et al., 2017). Therefore, the functional distinction between both circuits may extend beyond reaching versus grasping.

It has recently been hypothesised that V6A acts as a state estimator of the arm/hand movement by comparing inputs related to hand and arm movements with the actual configuration of the limb through visual and somatosensory signals (Galletti et al., 2022). V6A receives inputs from dorsolateral and dorsomedial streams, but does not receive input from ventral stream regions, nor from AIP (Gamberini et al., 2009; Passarelli et al., 2011). On the other hand, AIP has connections with IT, which can therefore provide object information to AIP to aid with object-directed actions (Rizzolatti & Matelli, 2003). Put together, it appears that the AIP-F5 dorsolateral circuit may be more suited to precise object-directed manipulation, such as when manipulating tools, whereas V6A is responsible for the fast, online control of object directed grasping (Galletti & Fattori, 2018).

1.4.4. Neural basis of Tool Use

Binkofski and Buxbaum’s (2013) VD ‘Use’ and DD ‘Grasp’ subsystems were based on the apparent dissociation between optic ataxia and apraxia and evidence of two sub-streams in the macaque (Rizzolatti & Matelli, 2003). A slightly different model of tool use was based on a meta-analysis of neuroimaging studies. Lewis (2006; see also Ishibashi et al., 2016; Reynaud et al., 2016) proposed that tool use was subserved by two largely left-lateralised networks in the ventral, VD and DD streams. Specifically, a conceptual and semantic network which includes bilateral FC, left-pMTG, and left IFG, which was proposed to support semantic knowledge of tools (e.g. words depicting tools and how a tool is manipulated). While the tool-use motor skill network involves the IPL, SPL, PMv and PMd, and is more typically activated during the retrieval of tool-use skills and when reaching, grasping, and using tools. While the two models appear to differ in which properties are represented in different regions, for instance in IPL, both models propose that tool use is subserved by regions in the ventral, VD and DD streams and highlight that the existence of separate streams for conceptual and motor skills.

Univariate neuroimaging studies have investigated the possible divisions in between the ventral, VD and DD streams in processing tool use knowledge. In the ventral stream, FC is commonly activated in studies involving viewing tools, naming tools, and when imagining pantomiming tool use (Chao et al., 1999; Creem-Regehr & Lee, 2005; Martin et al., 1996; Rumiati et al., 2004). pMTG, in the VD stream, is consistently activated in tool naming studies as well as lexical knowledge relating to tools, verbs and action words (Kellenbach et al., 2003; Martin et al., 1995). Moreover, bilateral pMTG is consistently recruited when processing manipulation knowledge, such as when hearing sounds associated with tools and producing words associated with specific object-related actions (Johnson-Frey et al., 2005; Kellenbach et al., 2003; Lewis et al., 2005; Martin et al., 1996). This suggests that pMTG may be responsible in integrating multisensory representations of tool use actions. The region also supports the recognition of tool use actions, e.g. using a comb to brush hair (Kalénine & Buxbaum, 2016; Reynaud et al., 2016; Tarhan et al., 2015). Given that the area also responds to images of hands, it is possible that pMTG is also responsible for processing tool manipulation knowledge in addition to conceptual knowledge. Finally, in Lewis' (2006) conceptual and semantic network, IFG was shown to be consistently activated in tool naming, suggestive of a role in semantic representations. However, the area is also activated during pantomime and tool use planning tasks, suggesting that the region also processes the goals of actions, or how objects are manipulated (Johnson-Frey et al., 2005).

In the DD stream, the left SPL is consistently activated when planning and executing tool-use movements or pantomimes with both left and right hands (Choi et al., 2001; Johnson-Frey et al., 2005), and is thought to be responsible for coding the location of the hand in relation to other body parts and objects during movement execution (Binkofski et al., 1999; Chao & Martin, 2000). While IPL in the VD stream appears to be involved in the planning stage of movements with tools, particularly when making judgements about objects' manipulability and pantomiming use of familiar tools (Buxbaum, Kyle, et al., 2005; Rumiati et al., 2004). IPS, which separates the SPL and IPL has been shown to support both the computation of hand postures for grasping (Culham et al., 2003), and the learned motor representations associated with the use of familiar tools (Valyear et al., 2007). Recently, an MVPA study in our lab found that hand-selective IPS coded grasp typicality of tools (i.e. by the handle), but not matched actions with non-tool bars (Knights et al., 2021). Typicality representations in IPS-hand were argued to be automatically evoked, as the representations were present in the absence of subsequent tool use.

The specific representations within the VD stream, particularly within IPL remain the subject of debate. According to the two action systems model (Buxbaum, 2017), the left IPL is responsible for storing tool manipulation knowledge (i.e. how to move a tool to use it). This manipulation-based approach assumes that tool use actions are based on stored representations of how to move a tool to achieve its function. Therefore, the VD stream may facilitate interaction of semantic knowledge and action representations within the IPL (Frey, 2007). However, an alternative view suggests that tool use actions are supported by a combination of mechanical knowledge based on the physical properties of the object (i.e. width, hardness) and online reasoning, rather than stored representations in memory (Osiurak & Badets, 2016). Through this online reasoning, tool use is mentally simulated and performed (Osiurak & Badets, 2016). The reasoning-based approach can explain how humans can utilise novel tools to perform a task (e.g. using a stick to acquire an object out of reach) or use multiple different tools for the same purpose. Moreover, a manipulation-based approach would predict that activity is higher in IPL when interacting with familiar compared to unfamiliar tools, however this has not been found to be the case (Vingerhoets et al., 2010). The reasoning-based approach postulates that IPL contains functionally distinct regions with an integrative area in aSMG, and technical reasoning (selecting the correct tool on the basis of abstract mechanical knowledge) in area PF (Osiurak et al., 2020; Reynaud et al., 2016). Both approaches stress the importance of premotor cortices and the VD stream in tool use processing, the key difference is the representations contained within IPL.

A recent review of neuroimaging, stimulation and lesion studies has questioned the role of aSMG in supporting the integration of semantic information, reasoning, and somatosensory feedback to support tool use actions (Lesourd et al., 2021). In particular, TMS studies have highlighted that disruption in SMG results in impairments in judging manipulation compatibility between two objects (Andres et al., 2013; Pelgrims et al., 2011), but not with hand-object compatibility (Pelgrims et al., 2011). This suggests that SMG is not critical for hand-object compatibility judgements and is thus not systematically impaired following lesions. Specifically, participants viewed pairs of images and performed conceptual judgements, which included contextual judgements (e.g., are a compass and a set square used in the same context?) and functional judgements (e.g. do a knife and a fork work together to achieve a common goal?). Additionally, participants performed manipulation knowledge judgements, such as hand configuration judgements (e.g., is the same hand posture required to use the two objects?) and hand-object judgements (is the presented hand posture compatible with the given object?). Reaction times were longer for hand configuration judgements, but not conceptual judgements or object-hand judgements, following TMS to SMG (Andres et al., 2013; Pelgrims et al., 2011). This suggests that SMG plays a specific role in tool manipulation, but not necessarily conceptual processing of tools, or manipulation judgements in the presence of images of hands.

However, IPL damage can impact hand-tool interactions, as observed in individuals with apraxia (Buxbaum, 2001) and is activated during fMRI when judging hand-tool compatibility (Kleineberg et al., 2018). Moreover, virtual lesions to SMG impairs the planning and execution of functional grasps to presented tools (McDowell et al., 2018; Potok et al., 2019). Therefore, Pelgrim et al.'s (2011) findings may be due to task requirements, for example judging object-hand compatibility from presented images may be a more perceptual shape matching task, rather than activating motor representations associated with the object (Lesourd et al., 2021). Put together, SMG appears to be a region supporting manipulation knowledge of tools (i.e., how a tool is grasped and moved for its use).

pMTG on the other hand is thought to be responsible for conceptual knowledge of tool tasks. Interestingly, a TMS study provided evidence of a double dissociation between SMG and pMTG, where TMS to pMTG impaired judgements on conceptual compatibility tasks but not on hand configuration judgements, with the opposite pattern observed following TMS to SMG (Andres et al., 2013). However, pMTG is also activated in response to judging manipulability of tools as well as conceptual judgements (Boronat et al., 2005; Kellenbach et al., 2003), and when pantomiming tool use (Johnson-Frey et al., 2005). Lesourd et al. (2021) suggested that this region may therefore represent the integrative hub between conceptual and manipulation tool knowledge, rather than SMG. However, they pointed out that it is unlikely that pMTG is the sole critical region for this, particularly as lesion studies highlight that IPL is critical for representing manipulation knowledge associated with tools (Ishibashi et al., 2016; Martin et al., 2017; Reynaud et al., 2016). Research has highlighted that structural connectivity exists between pMTG and IPL (Caspers et al., 2011; Vry et al., 2015), while passive viewing of tool images has been shown to lead to an increase in functional connectivity between pMTG/lateral occipitotemporal cortex (LOTC) and IPL (Chen et al., 2018; Garcea et al., 2018). This suggests that both conceptual and manipulation tool knowledge may involve reciprocal connections between pMTG and IPL (Lesourd et al., 2021).

Gallivan et al. (2013) conducted a study where participants planned and executed reach or grasp movements with either the hand, or a tool in hand. MVPA revealed that SMG and pMTG coded upcoming movements only with the tool in hand. This suggests that object-directed actions with a tool in hand are specifically represented in these interconnected regions. Using a wider range of 3D tools, Brandi et al. (2014) had participants use or move tool objects, or neutral ‘bars’ matched for colour and handle width. Activation was higher for use actions performed with a tool (vs a bar) in VD regions, PMv, SMG, pMTG, highlighting this network as particularly important for tool use. In addition, DD regions (SPL, PMd) were more activated during use actions than move actions, which is possibly due to the increased online control required in use actions. Interestingly, LOTC also exhibited higher activation for use compared to move actions, similar to what was observed in the DD regions (Brandi et al., 2014). Put together, it appears that the ventral, VD, and DD streams work together to achieve sophisticated tool use, with each stream specialising in conceptual knowledge, functional manipulation, and online visuomotor control respectively.

Overall, converging evidence from neuropsychological, neuroimaging and primate studies have provided evidence for the presence of a ventral stream responsible for visual perception, and a dorsal stream responsible for visually guided action. Complementary to the TVSH, the dorsal stream also appears to be subdivided into a DD stream responsible for visually guided reaching and online visuomotor control, while the VD stream concerns skilled movements, such as how to use tools (Binkofski & Buxbaum, 2013; Rizzolatti & Matelli, 2003). While Milner and Goodale’s (1992, 1995, 2006) model distinguishes the ventral and dorsal stream by their end goal (i.e. perception and action), research has highlighted several other key differences between the two visual streams.

1.5. How do the Two Visual Streams Differ?

1.5.1. Metrics and Timings

A key argument of the TVSH is that visual processing for perception in the ventral stream, and action in the dorsal stream require different transformations of visual input, and that the timings of these computations differ depending on the context. Milner and Goodale (1995, 2006) proposed that visuomotor representations in the dorsal stream decay rapidly and thus only allow for the control of immediate actions under visual guidance. This was based on the logic that only current spatial relationships between the observer and goal are relevant to performing successful interactions. The ventral stream, on the other hand, can inform working memory representations which enable long term memories of visual input to be formed. Therefore, the ventral stream is critical in storing visual information required when actions are based on previous information. Based on these assumptions, one would predict that patients with ventral stream lesions would be impaired in visuomotor tasks following a delay, while those with dorsal stream lesions may demonstrate improved performance in delayed reaching tasks.

Neuropsychological case studies have provided evidence that perceptual deficits can indeed affect actions under a time delay. For example, patient DF has been shown to exhibit impaired grip scaling to objects which have been removed from view following a two second delay, despite intact performance in tasks requiring immediate action towards the same objects (Goodale, Jakobson, et al., 1994; Rice et al., 2006). This was interpreted as evidence that DF was unable to perceive the object dimensions and thus store them in her visual memory to guide her future movements. DF was also unimpaired at pantomiming grasps of familiar objects, despite no delay in this task, this was assumed to be due to her ability to recall the size information stored in long-term, semantic memory (Goodale, Jakobson, et al., 1994). On the other hand, evidence of the opposite behaviour in those with dorsal stream lesions has provided support for this fast/slow distinction. For example, optic ataxic patient AT was unable to grasp unfamiliar objects, making awkward grips, but this was markedly improved when grasping familiar objects (Jeannerod et al., 1994). This demonstrates that while on-line visuomotor control may be compromised, due to a damaged dorsal stream, familiar object representations can be accessed from long term memory to program the action. Further neuropsychological evidence has found that optic ataxic patients' reaches to targets are markedly improved when a delay is introduced between the target and the movement (Milner et al., 2001; Revol et al., 2003), suggesting that the ventral stream may play a role in the 'offline' guidance of movements.

Interestingly, fMRI research has shown that LOTC and V1 are reactivated when performing delayed actions towards remembered targets in the absence of any visual stimulation, further suggesting that the ventral stream may be re-recruited to provide relevant information about object properties to guide memory-guided action (Singhal et al., 2006, 2013). Put together, Goodale et al. (2004) argued that the dorsal stream operates in 'real-time', taking visual signals into account during movement planning, while the ventral stream creates the object representations to be stored in memory to control later actions.

Behaviourally, the kinematics of immediate and delayed reach and grasp movements in healthy individuals also differ. The two second delay imposed in the study by Goodale, Jakobson, et al. (1994) showed that delayed movements are usually slower, while changes in grip aperture throughout the movement did not elicit the same 'overshoot' that is often observed in visually guided grasping. Further behavioural studies have corroborated this during reach to grasp movements in the dark, thus without visual feedback of the hand or object (Hu et al., 1999). Healthy individuals also show reduced accuracy and increased end-point variability following a delay, possibly because the ventral stream is utilised in delay conditions which is not optimised for visuomotor control (Westwood et al., 2001). These findings provide evidence that stored visual information, possibly stored in the ventral stream, is responsible for driving these delayed actions, rather than an online visuomotor analysis of the target object.

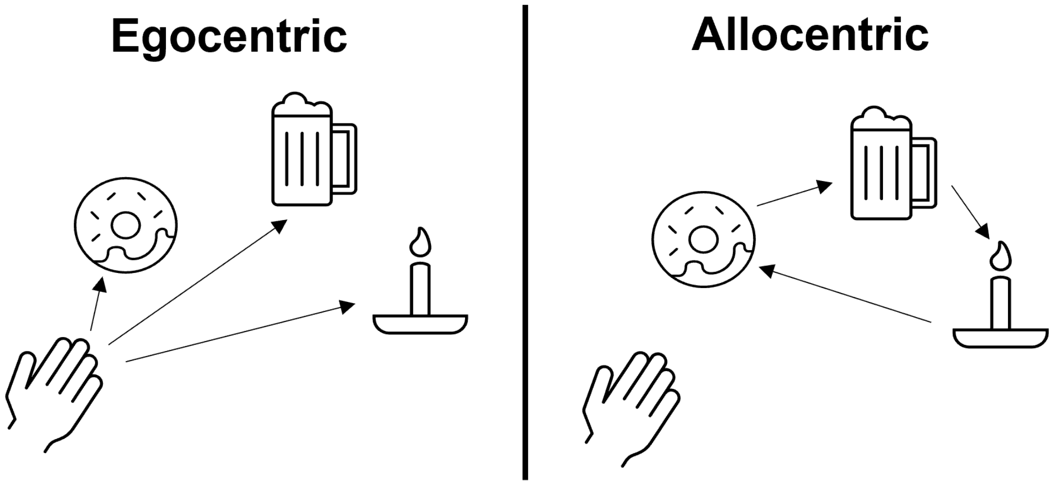
Given the 'fast' nature of the dorsal stream in visuomotor control, many researchers have investigated the neural underpinnings of the ability to make fast online corrections to target jumps during reaching. In double step reaching paradigms, participants are instructed to reach towards targets which are then sometimes displaced once the movement has commenced. The kinematic profile of healthy adults performing such paradigms suggests that there is a smooth movement trajectory following the target position change, with no abrupt changes in velocity profile, and these corrections typically occur 100-150ms following a change in target position (Desmurget et al., 1999; Goodale et al., 1986; Prablanc & Martin, 1992). Therefore, it is thought that these fast corrective movements are conducted without reprogramming the hand movement, are automatic, and escape intentional control (Gréa et al., 2002; Pisella et al., 2000).

Neuropsychological studies have found that optic ataxic patient IG is impaired at making online corrections to target jumps, instead reaching to the initial target location, suggesting that the dorsal stream may be responsible for the ‘fast’ online monitoring of visually guided movements (Gréa et al., 2002; Pisella et al., 2000; Rossetti et al., 2003). Moreover, as the bias was towards the initial target location, this suggests that those with dorsal stream damage but a spared ventral stream utilise ‘offline’ processing for visuomotor control (Rossetti et al., 2005). Further studies have highlighted impaired immediate visuomotor performance despite intact delayed performance in individuals with optic ataxia, for example impairments in obstacle avoidance, reaching, grasping, and saccades (Himmelbach & Karnath, 2005; Milner et al., 2001; Rice et al., 2008; Schindler et al., 2004). Moreover, TMS in healthy individuals to the PPC, particularly aIPS, leads to impairments in the online control of both reaching and grasping (Desmurget et al., 1999; Reichenbach et al., 2011). On the other hand, TMS to LO, but not PPC, affects kinematics of delayed reaches (Cohen et al., 2009).

1.5.2. Frames of Reference

Another key difference between the ventral and dorsal visual streams is the frame of reference utilised for spatial coding in each pathway. The dorsal stream is thought to compute coordinates in an egocentric frame of reference, whereby an object’s position is coded relative to the observer. This is thought to enable the fast programming of visually guided movements as the coordinates are computed in absolute metrics which is functionally advantageous when interacting with objects at a given time. On the other hand, the ventral ‘perception’ stream does not require information about the location of objects with respect to the self and rather computes object location in relation to other external landmarks in the scene, allocentric coordinates (Goodale, 2008; Goodale & Haffenden, 1998; Milner & Goodale, 2008; see Figure 1.2). Rather than absolute metrics, size and distances of the perceptual scene are coded relative to one another (Milner & Goodale, 2006; Schenk & McIntosh, 2010). This is a much more relevant way of encoding the visual scene for perception and memory of the external world. Research has shown that while DF was successfully able to guide two of her fingers into a disk with two holes, she was impaired when the task required three fingers and three holes (Dijkerman et al., 1998). This suggests that allocentric processing, even when guiding a motor response, requires a working ventral visual stream.

Figure 1.2 *A figure to show how objects are represented in egocentric and allocentric frames of reference.*



Some have argued that rather than two streams for perception and action, the key difference between the two streams regards the frame of reference they operate in. For example, Schenk (2006) argued that DF’s preserved ability to insert a card into a slot was achieved due to her ability to utilise a hand-centred egocentric representation of space. On the other hand, her impairment in perceptually matching the card and orientation of the slot, was due to the task requiring the use of allocentric representations. In support of this suggestion, Schenk (2006) reported findings from separate perceptual and visuomotor tasks completed by DF utilising either allocentric or egocentric information. In egocentric tasks, DF was required to point to a target from a given start position (visuomotor), or judge which of two dots was closest to the hand location (perceptual). In allocentric tasks, a target was presented at different distances from a cross. The visuomotor task required DF to begin movements at a separate start position, then reach to a position in space which mimicked the relative position of the target dot with respect to the cross. In the perceptual allocentric task, DF was required to judge which of two dots was closer to the cross. Remarkably, DF’s perceptual ability was similar to controls in the egocentric, but not allocentric perceptual task, while her visuomotor performance in the allocentric task was impaired. These findings highlighted that the crucial determinant of DF’s performance was the spatial mode, rather than the task (perceptual vs visuomotor) and questioned the traditional perception-action account. In response to this finding, it has been suggested that DF may have used a non-perceptual strategy, such as imagining pointing movements to each of the dots in the egocentric perceptual task (Milner & Goodale, 2008). Milner and Goodale (2008) also argued that the allocentric visuomotor task employed in Schenk's (2006) study was more of a manual, rather than verbal, report of her perceptual experience. Thus, caution needs to be made when interpreting the processing engaged when participants perform tasks.

The utilisation of egocentric and allocentric reference frames have been investigated behaviourally in neurologically intact individuals. In a reaching task, Thaler and Goodale (2011b) had participants reach from a start point to a target (egocentric), and to reach from a start point mimicking the distance and orientation between two visually presented reference targets. In the latter task, participants had to program their movements based on allocentric visual information. Participants were slower to initiate reach movements in the allocentric reaching task, which was taken as evidence that allocentric visuomotor performance depends on the slower ventral visual stream (Thaler & Goodale, 2011b). In line with these findings, fMRI research employing the same paradigm revealed that the allocentric task led to increased activation in LOC compared with the egocentric task, suggesting that the ventral stream is recruited for hand movements in allocentric conditions (Thaler & Goodale, 2011a).

fMRI research has supported a ventral-dorsal distinction in the representations of space in more perceptual tasks. Activation in dorsal stream regions including SPL, IPS and PMd has been consistently found in tasks requiring participants to make egocentric judgements, for example judging the relative position of stimuli with respect to the self (Committeri et al., 2004; Galati et al., 2000; Neggers et al., 2006; Zaehle et al., 2007). On the other hand, judging relative position of stimuli with respect to other objects more consistently activates ventral stream regions, including bilateral FG and LO, and also extending to hippocampal regions (Zaehle et al., 2007). Hippocampal place cells have consistently been shown to fire in specific spatial locations independent of the observer's orientation (Ekstrom et al., 2003). In line with propositions of different timings in the ventral and dorsal streams, there is a functional role for the processing of different frames of reference. Egocentric spatial maps of the environment have to be continuously updated as a result of head and eye movements, and is thus an online spatial updating process (Avraamides & Kelly, 2008). However, we are also able to build stable spatial representations based on the allocentric reference frames which can then be responsible for offline spatial updating.

1.5.3. Visual Field

Interestingly, research has also shown that there are asymmetries in the representations of different areas of the visual field (VF). This has been proposed as a feature of survival, given that most of the visual information we encounter is situated in the lower, compared to the upper VF. Previc (1990) suggested that vertical VF asymmetries in the representation of space represent a possible ventral-dorsal stream difference in the perceptual and motor processing that typically occurs in different areas of space. For example, the dorsal stream, which overrepresents the lower VF, is specialised for actions which are carried out within reach (peripersonal space). While the upper VF, was proposed to be specialised for visual scene processing (including visual scanning and search) and thus subserved by the ventral stream. Behavioural research has provided some support for this possible distinction. In particular, there is a lower VF advantage in spatial memory tasks (Genzano et al., 2001), while visually guided reaching movements have been shown to be faster and more accurate when performed in the lower, compared to upper, VF (Danckert & Goodale, 2001; Khan & Lawrence, 2005; Rossit et al., 2013; Stone et al., 2019). Others have found evidence of decreased end-point variability in visually guided reaching and grasping paradigms, but no evidence of timing or accuracy advantages in the lower VF (Binsted & Heath, 2005; Brown et al., 2005; Krigolson & Heath, 2006). This suggests that, while there may not be an advantage in the online control of actions, there may be lower VF spatial advantages possibly at the planning stage of movement.

At a neural level, this distinction is supported by evidence of asymmetric representations of the lower and upper VFs in the ventral and dorsal pathways (Curcio & Allen, 1990; Galletti, Fattori, Gamberini, et al., 1999; Previc, 1990; Rossit et al., 2013). In particular, the dorsal area of V1 represents the lower VF and projects to the dorsal stream, while ventral V1 represents the upper VF and projects to the ventral stream (Previc, 1990). Therefore, there are more projections from the lower VF in the PPC of the dorsal stream. In both primates and humans, area V6A represents largely the peripheral visual field, with a greater representation of the lower, compared to upper, VF (Galletti, Fattori, Gamberini, et al., 1999; Stenbacka & Vanni, 2007). Additionally, the density of cone and ganglion cells in the retina is approximately 60% higher in the lower, compared to upper VF (Curcio & Allen, 1990). In line with Previc's (1990) lower VF specialisation for action, Gallivan et al. (2009) found that SPOC and precuneus are more activated when stimuli are presented within reach, compared to out of reach, even when no action was carried out. While Rossit et al. (2013) found greater activation in these regions only when reaches were executed in the lower VF. The evidence therefore suggests that there is a greater representation of the lower VF in the dorsal visual stream which makes it specialised for action. Behavioural evidence has recently shown that up to 70% of our daily actions are performed in the lower VF (Mineiro & Buckingham, 2023). This is in line with the suggestion that the lower VF may be advantageous in tasks using stationary attention and visually guided reaching, but the upper visual field may be specialised for attention shifting (Danckert & Goodale, 2003).

Despite this, there is conflicting evidence as to whether there is an upper VF advantage in visual perceptual tasks, such as visual scanning which would be predicted under Previc's (1990) model. If there was a specialisation for each of the streams in processing the upper and lower VFs, one would expect evidence of a dissociation and thus advantages for perceptual tasks in the upper VF. For example, some research has indicated that visual search times are reduced, particularly in the upper right VF (Previc & Blume, 1994; Previc & Naegele, 2001), while others have not found such distinction (Walsh & Ellison, 2001). Moreover, LO does not appear to represent the upper and lower VFs differently, with similar populations of neurons representing the upper and lower VFs (Large et al., 2008). However, it has been suggested that the discrepancies may arise from the frame of references specialised for each of the VFs. Research has in fact provided some evidence for a egocentric reaction time facilitation in the lower VF, and allocentric facilitation in the upper VF, consistent with a ventral-dorsal specialisation for the upper and lower VFs respectively (Sdoia et al., 2004; Zhou et al., 2017).

1.6. Do the dorsal and ventral visual streams work together?

What has become evidently clear through my literature review thus far is evidence that the two (or three) visual streams collaborate with each other to perform relevant tasks. That is the ventral 'perception' stream does influence actions, while the dorsal 'action' stream in turn influences perception. Indeed, in developing the TVSH, Milner and Goodale (1995) never denied that the two visual streams cooperate to achieve their respective goals, however much of the research investigating the contributions and representations within each stream focuses on a perception/action dichotomy.

Many researchers for instance have argued that optic ataxia is not a specific visuomotor deficit. For example, many individuals with optic ataxia can still complete day to day visuomotor tasks particularly in central vision. Some have argued that the dorsal stream contains separate regions for visuomotor functioning in central and peripheral vision, for example, fMRI has identified the parieto-occipital junction (POJ) as a region which is activated when reaching in peripheral vision specifically (Prado et al., 2005). However, others have suggested that POJ and its connections are specifically involved in the ability to decouple movements with the eye and hand. This is demonstrated in research in optic ataxia patient IG who, while unimpaired in central reaching, and reaching tasks in differing spatial planes, shows a specific impairment when the task required her to point in a direction opposite to the direction of her saccade (Pisella et al., 2009). This has been observed in a number of patients with optic ataxia where they typically reach to a location in between the target and gaze direction, even when visual feedback is presented in a rotated manner (Blangero et al., 2010; Rossetti et al., 2005). Some have therefore argued that the dorsal stream is more specific to peripheral vision rather than simply vision-for-action (Pisella et al., 2009).

As discussed in previous sections, DF's ventral stream damage has also resulted in visuomotor impairments (e.g. Schenk, 2006). It is important to note that the classic dissociation between optic ataxia and visual agnosia has come from evidence using different paradigms. For example, while a visuomotor deficit characterises optic ataxia, this is mostly in peripheral vision (Perenin & Vighetto, 1988; Pisella et al., 2009; Rossetti et al., 2005), however, most of the evidence for DF's perceptual deficits have arisen from perceptual studies in central vision. Interestingly, when testing visuomotor performance in the peripheral visual field, researchers have shown that she exhibits misreaching and impaired online corrections similar to those observed in optic ataxia (Hesse et al., 2014; Rossit et al., 2018). Moreover, she demonstrates impairments in grip scaling for objects presented in the periphery (Hesse et al., 2012). This highlights DF may have visuomotor deficits associated with dorsal stream lesions, although this could be explained however by evidence of PPC damage, particularly in the right hemisphere (Bridge et al., 2013; James et al., 2003). It has therefore been argued that DF may not be an ideal candidate for demonstrating the effects of restricted ventral stream lesions (Hesse et al., 2012; Rossit et al., 2018).

On the other hand, perceptual deficits have also been identified in patients with optic ataxia. For instance, Rossetti et al. (2005) investigated reaching performance in two patients with optic ataxia. In the task, a target appeared, disappeared, and then reappeared in the same (congruent) or different (incongruent) location, participants were required to immediately point to the target after it had reappeared. They found that the patients with optic ataxia were heavily influenced in their reaches to the first target position, and the patients were unable to detect that the target had changed location, indicating the presence of a perceptual deficit in dorsal stream damaged patients. While there does appear to be evidence of a perceptual deficit here, this demonstrates how those with dorsal stream damage may have superior performance in performing visuomotor tasks under offline visual control which is subserved by the ventral stream (Rossetti et al., 2005).

While DF has a relatively intact ability to reach and grasp objects based on their physical properties, some research has highlighted that she does this in a manner that is not compatible with their acquired usage (Carey et al., 1996). In line with the finding that she demonstrates impairments orientating more complex objects to slots (Goodale, Jakobson, Milner, et al., 1994), these findings clearly highlight that her perceptual deficits may well result in impaired actions. fMRI functional connectivity research has found that tool manipulation knowledge in IPL in the VD stream relies on inputs from the ventral stream (Almeida et al., 2013). Further connectivity studies have highlighted increased functional connectivity between LOTC in the ventral stream and IPL in response to viewing tool images and pantomiming their use (Garcea et al., 2018; Hutchison & Gallivan, 2018). Therefore, it is important that we consider how the two streams work together to achieve their purpose, rather than considering them as isolated entities.

1.7. Normal and Pathological Ageing of Perception and Action

The classic deficits associated with dorsal and ventral visual stream lesions have provided significant insight into the functions of the streams regarding perception and visuomotor control. However, much of this research is based small sample sizes and case studies with lesions affecting a variety of regions (Karnath & Perenin, 2005; Milner et al., 2003). While these studies have provided valuable insights into visual stream related deficits and how they can be assessed, there may be other contributions, such as age, and larger groups with neurodegenerative conditions which could also lead to similar impairments. Indeed, naturally occurring lesions never fit the precise boundaries anatomically, thus there is not a precise complete lesion of either streams. As noted previously, while research with patient DF has been at the forefront of the TVSH, her lesions are not restricted entirely to the ventral stream which limits the generalisability of these findings. Indeed, it may be more appropriate to examine impairments in larger populations.

Healthy ageing is associated with declines in multiple areas of cognitive functioning (Grabowski & Mason, 2014), possibly due to progressive decline in brain volume which is thought to rapidly increase in rate at the age of 70 (Scahill et al., 2003). In particular, the ability to integrate information from multiple sensory modalities is thought to be reduced with age (Chaput & Proteau, 1996). Older adults have been shown to rely more heavily on visual information during reaching and grasping, for example older adults travel for a shorter distance before a change in target location and spend longer in the correction phase of movement compared to young adults (Pratt et al., 1994). Older adults have also been shown to reach and grasp more slowly and with greater final adjustments particularly when visual feedback is removed (Coats & Wann, 2011; Rossit & Harvey, 2008; Runnarong et al., 2019). This suggests that older adults rely more heavily on visual information during movements. Interestingly, a recent meta-analysis has found additional recruitment of the occipital lobe in older, compared to young, adults which the authors hypothesised could be due to additional mental visual imagery strategies engaged to perform visuomotor tasks (Zapparoli et al., 2022).

In addition to visuomotor performance variations, older adults also exhibit differences in automatic goal-directed movements. Research assessing performance in the double step paradigm has also found that older adults take longer to correct their movements in response to target changes (Rossit & Harvey, 2008; Sarlegna, 2006), however this may be a compensatory strategy to preserve accuracy (Rossit & Harvey, 2008). A number of studies assessing visually guided reaching has further found that ageing is associated with the slowing of reach movements, but spared accuracy, known as a speed accuracy trade-off (de Bruin et al., 2016; Rubinstein et al., 2014). Additionally, older adults increase their grip aperture during reach to grasp tasks, suggestive of another compensatory strategy (Grabowski & Mason, 2014). In line with this, EEG research has found that older adults performing visually guided reach movements recruit more widespread areas of the PPC and ipsilateral brain regions compared to younger adults, possibly reflecting a compensatory strategy to maintain accuracy (Labyt et al., 2004).

While it appears that visuomotor performance generally declines with increasing age, a growing body of research has been highlighted that visuomotor performance may also be specifically impaired because of neurodegenerative disease, such as dementia. Alzheimer’s disease (AD) is the most common form of dementia and is typically associated with observable memory decline, such as an inability to retain new information. Age is the most significant risk factor for the development of AD (Wang et al., 2008). Briefly, the pathological hallmarks of AD include the build-up of amyloid-beta (aβ) plaques, and neurofibrillary tangles caused by accumulating tau proteins which ultimately results in synaptic dysfunction and neuronal death (Jack et al., 2018). The medial temporal lobes, generally accepted as regions responsible for storage and retrieval of memory, have been frequently noted as particularly susceptible to AD pathology (Braak & Braak, 1991; Schöll et al., 2016). However, research shows that AD-related pathology may be present many years, even decades, before the onset of observable symptoms (Bateman et al., 2012; Becker et al., 2011; Jack et al., 2018; Mattsson et al., 2009). Additionally, dorsal stream regions in the PPC, particularly the precuneus, have been identified as regions exhibiting structural and functional abnormalities at an early stage of the disease (Jacobs, Van Boxtel, et al., 2012). It is therefore possible that people with AD-pathology may demonstrate impairments in visuomotor functioning associated with the dorsal stream.

While memory deficits are the most common area for behavioural research in AD, a growing body of research has investigated visuomotor performance, typically associated with the dorsal stream, in AD and MCI. In an early study, Ghilardi et al. (1999) found that people with AD were slower than controls to reach to targets under visual guidance, while they were more inaccurate in the absence of visual feedback, particularly at the end stage of the movement. This was interpreted as evidence that those with AD are particularly impaired in sustaining ongoing motor plans, having to therefore rely heavily on remembered spatial coordinates to maintain their limb control (Ghilardi et al., 1999). However, in comparison to age-matched controls, people with AD are typically slower to initiate and execute reaching movements, particularly when visual feedback is provided in increasingly dissociated spatial planes (Bartoli et al., 2017; Rogojin et al., 2019; Tippett et al., 2007, 2012; Tippett & Sergio, 2006). Similar studies have also identified deficits in those with MCI, considered a prodrome of AD, although deficits in plane dissociation tasks are restricted to the planning phase (longer reaction times), rather than both planning and execution (Salek et al., 2011). Additionally, timings and accuracy in plane dissociated tasks have been shown to discriminate between low-risk and high-risk of AD older adults (Hawkins et al., 2015; Hawkins & Sergio, 2014). Therefore, in tasks which don’t require a memory component as such, as visual feedback is provided, people with AD exhibit impairments in the ability to plan and sustain their motor plans after movement initiation. This also appears to be the case in preclinical populations.

Recently, Lu et al. (2021) assessed visuomotor integration preclinical AD (defined by the presence of amyloid protein) using a circle tracing task which had previously been used to assess the early stages of Huntingdon's disease (Say et al., 2011). Here participants traced the outline of a circle as quickly and as accurately as possible for 45 seconds. In direct conditions, they traced directly over the presented circle and can view their hand and tracing line. In plane dissociated (indirect) conditions, the circle is presented in a different spatial plane, and they have no visual feedback of the hand. Amyloid-positive, and therefore at risk of AD, participants were particularly slower and less accurate in plane dissociated conditions. This was found to correlate with white matter hyperintensity volume (Lu et al., 2021). Put together, a substantial body of research has found that people with AD, MCI and preclinical AD are particularly impaired in tasks requiring additional visuomotor transformations to accommodate differing spatial planes.

A possible explanation as to why people with AD may be particularly affected by plane dissociated tasks is that they may require a transformation of allocentric to egocentric coding. The egocentric frame of reference is thought to be adopted at an earlier stage of development than allocentric, with full maturation of allocentric frames during school ages. Some argue that there is an age related deficit in switching between the two reference frames, rather than specific allocentric impairments (Harris & Wolbers, 2014; Morganti & Riva, 2014). Indeed a meta-analysis of the effect of ageing on egocentric and allocentric navigation suggests that there is a preservation of egocentric strategies in spatial navigation but a specific deficit in allocentric spatial navigation strategies (Caffò et al., 2020). Studies comparing the performance of typically ageing older adults and those with MCI and AD seem to demonstrate a deficit involving both egocentric and allocentric reference frames in AD and MCI, but more involvement in allocentric frames of reference (Serino et al., 2014). Egocentric decline appears to more disease specific, given the role of the precuneus in egocentric frames of reference.

Further research has found that performance in hand eye coordination tasks is impaired in AD, in particular people with AD are unable to suppress eye movements towards targets to be reached, suggesting that people with AD are unable to inhibit automatic responses, such as looking towards a target (Verheij et al., 2012). Interestingly, we recently conducted research investigating reaching to targets under free and peripheral vision. Our hypothesis was that the susceptibility of the PPC to AD-related pathology could lead to impairments in visuomotor control in peripheral vision similar to that observed in optic ataxia. While no deficit was observed in reach accuracy in free or peripheral vision, we did observe increased movement times in the clinical groups, characterised by an extended deceleration phase (Mitchell et al., 2022). This suggests that patients with AD and MCI may have a reduced efficiency in feedback-based control, or that initial movement programming is impaired thus an increased reliance on visual feedback towards the end of movement is required. Overall, it is possible that people with AD and MCI may exhibit visuomotor impairments because of dorsal stream vulnerability to the disease. In particular, the research suggests that the ability to monitor movements online may be slowed, and moreover translating representations from allocentric to egocentric may also be impaired.

1.8. Current Projects

Overall, a growing body of evidence has highlighted the tight interplay between the ventral 'perception' streams, VD 'use' streams, and DD 'grasp' streams. In Chapter 2, I assessed the tight link between perception and action using a classic stimulus-response compatibility paradigm. Tucker and Ellis (1998) attributed speeded response times in trials where handles were facing the hand used to respond to an irrelevant task (a handle compatibility effect) to the automatic potentiation of motor representations afforded by the presented objects. The contributions of affordances to this SRC-paradigm has been the subject of much debate (see Chapter 2). Therefore, in Experiment 1, I designed a well powered and controlled replication of the classic Tucker and Ellis (1998) paradigm. In addition, the effects of VF on the SRC paradigm had never previously been investigated, thus I designed Experiment 2 to examine whether there was an advantage for affordances in the lower, compared to the upper, VF, given the overrepresentation of the lower VF in reach and grasp regions of the dorsal stream (see *Visual Field*). The methods and analysis plan of this experiment series were peer reviewed prior to data collection and accepted as a registered report. I hypothesised that we would observe a handle compatibility effect, and that this effect would be reduced when participants made low-level judgements about objects which are not thought to elicit affordances in this case. This would demonstrate that affordances do indeed contribute to the handle compatibility effect. Secondly, I hypothesised that there would be a greater handle compatibility effect in the lower, compared to upper VF, as there is an overrepresentation of the lower VF in the dorsal visual stream primed for action.

In Chapter 3, I investigated what regions within the ventral, VD, and DD streams represent in response to viewing images of manipulable tools or pantomiming their use. Specifically, it is unclear whether activation observed in DD and VD regions in response to viewing tools which has been demonstrated in numerous univariate experiments, reflects a general motor response, or specific action components related to the tools' use (i.e. how you would move the hand to use them). Moreover, whether these representations are task and modality specific remains elusive. Therefore, in Experiment 3, I conducted a secondary MVPA analysis on a pre-existing fMRI dataset from a task where participants were required view tool images, which were closely matched in terms of their low-level properties, such as orientation, colour, size, and pantomime the tool use in response to viewing the tool word without visual feedback of the hand. Firstly, I conducted a region of interest (ROI) based analysis focussing on category selective areas of the tool network based on each participant's activity in an independent visual localiser (Bracci et al., 2012; see Chapter 3). Secondly, I used a whole-brain searchlight approach. I hypothesised that tool use actions would be represented in the VD stream (e.g. SMG, pMTG) and, to some extent, the DD streams, from simply viewing tool images, as well as pantomiming, due to evocation of tool affordances. On the other hand, I expected visual, but not action, properties of tools to be represented in the ventral perception stream during tool viewing, but not pantomiming. Overall, our MVPA analysis sought to answer these questions: A) does MVPA allow us to reliably decode tool identity and/or tool use actions within tool and/or hand processing brain regions? B) in which regions of the brain can we reliably decode both tool identity and/or tool use actions? C) within those overlapping regions, can we cross-classify tool picture viewing by training on executed tool use pantomimes and vice-versa?

Finally, in Chapter 4, I investigated how individuals with possible dorsal stream degeneration due to AD and MCI, performed in a novel portable reaching task. In Experiment 4, I assessed how the frame of reference utilised (see Frames of Reference) may still affect visually guided reach movements in neurodegenerative conditions, even in the absence of a memory-based task. While in Experiment 5, I investigated whether AD and MCI was associated with impaired online corrections (see Metrics and Timings). I hypothesised that the clinical group would take significantly longer to correct movements based on a target jump, and that action based on allocentric processing may be particularly affected in the clinical group due to ventral, and dorsal, stream damage. Put together, this thesis aims to provide further evidence of a tight link between perception and action, as well as providing further insight into the specific representations contained within the ventral, VD and DD streams.

2. Chapter 2 - Is there a lower visual field advantage in object affordances?: A registered report.

Published in Quarterly Journal of Experimental Psychology on 26th January 2024 (Warman et al., 2024).

In everyday life, we are surrounded by thousands of objects that afford different types of interaction. For example, a spoon affords grasping, whereas a bed might afford lying. According to one of the most influential models of perception, when we look at an object, we not only process its colour, shape and size, but we also automatically perceive the potential action it affords, even before we act (Gibson, 1979). Much of the behavioural evidence expanding on Gibson's concept of affordance stems from the highly influential Tucker and Ellis (1998) handle compatibility effect which has been cited over 1500 times at the time of writing this thesis. The handle compatibility effect is characterised by faster reaction times (RTs) when the handle orientation of graspable objects is compatible with the hand used to respond, even when handle orientation is task irrelevant (see also Tucker & Ellis, 2001, 2004). Tucker and Ellis (1998) attributed the speeded RT for compatible conditions to an automatic triggering of a motor representation afforded by the object's handle (such as reach-to-grasp) and thus refers to a more representational account of affordances.

In line with this, several neuroimaging studies have reported that simply viewing graspable objects activates sensorimotor brain regions typically associated with reaching, grasping, and using objects (e.g., Chao & Martin, 2000; Creem-Regehr & Lee, 2005). In fact, we have recently reported that hand-selective visual areas in occipito-temporal and parietal cortices automatically encode how to grasp tools correctly for use (i.e., by their handles), even in the absence of subsequent tool use (Knights et al., 2021). This is interpreted as evidence that affordances are elicited even when there is no intent to act.

While the Tucker and Ellis (1998) handle compatibility effect has been widely replicated using various task manipulations (Cho & Proctor, 2010; Pappas, 2014; Saccone et al., 2016; Tipper et al., 2006), whether it is solely explained by affordances remains a subject of controversy. Evidence has shown that compatibility effects are driven by spatial compatibility, and it has been argued that spatial compatibility, rather than object affordances, explains the handle compatibility effect (Cho & Proctor, 2010, 2011; Proctor et al., 2017; see Azaad et al., 2019). Specifically, a well-known finding is that RTs are faster when the relative spatial location of a stimulus is compatible with the location of the response (e.g., stimulus and response locations are both on the left) even when spatial location is task irrelevant, a phenomenon known as the Simon effect (Simon, 1969). For example, if the handle of a graspable object (e.g., frying pan) protrudes into the right side of space, the right-hand RTs will be faster due to spatial compatibility between stimulus and response, rather than affordances alone.

In line with the spatial compatibility view, studies have found that the handle compatibility effect is affected by how object stimuli are centred. Specifically, when stimuli are centred with respect to their base or pixel area (thus handles protrude further to one side) the handle compatibility effects are larger compared to when stimuli are simply centred by their width (Kostov & Janyan, 2020; Proctor et al., 2017). Moreover, Cho and Proctor (2011) conducted a study where participants responded to upright and inverted teapot silhouettes and reported compatibility effects towards the spout, rather than handle, of the teapots as the spout protruded further towards the response location. Despite this, others have argued that outer shape of an object alone (such as a silhouette) may not be sufficient to elicit affordances. For example, Pappas (2014) found compatibility effects for silhouettes both when judgements were made using two fingers within one hand (within-hand) or separate hands (between-hands) and attributed this to spatial compatibility. However, when participants responded either with two fingers of the same hand or separate hands to photographs, the handle compatibility effect only arose when participants responded with separate hands, indicative of an affordance effect. Pappas (2014) therefore suggested that depth information was critical to eliciting the affordance effects, although this inference has recently been the subject of controversy given the differing distance between response keys when participants responded with one hand to when they responded with both hands (Bub et al., 2021).

To dissociate affordances from Simon effects, several manipulations have been added to the Tucker and Ellis' (1998) upright vs inverted judgement task, such as colour judgements. The idea here is that successful performance on upright vs inverted judgements is considered to elicit affordances, whereas colour judgements depend solely on low-level visual processing, thus not requiring object recognition or affordances (Saccone et al., 2016; Symes et al., 2005). In line with this, it has been shown that handle compatibility effects are larger for judgements of upright vs inverted, semantic categorisation or object shape than for colour judgements

(Saccone et al., 2016; Symes et al., 2005; Tipper et al., 2006). This demonstrates that spatial compatibility does not fully contribute to handle compatibility effects, highlighting a likely role of affordances. Nevertheless, this stance remains debatable given that differences in handle compatibility effects between shape and colour judgement tasks have not been replicated (Cho & Proctor, 2012). Therefore, more research is needed to resolve the controversy surrounding the contribution of affordances to the handle compatibility effect.

Another manipulation used to investigate affordances is reaching distance. Several studies have reported that the handle compatibility effect is smaller, or even eliminated, when objects are presented in far (out of reach), as opposed to near (within-reach) space (Ambrosini & Costantini, 2013; Costantini et al., 2010, 2011). Moreover, Saccone et al. (2018) did not find a difference between near and far objects when 'far' stimuli were still within reach. These findings suggest that the handle compatibility effect depends on an individual's ability to interact with objects.

Interestingly, to the best of our knowledge, object position in the upper vs lower visual field (VF) has never been compared during affordance tasks. This is important since humans are more efficient at reaching and grasping stimuli presented in the lower VF than in the upper VF, suggesting a functional advantage for the lower VF in visuomotor control (e.g., Brown et al., 2005; Danckert & Goodale, 2001; Krigolson & Heath, 2006). At an anatomical level, several brain areas involved in visuomotor processing (such as V6 and V6A) over-represent the lower VF in both macaques and humans (Galletti, Fattori, Kutz, et al., 1999; Gamberini et al., 2011; Pitzalis et al., 2010). In fact, we and others have found that visuomotor brain areas (along the medial surface of the parieto-occipital cortex) were significantly more activated when participants reached and grasped objects presented in the lower VF relative to the upper VF (Maltempo et al., 2021; Rossit, McAdam, Mclean, et al., 2013). Altogether, these findings are consistent with the proposed specialisation of the lower VF for analysis and execution of visuomotor responses (such as grasping and tool manipulation) within peri-personal space (Danckert & Goodale, 2003; Previc, 1990). Thus, it seems reasonable to hypothesize that the visual field in which graspable objects are presented may also modulate handle compatibility effects, but this has yet to be investigated.

Therefore, we ran a detailed investigation of handle compatibility effects as well as investigating the effect of visual field in two well-powered pre-registered studies. In Experiment 1, we contrasted upright vs inverted and colour judgements to separate the contribution of Simon and affordance effects and address the debate in the field. We expected to observe larger handle compatibility effects for upright vs inverted judgements than the colour task (e.g., Saccone et al., 2016) which would suggest that affordances contribute to the effects observed. In Experiment 2, we investigated, for the first time, whether the handle compatibility effect varies between the upper and lower VFs. Specifically, participants were asked to perform upright vs. inverted judgements while fixating on one of two fixation positions allowing objects to be presented in the upper or lower visual field. Crucially, by manipulating fixation position rather than the position of the objects, the proximity between stimuli and hands did not differ across conditions. Given the evidence supporting a lower VF advantage for action (e.g., Rossit et al., 2013; Previc, 1990), we hypothesised that the handle compatibility effect would be larger in the lower VF compared to the upper VF.

To our knowledge, this is the first registered report to assess the contribution of affordances to the handle compatibility effect while controlling for spatial compatibility. Some research favouring an affordance account has been subject to failed replications (e.g., Bub et al., 2018; Cho & Proctor, 2012), however it is possible that these replication studies were underpowered, or the original studies did not provide enough transparency to allow a full replication. Moreover, much of the object-based stimulus response compatibility (SRC) paradigm literature has employed different methods, for example, number of stimuli, design differences, judgement tasks, sample size justification (or lack of), different exclusion criteria, outlier detection and analyses. This highlights the importance of pre-registering our methods and analysis plans and using a well-powered design. By including our novel experiment manipulating visual field, our entire study design is fully reproducible and replicable to allow for researchers to build on the experiment's findings in the future.

2.1. Methods

2.1.1. Power analysis

An a priori power analysis was performed using *MorePower 6.0.4* (Campbell & Thompson, 2012) to determine the sample size required. As we were looking for a specific interaction between our independent variable (task or VF) and handle compatibility, we performed our power analysis based on the interaction reported by Pappas (2014; experiment 2 - η_p^2 = .143). Pappas' (2014) experiment 2 used a 2 x 2 within-subjects design manipulating handle compatibility and, to separate affordances from spatial compatibility, response mode (within vs between hands) which closely reflects our experimental design. The power analysis revealed that a sample size of 66 was required to detect a task x compatibility or VF x compatibility interaction with 90% power and $\alpha = .05$. To allow for equal counterbalancing of blocks, we chose a sample size of 68 for each experiment.

2.1.2. Participants

Participants were recruited through the University of East Anglia undergraduate participant pool and given course credits for their participation. Each participant was required to only take part in one of the two studies. All participants were aged between 18 and 50. Participants who reported colour blindness, history of neurological disease, motor impairments or coordination disorders (e.g., dyspraxia) were excluded from the study. Participants were also excluded from analysis if they failed to complete the entire experiment. Excluded participants were replaced until the desired sample size was obtained. All participants provided informed consent in line with the protocol approved by the University of East Anglia School of Psychology Ethics Committee.

2.1.3. Stimuli and piloting

Stimuli were photographs of common household objects with handles affording a unimanual grasp, presented on a white background. Exemplars were identified from a normative dataset of 296 images extracted from the Bank of Standardized Stimuli (Brodeur et al., 2010; Lagacé et al., 2013) of which 91 exemplars were identified as having handles affording a unimanual grasp. Of the remaining exemplars, 47 were excluded due to not having a clear upright-inverted orientation (e.g., a whisk or potato masher has no clear upright orientation when lying horizontally on a table), and duplicates were removed. Thus, fresh images of the 43 object exemplars were photographed using a Nikon D60 camera, fixed onto a tripod slightly above the object, at 52 centimetres distance to provide depth perspective. Objects were photographed in their upright and inverted orientations with handles oriented to the right, 45° towards the camera. Photographs were cropped to exclude the background and flipped horizontally to create symmetrical left-oriented handled objects. All objects therefore appeared in two horizontal (left, right) and two vertical orientations (upright, inverted), resulting in four unique stimuli for each object. All stimuli were black and white for upright vs inverted judgements (Tucker & Ellis, 1998) and coloured red and green for colour judgements (Saccone et al., 2016). Images were resized so that all objects had the same height, while maintaining aspect ratio, and centred on a transparent background. Since we compared across tasks and VF, we chose to centre objects by their width, rather than base or pixel area (e.g., Cho & Proctor, 2010; Pappas, 2014), thus any effects due to object centring were constant across tasks. Importantly, while the depth cues varied across the vertical axis – upright versus inverted, these cues remained constant across tasks.

To ensure that the vertical orientation of our objects and their names were easily identifiable, we ran a small pilot study to select the final stimulus set. Ten participants were presented with the objects in all four orientations for 100ms at the fovea. Participants were asked to name the object, identify whether it was upright or inverted, and specify whether the upright/inverted judgement was easy or a guess. Based on the results, we removed sixteen objects as the upright/inverted accuracy was less than 90%. A further two objects were excluded as their upright/inverted orientation was guessed by more than 10% of the sample, and one object was excluded because it was incorrectly named by more than 10% of the sample. Where there were multiple exemplars of the same object (e.g., knife, steak knife, cheese knife), we included the exemplar that was most accurately judged without guesses. As a result, 20 objects were selected for the final stimuli set. The number of stimuli closely matched that used in Tucker and Ellis' (1998) experiment, however many previous experiments have used a very limited stimulus set (e.g., a single object stimulus; Cho & Proctor, 2011; Tipper et al., 2006). We chose a larger stimulus set to improve ecological validity and include objects with varying handle size and orientations to reduce the salience of handle location between trials. All stimuli are available on Open Science Framework https://osf.io/bp8kq/.

2.1.4. Apparatus

In both experiments, we used a SR Research (Kanata, Ontario, Canada) Eyelink 1000 Plus with a desktop mount system to record participants' eye gaze and monitor fixation. Monocular vision was recorded at a sampling rate of 500 Hz. Participants sat with their head on a chin rest at a fixed distance of 60 cm from a 24" BenQ XL2411Z monitor.

2.2. Experiment 1

Our first experiment sought to replicate the handle compatibility effect while controlling for the spatial compatibility which has previously been shown to influence compatibility effects (Cho & Proctor, 2010; Kostov & Janyan, 2020; Proctor et al., 2017). Using a within-participants design, participants responded with their left- or right-hand to whether the handled object was upright or inverted or, in separate blocks, whether the object was red or green. Unbeknown to participants, handles were oriented towards the same side as the correct response (compatible), or the opposite side (incompatible).

2.2.1. Participants

68 participants aged between 18 and 46 took part in experiment 1 (18 male; M_{age} = 20.8, *SD* = 4.32). Participants were recruited through the University of East Anglia undergraduate participant pool and given course credits for their participation. 60 participants were right-handed, 6 were left-handed and 2 were ambidextrous based on the Edinburgh Handedness Inventory (mean laterality index = 67.4, *SD* = 55.6).

2.2.2. Procedure

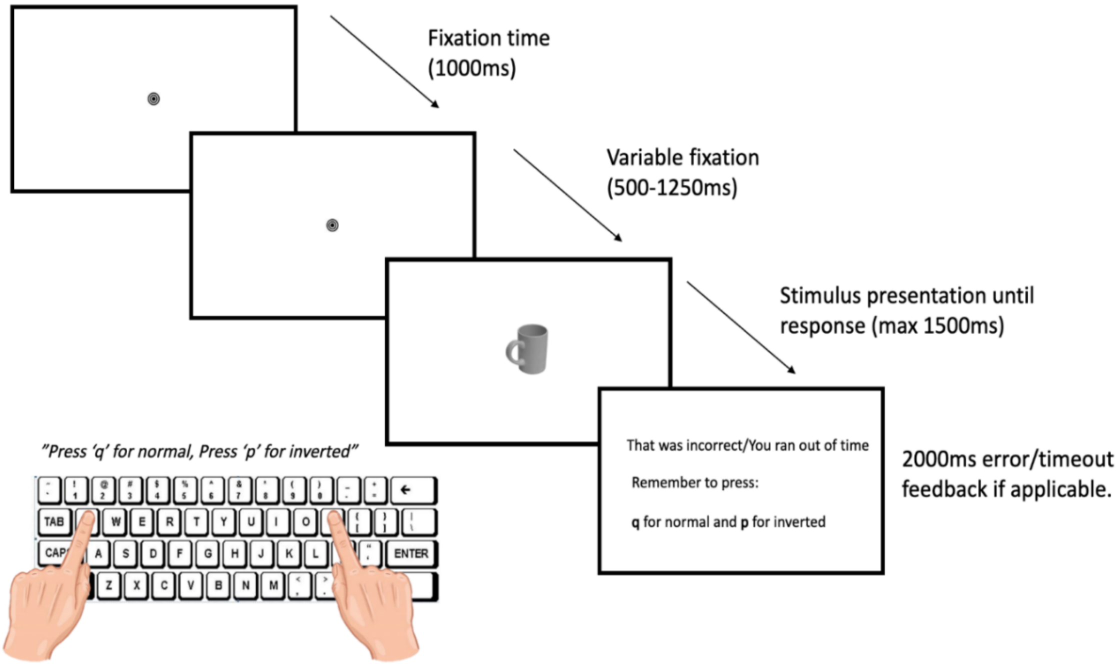
Following informed consent, participants completed a short demographics questionnaire to ensure they fulfilled the inclusion criteria. Following this, participants completed the eye tracking calibration procedure and the eye with higher spatial accuracy was selected for monocular recording.

In the main handle compatibility task, each trial began with a fixation bullseye (1°) presented at the centre of the screen for a fixed duration of 1000ms, followed by a variable delay of 500-1250ms (with a random delay of 250ms intervals). Then, a stimulus (maximum 15° x 5°) appeared in the centre of the screen until a response was made (maximum presentation time = 1500ms). In separate blocks, participants were asked to judge either whether the object is normal (upright) or inverted according to its canonical orientation or responded to the colour (red or green) by pressing either ‘q’ with their left index finger or ‘p’ with their right index finger on a QWERTY keyboard as quickly as possible. Note here that the task instructions used the term ‘normal’ instead of ‘upright’ to prevent any responses advantages due to the lexical similarity between ‘upright’ and objects presented in the ‘upper’ VF in our second experiment (Saccone et al., 2016). In addition, participants were required to maintain fixation throughout the trial. Feedback was provided reiterating the required response buttons in the event of an inaccurate response or when the response was not initiated within 1500ms. Participants were also informed of eye movement errors in the event of fixation errors greater than 1.5°. In the event of multiple consecutive eye movement errors due to calibration failure, a recalibration procedure took place, and if necessary, the selected eye was changed to the eye with higher spatial accuracy.

In a compatible trial, the hand used to respond was congruent with the orientation of the object handle, whereas for incompatible trials the hand used to respond, and the handle orientation was incongruent (see Figure 2.1). Response mapping was counterbalanced across blocks.

The experiment consisted of four blocks: in two consecutive blocks, participants performed upright vs inverted judgements, and in the other two blocks, participants performed colour judgements. Block order was counterbalanced so that half of participants began by judging object orientation (upright/inverted) and the other half began by judging colour. In each block, each stimulus was randomly presented once in each possible horizontal handle orientation (left, right) and vertical orientation (upright, inverted), resulting in 20 x 2 x 2 = 80 trials per block, and a total of 320 trials in the entire experiment. There were an equal number of compatible and incompatible trials per block. Each block commenced with 16 practice trials (2 independent stimuli x 2 handle orientations x 2 vertical orientations x 2 repetitions). Practice stimuli were independent exemplars that were excluded based on the pilot study. Participants initiated each block by pressing the spacebar and took a break between each block for a minimum of 20 seconds to reduce fatigue and eye discomfort. The experiment was developed using Experiment Builder (SR Research).

Figure 2.1 *Timing and sequence for Experiment 1 with example of a compatible trial.*



2.2.3. Data Analysis

Trials in which participants did not respond within 1500ms, responded incorrectly, or a fixation error of greater than 1.5° was detected, were excluded from all analyses. For a participant to be included in the final analysis, a minimum of 20 correct trials per condition was needed to compute a mean. Participants excluded at the data analysis stage were replaced until the sample size of 68 was achieved. For each participant, the mean RT for each condition (task: upright/inverted, colour; handle: compatible, incompatible) was calculated. RTs greater than two standard deviations away from each participant's condition mean were excluded as outliers (Pappas & Mack, 2008; Symes et al., 2005). A 2 (task: upright/inverted, colour) x 2 (handle: compatible, incompatible) repeated measures ANOVA was conducted on mean RTs with Bonferroni corrected post-hoc comparisons. In the event of null effects, non-rejection of the null hypothesis was clarified by using TOST (Lakens, 2018) giving a p-value which is the larger of the two one-sided p-values testing the null hypothesis that the effects were less than (in numerical value) that deemed to be minimally important. The smallest effect size of interest (SESOI) was set at dz = 0.106 for all TOST calculations, this is the effect size reported for the handle compatibility effect in a recent meta-analysis (Azaad et al., 2019). This was a deviation from the preregistration in which we specified the SESOI would be derived from the sample size calculation. We were unable to calculate the dz from the Pappas (2014) paper due to the lack of open data to calculate the correlation between the within-subjects measures. Moreover, the effect sizes reported would have been considerably larger than that reported in the meta-analysis, thus we adopted a more conservative approach. While using the lower bound estimate could deal with the bias reported in the meta-analysis, given the overall average effect magnitude was small (10ms), we deemed this the most appropriate SESOI to use.

2.2.4. Results

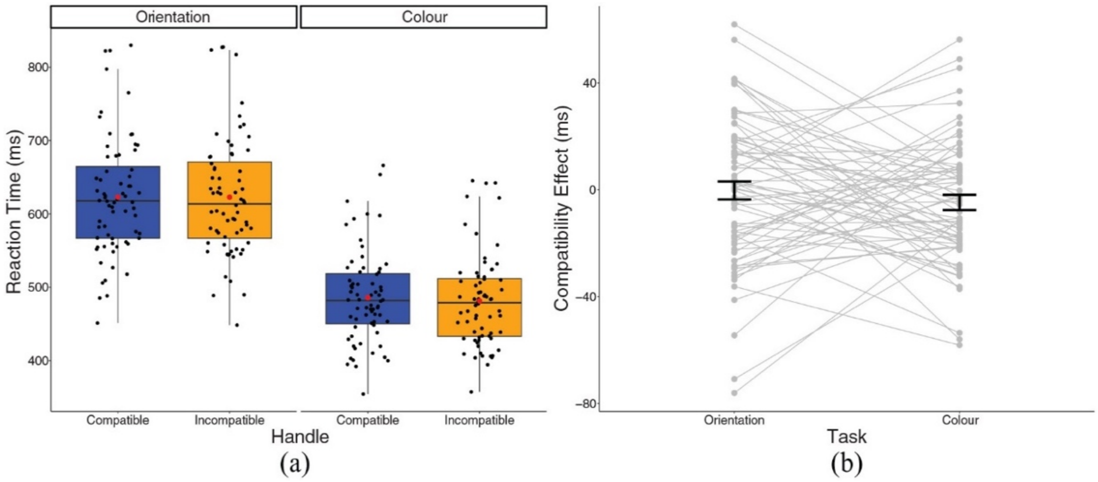
A total of 4713 (21.7%) trials were excluded from the main analysis. This included trials where participants made eye movement errors (11.2% of total trials), incorrect responses (6.3%), time outs (0.4%), and where RT was greater than two standard deviations from the participant's condition mean (3.8%).

2.2.5. Reaction Time

A 2 x 2 repeated measures ANOVA revealed a main effect of task, $F(1, 67) = 267.95$, $p < .001$, $\eta_p^2 = .800$. Unsurprisingly, RTs in the colour task ($M = 483.71$, $SD = 62.58$) were significantly faster than the orientation task ($M = 622.98$, $SD = 80.45$, $t(67) = 16.36$, $p < .001$, see Figure 2.2). There was no significant effect of compatibility, or task x compatibility interaction.

The TOST procedure revealed that the compatibility effect for orientation judgements was smaller than the SESOI ($t(67) = 2.48$, $p = .008$): RTs in the incompatible condition ($M = 622.86$, $SD = 80.86$) were similar to the compatible condition ($M = 623.09$, $SD = 80.65$). However, the compatibility effect for colour judgements was not statistically equivalent. We failed to reject the hypothesis that the true compatibility effect size for the colour task was at least as large as the SESOI (0.106; $t(67) = 0.68$, $p = .249$), although this was in the direction of a negative compatibility effect as RTs in the incompatible colour condition ($M = 481.35$, $SD = 63.27$) were slightly faster than in the compatible colour condition ($M = 486.07$, $SD = 62.26$).

Figure 2.2 *a) A box-plot displaying reaction times for Experiment 1 in the experimental conditions. Black dots represent individual data points, red dot represents the condition mean. b) A plot displaying the compatibility effect in the experimental conditions. Dots and lines represent individual data points, error bar represents standard error around the mean.*



2.3. Experiment 2

In experiment 2, we investigated whether the handle compatibility effect is larger in the lower VF, given the lower VF advantage in visuomotor control (e.g., Rossit et al., 2013). Participants responded with the left- or right-hand depending on whether the object was upright or inverted to stimuli presented in the upper or lower VFs. Crucially, to control for hand-object proximity effects, only the fixation position was manipulated, and all stimuli were presented centrally. As in experiment 1, the object's handle was either compatible, or incompatible, with the hand used to correctly respond.

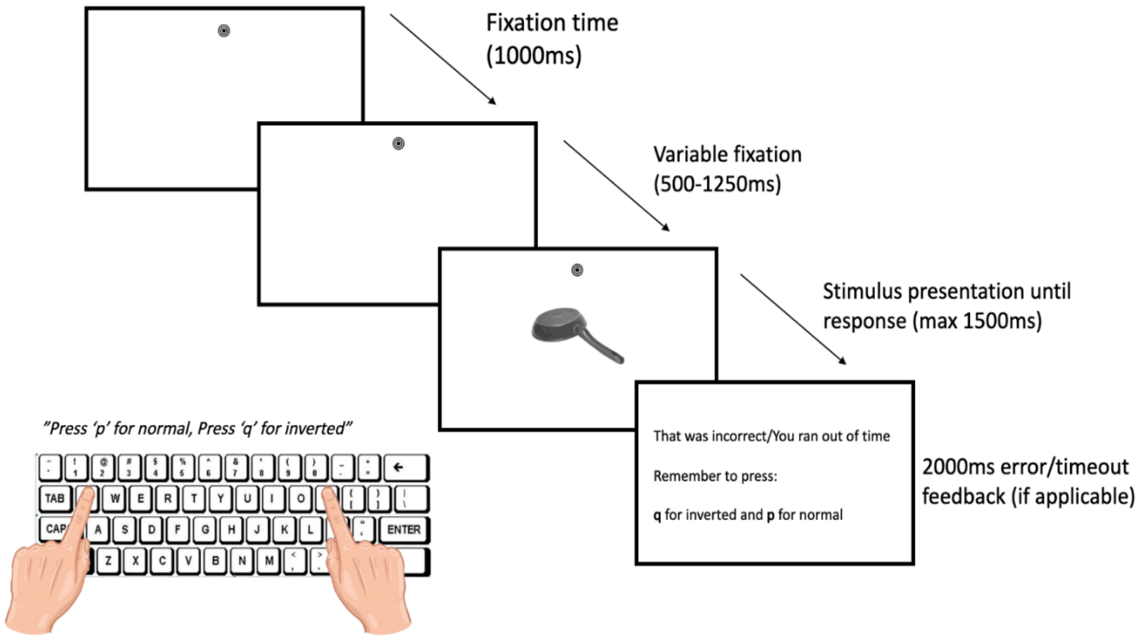
2.3.1. Participants

68 participants aged between 18 and 44 took part in experiment 2 (14 male, 1 non-binary; M_{age} = 21.8, *SD* = 5.87). Participants were recruited through the University of East Anglia undergraduate participant pool and given course credits for their participation. 54 participants were right-handed, 8 were left-handed and 6 were ambidextrous based on the Edinburgh Handedness Inventory (mean laterality index = 62.7, *SD* = 58.0).

2.3.2. *Procedure*

The procedure for experiment 2 remained the same as experiment 1. However, in the handle compatibility task, participants only performed upright vs inverted judgements and not colour judgements as we were simply interested in comparing the effects of VF. In a typical trial, the fixation bullseye was randomly presented either 7° above or below the centrally presented object and remained on screen throughout each trial. The next trial began with the fixation bullseye presented for 1000ms to allow participants to fixate, following which there was a variable delay period as in experiment 1 (see Figure 2.3).

Figure 2.3 *Timing and sequence for Experiment 2 with example of an incompatible trial in the lower VF.*



2.3.3. *Data Analysis*

Data exclusion criteria remained the same as experiment 1. A 2 (handle: compatible, incompatible) x 2 (visual field: upper, lower) repeated-measures ANOVA was conducted on mean RTs, post-hoc comparisons were Bonferroni corrected. Null effects were followed up with the TOST procedure with the SESOI set to 0.106 (Lakens, 2018).

2.3.4. Results

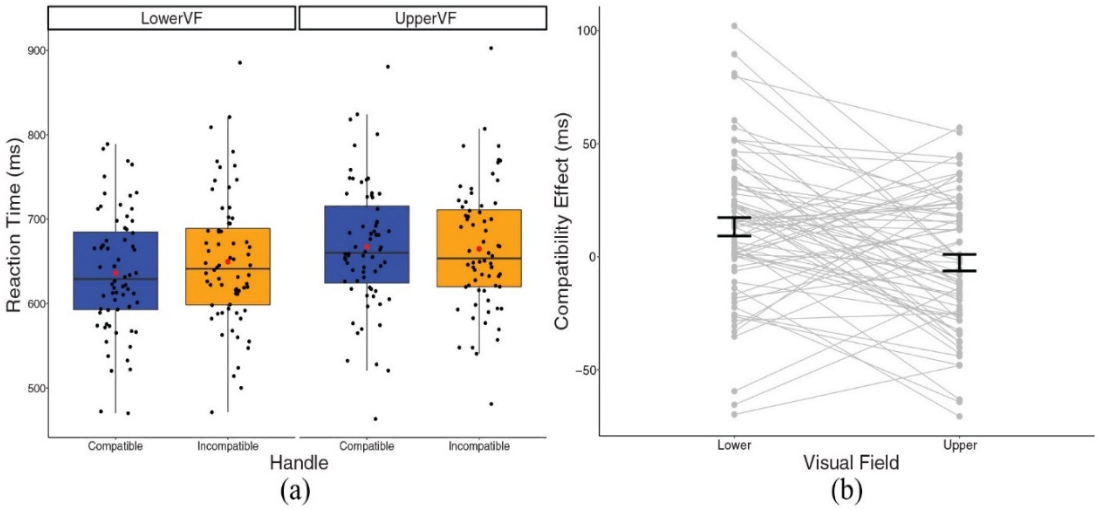
A total of 6914 (31.8%) trials were excluded from the main reaction time analysis. These included trials where participants made eye movement errors (12.8%), responded incorrectly (14.9%), timed out (0.5%) or responded more than two standard deviations away from the condition mean (3.5%), were excluded from the main analysis.

2.3.5. Reaction Time

A 2 x 2 repeated-measures ANOVA revealed there was a significant main effect of VF, $F(1,67) = 36.82$, $p < .001$, $\eta_p^2 = .355$, which was qualified by a significant compatibility by VF interaction $F(1, 67) = 11.26$, $p = .001$, $\eta_p^2 = .144$.

As hypothesised, we found a significant handle compatibility effect in the lower VF only: RTs in the incompatible condition ($M = 649.52$, $SD = 77.32$) were significantly higher than RTs in the compatible condition ($M = 636.27$, $SD = 70.87$), $t(67) = 3.25$, $p = .002$. On the other hand, in the upper VF, there was no significant difference between RTs in the incompatible condition ($M = 664.65$, $SD = 73.05$), and RTs in the compatible condition ($M = 667.29$, $SD = 74.58$), $t(67) = 0.726$, $p = .470$ (see Figure 2.4). The TOST was also non-significant, $t(67) = 1.42$, $p = .080$, thus we cannot reject a true effect at least as large, or larger, than the SESOI of 0.106, although this was in the direction of a negative compatibility effect.

Figure 2.4 *a) A box-plot displaying reaction times for Experiment 2 in the experimental conditions. Black dots represent individual data points, red dot represents the condition mean. b) A plot displaying the compatibility effect in the experiment 2 experimental conditions. Dots and lines represent individual data points, error bar represents standard error around the mean.*



2.4. Secondary Analyses (all studies)

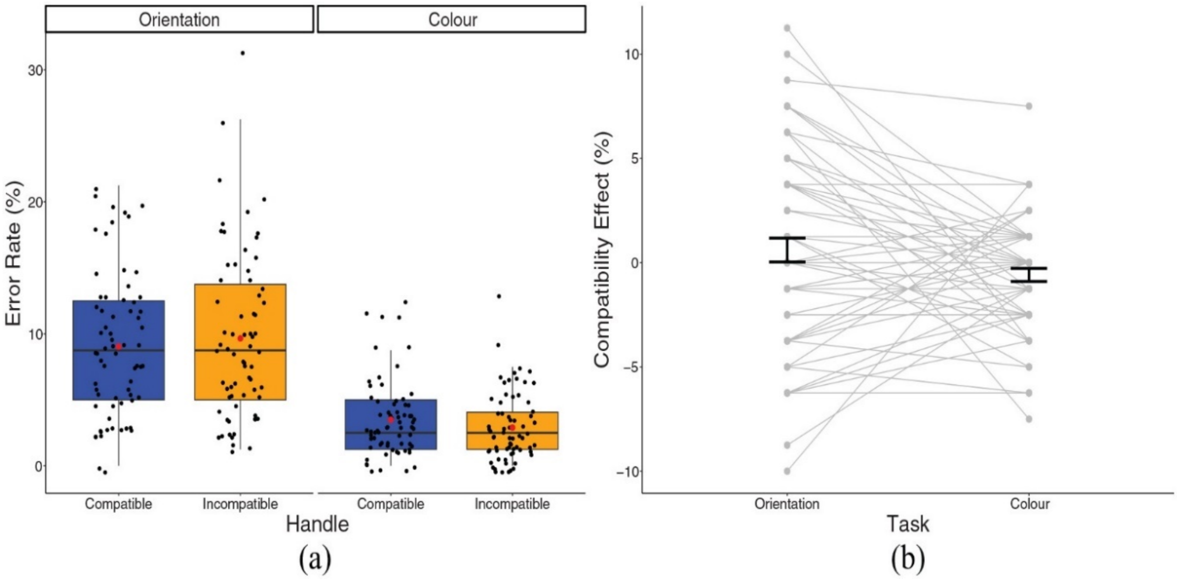
While some studies report handle compatibility effects on error rates, for example higher errors in incompatible conditions (Pappas, 2014; Tucker & Ellis, 1998), others have not replicated this (Goslin et al., 2012; Saccone et al., 2016). To clarify this, we explored the effect of handle-response compatibility on error rates in each experiment. A 2 (handle compatibility: compatible, incompatible) x 2 (task: orientation, colour) repeated-measures ANOVA was therefore conducted on percentage error (PE). Post-hoc comparisons were Bonferroni corrected, and null effects followed up using TOST (Lakens, 2018). All secondary analyses were planned prior to data collection and included within the Stage 1 report.

2.4.1. Percentage error - Experiment 1

In the orientation task, there was an average error rate of 9.04% (*SD* = 5.47) in the compatible condition, and 9.65% (*SD* = 6.21) in the incompatible condition. There was higher accuracy in the colour tasks, with an average error rate of 3.49% (*SD* = 2.89) in the compatible condition and 2.90% (*SD* = 2.56) in the incompatible condition.

In line with the findings from our RT analysis, a 2 x 2 repeated-measures ANOVA revealed a significant main effect of task $F(1,67) = 114.2$, $p < .001$, $\eta_p^2 = .630$, with significantly higher error rates in the orientation task compared to the colour task $t(67) = 10.69$, $p < .001$. There was no effect of compatibility or interaction (see Figure 2.5).

Figure 2.5 *a) A box-plot displaying percentage error in the experimental conditions in Experiment 1. Black dots represent individual data points, red dot represents the condition mean. b) A plot displaying the compatibility effect in the experimental conditions. Dots and lines represent individual data points, error bar represents standard error around the mean.*



The TOST procedure failed to provide evidence of statistical equivalence for the compatibility effect in the orientation condition ($t(67) = 0.03$, $p = .487$), or in the colour condition ($t(67) = 0.95$, $p = .826$).

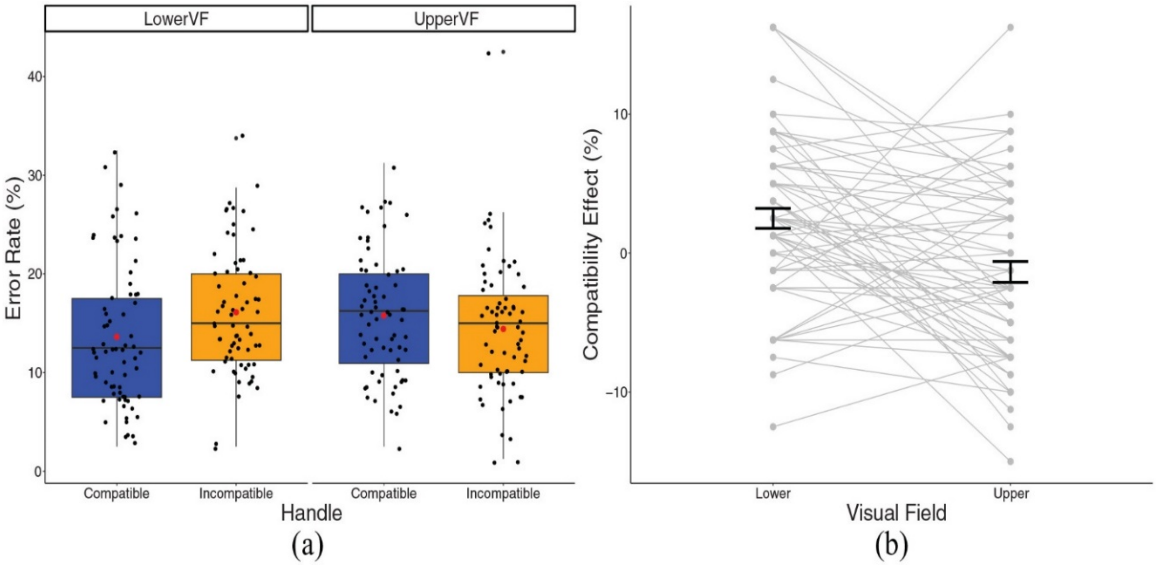
2.4.2. Percentage error - Experiment 2

Error rates were slightly higher in Experiment 2, possibly due to all tasks involving orientation judgements. In the lower VF, there was an average error rate of 13.62% (*SD* = 7.30) in the compatible condition, and 16.12% (*SD* = 6.26) in the incompatible condition. In the upper VF, there was an average error rate of 15.79% (*SD* = 6.35) in the compatible condition, and 14.43% *(SD* = 6.66) in the incompatible condition.

A 2 x 2 repeated-measures ANOVA found a significant VF by compatibility interaction, *F*(1, 67) = 17.07, $p < .001$, $\eta_p^2 = .203$ (see Figure 2.6). Bonferroni corrected post-hoc t-tests revealed a significant compatibility effect in the lower VF, significantly more errors were made in the incompatible condition, compared to the compatible condition, *t*(67) = 3.47, $p < .001$, however there was no significant compatibility effect in the upper VF, *t*(67) = 1.80, *p* = .076. The TOST procedure failed to provide evidence of statistical equivalence for the compatibility effect in the upper VF, *t*(67) = 0.89, *p* = .812, however this was in the direction of a negative compatibility effect.

Moreover, accuracy was significantly better in the lower VF than the upper VF, in the compatible condition, *t*(67) = 3.23, *p* = .002. However, in the incompatible condition, accuracy was significantly worse in the lower VF, compared to the upper VF, *t*(67) = 2.57, *p* = .012. There was no significant main effect of compatibility or VF.

Figure 2.6 *a) A box-plot displaying percentage error in the experiment 2 experimental conditions. Black dots represent individual data points, red dot represents the condition mean. b) A plot displaying the compatibility effect in the experiment 2 experimental conditions. Dots and lines represent individual data points, error bar represents standard error around the mean.*



2.5. Exploratory Analyses

To investigate the temporal development of handle effects in each condition, we also conducted a pre-registered distribution analysis. Participants' correct RTs for compatible and incompatible trials were rank ordered, divided into four equal bins, and the mean RT for compatible and incompatible trials in each bin was calculated. A handle compatibility effect was then calculated for each bin by subtracting the mean RT for compatible trials from the RT for incompatible trials, resulting in quartile effect sizes from experiment 1 for both the upright/inverted judgement task and the colour judgement task. Here, we expected that the handle compatibility effect will emerge over time when participants judge whether objects are upright/inverted. This pattern would be consistent with previous findings in distribution analyses for handle compatibility effects when tasks require object recognition (e.g., upright/inverted, kitchen/shed; Saccone et al., 2016; Symes et al., 2005). When the task is to judge colour, however, we expected the handle compatibility effect to be present in the earlier quartiles, but to rapidly dissipate in the latter quartiles, consistent with the literature on the temporal profile of the Simon effect (De Jong et al., 1994; Proctor et al., 2005). We had no predictions for the time course of effects in the upper and lower VFs. To statistically assess any effects across the RT distribution, participants' mean effect sizes for each bin and condition were entered into two 4 (bin: 1, 2, 3, 4) x 2 (Task or VF) repeated measures ANOVAs.

2.5.1. Experiment 1

Given that colour judgements were significantly faster than orientation judgements, we conducted a bin analysis to investigate whether there were different mechanisms contributing to the compatibility effect. There was a small negative compatibility effect across all four time bins in the colour task. In the orientation task, a small negative compatibility effect was observed in the earliest time bin, however as reaction time increased, the compatibility effect increased slightly (see Table 2.1).

Table 2.1 *Mean compatibility effects across the four time bins for both the colour and orientation tasks in Experiment 1.*

	Compatibility Effect (ms)	
Bin	Orientation Task	Colour Task
1	-7.80 (22.4)	-6.41 (19.4)
2	0.98 (23.7)	-5.23 (23.1)
3	4.76 (35.3)	-2.25 (29.9)
4	2.17 (52.0)	-4.19 (43.7)

Note: numbers show mean (SD)

A 4 x 2 repeated measures ANOVA revealed a small but significant effect of bin $F(1.77, 118.55) = 3.21$, $p = .05$, $\eta_p^2 = .046$. Post-hoc comparisons revealed that there was a significantly larger compatibility effect in bin 2 compared to bin 1 ($t(67) = 2.80$, $p = .007$), and in bin 3 compared to bin 1 ($t(67) = 3.08$, $p = .003$). There was however no effect of task or interaction.

2.5.2. Experiment 2

Our bin analysis for experiment 2 revealed a main effect of VF, $F(1, 67) = 8.26$, $p = .005$, $\eta_p^2 = .110$, where there was a significantly higher compatibility effect in the lower VF ($M = 11.94$, $SD = 54.87$) compared to the upper VF ($M = -2.78$, $SD = 55.14$), $t(67) = 2.87$, $p = .005$. There was no effect of bin or interaction (see Table 2.2).

Table 2.2 *Mean compatibility effects per bin in the lower and upper VFs in Experiment 2.*

	Compatibility Effect (ms)	
Bin	Lower VF	Upper VF
1	9.16 (61.0)	-2.15 (53.2)
2	14.22 (46.7)	2.07 (53.9)
3	9.38 (57.5)	-1.85 (57.5)
4	14.99 (54.1)	-9.18 (58.7)

Note: numbers show mean (SD)

2.6. Discussion

The functional specialisation of the lower VF for visuomotor control has been demonstrated by a number of neuroimaging and behavioural studies which have provided evidence for increased speed and accuracy for movements towards targets in the lower, compared to upper, VF (Brown et al., 2005; Danckert & Goodale, 2001; Krigolson & Heath, 2006; Stone et al., 2019), and increased activation in visuomotor brain regions when performing actions in the lower VF (Maltempo et al., 2021; Rossit, McAdam, Mclean, et al., 2013). Moreover, area V6A in the macaque, which is thought be involved in object affordances (Breveglieri et al., 2015), over-represents the lower VF (Galletti, Fattori, Kutz, et al., 1999). It is logical to assume that humans have developed this functional specialisation given that most of our actions with objects in day-to-day life are performed in the lower VF. Indeed, this has recently been quantified for the first time: over 70% of our actions with objects are performed in the lower visual field (Mineiro & Buckingham, 2023).

The findings of our experiment 2 demonstrate that a lower VF advantage for action, and possibly affordances, is present with images of graspable objects, even when the object orientation is irrelevant to the task goal. Firstly, reaction times were faster in the lower, compared to upper, VF, consistent with previous behavioural literature (Brown et al., 2005; Danckert & Goodale, 2001). Secondly, we observed a significant handle compatibility effect for both RTs and accuracy in the lower, but not upper, VF. However, we failed to replicate the handle compatibility effect in our Experiment 1, where participants were presented objects in their foveal vision; nor did we observe any differences in the compatibility effect between our two tasks (judging orientation vs colour), except for colour judgements being significantly faster than orientation judgements. Therefore, in conjunction with the findings of experiment 1, we can only speculate as to the possible explanations for the VF difference in the handle compatibility effect.

Our findings of a lower VF advantage in the handle compatibility effect are in line with previous research demonstrating that compatibility effects are reduced, or eliminated, when objects are presented in extra-personal, as opposed to peri-personal space (Ambrosini & Costantini, 2013; Costantini et al., 2010, 2011). In these experiments, objects in peri-personal space were presented lower on the vertical meridian than those in extra-personal space. In one sophisticated manipulation however, Costantini (2010) presented objects in the same position either in front of, or behind, a clear screen. In a striking case for the affordance account, a handle compatibility effect was only observed when the object was in front of the screen and thus manipulable. Put together, our findings provide complementary evidence for a lower VF advantage in reaching and object manipulation in peri-personal, reachable, space (Previc, 1990). Here, findings apply specifically to the VF of presentation, as we controlled for hand-object proximity by manipulating fixation position, rather than the object position, on the screen.

Given that we manually interact with and use objects mostly in the lower VF, the lower VF compatibility effect may therefore be reflective of activation of action-related information to allow for successful interaction with the object, in line with affordance accounts (Tucker & Ellis, 1998). This explanation seems plausible given all objects were centred on the screen with respect to their width (and thus a reduced salience of the handle towards a single side of space; Azaad & Laham, 2020). Numerous previous keypress response SRC paradigms have reported no compatibility effect, or even negative compatibility effects, when objects are centred by their width (Bub et al., 2021; Kostov & Janyan, 2020; Lien et al., 2014; Yu et al., 2014). These findings have been explained by a spatial account due to the functional end, rather than handle, protruding more to one side thus facilitating responses compatible with the functional end due to spatial coding. Therefore, a purely spatial account of our findings would predict a negative compatibility effect across all our tasks due to stimuli being centred by their width. Our findings therefore cannot be explained by a purely spatial account given that we failed to observe a negative compatibility effect across any tasks, and a significant compatibility effect was present when stimuli were presented in the lower VF. Despite this, we failed to observe a compatibility effect in Experiment 1 when the task was to judge orientation, and thus thought to elicit affordances, which questions the contribution of affordances to the handle compatibility effect.

It is possible that the lack of compatibility effect observed in Experiment 1 for both the colour and orientation task was due to the restriction of eye movements. To our knowledge, this is the first study using the SRC paradigm with handled objects while requiring participants to maintain fixation throughout trials thus the effects of restricting eye movements remain unknown. A number of eye-tracking studies have demonstrated that visuospatial attention is biased towards the action performing side of an object, as opposed to the handle (Pilacinski et al., 2021; van der Linden et al., 2015). Moreover, the bias towards the action-performing side of the object has been shown to increase over the time course, suggesting that the action related effects may be more likely to build up over time and when the object is foveated (van der Linden et al., 2015). This suggests that the eye is driven towards the functional part of the tool, potentially to recognise the tool's functional use. As participants were required to inhibit eye movements to either side of the object, it is possible that stimuli were harder to recognise, and action related information was less salient. For instance, by recognising an object by its functional end, one can adjust grip aperture and posture to successfully use the object (Belardinelli et al., 2016). Our finding of a lack of compatibility effect in Experiment 1, as well as no effect differences across the time course, could therefore be explained by the inhibition of eye movements restricting object identification, thus not eliciting affordances (Saccone et al., 2016; Symes et al., 2005). It is also possible that, given our findings from experiment 2, affordances are only elicited to objects in the lower VF. For example, it could be speculated that previous failed replications are a result of participants making eye movements towards a keyboard in the lower VF to respond, thus moving the stimulus into the upper VF and reducing the effect. Future studies could employ eye-tracking measures alongside the task to investigate how eye movements modulate RTs in keypress SRC paradigms.

Of course, our failure to replicate the handle compatibility effect in Experiment 1 further questions the reliability of using a keypress handle SRC paradigm as a measure of affordances. Despite this, there remains a growing body of literature providing a motor-based account of compatibility effects. The handle compatibility effect has recently been replicated in both lab-based experiments, and online (Littman et al., 2023; Littman & Kalanthroff, 2022). In both experiments here however, participants were primed by observing, or engaging in, hand-object interactions with the stimuli used. Moreover, only RTs for upright objects were included in their analyses as it is more natural to interact with an upright, rather than inverted, object. This may explain some of the differences observed between these recent findings and our experiment 1. In further support for a motor-based account, Zou et al. (2022) observed significant handle compatibility effects when handles were broken following 50ms of stimulus presentation, however this disappeared when the handle was broken at a later stage (150ms, 250ms). Despite this, a compatibility effect was present when the handle remained intact (and thus graspable), which was not observed with symmetrical objects and when 'handles' were protruding shapes. Therefore, it seems likely that both spatial coding and affordances contribute to handle compatibility effects, with affordance related effects occurring later than spatial effects.

More recent research has shown that compatibility effects also depend on participants' motor intentions. This has been demonstrated in experiments reporting a negative compatibility effect in keypress response paradigms, but a positive compatibility effect when participants are required to respond with a reach and grasp movement (Bub et al., 2021; Bub & Masson, 2010; Ferguson et al., 2021). These findings suggest that the compatibility effect depends on the action related information of the task demands, with compatibility effects only arising when participants' action intentions are to perform a reach-to-grasp movement, rather than a keypress with the index finger. Indeed, we do not typically interact with objects without a reach-to-grasp movement. Future research could assess VF differences in the handle compatibility effect using reach-to-grasp responses. It would also be interesting to assess movement kinematics to investigate which stage of a reach-to-grasp action these compatibility effects arise. It is possible that employing a reach-to-grasp paradigm would reduce the heterogeneity observed in our present experiments and generate more robust findings.

While judgements of object orientation have been commonly used in SRC handle compatibility paradigms (Saccone et al., 2016; Tucker & Ellis, 1998), one could question whether this is a purely perceptual judgement which triggers action related responses, or whether some form of imagining interactions is necessary to complete the task. For instance, it is possible that judging object orientation may require participants to imagine interacting with the object, making action more relevant to the task than colour judgements for example. Interestingly, EEG research has found that motor activation in response to viewing objects is greater when the object is in reachable, compared to unreachable space, however this only occurred when the perceptual task was action relevant (Wamain et al., 2016). Therefore, it is possible that rather than affordances being simply automatic motor responses to perceived objects, they depend on the action relevance of the perceptual task, even when no overt action is required. Future research could assess whether the handle compatibility effect is stronger in the lower VF, compared to the upper VF, when the perceptual task is to judge colour and thus not an action relevant property of the object. This could build on our current findings to establish whether the lower VF advantage in affordances is specific to the action relevance of the task, or whether it reflects an automatic evocation of object affordances in response to handled objects in the area most primed for action (lower VF).

Overall, using a well-powered, and well-controlled experimental design, we failed to replicate the highly cited Tucker and Ellis (1998) handle compatibility effect when participants fixated on the object centre while making keypress responses to the objects' orientation. Moreover, no compatibility effect was observed when participants responded to object colour. However, a significant compatibility effect, and faster responses, were observed when objects were in participants' lower VF. This adds to a body of evidence suggesting a lower VF advantage for action. While we cannot conclusively explain our findings in terms of a lower VF advantage in affordances, the presence of a compatibility effect in the lower VF cannot be explained by spatial compatibility. Future research should further investigate vertical VF differences in affordances using reach-to-grasp SRC paradigms as task demands will be more relevant for action. While caution should be used when interpreting handle compatibility effects in keypress SRC paradigms in terms of affordances.

3. Chapter 3 - Viewing tool pictures evokes action-specific activity in visual hand-selective occipitotemporal cortex: Neural representation of tool use actions from viewing and pantomime.

Throughout the course of our lives, we have countless experiences with different types of objects. Through these experiences we learn the predictable associations between how objects look, feel, and are used. Among all the objects we encounter, tools are unique because they are specifically designed for a function and, thus, tightly linked to highly predictable hand movements (Johnson-Frey et al., 2005). For example, based on the numerous individual exemplars of keys we interact with, we learn that a key opens a door and that to use it we need to make a hand rotation movement. In fact, the human ability to invent and build tools is viewed as a key milestone of brain evolution in humans (Peeters et al., 2009; Reynaud et al., 2016; Frey, 2007).

At a neural level, perception and action models hypothesize the existence of a left-lateralised network of brain regions for tool processing involving both ventral and ventro-dorsal (VD) and dorso-dorsal (DD) visual streams (Rizzolati and Matelli 2003; Buxbaum, 2017; Buxbaum and Kalénine, 2010; for a review see Lewis, 2006). Binkofski and Buxbaum (2013) characterised the VD and DD streams as the ‘Use’ and ‘Grasp’ systems respectively. The VD ‘Use’ system (comprising pMTG, SMG, and PMv) was proposed to be responsible for the storage of skilled actions associated with familiar objects. Specifically, to support tool use, VD regions were proposed to transform visual information from the environment and stored representations of action into sensorimotor representations to support tool use. The DD ‘Grasp’ stream on the other hand (comprising IPS and PMd) was thought to be responsible for transforming live visual input into sensorimotor representations to support reaching and grasping, thus the online control of actions towards objects.

This model has been supported by behaviours observed in individuals with apraxia, a disorder which is characterised by the misuse of everyday tools despite intact sensorimotor abilities (Dovern et al., 2012; Goldenberg & Hagmann, 1998). For example, people with apraxia may use the incorrect tools to perform a function, such as brush hair with a toothbrush; or use the tool incorrectly; such as using a knife in the incorrect orientation to slice bread (Bieńkiewicz et al., 2014; Goldenberg & Hagmann, 1998). Other characteristics of apraxia include deficits in pantomime of tool use actions and gesture imitation (Goldenberg, 2009), or using an incorrect handgrip when pantomiming tool use (Buxbaum, Johnson-Frey, et al., 2005). Despite this, semantic knowledge of tools, such as tool naming, remains unimpaired (Buxbaum & Saffran, 2002). Moreover, deficits in pantomiming tool use often coincide with a spared ability to handle and use real tools (Randerath et al., 2010).

Voxel-lesion symptom mapping has identified that lesions to the left hemisphere of the VD stream, in particular pMTG and IPL are associated with deficits in the ability to pantomime use of tools specifically, rather than meaningless gesture imitation (Buxbaum et al., 2014; Hoeren et al., 2014; Kalénine et al., 2010). Moreover, the pMTG and IPL has also been associated with tool use errors in left brain damaged individuals performing 3D tool use, such as moving the tool incorrectly for its functional use, or grasping the tool in an awkward posture for its use (Salazar-López et al., 2016). Interestingly, people with lesions to left SMG in the IPL are also impaired in mechanical problem solving (i.e. using novel tools) despite spared semantic knowledge about tools (Buxbaum & Saffran, 2002; Goldenberg & Spatt, 2009). While previous VLSM studies have isolated distinct regions which could be critical to the pantomime of tool use, multivariate approaches have identified a network of regions including AG, SMG, MTG and premotor cortices and white matter connecting the frontal, temporal and parietal lobes responsible for deficits in pantomiming tool use in apraxia, highlighting a collaborative network involved in tool use pantomime (Sperber et al., 2019). Crucially, apraxia can be dissociable from optic ataxia associated with DD stream damage. Patients with apraxia have an intact ability to grasp tools, possibly due to an intact SPL in the DD stream (Randerath et al., 2010). This provides support for the idea that the VD stream is responsible for the ability to perform skilled object-related actions towards familiar objects, with the DD stream more responsible for online control of actions and the processing of structural characteristics of objects for prehensile actions.

In neurotypical adults, imaging studies using univariate techniques have implicated regions within the ventral, VD and DD streams which are consistently activated when viewing, and pantomiming tool use actions. Given the constraints of interacting with real objects in MRI environments, pantomime has been considered a valid proxy for studying the neural underpinnings of real actions (Garcea & Buxbaum, 2019; Króliczak et al., 2007). For example, Johnson-Frey et al. (2005) used a go / no-go paradigm where participants were auditorily presented with several manipulable tools and instructed to plan a pantomime consistent with the tools' use. In a go trial, participants executed the pantomime, and in no-go trials, participants simply planned the movement but did not execute it. In control conditions, participants were instructed to plan and execute a meaningless limb movement in go trials, or simply plan in no-go trials. Tool use planning, which was the contrast between tool and control no-go trials, and execution (the contrast between tool go and no-go conditions), preferentially activated posterior temporal cortex (including superior temporal sulcus and pMTG) as well as VD and DD regions within the PPC (specifically IPS, SMG, AG and ventral SPL (Johnson-Frey et al., 2005). The authors suggested that SMG and AG within the VD stream was involved in representing motor programs for tool use, possibly by supporting the selection of appropriate hand configurations during hand-tool interactions.

In a similar study, Vingerhoets et al. (2010) compared activation for familiar tools with unfamiliar tools which do not have a typical use action. Participants viewed images of familiar or unfamiliar tools, or neutral shapes, and were instructed to plan a pantomime of how the tool would be used, and then execute the pantomime. Tool use planning and execution activated the left-hemispheric tool network including IPL, IPS, visual and sensorimotor regions. The only region that differed between familiar and unfamiliar tools was the cuneus during the planning phase, which was thought to reflect the increased visual processing in response to the novel object rather than action guidance. This network of regions however has also been shown to be preferentially activated in response to planning pantomimes of functional grasps of tools, compared to objects matched in shape and orientation but without associated tool functions (Przybylski & Króliczak, 2017). Put together, univariate studies have provided support for the existence of a network comprising the ventral, VD and DD streams in supporting the skilled use of tools. The same network has been shown to be activated in studies where participants are required to engage with 3D tools (Brandi et al., 2014; Hermsdörfer et al., 2007; Knights et al., 2021).

Further research has suggested that there is a clear interaction between the three streams. Indeed, this is in line with research showing that white matter tracts between the frontal, parietal and temporal cortices are related to deficits associated with apraxia (Sperber et al., 2019). For example, functional connectivity studies have identified increased functional coupling between LOTC and fronto-parietal regions during sensorimotor tasks, such as reaching to grasp objects, compared to resting state and visuo-perceptual tasks (Hutchison & Gallivan, 2018), and during tool pantomiming (Garcea et al., 2018). Increased connectivity between LOTC and aIPS has also been observed from passive viewing of tools (compared to non-tools;

Chen et al., 2018), suggesting that LOTC may play a critical role in the interaction between the ventral and dorsal streams for tool related tasks. Moreover, this highlights that communication between the ventral and dorsal streams are important for efficient tool use. It thus seems that while there may be a clear tool network in the brain, consisting of regions in the ventral, VD and DD streams, the streams are not distinct.

Moreover, functional connectivity between SMG and temporal and posterior parietal regions has been shown to be modulated by the type of movement required with tools (Garcea & Buxbaum, 2019). In an event-related fMRI study, participants were shown an image of a tool and instructed to pantomime how it would be used or how you would grasp it to transport it. For tool use actions, functional connectivity was strong between left SMG and the anterior temporal lobe, while tool transport actions elicited increased functional connectivity between the left SMG and posterior parietal (DD) regions. While this further supports the existence of two separate action systems in the brain, the authors hypothesised that SMG is a region which integrates the representations of tool features computed by the dorsal and ventral visual pathways (Garcea & Buxbaum, 2019). Further supporting this hypothesis, research has found that effective connectivity between SMG and aIPS in the DD stream is modulated by tool use experience (Bosch et al., 2023). Specifically, participants were scanned observing videos of an actor using chopsticks to move and drop a marble into a container in two sessions. In between sessions, participants were trained to use the chopsticks to complete the task themselves. Prior to training, effective connectivity was dominant in the direction from SMG to IPS, whereas after training, this was reversed to go from IPS to SMG. This further suggests that SMG is a region which integrates semantic learned knowledge of tool use with technical reasoning to achieve successful interactions with tools.

Grounded theories of cognition stipulate that the conceptual representations of tools involve brain regions associated with both tool perception and use, even when no hand movement is required (Martin, 2016; Barsalou et al., 2003). Therefore, this may explain the activation of a distributed network of brain regions and the increased functional coupling between them during pantomiming tool use movements (Garcea et al., 2018). Indeed, a substantial body of neuroimaging evidence has shown that merely viewing pictures of tools activates frontoparietal regions of the tool network (Chao & Martin, 2000; Creem-Regehr & Lee, 2005; Macdonald & Culham, 2015; Mruczek et al., 2013). This visual tool-selective activation has been proposed to reflect automatic and implicit retrieval of action properties about the hand movements that tools afford (Martin et al., 1996; Fang and He, 2005). These findings suggest that we may automatically process the potential actions that can be made with tools, even without intent to act (Warman et al., 2024). Despite this, the action-related response to viewing images of tools is broadly defined. For example, it is unclear whether this reflects a general action-related response, or the retrieval of a specific action property, such as how we would move a tool in a way that is functional for its use.

Studies using multivoxel pattern analysis (MVPA) have expanded on previous findings by revealing the specific properties regions in the tool network represent. An early MVPA study had participants reach to touch or grasp objects either with a hand or tool (Gallivan et al., 2013). Results found that the type of movement (grasp or reach) could be decoded in DD regions, including SPOC and aIPS, for movements using the hand, while SMG and pMTG in the VD stream represented type of movement using the tool. Interestingly, posterior IPS (pIPS) and PMd and PMv represented type of movement across effectors. This suggests that hand and tool related actions may be represented separately in early regions but become integrated in frontoparietal cortex (Gallivan et al., 2013). Further MVPA studies have found that hand-independent tool use actions (how a tool is moved for its use) during pantomime can be decoded in VD region IPL, close to the aIPS (Ogawa & Imai, 2016). Ogawa and Imai (2016) also conducted a separate finger tapping task and used MVPA to decode which finger was used to tap. They failed to observe significant decoding of finger tapping, this suggests that in line with Binkofski and Buxbaum's (2013) model, IPL specifically represents learnt actions associated with tools and not simply low-level visuomotor processes.

In an elegant fMRI study, Chen et al. (2018) presented participants with tool words and had them pantomime the action associated with the tool (e.g. rotate the wrist and forearm in response to the word 'screwdriver'). In separate runs, participants viewed tool images and were instructed to visually attend to the tool, silently name the tool and think about its features (such as weight and context in which they are found) and associated actions. Tools differed in terms of their function (to cut vs to open) and in terms of their tool use action (to rotate vs to squeeze). MVPA was used to assess whether tool use action or functions could be decoded in independently defined ROIs. Specifically, 'within-task' decoding of tool function and tool use action was performed, where the classifier was trained and tested on the same task (i.e. train on view and test on view), and 'cross-task' decoding was performed, where the classifier was trained on one task and tested on the other (i.e. train on view, test on pantomime). In the ROI analysis, successful within-task decoding of tool use action was observed in left IPL and pMTG in the view task, and in IPL and premotor cortex in the pantomime task. Tool function was only successfully decoded in the left medial FG in the view task. Interestingly, successful cross-task decoding of tool use action was observed in left IPL (mainly SMG). This was taken as evidence that IPL represents tool use actions in an abstract, rather than modality specific, manner, i.e. independent of task or stimulus modality (Chen et al., 2018). Despite this, it is not yet known whether VD regions also represent tool use action properties during passive viewing of tools, thus when not considering the tools' associated actions.

Interestingly, areas that respond to tools in the ventral and dorsal streams closely overlap with areas responding to hands (Bracci et al., 2012, 2016; Bracci & Op de Beeck, 2016; Bracci & Peelen, 2013). Research has found that images of hands and tools, compared to body parts, activate closely overlapping areas in LOTC, with hands and tools being represented more similarly in these regions than hands and other body parts (Bracci et al., 2012). This hand and tool selectivity is also observed in individuals born without hands (Striem-Amit et al., 2017), and in those who are blind (Kitada et al., 2014; Peelen et al., 2013), suggesting that hand and tool selectivity develops regardless of visual or sensorimotor experience. This overlap cannot be explained by stimulus features which have previously been shown to influence category selectivity such as manipulability (Mahon et al., 2007), animacy (Konkle & Caramazza, 2013) and low-level form (Coggan et al., 2016), because hands and tools differ in each of these aspects.

Moreover, closely overlapping patterns of activation have been found in IPS in response to images of tools and hands, but not for hands and other manipulable and non-manipulable objects matched for shape, size and elongation, nor for tools and other body parts (Matić et al., 2020). Therefore, the overlapping representations may be due to the functional relationship between tools and hands, in that tool use requires an object directed action that involve hands and tools. Recently, it has been shown that hand-, but not tool-, selective IPS represents how we typically grasp a tool (i.e. by its handle, rather than the functional end), which suggests that these visual hand-selective regions may code the hand configurations required for complex hand-tool interactions (Knights et al., 2021).

In Experiment 3, we investigated whether areas in the ventral, VD and DD pathways represent how we move tools for their functional use, both from simply viewing pictures of tools, and when pantomiming their use and whether these representations could be decoded independent of task and stimulus format. Moreover, we assessed for the first time whether tool use actions are represented specifically in either visual hand- or tool-selective cortex. We utilised a sophisticated stimulus set with tools differing in the actions required for their functional use, specifically tools affording a rotate action or a squeeze action, while carefully controlling for low-level differences such as colour, size, luminance, and orientation, as well as the grip type the tools afforded.

Using MVPA, we assessed whether tool use actions (rotate or squeeze) could be decoded from fMRI activity patterns within independently defined regions of interest (ROIs). We were also interested in whether tool use action was represented in an abstract, or modality-specific manner. To assess this, we firstly used MVPA within task (view and pantomime separately), and then used cross-task decoding (training the classifier on view and testing on pantomime). As a further control to ensure decoding was not simply due to low level differences between tool identities, we compared decoding of tool use action with decoding of tool identity in each ROI and task. Higher decoding of tool use actions compared to tool identity would suggest that specific action properties are represented, rather than simply low-level features such as shape and size.

Based on Gibson's (1979) theory of affordances, we hypothesised that simply viewing tools would elicit motor representations for actions within a frontoparietal network, including regions of the VD and DD stream. Thus, we expected to observe above chance decoding of tool use action (rotate vs squeeze) in the view task in VD and DD regions. We expected that tool identity, however, would be represented in ventral and VD regions in the view task, in line with Milner and Goodale's (1995, 2006, 2008) TVSH and the two action systems model proposed by Binkofski and Buxbaum (2013). We hypothesised that tool use action decoding would be significantly higher than tool identity decoding in the VD stream as VD regions are thought to specifically represent action properties associated with tools rather than simply shape and form. In the pantomime task, we hypothesised that tool use action decoding would be significantly above chance in regions in the VD stream (pMTG, SMG and PMv), as this network is associated with 'use' actions (Binkofski & Buxbaum, 2013). We were also interested in how representations of tool use actions differ in hand- and tool-selective cortices. Based on previous research in our lab, we expected significant decoding of tool use action in hand-selective LOTC and IPS (Knights et al., 2021), suggesting that hand- and tool-selective regions, while overlapping, are functionally distinct.

3.1. Experiment 3 - Methods

3.1.1. Participants

Eighteen healthy participants aged between 19 and 35 years [7 males; mean age = 24.7 (*SD* = 4.1)] recruited from the University of Maastricht (Netherlands) completed the fMRI study and a visual localiser study in the same session. All participants had normal or corrected-to-normal vision and no history of neurological or psychiatric disorders, were right-handed (Oldfield, 1971), and provided informed consent in line with procedures approved by the School of Psychology Ethics Committee at the University of East Anglia. Our sample size was based on similar motor studies using MVPA (Ariani et al., 2015, 2018; Chen et al., 2016, 2018; Gallivan et al., 2013; Knights et al., 2021), though no power analysis was performed before data collection.

3.2. Main experiment

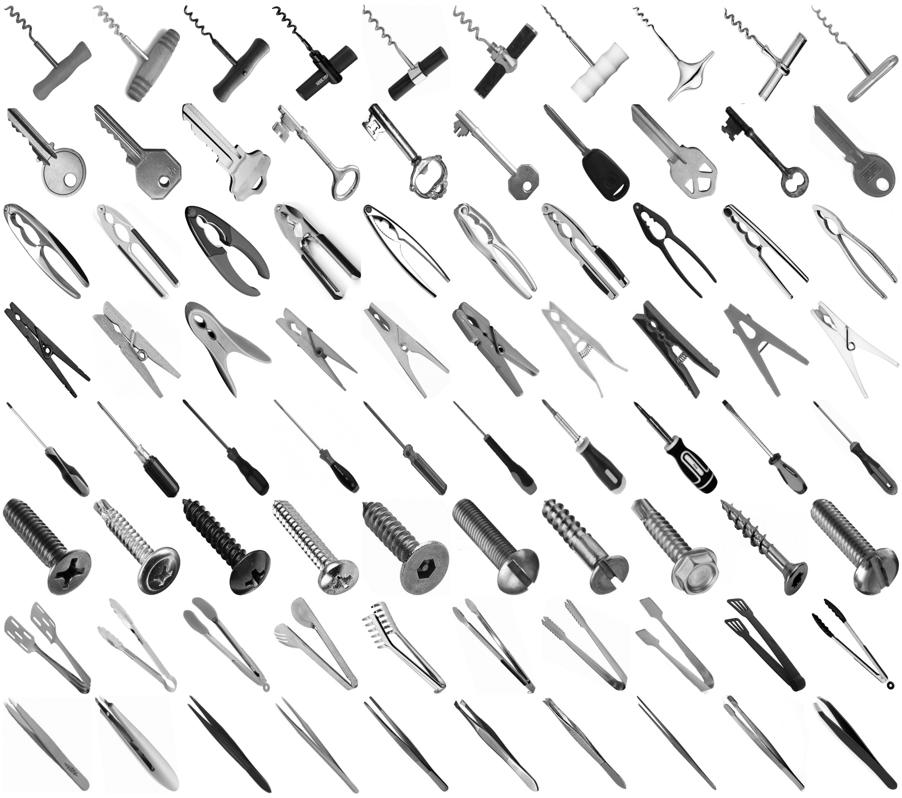
3.2.1. Stimuli

The main experiment included view runs, where participants viewed images of tools, and pantomime runs where participants pantomimed tool use actions (without tool in hand) in response to the names of the tools presented in the view runs. For the viewing task, ten exemplar images of eight different tool identities were selected from the BOSS database (Brodeur et al., 2010, 2014), the Konklab database (Konkle & Oliva, 2011, 2012), and Google Images. To control for low-level visual differences between stimuli, all images were grayscale (800 x 800 pixels, app. 15°) presented on a white background and matched for luminance. Tool handles were all orientated rightwards at an angle of approximately 45 degrees to control for any low-level visual effect of orientation. We chose to orient all tools to the right so that they would afford a right-handed action, given that all pantomime actions were performed with the right hand. To control for eye movements, participants were instructed to fixate on a bullseye (24 pixels, 0.5°) presented at the centre of the screen and superimposed on top of the centrally presented tool image. For the pantomime task, the English name of the tool was presented below the fixation bullseye in black on a white background (font size 32).

Our eight tool identities (tongs, screwdriver, tweezers, peg, key, screw, nutcracker, and corkscrew; see Figure 3.1) were selected from a larger dataset of 60 tools extracted from previous studies (Lagacé et al., 2013; Chen et al., 2016; Garcea & Mahon, 2012; McNair & Harris, 2012) that varied according to how the hand is moved to use the tool: half required a 'rotate' action (e.g. key and screwdriver), and the other half required a 'squeeze' action (e.g. peg and tongs). Specifically, from the original 60 tools, we selected the ones that: 1) had similar grip types for using and grasping actions (Lagacé et al., 2003), ensuring the actions afforded by our final tool set varied only in terms of the action property of interest (i.e. tool use action: squeeze vs rotation); 2) afforded between 0.9 and 1.5 actions ensuring that our tools afforded approximately one tool use action; 3) constituted a unique functional exemplar (e.g., spoon and wooden spoon are for the same function so only one was included); 4) afforded either a precision grip or power grip; and 5) did not involve interaction with the upper part of the body when using (e.g., lipstick, toothbrush, cup) or throwing actions to avoid excessive movements during actions in the scanner.

Using the twelve tools that fitted our criteria, we conducted a normative study at UEA [N = 15, 1, 1 male, mean age = 25.6 (*SD* = 6.5)] to match the final stimulus set in terms of familiarity and frequency of use. As such, our final eight tool identities were consistently correctly named (*M* = 97%, *SD* = 5.55), highly familiar (median ratings >6 on a 7-point Likert scale) and were rated as affording similar grasp types to both move and use the tool (median ratings >5 on a 7-point Likert scale). To control for grip type differences, half of our final stimulus set afforded a precision grasp, and half afforded a power grasp. Analyses were run using grip-matched pairs.

Figure 3.1 *Tool identities and their exemplars presented in the view task.*



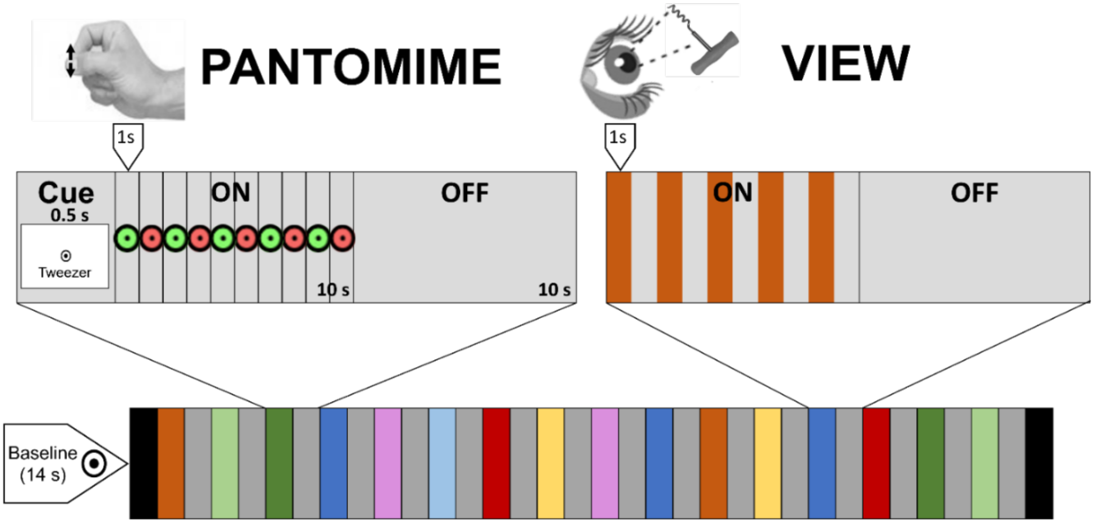
3.2.2. fMRI set-up and paradigm

Participants laid supine in the scanner (using a standard coil configuration; see MRI acquisition) with their right upper arm restrained and supported by cushions so that pantomime movements were performed by flexion around the elbow thus reducing the likelihood of motion artifacts (Culham, 2006). To control for eye movements, participants were required to maintain fixation on a red bullseye and this was monitored online via an eye-tracker (Avotech NANO RE-5721, Avotec Inc., Stuart, Florida). To verify that the correct tool use pantomime was performed, we filmed participants' actions using a video camera (Panasonic HD HVC-210) placed in the control room. The experiment was controlled using custom software written in MATLAB (MathWorks) using the Psychophysics Toolbox (Brainard, 1997). We used a powerful block design fMRI paradigm (10s ON, 10s OFF; as in Knights et al., 2021), which maximized the contrast-to-noise ratio to generate a reliable estimate of the average response pattern (Mur et al., 2009) and improved detection of blood oxygenation level-dependent (BOLD) signal changes without significant interference from artifacts during overt movement (Birn et al., 2004). Viewing and pantomime tasks were completed in separate runs, counterbalanced across participants so that the same task was never completed in two consecutive runs. Block timings were matched as much as possible across viewing and pantomime tasks (i.e. 10s ON, 10s OFF with 5 repetitions, see Figure 3.2).

In the viewing task, during the ON-block (10s), 5 image exemplars of a tool identity (e.g., 5 different pegs) were each presented for 1s with a blank inter-stimulus interval (ISI) of 1s. The ON-block was followed by a fixation OFF-block of 10s. The images were projected onto a screen (1920 x 1200 pixels) and viewed through a mirror mounted on the head coil (distance of mirror to screen = 60cm). Each run comprised 16 stimulus ON-blocks, with each tool identity being presented twice per run. Each exemplar was only presented once per run (thus 5 exemplars in one block, and the remaining 5 exemplars in another block). Each run started and ended with a 14s baseline block. Participants performed a 1-back repetition task by pressing their right index finger on the response box (2.5 x 13 x 6.4cm, fORP 932 response box system) whenever two successive blocks contained the same tool identity. Each viewing run lasted 348 seconds and participants completed on average 4.5 runs (minimum = 4 runs; maximum = 5 runs) for a total of 8-10 blocks per tool identity.

In the pantomime task, a block began with a preparation period (500ms) during which the tool name (e.g. tweezers) was presented cueing the action required (e.g. squeeze) and participants were instructed to lift their fist from their chest to prepare for the upcoming action. After this, the tool name disappeared, and fixation turned green 5 times (1s on, 1s off) to cue the participant to pantomime the tool use action. At the end of each block, the fixation turned red to cue the participant to return their fist to their chest. Thus, in each ON-block (10s), 5 pantomime actions were performed for 1s with a blank ISI of 1s. As in the view task, each run comprised of 16 stimulus ON-blocks, with each tool identity presented twice. A pantomime run lasted 356 seconds, slightly longer than the view task (given the extra 500ms required to present the tool names) and participants completed on average 4.66 runs (minimum = 4 runs, maximum = 5 runs) for a total of 8-10 blocks per tool identity.

Figure 3.2 *Trial sequence and timings for view and pantomime blocks within a run. Note that each run comprised only one task (view or pantomime).*



Each main experiment session lasted approximately 1.5 hours [including setup and anatomical scan]. Immediately before the fMRI experiment, participants were familiarised with the stimuli and tasks (procedure adapted from Lausberg et al., 2015). Firstly, they were asked to name each tool image and demonstrate how they would pantomime their use. Then, the experimenter demonstrated the required tool use action and participants repeated the pantomime in a comfortable and natural manner. Participants were then presented with the tool names and were required to perform the expected action when the word appeared on a screen until they reached 100% correct performance. Finally, participants completed up to eight trials of the pantomime task to familiarise themselves with the task. Three pantomime runs and two view runs were excluded from further analysis due to technical issues and/or excessive motion.

3.2.3. Visual localiser

Following the main experiment, participants immediately completed a bodies, chairs, tools, and hands (BOTH) visual localiser (Knights et al., 2021). Two sets of exemplar images were selected from previous stimuli databases (Bracci et al., 2012; Bracci & Op de Beeck, 2016; Bracci & Peelen, 2013) that were chosen to match, as much as possible, the characteristics within the tool (i.e., identity and orientation), body (i.e., gender, body position, and amount of skin shown), hand (i.e., position and orientation), and chair (i.e., materials, type, and style) categories. Different tool exemplars were used from the main fMRI experiment to avoid circularity. Using a mirror attached to the head coil, participants viewed separate blocks (14 s) of 14 different grayscale 2D pictures from a given category (800 × 800 pixels; 0.5 s). Blank intervals separated individual stimuli (0.5 s), and scrambled image blocks separated cycles of the four randomised category blocks. Throughout the runs, participants fixated on a superimposed bullseye in the centre of each image and, to encourage attention, performed a one-back repetition detection task where they made a right-handed button press whenever two successive images were identical. A single fMRI run included 24 category blocks (six repetitions per condition) with blank fixation baseline periods (14 s) at the beginning and the end of the experiment. Each localiser scan lasted 448 s, and each participants completed at least 3 runs (*M* = 3.05, *SD* = 0.23) for a total of 24 repetitions per condition. The entire localiser lasted approximately 30 minutes.

3.2.4. MRI acquisition

BOLD fMRI measurements were acquired using a whole-body 3T scanner (MAGNETOM Prisma Fit, Siemens) with a 64-channel head coil at the Scannexus imaging centre (Maastricht, The Netherlands). Functional images were acquired using a T2*-weighted echoplanar imaging sequence (35 horizontal slices; repetition time (TR) = 2000ms, echo time (TE) = 30ms, flip angle (FA) = 77°, field of view (FOV) = 216mm, matrix size (MS) = 72 x 72, voxel resolution = 3mm^3). High resolution T1-weighted anatomical images were also collected in the same session as functional scans (192 horizontal slices, TR = 2250ms, TE = 2.21ms, FA = 9°, FOV = 256mm, MS = 256 x 256, voxel size = 1mm^3).

3.2.5. Data pre-processing

Pre-processing and ROI definitions were performed using BrainVoyager QX (version 2.8; Brain Innovation). The BrainVoyager 3D motion correction (sinc interpolation) was used to align each functional volume within a participant to the functional volume acquired closest in time to the anatomical scan (Rossit et al., 2013). Slice scan time correction (ascending and interleaved) and high-pass temporal filtering (two cycles per run) were also performed. Functional data were superimposed on to the anatomic brain images that were previously aligned to the AC-PC plane and transformed into stereotaxic space (Talairach & Tournoux, 1988). Excessive motion was screened by examining the time-course movies and motion plots created with the motion-correction algorithms for each run. No spatial smoothing was applied.

To estimate activity in the localiser experiment, a predictor was used per image condition (i.e., bodies, objects (chairs), tools, hands, and scrambled) in a single-subject general linear model. Predictors were created from boxcar functions that were convolved with a standard 2*y* model of the hemodynamic response function (Boynton et al., 1996) and aligned to the onset of the stimulus with durations matching block length. The baseline epochs were excluded from the model, therefore, all regression coefficients were defined relative to this baseline activity. This process was repeated for the main experiment, using 16 separate predictors for each block of stimulation independently per run and 6 motion regressors (confound predictors). These estimates (β weights) from the main experiment were used as the input to the pattern classifier.

3.2.6. Regions of interest selection

Twelve regions of interest (ROIs) were defined at the individual participant level by drawing a cube (15mm^3) around the peak of activity from previously reported volumetric contrasts (see below) set at a threshold of $p < 0.005$ or, if no activity was identified, of $p < 0.01$ (Knights et al., 2021). In cases where no activity was observed, the ROI was omitted for that participant (see Table 3.1). Given the predominantly left-lateralised nature of tool processing (Lewis, 2006), all individual participant ROIs were defined in the left hemisphere (Bracci et al., 2012; Bracci & Op de Beeck, 2016; Bracci & Peelen, 2013; Knights et al., 2021; Peelen et al., 2013). Data from the independent BOTH localiser were used to define 6 visual regions of interest (ROIs) in the left hemisphere: lateral occipital temporal cortex (LOTC)-object, LOTC-tools, LOTC-hands, posterior middle temporal gyrus (pMTG), intraparietal sulcus (IPS)-hands, and IPS-tools. Two tool-selective ROIs were identified by contrasting tool pictures versus other objects or scrambled pictures [IPS-tool; LOTC-tools]. Moreover, two hand-selective ROIs were identified in LOTC (LOTC-hand) and IPS (IPS-hand) by contrasting activation for hand pictures versus pictures of other body parts (Bracci et al., 2012, 2018; Bracci & Op de Beeck, 2016; Palser & Cavina-Pratesi, 2018; Peelen et al., 2013) and a hand selective region was identified in pMTG by contrasting hand pictures with pictures of other objects (we were unable to find reliable activation in pMTG using the traditional tools > chairs contrast; Knights et al., 2021). Additionally, we defined an object-selective ROI [(LOTC-object); chairs > scrambled; Bracci & Op de Beeck, 2016; Hutchison et al., 2014]. Finally, an orthogonal contrast was applied to pantomime runs (all actions > baseline; Gallivan et al., 2011) to define tool processing ROIs in the DD and VD streams [i.e., supramarginal gyrus (SMG); ventral premotor cortex (PMv); dorsal premotor cortex (PMd)] and sensorimotor cortices [supplementary motor area (SMA); motor cortex (MC); somatosensory cortex (SC)]. This orthogonal contrast ensured that activity within each of the ROIs was not directly biased to show a pattern related to condition differences used in decoding analysis (Kriegeskorte et al., 2009). The ROI locations were verified by a senior author (S.R.) with respect to the following anatomical guidelines and contrasts:

*LOTC-object (*chairs > scrambled; Bracci & Op de Beeck, 2016; Knights et al., 2021) was defined by selecting the peak of activation near the lateral occipital sulcus (LOS; Hutchison et al., 2014; Bracci and Op de Beeck, 2016; Malach et al., 1995; Grill-Spector et al., 1999, 2001).

LOTC-hand [(hands > chairs) and (hands > bodies); (Bracci & Op de Beeck, 2016)] was defined by selecting the peak of activation near the LOS. These were often anterior to LOTC-body (bodies > chairs; Bracci et al., 2010; Bracci & Op de Beeck, 2016). LOTC-body was not included in the analysis.

LOTC-tool [tools > chairs; (Bracci et al., 2012; Hutchison et al., 2014)] was defined by selecting peak of activation near the LOS which closely overlapped with LOTC-hand (Bracci et al., 2012).

pMTG (hands > chairs) was defined by selecting the peak of activation on the pMTG, more lateral, ventral and anterior to EBA (Hutchison et al., 2014). We selected the peak anterior to the AOS, as the MTG is in the temporal lobe and the AOS separates the temporal lobe from the occipital lobe (Damasio, 1995).

SMG (pantomimes > baseline) was defined by selecting the peak of activation along the SMG, lateral to the anterior portion of the IPS (Gallivan et al., 2013).

PMv (pantomimes > baseline) was defined by selecting the voxels interior and posterior to the junction between the inferior frontal sulcus and pre-central sulcus (Gallivan et al., 2013).

IPS-Tools (tools > scrambled; Bracci & Op de Beeck, 2016) was defined by selecting the peak of activation close to the junction between the aIPS and post-central sulcus.

IPS-Hands (hands > chairs; Bracci & Op de Beeck, 2016) was defined by selecting the peak of activation along the IPS (Bracci & Op de Beeck, 2016).

PMd (pantomimes > baseline) was defined by selecting the peak of activation at the junction of the precentral sulcus and the superior frontal sulcus (Gallivan et al., 2013).

SMA (pantomimes > baseline; Fabbri et al., 2014) was defined by selecting the peak of activation on the medial wall of the posterior frontal gyrus, anterior to the medial end of the central sulcus and posterior to the vertical projection of the AC plane (Ariani et al., 2015).

MC (pantomimes > baseline) was defined by selecting the peak of activation around the "hand knob" area in the anterior bank of the central sulcus (Gallivan et al., 2013).

SC (pantomimes > baseline; Fabbri et al., 2014) was defined by selecting the peak of activation medial and anterior to the aIPS, including the post-central gyrus and post-central sulcus (Gallivan et al., 2013).

Table 3.1 *ROI Tailarach coordinates and ROI size (number of voxels).*

ROI	Subjects with ROIs (N)	Mean size (SD)	Mean peak coordinates (SD)		
			x	*y*	*z*
LOTC-Object	18	135 (34.6)	-43 (2.2)	-75 (2.8)	-4 (4.7)
LOTC-Tool	17	52 (31.6)	-45 (4.5)	-68 (3.7)	-2 (3.9)
LOTC-Hand	18	82 (37.7)	-47 (4.5)	-68 (4.1)	2 (4.6)
pMTG	18	81 (37.4)	-47 (4.4)	-59 (3.7)	5 (4.9)
SMG	17	138 (40.2)	-52 (3.9)	-33 (4.6)	31 (4.4)
PMv	17	101 (35.1)	-47 (4.6)	-4 (4.0)	36 (3.5)
IPS-Tool	18	66 (34.7)	-37 (4.8)	-38 (6.1)	40 (5.7)
IPS-Hand	18	90 (44.0)	-37 (3.6)	-44 (6.8)	43 (5.3)
PMd	17	125 (51.2)	-28 (4.7)	-16 (4.9)	51 (4.5)
SMA	18	117 (46.1)	-6 (2.3)	-11 (4.7)	48 (4.5)
MC	18	165 (30.7)	-35 (4.0)	-25 (4.9)	50 (4.5)
SC	18	143 (38.9)	-50 (4.3)	-25 (3.5)	43 (4.1)

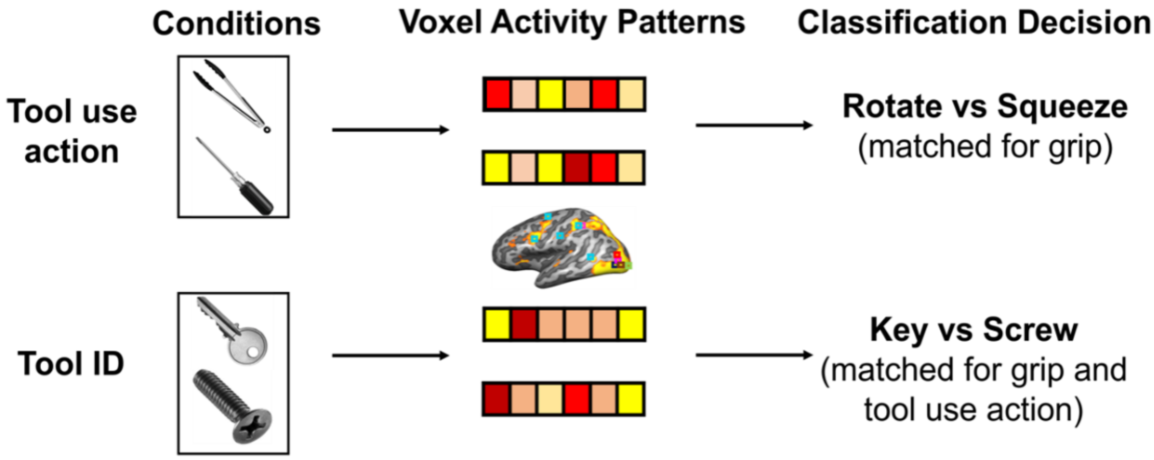
3.2.7. Pattern classification – Within-task decoding

MVPA was performed separately for view and pantomime runs. Independent linear pattern classifiers [linear support vector machine (SVM)] were trained to learn the mapping between a set of brain-activity patterns (β values computed from single blocks of activity) from the ROIs and the tool identities or tool use actions either depicted by the pictures (in the view task) or executed hand actions (in the pantomime task). Specifically, for each ROI and task separately, we decoded tool identity (e.g., screw vs key) or tool use action (squeeze vs rotation), while controlling for biomechanical differences between the actions afforded by the tool pairs. Specifically, to decode the tool use action, the classifier was trained and tested to distinguish between tool pairs that differed in the tool use action they afforded (rotate vs squeeze) but were matched for grip size (i.e., separate decoding analysis were run for tool pairs that afforded power and precision grips). Following this, the decoding accuracies were averaged across the power and precision tools, ensuring tool use action decoding was not confounded by grip size differences within pairs. To decode tool identity, the classifier was trained and tested to distinguish between tool pairs that differed in identity/shape but were matched for the tool use action and grip type the tool afforded (i.e., separate decoding analyses were run for tool pairs affording different actions). For example, the classifier was trained to distinguish between screw and key (both requiring a rotate action, and precision grip), and between tongs and nutcracker (both requiring a squeeze action, and power grip; see Figure 3.3). The decoding accuracies across the four pairs were then averaged to ensure that tool identity decoding was not confounded by differences between the actions afforded by the tools. Note that due to our decoding procedure the chance level was always 50%.

To test the performance of our classifiers, decoding accuracy was assessed using an *n*-fold leave-one-run-out cross-validation procedure; thus, our models were built from *n* – 1 runs and were tested on the independent *n*th run (repeated for the n different possible partitions of runs in this scheme; Duda et al., 2001; Gallivan et al., 2016; Knights et al., 2021; Smith & Goodale, 2015; Smith & Muckli, 2010) before averaging across *n* iterations to produce a representative decoding accuracy measure per participant and per ROI. Beta estimates for each voxel were normalised (separately for training and test data) within a range of −1 to +1 before input to the SVM (Chang & Lin, 2011) and the linear SVM algorithm was implemented using the default parameters provided in the LibSVM toolbox (C = 1). Pattern classification was performed with a combination of in-house scripts (Smith and Muckli, 2010; Smith and Goodale, 2015) using MATLAB with the Neuroelf toolbox (version 0.9c; http://neuroelf.net) and a linear SVM classifier (libSVM 2.12 toolbox; https://www.csie.ntu.edu.tw/~cjlin/libsvm/).

For each ROI, missing data were replaced with the task and condition mean, and one-tailed one-sample *t* tests were used to test for above-chance decoding for tool use action and tool identity classifications in each task independently. Additionally, to control for shape differences between tools, we contrasted tool use action and identity in each task and ROI by running a 2 x 2 x 12 repeated-measures ANOVA with property decoded (tool identity, tool use action), task (view, pantomime), and ROI (LOTC-object, LOTC-hand, LOTC-tools, pMTG, IPS-hand, IPS-tools, SMG, SC, SMA, PMv, PMd, MC) as within-subject factors. We corrected for multiple comparisons with false discovery rate (FDR) correction of $q \leqq 0.05$ (Benjamini & Hochberg, 1995; Benjamini & Yekutieli, 2001).

Figure 3.3 *MVPA classification example for tool use action and tool identity.*



3.2.8. Cross-task decoding

To test if the distributed activity patterns used to represent the inferred actions associated with tool pictures were the same as, or reliably like, the activation patterns which represent tool use actions, we conducted cross-task decoding by training our classifier in the view task and testing on the pantomime tasks (or vice-versa) using the leave-one-run-out procedure as mentioned in the Pattern Classification section. As in our within-task MVPA, we conducted a series of one-tailed one-sample *t* tests against chance in each of our ROIs.

3.2.9. Univariate analysis

To investigate whether our decoding results could have been a result of univariate differences, we extracted participants' beta weights for each tool identity, task and ROI. We calculated univariate difference scores for tool identity and tool use action to ensure that above chance decoding accuracy was not simply due to the univariate differences between our tool identities. More specifically, to calculate difference scores for tool identity, we calculated the average beta weight for each of the eight tools. Following this, we calculated the difference in beta weights between each tool identity matched for grip type and the tool use action. Specifically, we calculated the beta weight difference between tongs and nutcracker, key and screw, screwdriver and corkscrew, and tweezers and peg separately, and then averaged the difference scores. This method was employed to remain consistent with the pairs entered in to our MVPA analysis. For tool use action, we firstly averaged the beta weights across tools matched for grip type and tool use action. Thus, we averaged beta weights for key and screw (precision grip and rotate), screwdriver and corkscrew (power grip and rotate), peg and tweezers (precision grip and squeeze), and tongs and nutcracker (power grip and squeeze). The univariate difference scores were then calculated by finding the difference between rotate and squeeze tools matched for grip type and averaging the difference scores across both grip types. Again, this was in a manner which was consistent with our MVPA analysis.

We entered the beta difference scores into a (property: tool ID, functional manipulation) x 2 (task: view, pantomime) x 12 (ROI) repeated-measures ANOVA to see if the beta difference scores varied as a function of property, task or ROI. Post-hoc comparisons were FDR corrected (Benjamini & Yekutieli, 2001).

3.2.10. Whole-brain searchlight decoding

Finally, to test across the whole-brain which regions code tool use actions and tool identity for viewing and pantomiming, we performed a whole-brain searchlight MVPA independently, per participant, using separate linear pattern classifiers for the view and pantomime tasks (as in the within- task decoding above). A cube mask (5 x 5 x 5 voxel length, 125 voxels) was shifted through the entire brain volume, applying the classification procedure at each centre voxel (Smith & Goodale, 2015) to measure the accuracy that a given cluster of activity patterns could be used to discriminate between different tool use actions OR different tool identities within either the viewing or pantomime tasks. We also conducted further cross-decoding analyses (as above). To test performance of the classifiers the same procedures were used as the within and cross task decoding (i.e. leave one run out cross-validation) and this produced a decoding accuracy value per voxel for each analysis. Searchlight analysis space was restricted to a common group mask within Talairach space, defined by voxels with a mean BOLD signal > 100 for every participant's fMRI runs to ensure that all voxels included in searchlight MVPA contained suitable activation. Beta estimates for each voxel were normalised (separately for training and test data) within a range of − 1 to 1 before input to the SVM, and the linear SVM algorithm was implemented using the default parameters provided in the LibSVM toolbox (C = 1). Pattern classification was performed with a combination of in-house scripts (Knights et al., 2022; Smith & Goodale, 2015) implemented in Matlab using the SearchMight toolbox (Pereira & Botvinick, 2011).

Voxel accuracies from the searchlight MVPA for each participant were converted to unsmoothed statistical maps. To assess where in the brain coded information about tool identity and tool use action, we used one-sampled *t* tests (across participants) against chance level performance (50%; see Smith & Goodale, 2015). The BrainVoyager cluster-level statistical threshold estimator (Forman et al., 1995; Goebel et al., 2006) was used for cluster correction (voxelwise thresholds were set to $p = 0.01$ and then the cluster-wise thresholds were set to $p < 0.05$ using a Monte Carlo simulation of 1000 iterations), before projecting results on to a standard surface.

3.3. Results

It is well-known that tool pictures elicit activation in both perceptual and sensorimotor regions (Chao & Martin, 2000; Lewis, 2006) and that similar brain areas respond to hand pictures (Bracci et al., 2012, 2016; Bracci & Op de Beeck, 2016; Bracci & Peelen, 2013).

3.3.1. ROI decoding

We first tested which ROIs had decoding accuracy (FDR corrected) greater-than-chance (50%) when discriminating tool identity during picture viewing and pantomiming tool use. Interestingly, as shown in Figure 3.4, LOTC-hand and SMG were the only ROIs where tool identity could be decoded significantly above chance for both viewing and pantomiming tasks [mean ± SD (LOTC-hand accuracies: view = 58.16 ± 7.49%, $t(17) = 4.62$, $p < .001$, $d = 1.09$; pantomime = 52.71 ± 5.88%, $t(17) = 1.96$, $p = .034$, $d = .461$); SMG accuracies: view = 53.47 ± 7.23%, $t(17) = 2.04$, $p = .029$, $d = .481$; pantomime = 54.49 ± 5.63%, $t(17) = 3.38$, $p = .002$, $d = .797$)]. Moreover we found a different pattern of results for tool identity decoding between ventral and dorsal ROIs depending on task: while in the view task significant above chance accuracy was observed only in ventral ROIs including LOTC-object, -tool and -hand and pMTG, in the pantomime task above chance decoding was only found in dorsal ROIs such as tool- and hand-selective IPS, PMd, SC and MC [view LOTC-object accuracy = 62.57 ± 8.83%, $t(17) = 6.04$, $p < .001$, $d = 1.42$; view LOTC-tool accuracy = 59.72 ± 8.10%, $t(17) = 5.10$, $p < .001$, $d = 1.20$; view pMTG accuracy = 55.42 ± 7.09%, $t(17) = 3.24$, $p = .002$, $d = 0.764$); pantomime IPS-tool accuracy = 54.60 ± 6.97%, $t(17) = 2.80$, $p = .006$, $d = 0.660$; pantomime IPS-hand accuracy = 55.10 ± 6.37%, $t(17) = 3.40$, $p = .002$, $d = .801$; pantomime MC accuracy = 60.35 ± 9.11%, $t(17) = 4.82$, $p < .001$, $d = 1.14$; pantomime SC accuracy = 62.34 ± 9.53%, $t(17) = 5.50$, $p < .001$, $d = 1.30$, pantomime PMd accuracy = 57.02 ± 9.25%, $t(17) = 3.22$, $p = .003$, $d = .759$].

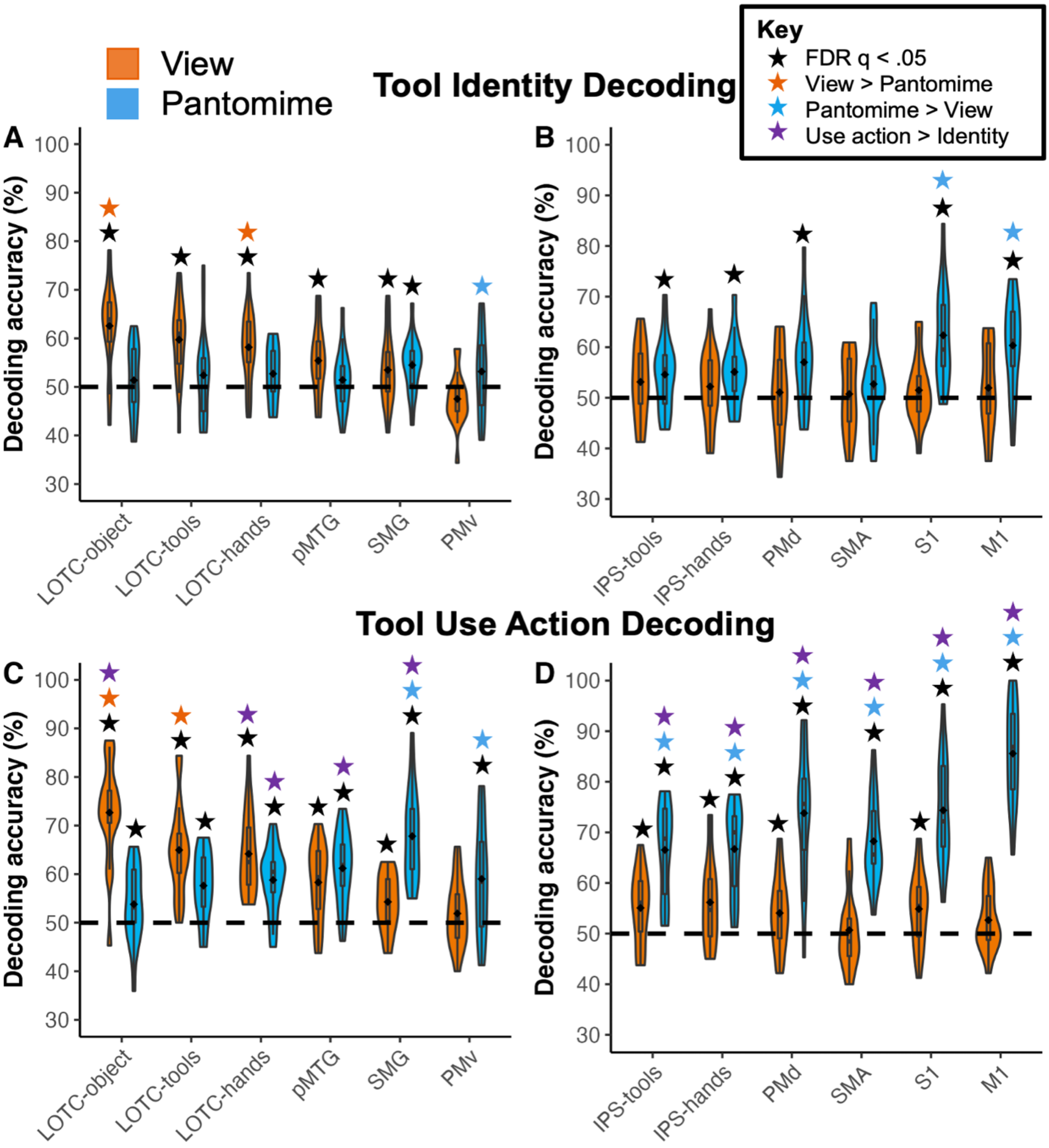
Next, we examined decoding accuracies for tool use actions for both tasks. In line with our predictions, and as can be seen in Table 3.2, tool use actions could be discriminated above chance during picture viewing in both hand- and tool-selective LOTC and IPS ROIs. Moreover, tool use actions could be decoded significantly above chance during picture viewing in LOTC-object, pMTG, SMG, and, remarkably, even SC [see Table 3.2; Figure 3.4]. In the pantomime task, we successfully decoded tool use actions in all ROIs, even in ventral visual areas such as LOTC.

Table 3.2 *Decoding accuracies and effect sizes in all ROIs for tool use action.*

Task	ROI	Accuracy (%)	SD (%)	t-statistic	Cohen's d
View	LOTC-Object	72.67	10.33	9.31***	2.20
	LOTC-Tools	64.96	9.40	6.75***	1.59
	LOTC-Hands	64.17	8.47	7.10***	1.67
	pMTG	58.30	7.73	4.56***	1.07
	SMG	54.28	5.67	3.20**	0.76
	PMv	51.89	6.95	1.19	0.13
	IPS-Tools	55.07	7.09	3.03**	0.72
	IPS-Hands	56.16	8.30	3.15**	0.74
	PMd	54.06	7.21	2.39*	0.56
	SMA	50.68	7.70	0.357	0.09
	SC	54.86	7.10	2.90**	0.68
	MC	52.66	6.00	1.88	0.04
Pantomime	LOTC-Object	53.78	7.68	2.09*	0.49
	LOTC-Tools	57.63	6.91	4.68***	1.10
	LOTC-Hands	58.78	6.75	5.52***	1.30
	pMTG	61.2	7.49	6.35***	1.50
	SMG	67.81	9.31	8.11***	1.91
	PMv	59.01	11.01	3.47**	0.82
	IPS-Tools	66.53	9.08	7.73***	1.82
	IPS-Hands	66.7	8.73	8.12***	1.91
	PMd	73.81	12.62	8.00***	1.89
	SMA	68.25	8.32	9.31***	2.19
	SC	74.36	10.15	10.18***	2.34
	MC	85.59	7.93	15.52***	3.66

Note: * = p < .05, ** = p < .01, *** p < .001

Figure 3.4 *A) Tool identity decoding accuracies in ventral and VD regions. B) Tool identity decoding in DD regions. C) Tool use action decoding accuracies in ventral and VD regions. D) Tool use action decoding accuracies in DD regions. Dashed line represents chance (50%) in all plots.*



Then, to test if these effects were driven by low-level shape differences between our tool stimuli and investigate how decoding accuracies varied per property, task, and ROI, we ran a 2-property decoded (tool identity, tool use action) x 2-task (view, pantomime) x 12-ROI repeated-measures ANOVA. This revealed a significant three-way interaction [$F(11, 187) = 6.293$, $p < .001$, $\eta_p^2 = .270$]. Post-hoc tests (FDR corrected; see Table 3.3) showed that LOTC-hand was the only region where tool use action decoding was significantly higher than tool identity decoding in both the view and pantomime tasks. This demonstrates that tool use action representations in LOTC-hand cannot simply be explained by visual shape differences between stimuli and are task-invariant. Moreover, the ANOVA also revealed that our ROIs showed a task-based gradient with better decoding in ventral visual areas in the view task and better decoding in ventro-dorsal or dorsal regions in the pantomime task (see Table 3.4).

Table 3.3 *Regions showing a significant difference in decoding accuracy across action property decoded.*

Task	ROI	Comparison	Mean Difference (SE; %)	*p*
View	LOTC-object	Use > Identity	10.10 (2.43)	.001
	LOTC-hand	Use > Identity	6.01 (2.06)	.010
	PMv	Use > Identity	4.38 (1.65)	.017
Pantomime	LOTC-hand	Use > Identity	6.08 (1.96)	.007
	pMTG	Use > Identity	9.77 (1.91)	< .001
	SMG	Use > Identity	13.33 (2.63)	< .001
	IPS-tool	Use > Identity	11.93 (2.26)	< .001
	IPS-hand	Use > Identity	11.60 (1.81)	< .001
	PMd	Use > Identity	16.78 (3.57)	< .001
	SMA	Use > Identity	15.54 (2.45)	< .001
	SC	Use > Identity	12.01 (2.71)	< .001
	MC	Use > Identity	25.24 (3.88)	< .001

Specifically, for tool identity decoding, while LOTC-object and LOTC-hand showed significantly higher decoding for view than pantomime, the opposite was true for PMv, SC and MC. Similarly, for tool use action decoding, while ventral areas LOTC-object and LOTC-tool had higher decoding in view than pantomime, ventro-dorsal and dorsal areas such as SMG, PMv, IPS-tool, IPS-hand, PMd, SMA, SC and MC showed higher tool use action decoding in pantomime than view. Finally, in the pantomime task only, decoding of tool use actions was significantly higher than tool identity decoding in pMTG, SMG, IPS-tool, IPS-hand, PMd, SMA, SC and MC, while in the view task this pattern was found in LOTC-object only.

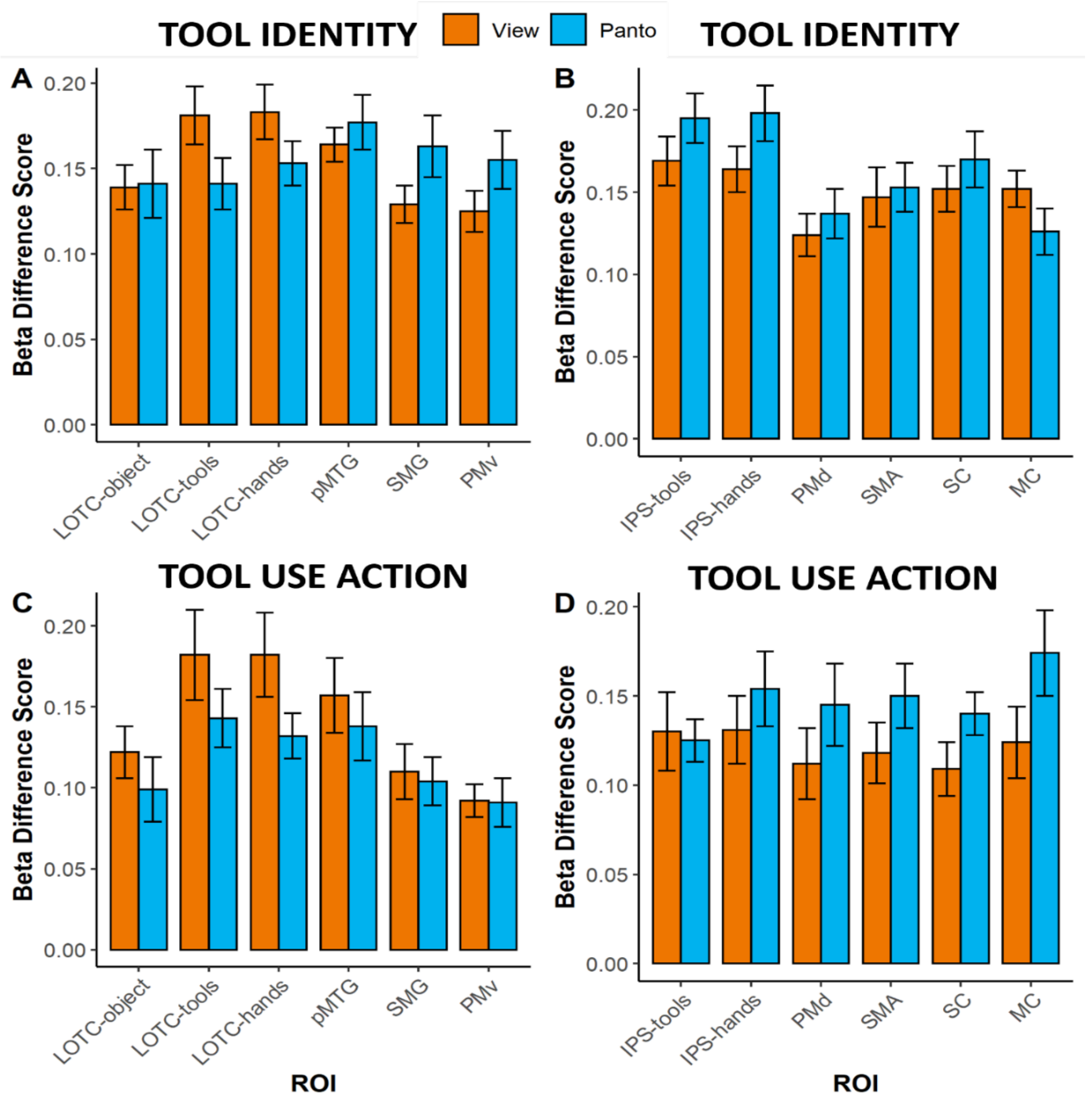
Table 3.4 *Regions in which decoding accuracy significantly differed between task.*

Decoding Type	**ROI**	**Comparison**	**Mean Diff (SE; %)**	***p***
Tool Identity	LOTC-object	View > Panto	11.22 (2.76)	< .001
	LOTC-hand	View > Panto	5.45 (1.85)	.009
	PMv	Panto > View	5.64 (2.02)	.012
	SC	Panto > View	10.85 (2.81)	.001
	MC	Panto > View	8.41 (2.74)	.007
Use Action	LOTC-object	View > Panto	18.89 (2.37)	< .001
	LOTC-tool	View > Panto	7.34 (2.46)	.008
	SMG	Panto > View	13.53 (2.25)	< .001
	PMv	Panto > View	7.11 (2.69)	.017
	IPS-tool	Panto > View	11.46 (3.00)	.001
	IPS-hand	Panto > View	10.54 (2.83)	.002
	PMd	Panto > View	19.74 (3.16)	< .001
	SMA	Panto > View	17.56 (2.34)	< .001
	SC	Panto > View	19.50 (2.80)	< .001
	MC	Panto > View	32.93 (2.91)	< .001

3.3.2. Univariate analysis

Finally, we tested if these significant decoding accuracies simply reflected the response amplitudes within each ROI. To do this we analysed the mean β-weights in ANOVAs in a manner consistent with the MVPA analysis by calculating β-difference scores between the tool pairs used for MVPA classification. This revealed a significant ROI x task interaction ($F(4.86, 82.59) = 2.455$, $p = .041$, $\eta_p^2 = .126$) and a significant ROI x property interaction ($F(11, 187) = 2.168$, $p = .018$, $\eta_p^2 = .113$; see Figure 3.5). FDR corrected post-hoc comparisons revealed a larger difference in activation between the tool identities in IPS-hand compared to PMd (mean difference = .051, *SE* = .011, $p < .001$), and that in PMv, there was a greater activation difference between tool identity than tool use action (mean difference = .049, *SE* = .010, $p < .001$). There were no significant post hoc effects of task on activation differences.

Figure 3.5 *A) Univariate differences between tool identities in the ventral and VD streams. B) Univariate differences between tool identities in the DD stream. C) Univariate differences between tool use action (rotate vs squeeze) in the ventral and VD streams. D) Univariate differences between tool use action in the DD stream. Error bars represent standard error in all plots.*



3.3.3. *Whole-brain searchlight decoding.*

Results from the whole-brain searchlight analysis replicated our ROI findings (see Table 3.5 and Figure 3.6). Tool identity was successfully decoded during the view task in a large area of occipital cortex, including early visual cortex (EVC), extending bilaterally to ventral stream regions LOTC, FG and MTG. Significant decoding was also observed in dorsal regions bilaterally along IPS and SPOC. Posterior clusters of significant decoding were larger in the right than left hemisphere. Successful decoding of tool use action in the view task was observed in a large area of the occipital cortex bilaterally, this extended to ventral regions LingG, LOTC, FG bilaterally, and left MTG. In dorsal regions, successful tool use action decoding was observed in the right IPS, left MC. We also observed successful decoding in bilateral somatosensory cortex.

For the pantomime task, tool identity was successfully decoded in motor cortex, somatosensory cortex and PMv. This was largely left-lateralised; however a cluster was also found in right SC. Decoding of tool use action in the pantomime task was also observed in bilateral MC and SC, however this was much more widespread than tool identity decoding. We also observed clusters of significant decoding in left SMA, left IPS, left PMd and SPOC bilaterally. More ventral regions exhibiting significant decoding included bilateral LOTC, extending to the left MTG, bilateral para-hippocampal gyrus (PaHG) and right FG and AG. Successful decoding of tool use action in the pantomime task was also observed in the right cerebellum.

We were unable to observe any regions exhibiting significant cross-task decoding in the whole-brain searchlight analysis, however our searchlight analysis revealed overlapping regions where significant decoding was observed for both view and pantomime tasks when decoding tool use action. We therefore examined a conjunction of the searchlight classification accuracy maps which revealed significant decoding of tool use action in both tasks in left MC, bilateral somatosensory cortex, ventral and VD stream regions including LOTC, FG and MTG, and IPS and SPOC in the DD stream.

Figure 3.6 *Regions where decoding was observed in the searchlight analysis for both tasks, and conjunction regions.*

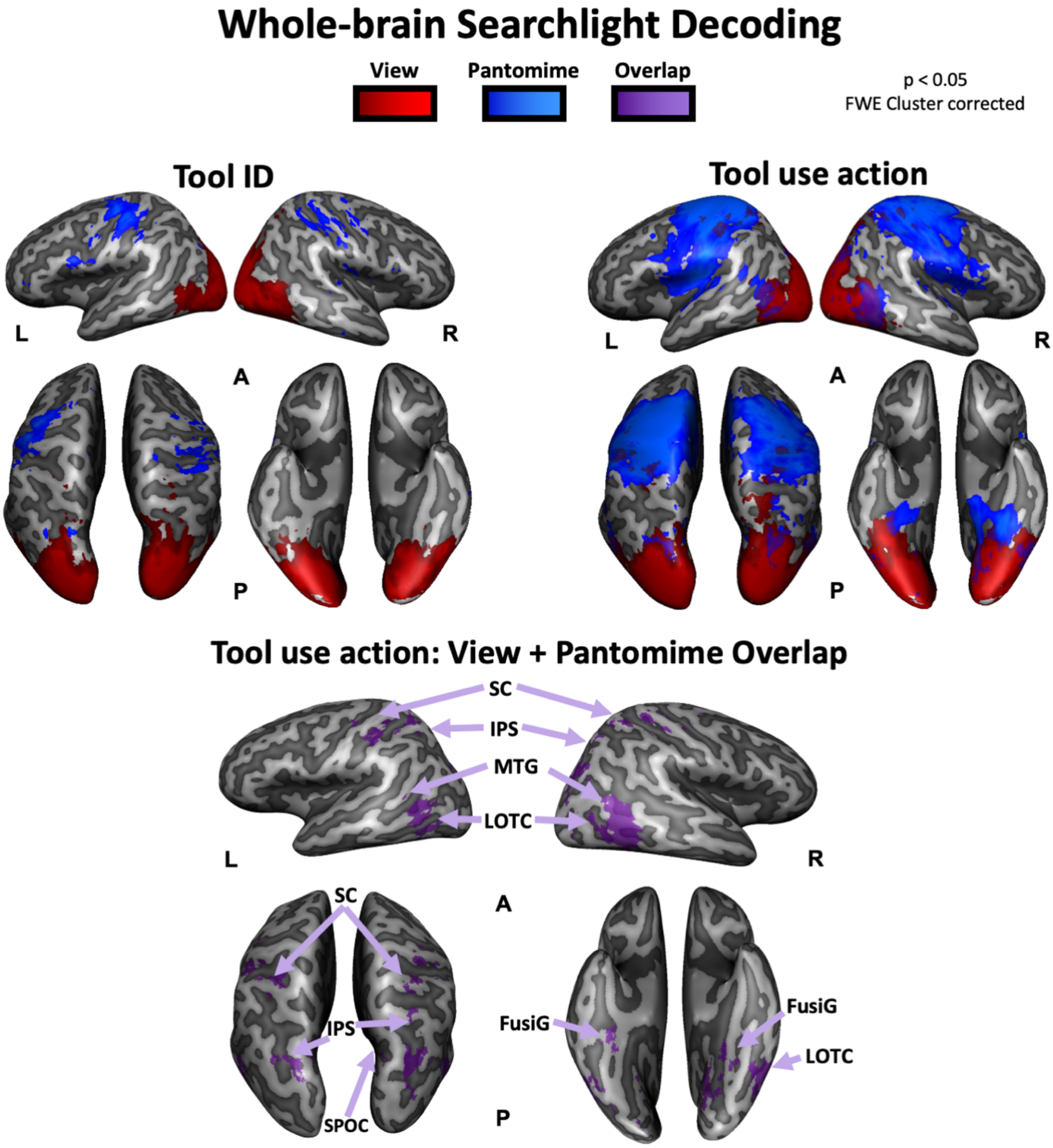


Table 3.5 *Searchlight peak coordinates (Talairach) and statistics for decoding tool identity and tool use action categories for viewing and pantomiming tasks.*

Searchlight	**Region**	X	Y	Z	t-statistic	*p*
Tool Identity: View	L-EVC	-10	-86	-3	34.03	< .001
	R-EVC	20	-83	9	24.73	< .001
	L-LOTC	-46	-71	-3	9.97	< .001
	R-LOTC	35	-74	3	15.9	< .001
	L- AOS/ITG	-40	-56	-9	7.17	< .001
	R-AOS/ITG	41	-56	-9	9.55	< .001
	L-FG	-21	-44	-9	5.02	< .001
	R-FG	21	-59	-9	9.52	< .001
	L-MTG	-40	-56	3	7.77	< .001
	R-MTG	41	-56	-1	7.52	< .001
	L-SPOC	-13	-80	42	5.46	< .001
	R-SPOC	17	-80	42	8.40	< .001
	L-IPS	-19	-68	42	5.16	< .001
	R-IPS	29	-68	39	5.63	< .001
Tool identity: Pantomime	L-IPS	-25	-77	39	9.49	< .001
	L-SC	-43	-38	51	7.90	< .001
	R-SC	44	-32	48	6.72	< .001
	L-MC	-40	-20	48	9.61	< .001
	L-S2	50	-23	21	6.50	< .001
	L-PMv	50	-17	30	6.15	< .001
Tool use action: View	L-EVC	-4	-83	3	32.84	< .001
	R-EVC	7	-86	0	29.10	< .001
	L-LingG	-19	-74	-9	19.32	< .001
	R-LingG	17	-68	-3	20.12	< .001
	L-FG	-32	-51	-15	9.54	< .001
	R-FG	35	-44	-9	9.08	< .001
	L-LOTC	-43	-62	-3	12.53	< .001
	R-LOTC	36	-77	3	14.99	< .001
	L-MTG	-49	-60	6	8.24	< .001
	R-IPS	23	-68	48	6.83	< .001
	L-SC	-28	-47	48	6.56	< .001
	R-SC	32	-44	51	7.24	< .001
	L-MC	-37	-32	42	7.63	< .001
	L-LOTC	-49	-62	-3	9.65	< .001

Searchlight	**Region**	X	Y	Z	t-statistic	*p*
Tool use action:	R-LOTC	44	-62	-6	7.09	< .001
Pantomime	L-MTG	-49	-53	6	8.34	< .001
	L-PaHG	-22	-35	-9	8.25	< .001
	R-PaHG	20	-41	-12	10.99	< .001
	R- FG/TOG	35	-38	-12	9.03	< .001
	L-SPOC	-16	-77	27	6.94	< .001
	R-SPOC	17	-72	30	7.68	< .001
	L -IPS	-28	-77	35	5.15	< .001
	R-AG	35	-74	33	6.71	< .001
	L-SC	-22	-35	49	10.97	< .001
	R-SC	29	-41	54	17.2	< .001
	L-MC	-34	-26	48	16.68	< .001
	R-MC	35	-26	49	10.10	< .001
	L-PMd/FEF	-25	-17	66	21.23	< .001
	L-SMA	-7	-17	54	16.92	< .001
	R-Cerebellum	5	-44	-3	12.04	< .001
Tool Identity: View + Pantomime Overlap	Not significant					
Tool use action:	L-FG	-31	-41	-12		
View + Pantomime	R-FG	34	-39	-12		
Overlap	L-LOTC	-49	-62	-3		
	R-LOTC	35	-77	0		
	L-MTG	-50	-54	6		
	R-MTG	47	-59	7		
	L-SPOC	-17	-78	27		
	R-SPOC	24	-75	24		
	L-IPS	-28	-74	15		
	R-IPS	27	-77	24		
	L-SC	-35	-38	50		
	R-SC	29	-41	54		
	L-MC	-34	-29	45		

3.4. Discussion

The neural mechanisms underlying humans' ability to reach, grasp, and use tools have been studied for several decades. Neuroimaging and lesion studies have provided support for the specific roles of the ventral, VD and DD streams in tool related processing and use action (Binkofski & Buxbaum, 2013; Rizzolatti & Matelli, 2003). However, far less is known about whether regions in these pathways code general motor and/or visual responses, or specific action properties, such as how we would move a tool for use. Moreover, it is unclear whether these action representations are task or modality specific, or generalisable across simply viewing pictures of tools and pantomiming their use. Here, we defined visual category-selective areas in the ventral, VD and DD streams, and regions responding preferentially to pantomime including MC, PMd, SMG and SMA, and investigated whether these regions contained representations of tool use actions, such as whether a tool is rotated or squeezed to fulfil its function, while participants simply viewed tool images and pantomimed their use. Importantly, to control for representations of low-level visual features, such as object shape, size, orientation, and grip type, we carefully selected a stimulus set matched as much as possible for low-level features. In addition, we compared decoding accuracies for tool use action with decoding of tool identity, to ensure that our representations were of action properties rather than simply object shape. We found that ventral, VD and DD regions represent how to use a tool both when viewing and pantomiming and most notably, provide the first evidence that visual region LOTC-hand represents tool use actions both when viewing tool images and pantomiming their use.

Our results support the long-standing hypothesis that simply viewing pictures of graspable objects triggers action representations even when there is no intent to act (Chao & Martin, 2000; Gibson, 1979). In particular, we were able to reliably decode tool use action in frontoparietal regions SMG, IPS, PMd and even in SC when participants simply viewed images of tools. Importantly, given that we were unable to decode tool identity in any of these regions (except SMG) during viewing, this suggests that viewing tool images triggers functional action representations of how to move hands to use them (i.e. rotate or squeeze) rather than simply the tool identity itself. Decoding of these functional representations cannot be simply due to differences in shape, elongation, graspability, or object weight, as if this was the case, we would expect significant decoding of tool identity in these regions too. Instead, this suggests that the tool images elicit learned motor representations in dorsal areas about how we move our hands to functionally interact with them

(Valyear et al., 2007). Given that we were able to decode tool identity in SMG during viewing, it is possible that this is in line with recent research suggesting that SMG is the region which integrates semantic and action related tool information, containing representations of both (Garcea & Buxbaum, 2019).

As expected, we were also able to reliably decode tool use action in all our ROIs in the VD and DD streams during pantomime. Decoding of tool use action was significantly higher than decoding of tool identity in all regions within the DD stream, both IPS-tools and hands, and PMd. We were also able to observe significantly higher decoding of tool use action compared to tool identity in SMG in the VD stream during pantomime. This suggests that regions in the DD and VD stream do represent the actions required to successfully use a tool when pantomiming. Binkofski and Buxbaum's (2013) model would suggest that regions of the DD are responsible for utilising online visual feedback to aid actions, however, here we show that regions in the DD stream (such as IPS and PMd) represent tool use actions in the absence of visual feedback of the hand or tool. Given that the pairs entered into our analyses were matched for grip type (e.g. power and precision), it is possible that these representations extend beyond simply hand posture to the actual hand actions involved to use a tool. These findings align with previous research showing that IPS, specifically, IPS-hand, represents how we would correctly grasp a tool for its use (Knights et al., 2021). Put together, this suggests that regions in the DD stream also represent more complex hand kinematics involved in learned skilled motor actions such as tool use even in the absence of visual feedback of the hand action.

Interestingly, we found that both hand- and tool-selective LOTC in the ventral stream represents tool use actions during pantomiming. Despite being a visual-perceptual area, LOTC has been implicated in hand and arm movements even in the absence of visual feedback (Astafiev et al., 2004; Gallivan et al., 2016), and responds selectively to auditorily presented tool words even in those who are congenitally blind (Peelen et al., 2013). Moreover, recent research has implicated LOTC in containing effector-independent representations of grasping movements during real action (Turella et al., 2020). In line with previous research, it appears that specific, rather than generalised category-level, sensorimotor representations are stored in LOTC which need to be accessed in order to pantomime tool use (Perini et al., 2014). It has recently been proposed that there are two subdivisions of the ventral visual stream, with ventral OTC responsible for processing features associated with using tools, such as size and weight, and LOTC responsible for processing the actions associated with tools, i.e. its function (Wurm & Caramazza, 2022). It is possible that these development of action representations in the brain are independent of the visual experience. Particularly as research has shown action representations such as reach direction can be decoded in EVC as well as DD regions in the congenitally blind (Bola et al., 2023).

Moreover, to confirm whether tool use actions are represented in LOTC, fMRI guided TMS to LOTC could be used to examine whether there is a causal link between LOTC and tool use actions. Interestingly, a recent TMS study found that TMS to body-selective LOTC slowed object recognition for images of hands and tools (teapots were used as tool stimuli), but not for images of other objects (cars; Atilgan et al., 2023). This highlights a causal functional relevance for the overlapping representations of hands and tools in LOTC. However, it would be interesting to further our understanding as to how and why LOTC may be involved in tool use actions. If tool use actions are represented in LOTC even during pantomime, it is possible that TMS to LOTC could impair functional tool use actions even when the tool is not viewed (for instance when performed in the dark). This could provide further complementary but causal evidence highlighting a role of the ventral stream (LOTC) in tool use action processing (Wurm & Caramazza, 2022).

Interestingly, we were also able to decode tool use action in visual region pMTG during both view and pantomiming. These findings are in line with previous research where pMTG has been shown to discriminate upcoming actions performed with a tool in hand (Gallivan et al., 2013), and when observing hand-tool interactions (Wurm & Lingnau, 2015). Here, we have expanded on this research to show that pMTG also represents hand actions required to use a tool during pantomime, and thus in the absence of visual feedback of the hand or tool. This is in line with recent research showing that tool actions, and goals (to move or to use), are represented in pMTG during planning and execution of pantomimes (Malfatti & Turella, 2021). While the functional role of pMTG in motor control remains elusive, there is evidence of bidirectional connectivity between pMTG and PMv and aIPS during pantomimed movements (Malfatti & Turella, 2021). Put together, our findings expand on a growing body of evidence suggesting that ventral visual regions are involved in action planning and execution.

Moreover, previous research has found that ventral stream regions such as LOTC and pMTG are preferentially activated in response to viewing tools being used consistent with their typical use, compared to atypically (Valyear & Culham, 2010). These findings were interpreted as regions in the ventral pathway being associated with stored semantic knowledge of object-specific actions (Valyear & Culham, 2010). Our findings corroborate these previous findings given that we could decode tool use actions in ventral region LOTC both during viewing and pantomiming. This suggests that the ventral stream contains representations of semantic knowledge of actions associated with tools based on previous interactions even in the absence of a viewed tool.

As expected, we were able to decode tool identity and tool use actions from viewing tool images in ventral region LOTC in line with Goodale and Milner's (1992; Milner & Goodale, 2006, 2008) TVSH which posits that ventral stream regions contribute to visual perception (Goodale & Milner, 1992). Interestingly, although tool identity was successfully decoded in all ventral ROIs, tool use action was decoded significantly higher in object and hand-selective LOTC, and pMTG. This highlights that action representations, as well as properties such as shape and size, are represented in visual areas, in line with research showing that LOTC represents both action and category related hand-tool information (Bracci et al., 2016).

Interestingly, LOTC-hand was the only region where tool use action was decoded significantly higher than tool identity in both the view and pantomime tasks. Therefore, it is possible that this hand-selective area contains representations of the hand actions associated with tools both when viewing and pantomiming tool use in the absence of visual feedback. Previous real-action fMRI studies have found that hand-selective LOTC contains representations of movement goals of planned reach to grasp actions carried out with hands, although not movement goals of actions carried out with a tool in hand (Gallivan et al., 2013). While hand- and tool-selective areas are present in those born without hands (Striem-Amit et al., 2017), activity in hand-selective visual regions, and functional connectivity with hand selective sensorimotor regions, increases with increased prosthetic usage, thus with experience of having and using the hands (van den Heiligenberg et al., 2018). Moreover, previous research in our lab found that LOTC-hand, but not LOTC-tool, represents how to grasp a tool correctly for its use (i.e. by its handle rather than the functional end; Knights et al., 2021). Put together with our present findings, it seems that hand-selective LOTC, while overlapping with tool-selective LOTC, more likely represents the hand actions required to effectively use a tool. Future research could assess whether LOTC-hand, as well as LOTC-tool represents the hand-actions required for the functional use of 3D tools. It is possible that the tool preferring region would be more likely to represent these actions when the tool is in hand, but in the absence of visual feedback.

Despite observing significant decoding in ventral areas for the pantomime task, and DD regions for the view task, our results suggest a preference for the representation of functional tool use in brain regions depending on their underlying sensory modality preference. For example, decoding of tool use action was significantly higher in visual LO regions (except for LOTC-hand) in the view, compared to the pantomime task. On the other hand, tool use action was decoded significantly higher in frontoparietal regions in the pantomime task. This supports the classic perception action dissociation to an extent, however there is a clear involvement of both streams in the representation of action related concepts during both viewing and pantomiming.

Remarkably, we were able to decode tool use action during picture viewing in SC. This is in line with previous work finding that SC represents familiar, but not unfamiliar, object category information despite the absence of any haptic interaction (Smith & Goodale, 2015). Moreover, object texture is also represented in somatosensory cortex from simply viewing images, although this is not the case when imagining textures (Sun et al., 2016). It is possible that our finding of tool use action decoding during viewing in SC reflects an automatic evocation of the learnt haptic experiences associated with using the tools pictured, which is in line with EEG studies of affordances (Proverbio, 2012; Proverbio et al., 2011). More recent fMRI research has identified that the effector used in movement planning can be decoded in SC during movement planning, therefore providing some evidence that SC may be involved in anticipating sensory information to be received in the upcoming movements, before an action occurs (Gale et al., 2021).

Surprisingly, we were unable to reliably decode tool identity or use action across tasks. This suggests that while ventral and dorsal visual regions represent how we use a tool, they do so using distinct patterns of activation even when the inferred and experienced actions represent the same basic information (e.g. squeeze). One possibility for our inability to decode across tasks is due to our stimuli being presented in different modalities for the view and pantomime task (e.g. words versus images). However previous studies using cross-decoding to investigate neural representations in response to viewing words and images of objects and/or scenes (e.g. train the classifier on ‘images’ and test on ‘words’) have successfully decoded semantic categories of stimuli across both images and words particularly in ventral stream ROIs (Fairhall & Caramazza, 2013; Kumar et al., 2017; Shinkareva et al., 2011). This has been interpreted as evidence of a common neural representation of semantic categories across the input modalities. Therefore, our lack of decoding across tasks is unlikely to be explained by differing stimulus modalities. Instead, our findings could represent a necessary mechanism by which inferred (view) and experienced (pantomime) sensations are kept distinct at the neural level in order to prevent inappropriate physiological or behavioural responses to inferred sensations (similarly to what has been reported for viewing images of foods in Avery et al., 2021). For example, to inhibit automatic actions while simply viewing a tool.

Despite this, our lack of significant cross-task decoding contrasts with the findings of a recent similar study in which tool use actions were successfully decoded across view and pantomime tasks in left-IPL (Chen et al., 2018). However, there are several differences between our study and that reported by Chen et al. (2018). Firstly, we did not include IPL in our ROI analysis, and we defined our ROIs based on a different functional localiser. Secondly, in the view task, Chen et al. (2018) instructed participants to think about the objects' features, including their associated actions. In contrast, participants in our experiment were solely focussing on tool identity to complete the 1-back task. It is thus possible that conscious processing of tool-use is represented in a manner that is more abstract rather than modality specific in IPL. Nevertheless, put together with the findings of Chen et al. (2018), our present findings suggest that task-independent patterns of action representations may only be evoked by pictures of tools when participants are explicitly asked to think about object features, such as how we would interact with them. Despite this, other research has used MVPA to classify manipulable vs non-manipulable objects during continuous flash suppression. Here, successful decoding of manipulability was found in IPL even when there was no conscious awareness of the tool stimuli being present (Tettamanti et al., 2017). While manipulability was decoded in IPL in the absence of conscious awareness, it is still possible that specific actions associated with tools may not be represented in IPL similarly to execution of their use unless tool use action is imagined. To test whether tool use action representations differ when imagining tool use compared to passively viewing, future research could directly compare tool use action representations in IPL in response to passively viewing tool images and imagining tool actions, stimuli could be tool images but also in other modalities, such as words or auditory input. This could confirm whether tool use action representations from passively inferred actions (passively viewing objects, and their affordances) are represented using distinct patterns of activation to imagined actions.

Our searchlight analysis largely complemented our ROI analysis; however, the findings challenge the longstanding notion that the tool use cortical network is left-lateralised. Despite this, recent fMRI research does suggest that the tool use may engage a bilateral cortical network (Garcea & Buxbaum, 2019; Michalowski et al., 2022). One possibility is that while execution of tool use is bilateral, the left-lateralised network is only involved in complex tool use planning (Frey, 2007). While patterns of neural responses are not necessarily similar across both tasks, we observed several overlapping regions which represented tool use action during pantomime and viewing. Within the ventral stream, we found overlapping representations in LOTC and MTG in line with our ROI analysis. We also observed significant decoding of tool use action in both tasks in bilateral fusiform gyrus. The FG is a visual area typically associated with low-level visual properties such as colour and shape (Martin et al., 1995). However, fMRI research has found repetition suppression for tools, but not other manipulable objects, in the medial FG (Mahon et al., 2007). This suggests that higher level information, such as action-related properties, is stored within this ventral stream region.

In the dorsal stream, significant decoding in both tasks in the searchlight analysis was observed in DD regions, but not VD regions. In line with our ROI analysis, IPS represented tool use actions during both view and pantomime. We also observed an overlapping region in SPOC for decoding tool use action. Neurons in monkey V6A, which is thought to correspond to SPOC, have been shown to discriminate reach direction of hand actions even before movement onset (Fattori et al., 2005). In humans, SPOC has been shown to discriminate upcoming reach vs grasp actions with the hand but not with a tool in hand (Gallivan et al., 2013). Additionally, V6A neurons have been shown to be sensitive to grip formation and wrist rotation (Breveglieri et al., 2016, 2018; Fattori et al., 2009, 2010). In line with these findings, and in conjunction with our findings, it is possible that SPOC contains representations of the hand actions associated with the tools' functional use, and that these representations are also elicited in response to simply viewing tool images. Albeit the representations consist of different neural patterns of activation.

A further, but not mutually exclusive, explanation for lack of significant cross-decoding between tasks is that it is impossible to grasp and use an image of a tool, while pantomiming tool use is merely a proxy for real tool use. Action representations from passively viewing tool images may therefore differ from those of pantomimed actions firstly due to the inability to interact with the tool image, and secondly due to the lack of a presence of a real tool during pantomime. Indeed, it is possible that there are differing mechanisms involved in real tool use compared to pantomime, for example symptoms of apraxia notably improve when using a real tool compared to pantomiming (Goldenberg et al., 2004). Research has generally found that regions in the dorsal stream have higher activation when using real tools compared to pantomiming (Hermsdörfer et al., 2007; Króliczak et al., 2007). Moreover, pantomime of tool use may recruit more of the right hemisphere when compared to grasping real objects which may explain our findings of bilateral representations in the searchlight analysis (Króliczak et al., 2007). There is also a growing body of evidence that neural and behavioural responses to 2D images differ from real graspable objects (for a review, see Snow & Culham, 2021). For instance, greater flanker effects have been observed in response to real objects, compared to 2D and 3D images of the same objects (Gomez et al., 2018). Moreover, real objects have been shown to be more readily detected from continuous flash suppression than 2D counterparts (Korisky & Mudrik, 2021). Therefore, future research could investigate patterns of activity in response passive viewing and using 3D tools. It is possible that responses to viewing and using 3D tools could potentiate more similar representations in the tool network to real tool use actions due to the genuine possibility of successful interaction with the tool.

In summary, our results suggest that areas in the occipitotemporal and frontoparietal tool network contain representations for how we interact with tools for their functional use. These representations are present in the tool network from simply viewing images of tools and from pantomiming their use and cannot be purely due to low-level visual differences given that action decoding was significantly higher than tool identity decoding in most regions. Despite this, the patterns of neural activation elicited during viewing and pantomiming differ, potentially as a mechanism to prevent inappropriate behavioural responses to stimuli. We observed that hand selective visual occipito-temporal cortex represented tool use actions significantly higher than tool identity in both viewing and pantomime. This adds to a growing body of evidence that ventral stream regions are involved in planning and executing hand actions. Future research should investigate representations in response to viewing and performing actions with real tools as well as investigate the effective connectivity between ventral and dorsal regions of the tool network.

4. Chapter 4 - Assessment of online, ego-, and allocentric visuomotor performance in Alzheimer’s dementia and Mild Cognitive Impairment.

Dementia is an ever-increasing global health challenge, estimated to affect approximately 50 million people globally (Patterson, 2018). Alzheimer’s Disease (AD), the most common type of dementia, is estimated to account for 50-70% of dementia cases (Winblad et al., 2016). While the above estimates account for AD during the clinical stage, recent modelling has estimated that an additional 69 million individuals are in the prodromal stages of AD, and over 300 million people are in a preclinical AD stage, equating to approximately 22% of individuals over the age of 50 (Gustavsson et al., 2023). AD is characterised by observable episodic memory decline, usually presenting as an inability to retain new information, as well as limited attention and poor spatial navigation (Coughlan, Laczó, et al., 2018). Mild cognitive impairment (MCI) is often considered a prodrome of dementia. A diagnosis for MCI requires higher degree of impairment in a cognitive domain than is normal for one’s age, although, unlike a dementia diagnosis, this does not impair day-to-day independence (Anderson, 2019; Petersen, 2004). While not all individuals with MCI develop dementia, it has been estimated that around 55% of MCI cases are due to AD related pathology, such as aβ and pathological tau (Gustavsson et al., 2023).

4.1. Vulnerability of the PPC in MCI and AD.

While research into AD pathology commonly focusses on medial temporal regions typically associated with memory deficits, a growing body of evidence has implicated the precuneus in posterior parietal cortex (PPC) as an area exhibiting structural abnormalities at an early stage of AD and even in preclinical populations (Becker et al., 2011; Bruner & Jacobs, 2013; Doré et al., 2013; Jacobs, Van Boxtel, et al., 2012). Recent modelling suggests that these parietal changes, for example alterations of aβ levels, could occur approximately 20 years before the onset of symptoms such as memory loss (Gordon et al., 2018). In addition to structural changes, functional changes in the PPC have been noted in those with MCI and AD. For example, in a longitudinal study, Corriveau-Lecavalier et al. (2019) recorded fMRI activity while completing a word pair memory task in those with MCI, and assessed performance two years later. Hyperactivation was observed in right SMG in individuals who progressed to dementia compared to healthy controls, while hypoactivation was observed in the hippocampus. Interestingly, Belleville et al. (2011) found that higher activation in IPL correlated with improvements in memory performance in people with MCI. Put together, these findings suggest that people in the preclinical stage of dementia may need to recruit additional brain regions that are not typically required to be successful in the task. This could act as a compensatory strategy to preserve normal cognition (Elman et al., 2014).

Similar findings have been observed in visuospatial tasks known to recruit temporal and parietal regions. For example, research using a mental rotation task has shown that individuals with MCI exhibit hyperactivation in parietal and temporal regions, compared to healthy controls, but similar levels of performance (Jacobs et al., 2012). Interestingly, the same study found increased intraparietal and parietal-temporal effective connectivity in those with MCI during the task but decreased effective connectivity surrounding the posterior cingulate gyrus. More recently, another study assessed functional connectivity during a memory encoding task of images. Interestingly, left hippocampal activation and connectivity with fronto-temporal regions were associated with poorer memory in those with subjective cognitive decline (SCD; characterised by a subjective impairment in memory but no sign of cognitive impairment) and MCI, while left superior parietal regions and its connections to fronto-temporal regions were associated with increased memory performance in SCD only (Corriveau-Lecavalier et al., 2021). This was interpreted as evidence that activation in the parietal lobe acts as a compensatory mechanism for AD pathology in the hippocampus. However, as the disease progresses, the hyperactivation does not result any cognitive benefit (Corriveau-Lecavalier et al., 2021). Indeed, it has been proposed that parietal areas could play a compensatory role in the early, preclinical, stages of AD, but this is only for a transient period (Jones et al., 2016). One possibility is that due to hyperactivation in the PPC for tasks that do not typically recruit the PPC, performance in tasks typically associated with the PPC could in turn be impaired.

4.2. Functions of the PPC

4.2.1. Online Visuomotor Control

The PPC is a key area of the dorsal visual stream, a network of regions involved in visuomotor control (Culham & Valyear, 2006; Goodale & Milner, 1992). Lesions to the superior parietal lobe (SPL) within the PPC are most often associated with optic ataxia, characterised by impaired reaching towards objects in the periphery despite an often preserved ability to reach in foveal vision (Perenin & Vighetto, 1988).

These impairments are present in the absence of primary visual, proprioceptive or motor deficits (Rossetti et al., 2019). One explanation of optic ataxia is that of impaired online visuomotor control (Pisella et al., 2000). Online visuomotor control is defined as the ability to make corrections to movements ‘in-flight’, for example when a target object changes location during a reach, and we must catch it. Pisella et al. (2000) found that in comparison to healthy controls, patient IG who had bilateral PPC lesions, was particularly impaired in smoothly correcting her hand movements in response to target jumps. Despite this, she was successfully able to inhibit online corrections when required by the task. On the other hand, healthy controls were less able to voluntarily inhibit these online corrections in response to the change in target position, suggesting that this is usually an automatic process. This suggests that optic ataxia results in a specific impairment in the ability to correct movements online and patients utilise slow offline cognitive control when engaging in reaching tasks. Pisella et al. (2000) suggested that in foveal vision, reaching movements only need to be corrected towards the end of the movement, while in peripheral vision, actions are programmed based on less precise visual information which requires a greater degree of online visuomotor control to perform a movement in the periphery with spared accuracy. This provides a possible explanation for why individuals with optic ataxia may be unimpaired in visuomotor control in foveal vision. In line with this, further research has found that reach to grasp movements are also impaired when a target object is suddenly displaced (Gréa et al., 2002). Instead, patients with optic ataxia tend to complete their movement to the original target location before redirecting towards the new target location. IG, in both experiments, typically completed movements towards the initial target location before redirecting her movements towards the new target location (Gréa et al., 2002; Pisella et al., 2000).

In line with the findings in patient IG, TMS to the PPC in neurologically intact individuals has been shown to disrupt movement trajectory corrections in response to changes in target position, but not movements towards stationary objects (Desmurget et al., 1999; Tunik et al., 2005). Moreover, the extent of these disruptions as a result of TMS have been correlated with fMRI activation in response to jump trials in aIPS and anterior SMG (Reichenbach et al., 2011). Given that movements towards stationary objects remain unimpaired following PPC lesions and TMS, this suggests that deficits observed following PPC disruption are not reflective of a movement planning deficit, or purely visual or motor impairments. It has therefore been argued that the PPC represents target position in an egocentric frame of reference and computes current motor error to allow updating of the muscle activation pattern required for a successful reach (Desmurget et al., 1999).

4.2.2. Egocentric and Allocentric Visuomotor Control

It has been suggested that processing within the dorsal and ventral visual streams can be distinguished based on the frame of reference used for spatial coding, with a dorsal stream responsible for egocentric, and the ventral stream responsible for allocentric coding (Schenk, 2006). Egocentric frames of reference refer to a subject-to-object relationship, such as one's own position in relation to objects in the environment; while an allocentric frame of reference reflects an object-to-object relationship which relies on the relationship between external objects in the environment irrespective of one's own position in space (Goodale, 2008; Milner & Goodale, 2008). Coding in egocentric frames of reference is thought to facilitate visually guided actions at a given time as continuous updating of spatial coordinates is required to control for head or eye movements, and is thus associated with processing in the dorsal visual stream (Milner & Goodale, 2006). On the other hand, allocentric representations remain stable over time despite an individual's movement and thus may rely more on visual working memory which can facilitate encoding of the visual scene for perception, and thus may be more subserved by the ventral stream (Milner & Goodale, 2006; Schenk & McIntosh, 2010).

Research in patient DF, who sustained bilateral ventral visual stream damage, found that while she could correctly perceive targets and execute manual responses to targets presented in an egocentric frame of reference, this was impaired when performing the same tasks in an allocentric reference frame (Schenk, 2006). Schenk (2006) argued that DF's ventral stream damage led to an allocentric rather than perceptual deficit, challenging the traditional perception-action model. Further observations in patient GP, who sustained bilateral occipito-parietal lesions, found a significant impairment in short-term egocentric perceptual judgements about objects, while allocentric judgements and delayed egocentric judgements were similar to controls (Ilardi et al., 2021). Given that long-term egocentric judgements were unimpaired in GP, Ilardi et al. (2021) argued that long-term egocentric judgements could be based on the stored representation of the visual information in the ventral stream. Put together, these observations suggest that the ventral stream subserves allocentric processing, while the dorsal stream mediates egocentric processing.

In neurologically intact individuals, behavioural studies have provided evidence of a possible ventral/dorsal distinction between egocentric and allocentric reference frames. For example, research has found that individuals are generally slower and less effective at performing allocentric reaching tasks compared to egocentric tasks, possibly suggestive of allocentric reference frames being mediated by the slower networks of the ventral visual stream (Manzone & Heath, 2018; Thaler & Goodale, 2011b). In these tasks, participants are required to reach directly to a target (egocentric) or are presented with a reference target and must make a reach based on the distance and orientation between the reference target and reach target (allocentric). In line with this, Thaler and Goodale (2011a) conducted the same egocentric and allocentric reaching tasks during fMRI, and found that allocentric reaching was indeed associated with greater activation, compared to egocentric reaching, in ventral visual region LOC.

A number of fMRI studies have found that egocentric spatial judgements activate a parietofrontal network of regions including precuneus, the SPL, IPS, and PMd (Committeri et al., 2004; Galati et al., 2000; Zaehle et al., 2007). On the other hand, allocentric judgements have been shown to additionally recruit ventrolateral occipito-temporal cortex and IPL (Committeri et al., 2004; Zaehle et al., 2007), while also displaying some recruitment of regions in the dorsal visual stream (Committeri et al., 2004; Galati et al., 2000). A recent meta-analysis of neuroimaging studies has shown that both egocentric and allocentric spatial navigation tasks recruit common areas in the precuneus and superior frontal gyrus, suggesting that the PPC may mediate coding both frames of reference (Derbie et al., 2021).

These findings have been extended in reaching based fMRI tasks. In a study by Chen et al. (2014), participants were first cued to either reach to a target (egocentric) or reach relative to a landmark (allocentric). Following this, the landmark and target were presented, after which there was a delay phase where participants had to remember the location of the reach target, before executing the reach. Activation in the delay phase was higher in dorsal stream regions SPOC, IPS and in PMd for egocentric, compared to allocentric, encoding of target position. On the other hand, allocentric specific activation was observed in the ventrolateral occipito-temporal cortex (Chen et al., 2014). This provides evidence that while egocentric frames of reference are coded solely in the dorsal visual stream, ventral stream regions are additionally required in cases where allocentric spatial representations are required. However, some overlapping activation was also observed in the dorsal stream for both egocentric and allocentric encoding. The authors suggested that these regions may be therefore involved in an allocentric-to-egocentric conversion for reaching. In a follow up study, Chen et al. (2018) had participants always encode the position of a target relative to a landmark (allocentric), however all reaches were conducted following a delay in an egocentric reference frame which allowed the researchers to assess allocentric to egocentric conversion. Here, while ventral stream regions encoded allocentric coordinates, the right precuneus, pre-SMA and bilateral PMd were activated at the phase of transforming allocentric codes to egocentric reach plans (Chen et al., 2018). As the PPC is thought to be associated with AD pathology an early stage of the disease (Gordon et al., 2018). It is therefore possible that both egocentric and allocentric visuomotor performance is affected in AD. On the other hand, allocentric visuomotor performance could be particularly affected in AD given that regions in the medial temporal lobe are also susceptible to AD pathology at an early stage of the disease (Braak & Braak, 1991; Schöll et al., 2016).

4.2.3. Visuomotor performance in neglect

Lesions to the inferior parietal lobe (IPL) within the PPC are often associated with neglect, a condition commonly characterised by an inability to attend to the contralesional side of space despite a lack of pure visual deficits (Husain, 2008). Despite being thought of as a more perceptual deficit, research has found that people with neglect do display some visuomotor impairments. Interestingly, using a double-step reaching paradigm, adapted from Pisella et al. (2000), patients with neglect performed similarly to those with right hemisphere damage but no neglect, and neurologically intact individuals (Rossit et al., 2012). A lesion overlap analysis revealed that lesions in the neglect group were mostly overlapping in the IPL, MTG and STG. Behaviourally, all groups demonstrated automatic corrections when the task was to inhibit corrective movements and were able to conduct one ballistic movement in response to the change in target position, which is impaired in those with optic ataxia. However, corrections towards the contralesional side of space were markedly slower in those with neglect, compared to control groups (Rossit et al., 2012). This suggests that IPL, MTG and STG lesions may also result in some slowing of online visuomotor control functioning.

Moreover, offline actions such as anti-pointing, which are thought to recruit more ventral regions, have been associated with longer RTs and greater end-point errors, in individuals with neglect, compared to those with right hemisphere damage and no neglect, and neurologically intact participants (Rossit et al., 2011). These deficits were associated with lesions in the MTG and parahippocampal gyri. It has been suggested that the longer RTs during offline visuomotor tasks in people with neglect could reflect 1) a deficit in offline visuomotor control, which has previously been identified as requiring ventral stream input (Culham & Valyear, 2006; Goodale, Jakobson, & Keillor, 1994); or 2) a deficit in coding target location with respect to the imaginary centre point which had to be represented in an allocentric frame of reference during the anti-pointing task (Rossit et al., 2011; Schenk, 2006). These two explanations may not be mutually exclusive, and overall, it appears that VD stream lesions can lead to subtle impairments in visuomotor control, particularly in increasingly complex visuomotor tasks.

4.3. Assessment of Cognitive Functioning in AD and MCI

Traditionally, paper-and-pencil tests have been used to assess cognitive functioning and to identify possible markers of MCI and AD. These include subtests in various cognitive domains, such as memory, attention, orientation, language and fluency, and visuospatial abilities. In particular, the Addenbrookes Cognitive Exam-III (ACE-III; (Hodges & Larner, 2017), which assesses five cognitive domains, providing an overall score out of 100, has been shown to be particularly successful in distinguishing AD from MCI and cognitively unimpaired individuals (Senda et al., 2020). Despite this, research has shown that the ACE-III, along with other traditional neuropsychological tests, are associated with levels of education (Matias-Guiu et al., 2015; Pigliautile et al., 2019) and IQ (Stott et al., 2017). Moreover, the ACE-III has been shown to have high inter-rater variability (Say & O'Driscoll, 2022), particularly in the fluency, visuospatial, and attention domains. Given the nature of the test, detailed objective measures such as timings cannot be gathered which could provide a greater insight into the nature of cognitive decline. This highlights the importance of developing clinical assessments which are robust to individual differences in IQ, education level, and language, and provide objective measures of cognitive functioning.

4.3.1. Visuospatial processing in AD and MCI

While memory problems are most commonly associated with AD, people with AD also show difficulties in visuospatial processing (Rizzo et al., 2000), and spatial navigation (Lithfous et al., 2013). In particular, spatial navigation deficits may distinguish between those at higher risk of AD from those with low risk (Lithfous et al., 2013). It is therefore possible that spatial navigation deficits may be present before observable memory deficits associated with AD become apparent. To successfully navigate the environment, egocentric and allocentric representation strategies need to be employed, and often reference frames are switched depending on the optimum method in a certain context. In line with this, several researchers have investigated spatial navigation utilising egocentric and allocentric processing in MCI and AD.

Research assessing visuospatial abilities in egocentric and allocentric reference frames commonly employ the Hidden Goal Task (HGT; Kalová et al., 2005; Serino et al., 2014; Tuena et al., 2021). Here, participants locate a hidden target relative to the start position (egocentric), or relative to landmarks in the periphery (allocentric). Individuals with AD and amnestic MCI (aMCI) affecting multiple domains perform significantly worse than healthy controls in all tasks, whereas those with single domain aMCI are affected in the allocentric task only (Hort et al., 2007; Laczó et al., 2017). Additionally, the presence of the APOE4 gene, a significant risk factor for AD, also affects egocentric performance, with MCI individuals performing worse if they are APOE4 positive (Laczó et al., 2011). This highlights that the coding of egocentric and allocentric spatial representations for navigation may be particularly impaired at the early stage of dementia, with allocentric representations being particularly susceptible to impairment when cognitive impairments relate solely to memory deficits.

Virtual reality (VR) studies, which aim to provide more real world like scenarios, have also revealed impairments in egocentric and allocentric navigation in those with AD, with egocentric impairments linked to structural differences in the posterior cingulate and retrosplenial cortex (Tu et al., 2015, 2017). This suggests a possible allocentric-to-egocentric translation deficit in AD, possibly related to temporal/hippocampal pathology and dorsal visual stream degeneration (Weniger et al., 2011). Indeed, a review of egocentric and allocentric abilities in AD and MCI, revealed that people with AD were particularly impaired in allocentric tasks, however there also appears to be an impairment in allocentric to egocentric translation (Serino et al., 2014). Nevertheless, it remains unclear whether these findings reflect spatial memory issues or deficits in reference frame utilisation. One possible avenue of research therefore is to assess performance on a purely visuomotor task with no memory requirements using egocentric and allocentric reference frames.

4.3.2. Visuomotor Research in MCI and AD

Visuomotor functioning in AD and MCI has been assessed using a multitude of paradigms. For example, Tippett and colleagues (2007) investigated reaching to targets presented vertically in AD under three increasingly complex conditions. In the first condition, participants conducted their movements to the target in the vertical spatial plane which provided full correspondence and visual feedback of the hand position relative to the target. In the second condition, participants reached in the same spatial plane after the target had disappeared, thus to a remembered position. In the third condition, participants reached to a remembered position but this time their reach was carried out in the horizontal spatial plane, and visual feedback of the hand position was provided in the form of a cursor on the screen. This reflected an increased dissociation between the visual target stimulus and required motor response. Those with AD took significantly longer to initiate and execute reach movements in all conditions compared to controls. However, end-point error was only significantly worse than controls as the task complexity increased, thus when the target was not visible, and the spatial plane was dissociated (Tippett et al., 2007). Put together, these findings suggest that those with AD exhibit subtle visuomotor deficits associated with the PPC which become more apparent when additional processing, such as visual short-term memory and visuomotor transformations, is required.

Further studies have used similar paradigms in different spatial planes but with added complexities, such as rotating visual feedback of the hand position. These studies have also demonstrated that people with AD take longer to plan and execute movements, and make more errors in all conditions (Tippett et al., 2012; Tippett & Sergio, 2006). People with AD were found to be particularly affected by feedback reversal, even with only mild impairments in cognitive measures (Tippett & Sergio, 2006). This suggests that these additional visuomotor task complexities may be sensitive to AD at an early stage. Interestingly, research using similar plane dissociated and feedback reversal paradigms have found that people with MCI are more impaired at the planning stage of movements, compared with execution in more complex tasks (Salek et al., 2011). Therefore, it is possible that performance on complex visuomotor tasks becomes more impaired as the disease progresses, similar to what has been found in research comparing healthy controls with people MCI and mild AD (Kluger et al., 1997). Interestingly, performance on these increasingly complex tasks have also been shown to discriminate between people with low risk and high risk of AD (defined by a family history or presence of MCI) (Hawkins & Sergio, 2014). Put together, these findings suggest that visuomotor assessments may be a sensitive measure of AD, even at a preclinical stage.

Similar findings have been observed in a visuomotor paradigm where participants pressed one of five buttons in a horizontal plane based on the position of targets presented in a vertical plane on a computer screen (Mollica et al., 2017). Participants with AD performed significantly slower and with greater errors compared to controls, while those in the preclinical stage (defined by aβ and tau in cerebral spinal fluid) were slower than controls despite scoring similarly on cognitive batteries. This provides further evidence that subtle deficits in visuomotor performance, followed by a progressive decline, may be present in early AD. Recently, in a circle tracing task with differing levels of visual feedback and plane dissociation, aβ-positive older adults performed with poorer accuracy when the plane of response was dissociated from the plane of the circle presentation, compared to aβ-negative adults (Lu et al., 2021). Despite this, there were no differences in tracing speed between groups, suggesting that findings cannot be explained by a speed-accuracy trade-off, where a deficit in accuracy is compensated for by reducing the movement speed. Put together, these findings highlight that visuomotor performance differences can be present in a preclinical stage of AD and further research is needed to fully assess these differences.

Recently, we investigated kinematics of reach movements in participants with AD, MCI and healthy age-matched controls. In line with previous research observing longer movement times to targets in AD (Tippett et al., 2007, 2012), we also observed longer movement times in those with AD and MCI. Additionally, while acceleration times were similar across groups, participants with MCI and AD had longer deceleration times than healthy controls (Mitchell et al., 2022). This could reflect a planning deficit, which in turn leads to a greater reliance on visual feedback to maintain accuracy which increases the deceleration phase. In line with this, evidence has shown that reaching accuracy is significantly worse in individuals with AD when feedback of the hand is absent and thus cannot rely on online visuomotor control (Ghilardi et al., 1999). Moreover, recent research investigating reach-to-grasp movements found that those with early-stage AD are slower to initiate and execute movements compared to healthy controls, particularly in the absence of visual feedback (Zhang et al., 2022). Accuracy was only significantly worse than controls in the absence of visual feedback, and this correlated with scores on cognitive tests (Zhang et al., 2022). Put together, this highlights that a planning deficit may explain our recent findings. An alternative, but not mutually exclusive explanation, is that the ability to implement feedback-based online corrections at the phase when the hand approaches the target is impaired in individuals with AD, resulting in longer deceleration times. It would be therefore interesting to investigate specifically the ability to make fast online corrections in individuals with MCI and AD.

It is possible that visuomotor deficits could explain several functional difficulties observed in preclinical AD. For example, subtle visuomotor impairments could explain the decline in driving abilities in individuals with preclinical AD (Roe et al., 2019), and the increased risk of falls (Stark et al., 2013). Unsurprisingly, the slowed planning and execution of reach movements in people with early stage AD has been shown to be associated with decline in activities of daily living, such as meal preparation, and housework, which are essential for functioning independently (de Boer et al., 2015). Therefore, the assessment and possible detection of visuomotor impairments at an early stage are of particular importance due to their relevance with functional abilities.

4.4. Aims and Hypotheses

The aims of Experiments 4 and 5 were to investigate visuomotor functioning differences between participants with early-stage AD, and healthy older adults. Two novel portable tablet-based tasks were developed to investigate visuomotor performance in egocentric and allocentric frames of reference, and online visuomotor control. These were designed to be easily accessible assessment tools for use in clinical settings. Clinical drug trials on AD are usually focussed on preclinical populations, and thus identification of early stage deficits could be particularly important in supporting progress in this area (Huang et al., 2020), for this reason our clinical group also included participants with a diagnosis of amnestic MCI.

In Experiment 4, we investigated performance in egocentric and allocentric iPad based reaching tasks. Although past research has suggested that egocentric and allocentric spatial representation deficits may be a characteristic of early AD (Hort et al., 2007; Tu et al., 2015, 2017; Tuena et al., 2021), this has not been tested in a visuomotor task, without the requirement of visual working memory. We hypothesised that our clinical group would have reduced egocentric and allocentric reaching accuracy, and that movement times and reaction times would be longer compared to controls. This could be reflective of a dorsal visual stream deficit. In Experiment 5, we investigated online corrections using an iPad-based double-step reaching task to compare performance between our clinical group and healthy controls. As online motor control has been shown to be a key function of the dorsal stream, and evidence suggests that PPC may be one of the earliest regions to exhibit pathological changes in AD and MCI (Gordon et al., 2018), we hypothesised that corrections to target perturbations would be delayed in people with our clinical group compared to controls. This would be reflected in an increase in overall movement time, and significantly longer time to make a correction towards the new target location. If longer correction times are observed, this could provide explanation for our recent findings of extended deceleration time for reaches in AD and MCI (Mitchell et al., 2022). Finally, we aimed to investigate whether reaching performance was related to performance on traditional neuropsychological tests.

4.5. Methods

4.5.1. Participants

The performance of a clinical group (N=21) of 13 participants diagnosed with AD and 8 participants diagnosed with aMCI aged between 51 and 81 (14 male; *M* = 71.43, *SD* = 8.30) was compared with 17 healthy age-matched controls aged between 57 and 79 (3 male; *M* = 67.71, *SD* = 6.59; see Table 4.1). One participant in the clinical group (65yo, female, AD diagnosis) was excluded from Experiment 4 due to a failure to complete the allocentric task. One control participant (79-year-old, female) was unable to take part in Experiment 5 due to technical difficulties, thus there were 16 healthy controls included in the analysis for Experiment 5 (*mean age* = 67.00, *SD* = 6.11). All participants had no uncorrected visual impairments (e.g. cataracts, amblyopia), or other medical conditions which could interfere with task performance e.g. arthritis, or history of stroke.

Data were collected across two sites, the UEA and University of Edinburgh (UoE). Participants in the clinical group were recruited via the Julian Hospital (Norwich) and the Anne Rowling Regenerative Neurology Clinic (Edinburgh). Healthy controls were recruited through opportunity sample at UEA paid panel, had normal or corrected to normal vision, and no reported neurological or neurodegenerative conditions. The research was approved by the UK Health Research Authority, the East of England Central Cambridge Research Ethics Committee and Research & Development for NHS Lothian and NHS Norfolk & Suffolk Trusts (REC 19/EE/0170) and the University of East Anglia School of Psychology Ethics Committee (2019-0674-001577).

Table 4.1 *Participant demographics*

	Control (N = 17)			Clinical (N = 21)		
Demographics	**Mean**	**SD**	**Range**	**Mean**	**SD**	**Range**
Age (years)	67.71	6.59	57-79	71.43	8.30	51-81
Gender (M/F)		3/14			14/7	
Education (years)	17.06	3.62	12-25	14.41	3.50	10-22
ACE total (%)				78.38	8.30	31-96
ACE attention (%)				82.01	17.02	27-100
ACE memory (%)				66.30	22.72	12-100
ACE fluency (%)				66.33	22.94	7-100
ACE language (%)				87.18	19.01	30-100
ACE visuospatial (%)				90.18	16.13	38-100

Note: SD = Standard deviation, ACE = Addenbrookes Cognitive Exam.

4.5.2. Materials

Participants completed the tasks on a 9.7 inch iPad 6th Gen (2048x1536 pixel resolution, 264 ppi) with a stylus (Apple Pencil, 1st Gen). 6 control participants completed the tasks on a 10.2 inch iPad 9th Gen (2160x1620 pixel resolution, 264 ppi). All tasks were created with iOS processing and Solar2D (formerly Corona SDK). Target sizes and location on the screen remained the same between both iPads. Reach movements in all tasks were recorded at the screen refresh rate of 60Hz. Participants were seated approximately 40cm from the iPad. A start-box (1cm^2) was presented at the bottom centre of the screen, aligned to the participant's midline. Targets were presented as red circles (1.4cm^2).

4.5.3. Procedure

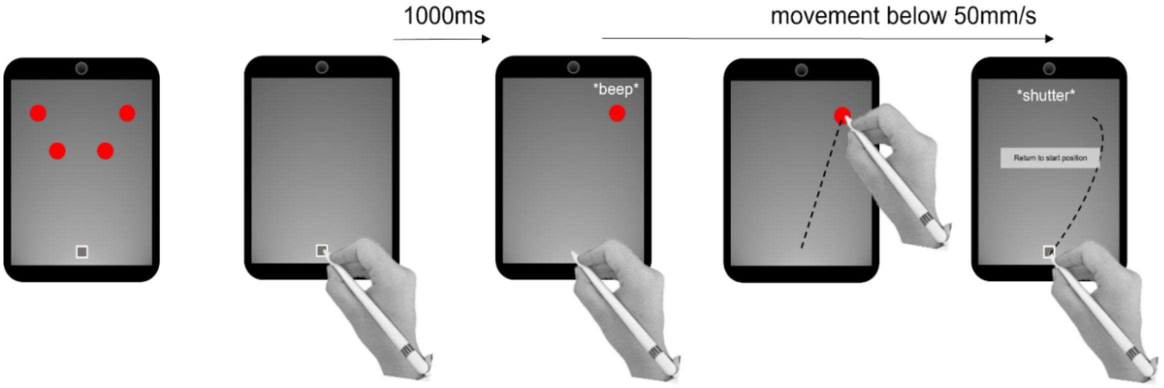
Participants in the clinical group first completed the ACE-III (Hodges & Larner, 2017) before completing both experiments in the same session.

4.5.4. Experiment 4: Egocentric and Allocentric Reaching

The egocentric and allocentric reaching tasks were adapted from Thaler and Goodale (2011). All participants completed the egocentric task before the allocentric task as the ability to perform on the egocentric task was a requirement for the allocentric task. All reaching tasks were performed with the participants' dominant hand.

In the egocentric task, participants were provided with written and verbal instructions where they were instructed to draw a line with the stylus to the target as quickly and accurately as possible. Targets were presented in one of four locations (see Figure 4.1). The targets closest to the start button were 80mm above, and 20mm to the left or right of the start button. The top two targets were 120mm in depth and 35mm to the left or right of the start button. Participants initiated a trial by holding down the stylus in the start-box. After the stylus had been held down for 1000ms, a beep tone was played (500Hz, 0.15ms) and the target appeared at one of the four locations on the screen which cued the participant's reach movement. Participants reached to the target with the stylus remaining in contact with the screen throughout and were required to hold the stylus on the target until they heard a 'shutter' sound and the target disappeared. This occurred after the participant's movement fell below the movement threshold (50mm/s in the last 5 frames), or 3000ms after the presentation of the target (see Figure 4.1). This cued participants to lift the stylus and return to the start-box signalling the end of the trial.

Figure 4.1 *Target positions and example trial timeline of the egocentric task, dashed line represents required hand movement.*

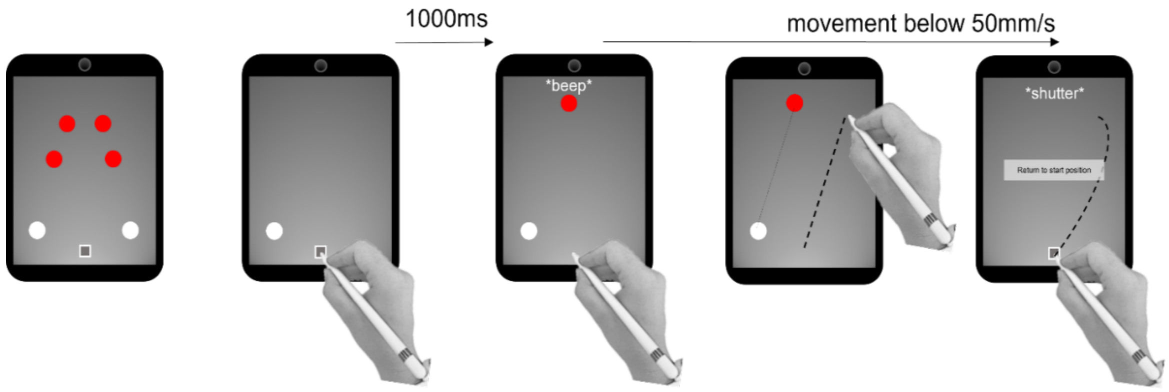


Participants began with four practice trials, one in each target position before completing the experimental trials. The target was presented in each target position 10 times, and participants completed a total of 40 experimental reaching trials. Target presentation order was pseudorandomised avoiding 2-back repetitions.

In the allocentric reaching task, a white reference dot (1cm^2, circle) was presented 50mm above and 50mm to the left or right, the start-box. Participants were instructed to draw a line that mimicked the orientation and length between the reference dot and target but from the start-box instead. In other words, participants used allocentric visuospatial information to program their reach movements (i.e., the location of the red target in relation to the white reference point). Lower targets were presented 130mm above and 30mm to the left or right of the start box. Upper targets were presented 170mm above and 15mm to the left or right of the start box. Importantly, the four targets were positioned so that ideal reach coordinates in the allocentric task matched the biomechanics of the egocentric task.

Participants initiated a trial by pressing the stylus down on the start-box. The white reference dot was also presented to the participants in its left or right location at this time. After 1000ms of the stylus being held down in the start-box, the red target appeared in one of the four target locations. Participants were then required to perform the reaching movement reflecting the distance and orientation between the reference point and target (see Figure 4.2). Again, the trial ended when the participant's movement fell below 50mm/s.

Figure 4.2 *Target and reference point positions, and example trial timeline of the allocentric task. Dashed line represents required hand movement, dotted line represents distance and orientation between reference point and target to be mimicked by the hand movement.*



Participants began the task with 4 practice trials and were also instructed to complete 4 practice trials using a pencil and paper as the nature of the task was more complex than the egocentric task. Participants completed 40 trials of the allocentric task, 10 trials per target location. Trials were presented in a pseudorandomised order to avoid 2-back repetitions.

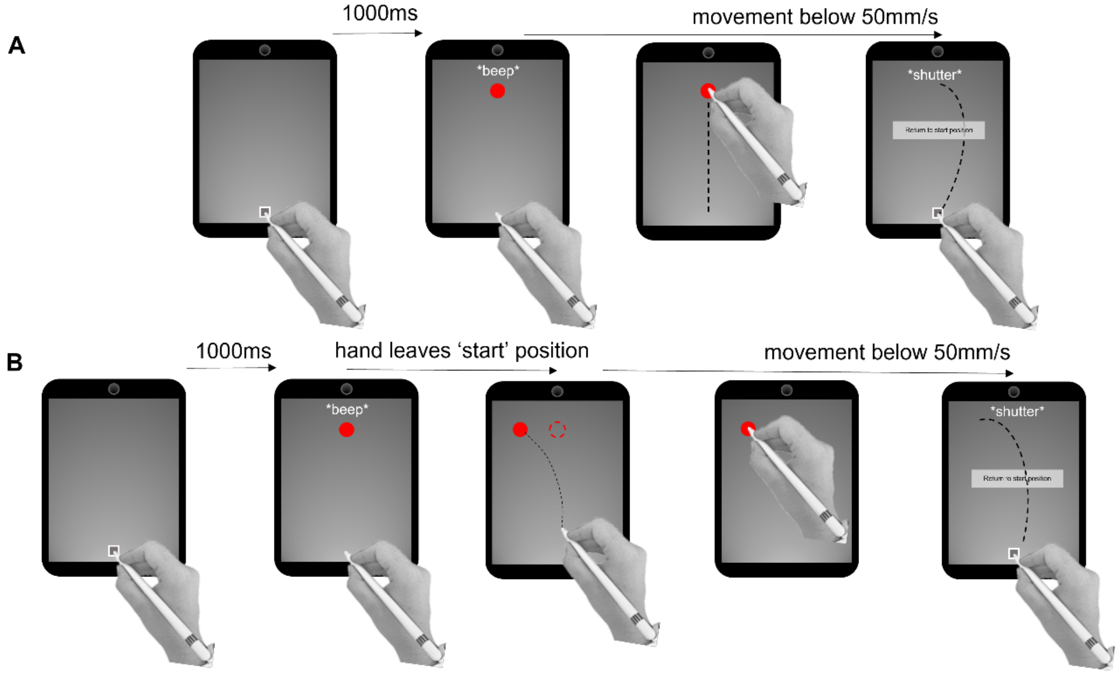
4.5.5. Experiment 5: Online Corrections

The online correction task was adapted from (Rossit et al., 2012). Participants were provided with written and verbal instructions where they were instructed to draw a line with the stylus to the target as quickly and accurately as possible. They were also informed that the target may change position, in which case they should adjust their movement to try and 'catch' the target as fast as possible. All trials were performed with the participants' dominant hand.

Participants initiated a trial by holding down the stylus in the start-box. After the stylus had been held down on the start-box for 1000ms, a beep tone was played (500Hz, 0.15ms) in conjunction with the red target appearing at the top centre of the screen. This cued the participant to initiate their reach movement, which was completed with the stylus remaining in contact with the touchscreen throughout the trial. In 'static' trials, the red target remained at the top centre of the screen, 165mm above the start box, thus participants were simply required to reach as quickly and as accurately as possible to the central target (see Figure 4.3a). However, in 'jump' trials, the target moved to the 50mm to the left or right of the original static target when the participant's stylus had left the start-box. Participants were therefore required to adjust their reach trajectory 'in-flight' to the new target position (see Figure 4.3b). A trial ended with a shutter sound, and the target disappearing, when the reach movement was below the movement threshold of 50mm/s, or when a reach was not initiated within 3000ms of the target appearing. Participants were then required to lift the stylus and return it to the start position to initiate the next trial. If a movement was not initiated within 3000ms, this was classed as a timeout and the trial was recycled to the end of the block.

Participants first completed 10 practice trials before moving on to the experimental task. Practice trials were repeated until the task was fully understood by participants. The experiment consisted of two blocks of 50 trials with a rest break in between. Overall, there were a total of 68 'static' trials, 16 'jump' trials to the left, and 16 'jump' trials to the right. Trials were presented in a pseudorandomised order avoiding 2-back 'jump' trial repetitions.

Figure 4.3 *a) Timeline of a 'static' trial in the jump-go task. Dashed line represents required hand movement. B) Example timeline of a 'jump' trial in the jump-go task. Dashed line represents required hand movement. Dotted red circle represents original target position prior to the 'jump'.*



4.5.6. Data Analysis

Movement onset and offset for all tasks were determined using a velocity threshold of 50mm/s. Subsequently, data with incomplete kinematic information (less than 5 frames recorded in a trial, or movement time below 150ms) were removed from further analyses (egocentric: 2%, allocentric: 13.9%, jump-go: 2.7%).

For all tasks, reaction time was calculated as the time, in milliseconds (ms), between the target onset and the first frame in which the participant exceeded the movement threshold. Movement time was calculated as the time, in ms, between the movement onset and movement offset. The movement endpoint was defined as the coordinates at the movement offset in x and y dimensions. Absolute error was calculated as the 2D distance, in millimetres (mm), from the centre of the target (or 'ideal' endpoint in the allocentric task) using the following equation:

$$AE = \sqrt{x\_\mathrm{error}^2 + y\_\mathrm{error}^2}.$$

4.5.7. Experiment 4: Egocentric and Allocentric Analysis

For each variable (RT, MT, and AE), median scores were calculated for each participant at each target location (providing four median scores) for the egocentric and allocentric tasks separately. For each participant and variable, median scores were averaged to provide a single measure for each variable. A series of 2 (group: Control, Clinical) x 2 (task: Egocentric, allocentric) mixed ANOVAs were carried out to assess the effects of group and task on RT, MT and AE. Post-hoc tests were Bonferroni corrected for multiple comparisons.

4.5.8. Experiment 5: Online Correction Analysis

As in the egocentric and allocentric analyses, median scores for the left and right jump targets were calculated and then averaged to provide a single measure for each variable in the jump condition. In the static condition, as there was only one target location, the median of each variable for each participant was calculated. A series of 2 (group: control, clinical) x 2 (condition: Jump, Static) mixed ANOVAs were carried out on RT, MT and AE. Post-hoc tests were Bonferroni corrected for multiple comparisons.

An additional analysis (adapted from McIntosh et al., 2011) was conducted assessing correction trajectories and time it took for participants to correct their movements in response to a jump. Firstly, the x and y coordinates of each trajectory were translated so that the origin (0,0) was the start button. Therefore, leftward lateral displacement was negatively signed, and rightward displacement was positively signed. Depth displacement towards the targets was signed positively.

The analysis of online corrections in individual jump trials was based on hand path deviations based on the average path on static trials with a bandwidth based on the movement variability of control participants. Firstly, the spatial trajectories for all static trials were normalised to 1mm increments along the y axis, an estimate of the x position at each increment was calculated using linear interpolation. Secondly, for each participant, the average x coordinate at each y increment was calculated, along with the standard deviation. Standard cut-offs were then calculated by averaging the standard deviations of all control participants at each depth increment. Lower and upper bound cut-offs were calculated at 2.81 average standard deviations from the participant's average hand path.

For each jump trial, movements were classed as 'corrected' if they exceeded the cut-off in the direction of the jump, otherwise they were classed as uncorrected.

The position of the final frame of movement defined the terminal correction status. Correction time was calculated as time at the first frame which exceeded the lateral bandwidth position. The median correction time was calculated for each jump position (left, right) and averaged across both positions. Correction time was compared between groups using an independent samples t-test.

4.5.9. Additional analyses (all experiments)

For all variables, individual patient-level assessments were performed using case-control Bayesian tests of deficit (Crawford & Howell, 1998) implemented in the *singcar* package in R (Rittmo & McIntosh, 2023). Here, each patient's performance for each variable (e.g. AE, MT, RT) in the egocentric and allocentric task, and correction time in the online correction task, were compared against the distribution of that variable in the control group using a one-tailed test. This gives an indication of the proportion of individuals in the clinical group who exhibit a deficit.

Finally, FDR corrected Pearson's correlations were conducted to assess the relationship between score on the ACE domains and performance on reaching tasks in Experiments 4 and 5.

4.6. Results

4.6.1. Experiment 4: Egocentric and Allocentric Reaching

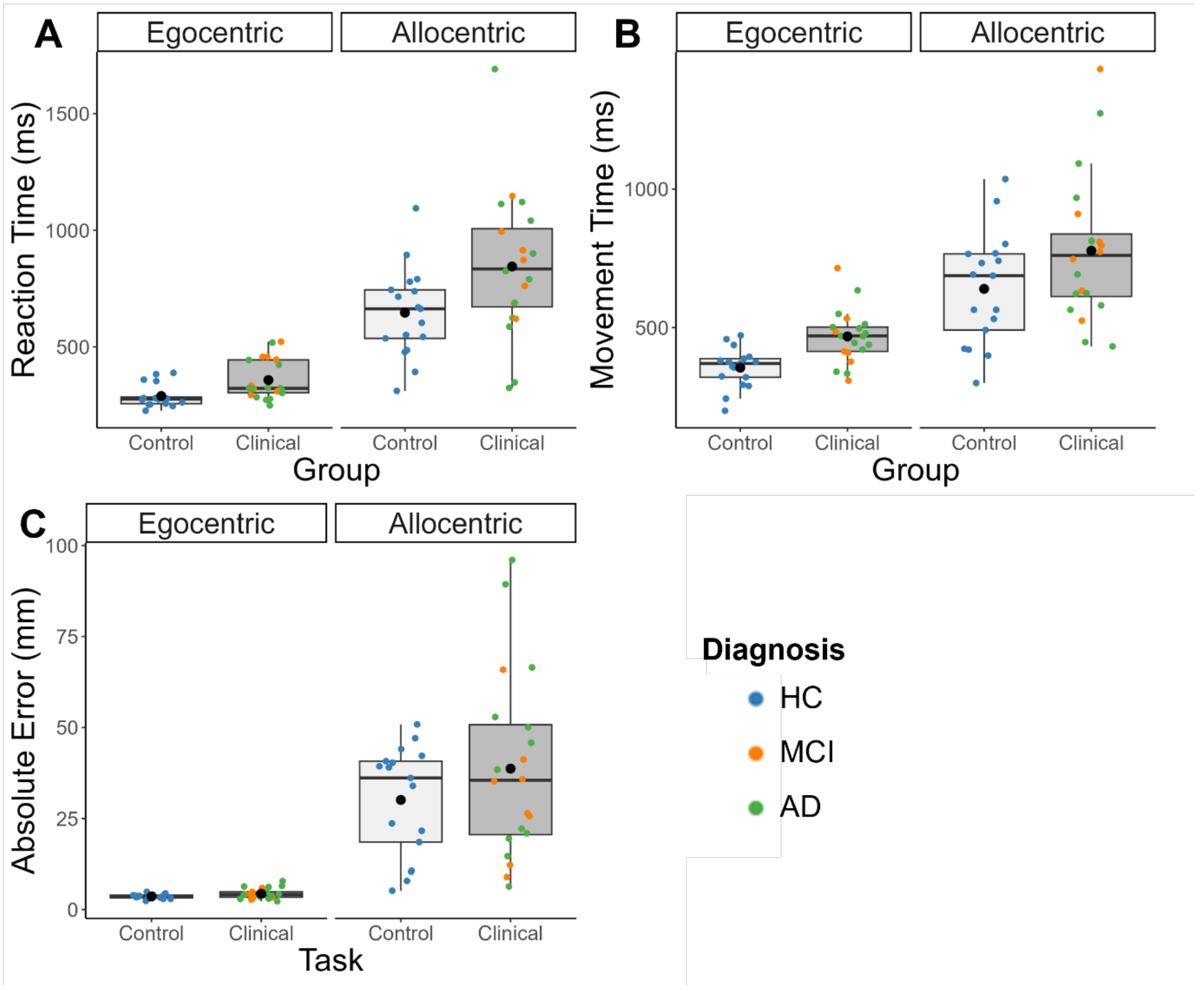
For RT (see Figure 4.4A), there was a significant main effect of group $F(1,35) = 6.79$, $p = .013$, $\eta_p^2 = .162$, with the clinical group exhibiting significantly slower RTs compared to controls (*mean diff* = 133.80 ms, $SE = 49.78$, $p = .011$). There was also a main effect of task $F(1,35) = 129.52$, $p < .001$, $\eta_p^2 = .787$, with RTs significantly longer in the allocentric, compared to egocentric, task (*mean diff* = 422.56 ms, $SE = 36.94$, $p < .001$) in line with previous literature (Thaler & Goodale, 2011b). There was no significant interaction between task and group, $F(1, 35) = 3.19$, $p = .083$, $\eta_p^2 = .083$.

Regarding MT (see Figure 4.4B), there was a significant main effect of group, $F(1,35) = 6.29$, $p = .017$, $\eta_p^2 = .152$, with longer MTs in the clinical group compared to controls (*mean diff* = 126.05 ms, $SE = 48.36$). There was also a significant main effect of task, $F(1,35) = 89.22$, $p < .001$, $\eta_p^2 = .718$, with MT in the allocentric task significantly longer than the egocentric task (*mean diff* = 297.70 ms, $SE = 31.41$). There was no significant group by task interaction, $F(1, 35) = .210$, $p = .650$, $\eta_p^2 = .006$.

For AE (see Figure 4.4C), there was a significant main effect of task $F(1,35) = 75.87$, $p < .001$, $\eta_p^2 = .684$. End-point accuracy was significantly worse in the allocentric task compared to the egocentric task (*mean diff* = 30.43 mm, *SE* = 3.45, $p < .001$). There was no significant main effect of group, $F(1, 35) = 1.78$, $p = .191$, $\eta_p^2 = .048$, nor a significant interaction, $F(1, 35) = 1.23$, $p = .274$, $\eta_p^2 = .034$.

Case-control comparisons revealed a total of 4/20 (20%) participants in the clinical group had significant deficits for AE in the allocentric task. Three of these had a diagnosis of AD and one had a diagnosis of aMCI. For MT, 3/20 (15%) participants in the clinical group were impaired, 2 of these had AD, one had MCI. For RT in the allocentric task, 6/20 (30%) participants in the clinical group had a significant deficit, 4 with AD and 2 with MCI. Interestingly, for the egocentric task, 7/20 (35%) participants had a significant deficit for AE, 5 of these had a diagnosis of AD and 2 had an MCI diagnosis. For MT, 10/20 (50%) participants had a deficit, 6 with AD and 4 with MCI. While for RT, 6/20 (30%) participants were impaired, 4 with MCI and 2 with AD.

Figure 4.4 *Boxplots displaying A) RT, B) MT, C) AE, for each group and task. Dots represent individual participants, colour coded by diagnosis. Black dots represent group and task mean.*



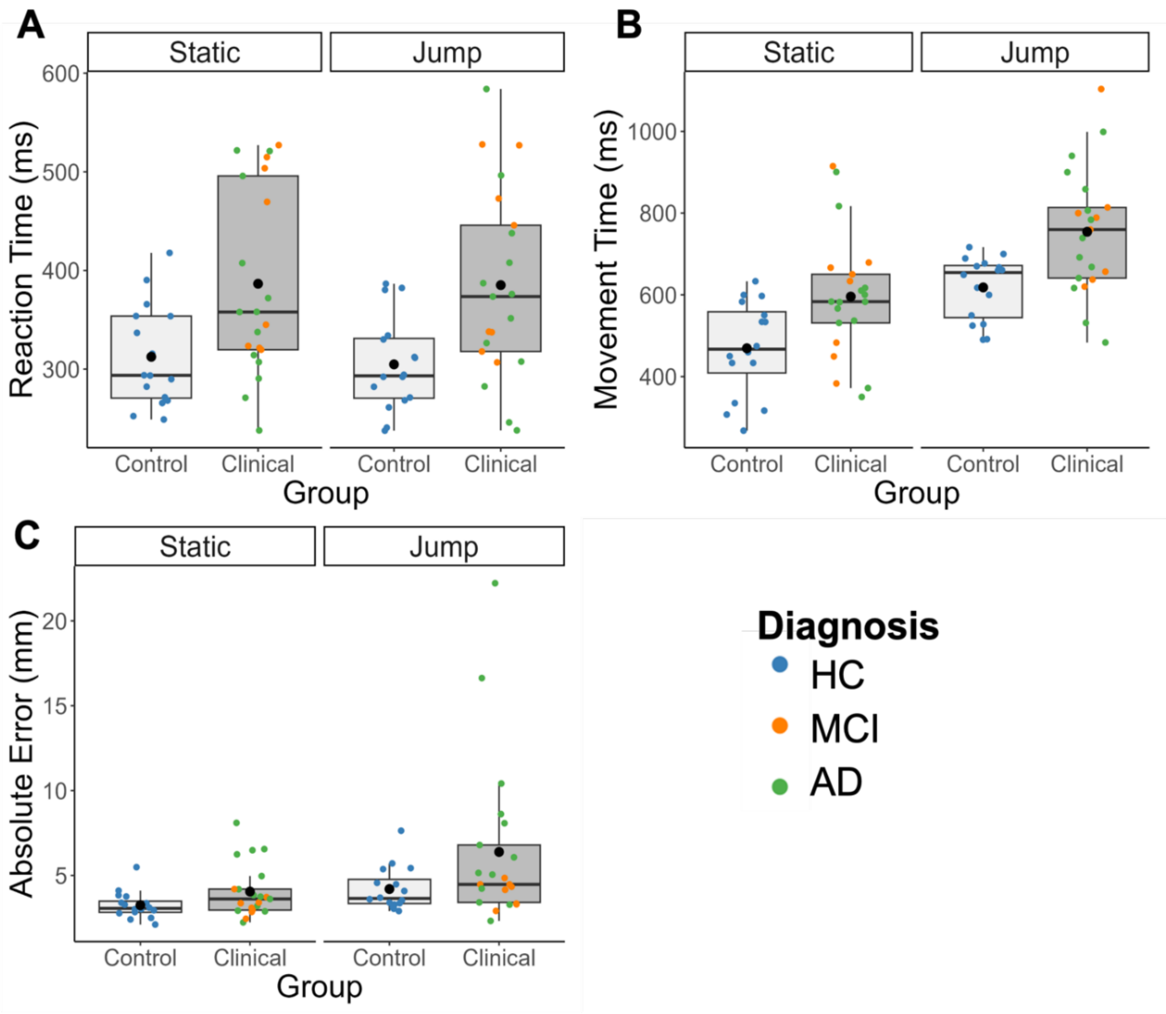
4.6.2. Experiment 5: Online Corrections

For RT (see Figure 4.5A), there was a significant main effect of group, *F*(1, 35) = 8.82, *p* = .005, η_p^2 = .201, with the clinical group taking significantly longer to initiate their movements compared to controls (*mean diff* = 77.18 ms, *SE* = 26.98, *p* = .005). There was no significant effect of jump condition, *F*(1, 35) = 1.41, *p* = .243, η_p^2 = .039. This finding was expected as participants were unaware of the jump condition until after the movement was initiated. There was also no significant group by jump condition interaction, *F*(1, 35) = .683, *p* = .414, η_p^2 = .019.

For MT (see Figure 4.5B), there was a significant effect of group, *F*(1, 35) = 9.90, *p* = .003, η_p^2 = .221, with the clinical group exhibiting significantly longer movements compared to controls (*mean diff* = 131.25 ms, *SE* = 41.71, *p* = .003). There was also a significant effect of jump condition, *F*(1, 35) = 138.4, *p* < .001, η_p^2 = .798, with significantly longer MTs in jump conditions compared to static (*mean diff* = 153.73 ms, *SE* = 13.10, *p* < .001). There was no significant group by jump condition interaction, *F*(1, 35) = .136, *p* = .714, η_p^2 = .004.

For AE (see Figure 4.5C), there was a significant effect of group, *F*(1, 35) = 4.23, *p* = .047, η_p^2 = .108. The clinical group made larger errors than controls (*mean diff* = 1.49 mm, *SE* = .726). There was also a significant effect of jump condition, *F*(1, 35) = 7.84, *p* = .008, η_p^2 = .183, with significantly larger error in the jump condition compared to static conditions (*mean diff* = 1.65 mm, *SE* = .588). There was no significant group by jump condition interaction, *F*(1, 35) = 1.38, *p* = .248, η_p^2 = .038.

Figure 4.5 *Boxplots displaying A) RT, B) MT, C) AE, for each group and jump condition (static and jump). Dots represent individual participants, colour coded by diagnosis. Black dots represent group and condition mean.*

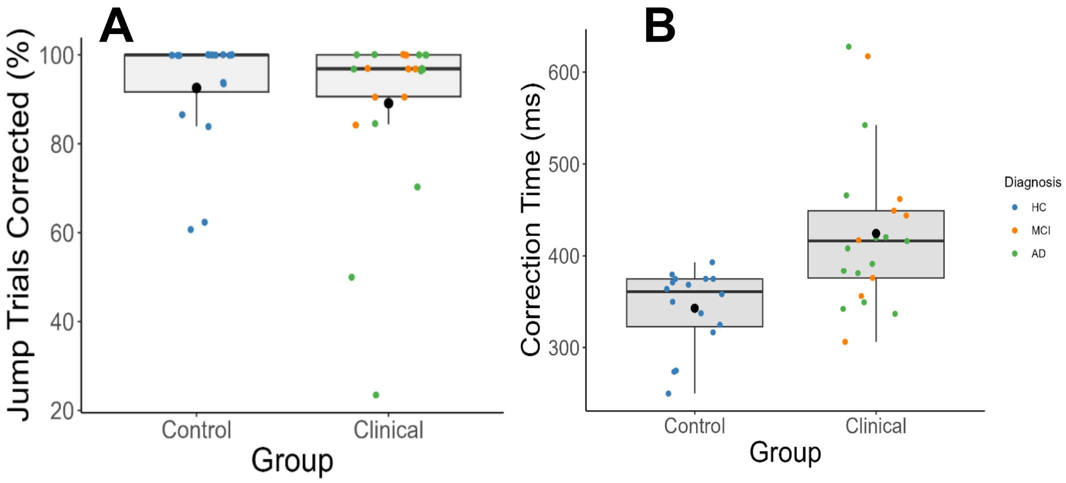


4.6.3. Trajectory Analysis

There was no significant difference in terminal correction status in the jump conditions between the clinical group and controls *t*(34.6) = .645, *p* = .523 (Controls: *M* = 92.57%, *SD* = 13.10, Clinical: 89.12%, *SD* = 19.37, see Figure 4.6A). However, correction time was significantly slower in the clinical group compared to controls (*mean diff* = 81.47, *SE* = 14.58), *t*(31.2) = 3.81, *p* < .001.

Case-control comparisons revealed that 7/21 (33%) had significant deficits in correction time. 3 of these had a diagnosis of AD, while 4 had a diagnosis of MCI.

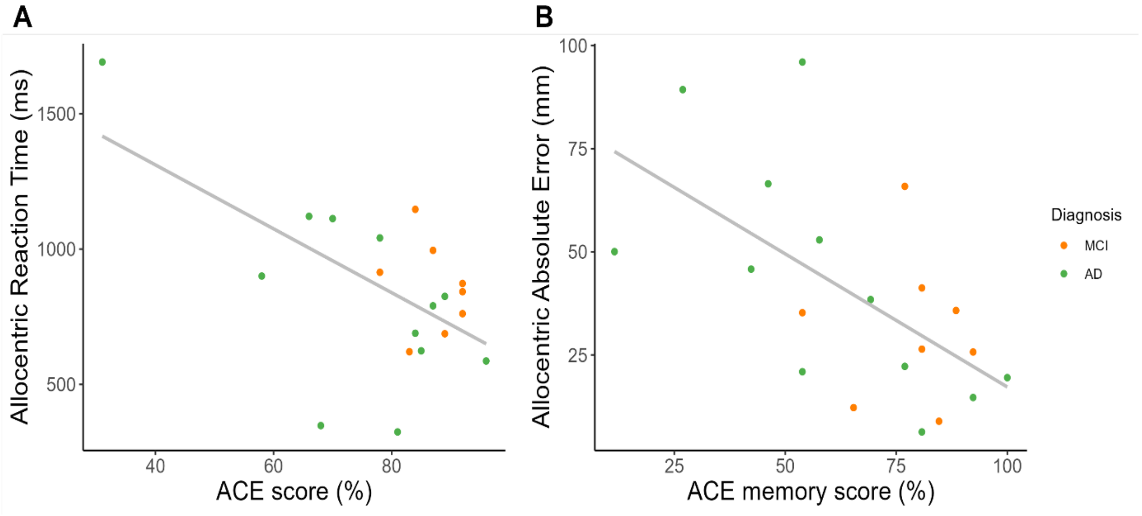
Figure 4.6 *Boxplots showing A) percentage of jump trials corrected, B) correction time, for both groups. Dots represent each participant, colour coded by diagnosis. Black dots represent group means.*



4.7. Correlation with cognitive measure (ACE scores)

FDR corrected correlations revealed a significant negative correlation between RT in the allocentric task and overall scores on the ACE, *r*(18) = -.580, *p* = .042, with poorer performance on the ACE being associated with longer RTs in the allocentric task (see Figure 4.7A). There was also a significant negative correlation between AE in the allocentric task and scores in the memory domain of the ACE, *r*(18) = -.590, *p* = .040 (see Figure 4.7B), poorer memory scores were associated with increased error in the allocentric task. As expected, scores in the ACE domains correlated significantly with the overall ACE scores, and there were several significant correlations between the ACE domains.

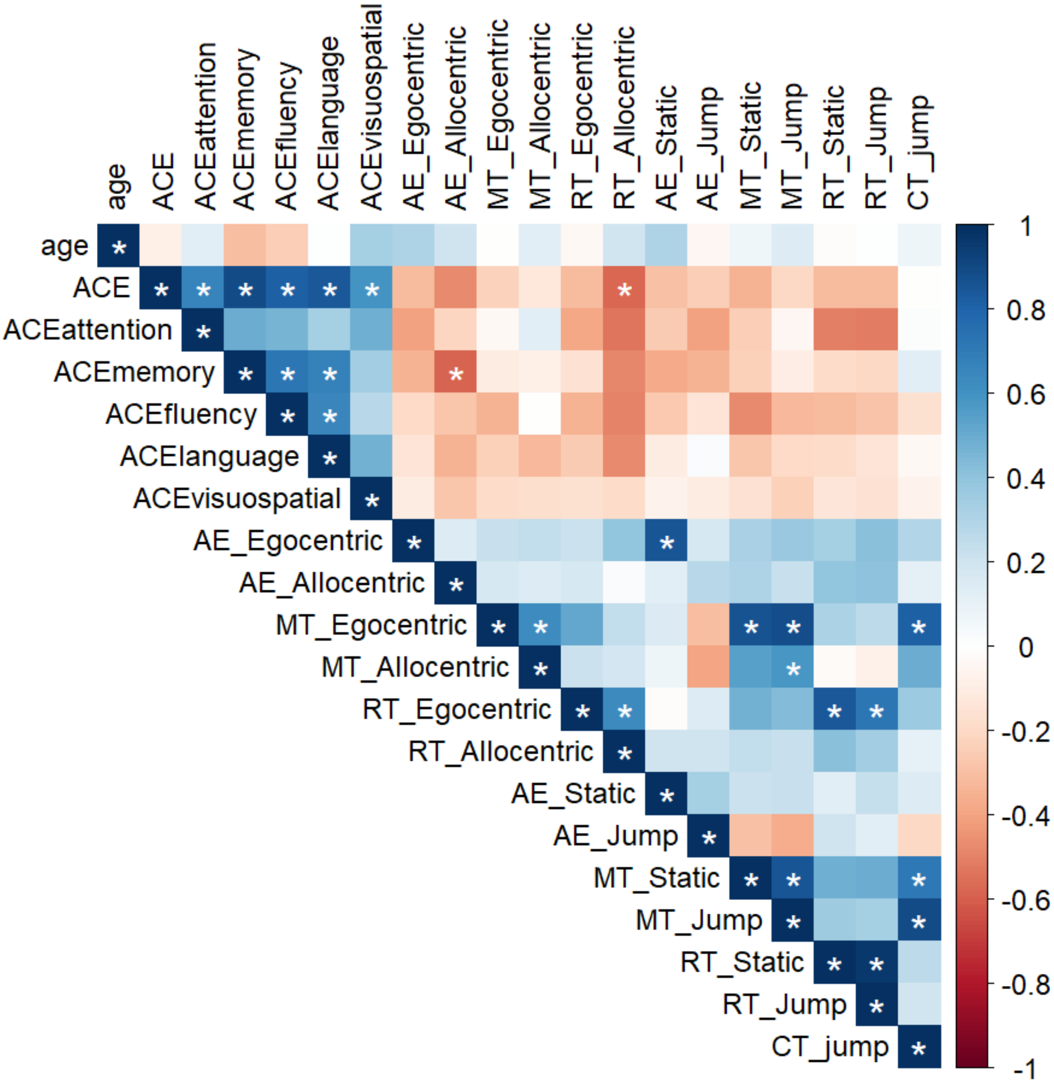
Figure 4.7 *Scatterplots showing the relationship between A) Allocentric RT and overall ACE score B) Allocentric AE and ACE memory domain score.*



Across experiments 4 and 5, there were also several significant correlations between kinematic variables (see Figure 4.8). More specifically, a significant positive correlation was found in accuracy between tasks: AE in the egocentric task significantly correlated with AE in the static condition of the online correction task *r*(18) = .850, *p* < .001. Movement time was also significantly correlated between the two tasks: MT in the egocentric task was positively correlated with MT in the static condition of the online correction task *r*(18) = .860, *p* < .001, with MT in the jump condition of the online correction task *r*(18) = .880, *p* < .001, and with correction time in the online correction task *r*(18) = .810, *p* < .001. There was also a significant positive correlation between MT in the allocentric task and MT in jump condition of the online correction task *r*(18) = .580, *p* = .046.

In experiment 4, MT in the egocentric task was significantly positively correlated with MT in the allocentric task, *r*(18) = .620, *p* = .025. RT in the egocentric task was positively correlated with RT in the allocentric task, *r*(18) = .630, *p* = .020. In experiment 5, there was a significant positive correlation between MT in the static and MT in the jump condition, *r*(18) = .850, *p* < .001. Longer MTs in the static condition were associated with longer correction time in jump conditions *r*(18) = .710, *p* = .002. MTs in the jump condition were positively correlated with correction time *r*(18) = .890, *p* < .001.

Figure 4.8 *A correlogram indicating Pearson's correlations between scores on the ACE domains and performance on the tasks in Experiment 4 and Experiment 5. Asterisks represent significant correlations following FDR correction.*



4.8. Discussion

The aim of the current series of experiments was to investigate whether individuals with AD and MCI display behavioural deficits in egocentric and allocentric visuomotor functioning (Experiment 4) and online visuomotor control (Experiment 5). Such deficits could be indicative of dysfunction in the dorsal visual stream which has been found to exhibit AD related pathology at an early stage of the disease, possibly before symptoms such as memory loss arise (Gordon et al., 2018). We used a novel portable iPad task which could easily be transferred to clinical settings to address these questions. In both experiments, we found that the clinical group were slower to initiate and execute reaching movements irrespective of the task or condition. That is, RTs and MTs were significantly longer in the clinical group compared to healthy controls. Despite this, end-point error remained comparable between the clinical and control samples throughout the tasks. In experiment 4, slowing of initiation and movement execution was apparent across egocentric and allocentric tasks, suggestive of a deficit in visuomotor performance irrespective of the reference frame employed to plan accurate reaching movements. In experiment 5, we observed that the clinical group took significantly longer than controls to correct movements in response to changes in target position, possibly indicating a deficit in online motor control.

4.8.1. Egocentric and Allocentric visuomotor performance

Interestingly, increased RTs in the allocentric reaching task were associated with lower total scores in the ACE, while poorer accuracy in the allocentric task was associated with lower scores on the ACE memory domain. Despite this, the clinical group exhibited significantly longer RTs and MTs in both egocentric and allocentric tasks. These findings suggest that while those in the clinical group take longer to initiate and execute movements in general, allocentric visuomotor performance may be particularly sensitive to cognitive decline and observable memory deficits. This is perhaps surprising given that the task did not rely on a memory component, however these findings could align with those previously reported in spatial navigation tasks using the HGT (Hort et al., 2007; Laczó et al., 2011). Here, allocentric deficits have been found to be characteristic of individuals with AD, aMCI affecting multiple domains, and single domain aMCI, whereas egocentric deficits have not been observed in those with single domain aMCI (Hort et al., 2007; Laczó et al., 2011). Indeed previous studies employing the HGT rely on memory and learning of landmark locations to successfully complete the task, while other tasks employed have assessed more perceptual judgements (Serino et al., 2014). Therefore, our findings expand on this past body of research to provide the first evidence to our knowledge that visuomotor performance using an allocentric reference frame is sensitive to memory impairments in a task that does not rely on memory.

It is possible that both longer RTs and increased AE in the allocentric task are reflective of a visuomotor planning deficit. Interestingly, when similar tasks have been performed by healthy controls in both the presence and absence of visual feedback of the hand, visual feedback reduced movement variability more in egocentric tasks than allocentric tasks (Thaler & Goodale, 2011b). This suggests that allocentric tasks rely less on the presence of visual feedback and thus more heavily on the planning stages of the reach. This is in line with recent findings that reach-to-grasp kinematics are particularly affected in early-stage AD in the absence of visual feedback (Zhang et al., 2022). Our findings can therefore corroborate those of Zhang et al. (2022), for example it is possible that the movement planning stage is particularly affected in AD. As we found reaction times correlated with overall ACE scores in the allocentric task only, this could reflect a greater degree of planning required to carry out an allocentric reach due to less reliance on online control to complete the movement. In line with this, Zhang et al. (2022) noted that correlations with cognitive measures heavily relied on the visual feedback condition, with much stronger correlations noted between performance and cognitive measures in the absence of visual feedback, compared to when visual feedback was available. It is therefore possible that the allocentric reaction times can be a sensitive measure to cognitive decline and reflective of a movement planning impairment when there is less reliance on online control.

Additionally, Zhang et al. (2022) found that end-point accuracy was related to neuropsychological test scores in the absence of visual feedback, this could again reflect a deficit at the planning stage of the reach to grasp movement. Our finding that end-point accuracy in the allocentric task only was negatively associated with performance on the memory subtest of the ACE is in line with these findings. Memory impairments are one of the first observable symptoms of AD (Jahn, 2013), as the deficits associated with Alzheimer’s become more apparent, it is possible that at this stage, end-point accuracy cannot be compensated for by increased planning time. It could therefore be the case that while there is a subtle allocentric visuomotor deficit, this manifests in reduced accuracy as key observable impairments associated with AD progression.

An alternative explanation for our finding that allocentric RT and AE may be sensitive to cognitive decline is that of a deficit in the translation of allocentric to egocentric representations. While allocentric coding was required in the task to plan the reach, this may have been translated to egocentric coordinates during movement execution for online monitoring. fMRI and behavioural research during allocentric and egocentric reach paradigms has identified that the brain converts allocentric codes to egocentric reach plans at an early stage, with frontoparietal areas including precuneus being involved in this step (Chen et al., 2011, 2018). It is therefore possible that the allocentric reaction time and errors which correlated with ACE scores could be due to a deficit in allocentric to egocentric transformations, rather than a reach planning deficit, possibly due to pathology in the precuneus.

Previous research has found that spatial judgements about objects are particularly impaired in AD and aMCI when a switch between reference frames is required (Ruggiero et al., 2018). Specifically, participants were required to make two judgements about remembered object locations, these were either in the same reference frame, or switched. Both clinical groups performed significantly less accurately than controls for allocentric judgements, and when the task involved a switch from allocentric to egocentric judgements. However, when the switch was from an egocentric to allocentric reference frame, those with aMCI performed similarly to controls. This suggests that there could indeed be a deficit in switching between reference frames leading to greater error in allocentric tasks associated with observable memory decline, however this would not explain our findings of increased RTs. It would be difficult to clarify whether our findings are due to an allocentric-to-egocentric conversion deficit as tasks investigating conversion use delayed reaching paradigms which could be explained by memory confounds in our clinical population (Chen & Crawford, 2020; Ruggiero et al., 2018).

Despite this, we found that our clinical group had significantly longer RTs and MTs irrespective of the frame of reference employed. This suggests that visuomotor performance deficits are present in early AD, while allocentric reaching is sensitive to observable cognitive impairments assessed in the ACE. It is not yet clear whether this relationship is a result of AD pathology specifically, or general neurodegenerative disease. For instance, previous research has found that performance for egocentric navigational judgements can discriminate between AD and behavioural variant fronto-temporal dementia (bvFTD), and AD and vascular cognitive impairment (VCI; Coughlan, Flanagan, et al., 2018; Lowry et al., 2020; Tu et al., 2017). While allocentric judgements appear to be impaired in all groups, findings suggest that people with AD perform significantly worse in egocentric tasks than those with bvFTD, but those with VCI perform significantly worse than those with AD. Put together, this suggests that performance in tasks requiring an egocentric reference frame may be more sensitive to different forms of dementia, while allocentric judgements may be more reflective of general cognitive impairment. Future research could assess the diagnostic specificity of our reaching based tasks in a broader range of populations. It would also be interesting to investigate how removing visual feedback of the hand, but not the target, would affect performance in both tasks. This would help to clarify whether a visuomotor planning deficit may be attributable to the timing differences observed between our groups.

4.8.2. Online Visuomotor Control

Given that our clinical group took significantly longer to initiate corrections compared to controls, it is possible that impaired visuomotor performance in our clinical group is a result of an impairment in online visuomotor control. As terminal correction status did not significantly differ between groups, it appears that the deficit is not as severe as that observed in patient IG, who initially reached towards the initial target before correcting towards the second target position (Gréa et al., 2002). Despite this, several patients in our clinical group did appear to fail to correct their movements. It is possible that in these cases, participants made a reach towards the initial target and then stopped their movement before reaching towards the new target position, as was observed in patient IG. This is the first study to our knowledge utilising the double step paradigm in a dementia population.

Recent research has found that online corrections to targets redirected towards the body midline are more effective than those away from the midline, possibly because functional actions are most likely directed at the body midline (Maselli et al., 2023). It would therefore be interesting to observe the performance of clinical populations in a task where the target redirects towards the centre of the screen. Given that this should be an easier task in the absence of any deficits, it is possible that an online control deficit would therefore be more pronounced in clinical groups. On the other hand, it could be that moving the target away from the body midline is a more complex task which could be a more sensitive manipulation to detect subtle deficits.

We would argue that although MT was also increased in the clinical group in our online correction task, the longer correction times observed in the clinical group are not solely due to a slowed movement in general. Indeed, online corrections are generally considered a smooth movement without abrupt changes to velocity profile (Prablanc & Martin, 1992). Despite this, our findings show that the impairments associated with online corrections in our clinical group are not as profound as that observed in individuals with optic ataxia. However, research using a similar double step paradigm in individuals with neglect, found longer correction times to changes to target position in the contralesional field (Rossit et al., 2012). Rossit et al. (2012) suggested that this could be a result of perceptual deficits which affect processing of stimuli required for online corrections. It is thus possible that our findings could be reflective of a slowed, or impaired, transfer of visual perceptual information into visuomotor commands. Interestingly, individuals with optic ataxia are also slow to perceptually discriminate target jumps, in addition to their visuomotor deficit, which was interpreted as an impaired orienting of attention (McIntosh et al., 2011). It would therefore be interesting to investigate whether there is a presence of this kind of perceptual deficit in our clinical populations.

4.8.3. General slowing in the planning and initiation of movements

In both of our experiments, we observed that the clinical group had increased RTs and MTs compared to controls. Our findings are line with a number of studies which have reported slowed movement planning and execution in both individuals with AD (Mitchell et al., 2022; Tippett et al., 2007, 2012; Tippett & Sergio, 2006). While this could be attributed to general bradykinesia associated with cognitive decline (Bologna et al., 2020), our recent research found that longer movement times were associated with an extended deceleration period compared to controls which could be more suggestive of an online control deficit (Mitchell et al., 2022). In line with this, we demonstrated here that the clinical group take significantly longer to adjust their trajectories in response to a change in target position.

Despite this, contrary to our hypothesis, end-point error did not significantly differ between our clinical and control groups. This could indicate a speed-accuracy trade off, whereby movements are slowed to compensate for a planning deficit but to maintain accuracy. For example, people with optic ataxia show improved reaching accuracy when reaching towards a target following a delay period and thus allowing for time to program a reach (Milner et al., 1999). Therefore, our clinical group may have performed a similar strategy, where end-point accuracy was prioritised over time taken to execute the movement. In future, it would be interesting to investigate how reaching accuracy is affected by time limits imposed on our visuomotor tasks. In this case, movement speed would have to be prioritised over accuracy and reaching error due to planning deficits may be more likely to be observed.

While we do provide some evidence of an impairment in the ability to make fast online trajectory corrections, the sampling rate of our tablet did not allow us to investigate the in-depth kinematics of reaching performance in the task. It would have been particularly useful to investigate how the kinematics of movements in each of our tasks differed between groups. For example, it would be interesting to investigate whether our clinical group extended the deceleration phase in all our tasks, even in the allocentric task which is usually characterised by less reliance on online control (Thaler & Goodale, 2011b). Future studies could therefore investigate performance in the double step paradigm using more sophisticated motion tracking technology to investigate whether the observation of a longer correction time also coincides with extended deceleration, possibly due to poor online control.

A possible alternative explanation for our findings stems from research suggesting that untreated poor vision is a significant risk factor for AD (Nael et al., 2019). In turn, it may have been more likely that those in our clinical group had undetected visual impairments which could have affected task performance. For instance, research has shown that reducing visual acuity impairs performance in fine visuomotor tasks, such as threading a small bead onto a needle (Piano & O'Connor, 2013). Moreover, a recent review has highlighted that visually guided reaching and grasping movements are significantly slower in those with amblyopia (Rakshit et al., 2023). It is therefore possible that our observation of slowed movements in the clinical group could be a compensatory strategy for reduced visual acuity but to maintain accuracy. Future studies should control for this possible confound by assessing visual acuity in all participants and ensuring that groups are matched in terms of visual abilities. Despite this, observation of the variability in the MT plots in Experiment 4 seems to indicate that increased MT, particularly in the egocentric task is a stable group level deficit. We did attempt to control for visual impairments at the recruitment stage by excluding individuals with diagnosed uncorrected visual impairments, however it is possible that visual impairments may have been undiagnosed.

Regarding the feasibility of using our novel iPad application as an assessment tool for reaching in clinical populations, all participants were successfully able to interact with the technology used in our reaching assessments, and able to complete the tasks after very brief training. Moreover, the task is brief (< 10 minutes) and could be administered at home which is in line with recent recommendations for digital assessments of dementias (Staffaroni et al., 2020). This could therefore ultimately be used as an assessment tool which provides rich information on visuomotor functioning which could be accessible by a wide range of people. Moreover, we replicated previous findings that allocentric reach programming takes longer than egocentric reach planning, as demonstrated by increased reaction times in allocentric compared to egocentric tasks in our healthy control group (Thaler & Goodale, 2011b). This provides some evidence for the validity of our iPad-based assessment. However, to confirm this, a larger validation study should be carried out to assess the validity, provide normative data, and differences in timings that occur due to natural ageing and other forms of neurodegenerative disease.

It would also be interesting to compare performance between those with AD and MCI. The current study was not sufficiently powered to perform this comparison, due to data collection being impacted by the COVID-19 pandemic. However, previous research suggests that RT, and thus the planning stage of movements, is more impaired in MCI, compared to healthy controls (Salek et al., 2011). This could be a potential compensatory strategy by increasing planning time to preserve end-point accuracy as discussed earlier. It may be the case that performance on these tasks could predict progression into AD, or that there are specific differences in visuomotor planning and execution between the two populations.

Overall, using a novel portable iPad-based task, we were able to identify that people with AD and MCI show an overall slowing in the planning and execution of movements and corrections to target jumps, possibly reflective of impaired online motor control due to dorsal visual stream damage. Moreover, performance on the allocentric task was specifically related to overall cognitive decline in a traditional neuropsychological test. These findings suggest that the allocentric task may be a sensitive measure to assess cognitive decline resulting from AD pathology. These deficits may be associated with impaired planning of movements which is particularly affected in allocentric reference frames, or a deficit in allocentric to egocentric transformations which could be a result of pathology in the precuneus. Future research should assess performance using task manipulations such as removing visual feedback, and introducing a time limit, as well as investigate the sensitivity of the task in discriminating between different forms of dementia.

Ultimately, we provide tentative evidence that our portable iPad task could be sensitive to early-stage AD.

5. Chapter 5 - General discussion

Our interactions with objects in the environment demonstrate an important link between perceiving the environment and interacting with the objects within it. Overall, the aim of this thesis was to investigate how perception may affect action, and how action may affect perception using different approaches. Firstly, I investigated how simply perceiving objects that we can interact with can influence motor responses using a commonly utilised behavioural paradigm (Chapter 2). Secondly, I investigated how tool use action properties are represented in the ventral ‘perception’ stream, and dorsal ‘action’ stream in tasks where participants were simply perceiving objects, and when participants pantomimed tool use (Chapter 3). Finally, I investigated how action, but also perception, may be affected due to neurodegenerative disease (Chapter 4). Put together, this thesis highlights the importance of considering the ventral and dorsal streams, as well as the VD and DD streams, as collaborative networks. These collaborative networks should also be considered behaviourally, by understanding how perception may affect action and vice versa, rather than considering them as isolated processes.

5.1. Summary of findings

In Experiment 1 (Chapter 2), I aimed to replicate the highly cited, but controversial (Azaad et al., 2019), handle compatibility effect (Tucker & Ellis, 1998). In this paradigm, a common finding is that reaction times are faster when the handle of a perceived object is compatible with the hand used to respond in an irrelevant task. This has been interpreted as a behavioural demonstration of Gibson’s (1979) concept of affordances, which proposes that perception of objects carries direct information about its afforded actions. In Experiment 2, I introduced a novel manipulation to the classic paradigm. Here, objects were presented in either the upper or lower VFs. An abundance of research in macaques, as well as humans, has identified that the lower VF is more specialised for action, whereas the upper VF is more specialised for perceptual tasks. In line with this, we observed a significant handle compatibility effect in the lower, but not the upper, VF in Experiment 2. This demonstrates a possible lower VF advantage in the direct perception of afforded actions. However, we were unable to replicate the handle compatibility effect when objects were presented in the central VF (Experiment 1).

In my third experiment (Chapter 3), I used a block-design fMRI paradigm, and analysed using ROI-and searchlight-based MVPA which regions represented tool use action properties (i.e., rotate or squeeze) during both passive viewing of tool images, and tool use pantomiming without tool in hand in response to tool names. I further investigated whether tool use action neural representations could be generalised across tasks (viewing or pantomime) and modality input (tool image or word), or whether they were modality/task specific. We found several regions in the ventral, VD and DD streams which represented tool use actions during both viewing and pantomiming. In particular, we found that decoding of tool use action in hand selective LOTC within the ventral stream was significantly higher than decoding of tool identity for both viewing and pantomiming. This provides evidence that visually defined category-based regions within the ventral stream contain higher-level information about possible actions towards objects, and not simply their shape, size, and orientation. We were unable to observe significant cross-task decoding in any region in both our ROI analysis and our searchlight. This suggests that while areas in the ventral, VD, and DD streams contain action representations, they use distinct patterns of activation.

In Experiments 4 and 5 (Chapter 4), I investigated visuomotor performance in individuals with AD and MCI, using an iPad based reaching task. Here I compared the performance of a clinical group (characterised by a diagnosis of AD or MCI) with healthy age matched controls in several tasks thought to involve the dorsal stream. In particular, in Experiment 4, I assessed visuomotor control in both egocentric and allocentric reference frames. The representation of the environment in allocentric reference frames are thought to recruit the ventral visual stream, while the dorsal visual stream is thought to represent space in an egocentric reference frame. In Experiment 5, I investigated the ability to make fast online trajectory corrections to target jumps, associated with the dorsal visual stream. Overall, in both studies, participants in the clinical group were slower to initiate and execute reach movements, irrespective of the reference frame employed. The clinical group were also slower than controls to correct their movements in response to target jumps. Interestingly however, performance in the allocentric reaching task was the only task associated with cognitive decline. Here, we found that allocentric reaction times correlated negatively with overall ACE scores, while absolute error was negatively associated with scores on the memory domain of the ACE.

Put together, my three studies have highlighted, using different approaches, that perception and action can be considered as integrated and collaborative processes. Moreover, I add to a growing body of evidence suggesting that the ventral ‘perception’ stream contributes to actions, and the dorsal ‘action’ stream contributes to perception. In the following sections, I will discuss how my findings can be interpreted as perception in the action stream, and action in the perception stream, and how my tool use action findings relate to the two-action systems model (Binkosfki & Buxbaum, 2013; Buxbaum, 2017). Moreover, I will address some of the limitations of my studies and provide suggestions for future research.

5.2. Perception in the action stream

In line with Gibson's (1979) concept of affordances, our findings from Experiments 2 and 3 provide evidence that perception of manipulable objects trigger action properties and this can be demonstrated at a neural and behavioural level. At a neural level, we found that tool use actions can be decoded in regions of the DD and VD stream, even during passive viewing of tool images. Moreover, our ROI and searchlight based MVPA analyses revealed significant decoding of tool use action in IPS, SPOC and PMd in the DD stream, and SMG in the VD stream from passive viewing of tool images. Given that no tool use action was required in the view task, this questions the propositions of the two action systems model (Binkofski & Buxbaum, 2013), and TVSH (Goodale & Milner, 1992). Specifically, both models state that the superior regions in the PPC are responsible for the online control of visually guided actions. However, here we showed that simply perceiving tool images leads to action related representations in the DD stream. We were unable to reliably decode tool identity in DD regions from viewing however, so this suggests that DD regions contain information relevant for tool use actions rather than simply low-level features (object shape/identity). Nevertheless, it appears that perceptual properties of objects are computed in the dorsal stream to some extent.

Our MVPA findings fit well with evidence from monkey physiology showing that visual neurons in dorsal region AIP represent object shape, orientation, and size (Murata et al., 2000). Moreover, in humans, dorsal stream regions are reliably activated in response to viewing tool images (for a review, see Lewis, 2006). In addition, tool use actions can be decoded in IPL and SPL in response to viewing tool images and imagining their associated actions (Chen et al., 2018). We expanded on these findings to show that similar regions also represent tool use actions when viewing tool images, without imagining their associated actions. Put together, this highlights that the dorsal 'action' stream is also involved in visual perception to an extent.

This suggestion is in line with a growing body of literature suggesting that dorsal stream regions represent perceptual attributes, possibly independent of action (Freud et al., 2020). fMRI research has shown that dorsal areas including parieto-occipital junction and pIPS are sensitive to changes in object orientation, but not object identity (Valyear et al., 2006). Moreover, dorsal stream regions show shape selectivity in response to viewing object images (Bracci & Op de Beeck, 2016; Freud et al., 2017), and novel shapes (Freud et al., 2015). The dorsal stream has been suggested to represent shape following a posterior to anterior gradient. Posterior regions have been suggested to contribute to perceptual functions through connections with ventral regions, and anterior regions use these shape representations in a way that subserves visuomotor control (Freud et al., 2017).

A recent model by Ayzenberg and Behrmann (2022) hypothesises that global shape (i.e. the overall form of an object) is represented in IPS before being transferred to connected ventral stream regions for more detailed analysis of its local features. This model suggests that global shape can be represented in the absence of any ventral stream involvement, and that this dorsal stream processing is used primarily to inform perception. While this could be considered contrary to the arguments of the TVSH, it is also likely that the global shape computations are primarily responsible for the visual guidance of actions (Goodale & Milner, 2023). Put together, there is a growing consensus that perception of action relevant properties of objects is computed in the dorsal visual stream, particularly IPS. In Project 2, we were unable to decode tool identity from viewing in IPS, or any dorsal stream regions. However, tool use actions were reliably decoded in IPS, as well as SPOC from simply viewing. This provides evidence that the dorsal visual stream may compute perceptual properties of objects, but only properties that are action relevant, to facilitate the guidance of action.

In line with this, our behavioural findings from Experiments 1 and 2 demonstrate that perception of graspable objects leads to a facilitation of motor responses when the object position is primed for action (i.e. the handle oriented to the hand of response and in the lower VF). fMRI research, where participants were presented with images of objects affording a power or precision grasp, has found greater activation in IPS and PMd is associated with a greater compatibility effect (Grèzes et al., 2003). In this case, the compatibility effect was characterised as faster reaction times to perform a precision or power grip which was compatible with the object presented in an irrelevant object categorisation task (Grèzes et al., 2003). This highlights that regions in the DD stream may automatically compute object affordances even when the action is not relevant for the task. Again, this is in line with our finding in Experiment 3 that tool use actions are represented in IPS from passive viewing. It is important to note the deviations from Gibson's (1979) definition of the term here. Given our findings in Experiments 1 and 2, it is likely that affordances vary depending on the environment. As we only observed a significant compatibility effect in the lower VF, this suggests that the evocation of object affordances in our study depended on the context, rather than the intrinsic features of the object alone. This is in line with previous handle compatibility research suggesting that handle compatibility effects are enhanced when action is implied (depressed door handles; Tipper et al., 2006), and when objects are situated within reach (Ambrosini & Costantini, 2013; Costantini et al., 2010, 2011). Put together, we expanded on this evidence by showing that handle compatibility effects are present in the lower, but not upper, VF, suggesting that the elicitation of affordances depends on the context, and how suited the objects' positioning is for action. Moreover, we included a larger stimulus set than previous similar studies (which were limited to one object) which increases the ecological validity of our findings.

5.3. Action in the perception stream

An interesting finding in Experiment 3 was that patterns of activity in the ventral stream represented tool use actions even when pantomiming tools' use without visual feedback. Tool use action was represented in hand-selective LOTC during both view and pantomime, and decoding was significantly higher for tool use action than tool identity. This was also the case in pMTG in the pantomime task. This suggests that the ventral stream may not solely process semantic and visual associations with tool identities, but also tool use action knowledge for the purpose of engaging in skilled object-directed actions. These findings expand on a growing body of evidence highlighting ventral stream involvement in action planning and execution, as well as action observation (for a review, see Lingnau & Downing, 2015). Moreover, activation in LOTC has been observed during action execution in the absence of visual feedback of the hand (Astafiev et al., 2004; Cavina-Pratesi et al., 2010; Peelen & Downing, 2005). Expanding on this, MVPA studies have found reliable decoding of actions (e.g. reach to grasp, reach to touch) and action sequences (e.g. grasp-to-hold, grasp-to-place left, grasp-to-place right) in LOTC during the planning phase of movement (Gallivan et al., 2013, 2016). These action sequences can also be decoded in LOTC when the tool is in hand (Gallivan et al., 2013). This suggests that movement sequences may be represented in ventral regions prior to engaging in movement, and not necessarily simply due to the visual information that arises during movement execution. We built on this evidence by showing sequences of movements (such as tool use) can be decoded in visually defined LOTC and pMTG during pantomime.

Recently, Wurm and Caramazza (2022) have proposed that the occipito-temporal cortex contains two pathways. Specifically, a ventral pathway which supports object recognition, and a lateral pathway which encompasses LOTC supporting action recognition. Previous research has shown that activity in LOTC represents action-related categories such as tools and hands (Bracci et al., 2011, 2016), and that tool selectivity in LOTC can develop without visual experience, in those who are congenitally blind (Peelen et al., 2013). Moreover, it has been shown that the type of action (e.g. lift versus pull) is represented in LOTC, regardless of the viewpoint (Oosterhof et al., 2012). Additionally, grasping related properties such as elongation, grasp axis and number of digits used during grasping is also represented in LOTC (Fabbri et al., 2016; Monaco et al., 2015). Put together, results from our Experiment 3 align with the view that the LOTC codes action relevant properties regardless of the visual input.

In line with this, Klein et al. (2023) conducted a recent study where participants planned and executed precision grasps of L-shaped blocks comprised of differing materials, masses, and orientations. Representational similarity analysis found that both visual streams represent distinct grasping related factors, such as grasp axis, size, and object mass during both planning and execution, but at different stages. For instance, grip size was encoded in the ventral stream and aIPS during planning, but in ventral stream regions and premotor cortices during execution. Grasp axis was only correlated with neural representations in dorsal regions during planning, but not execution. However, grasp axis was encoded in ventral LOC during both planning and execution. While object mass was only encoded in ventral and dorsal regions during execution. Interestingly, during planning, representations between V1 and the dorsal stream network were strongly associated with one another, while only weak correlations were observed among ventral regions. The opposite pattern was observed during execution, with representations within dorsal stream regions becoming more independent of one another. This was speculated to represent a shift from extraction of action relevant information (such as grip selection) during planning in the dorsal visual stream to monitoring sensory feedback to assess whether corrections are needed in the ventral stream during execution (Klein et al., 2023). In Experiment 3, we were able to decode tool use actions during pantomime execution, in the absence of sensory visual or haptic feedback. Therefore, while we corroborate previous findings of LOTC involvement in action execution, the functional role of this activity remains unclear. Our findings are more in line with those of Gallivan et al. (2013, 2016), suggesting that ventral stream regions represent movement sequences, rather than being engaged in sensory feedback processes.

5.4. Theoretical implications for perception and action models

Put together, the overall findings in this thesis have highlighted that both the dorsal and ventral visual streams contribute to both perception and action. In the classic TVSH, perception and action are subserved by two separate but interacting cortical pathways (Goodale & Milner, 1992; Milner & Goodale, 2008). Despite this, much of the neuropsychological evidence for the TVSH has been based on behavioural dissociations between the two streams, thus considering them as isolated, rather than interacting, systems. However, functional connectivity studies have clearly highlighted interactions between the streams (Amaral et al., 2021; Chen et al., 2018; Hutchison & Gallivan, 2018; Zimmermann et al., 2018). For instance, body-selective occipitotemporal cortex (i.e. EBA), but not object-selective LOTC, shows connectivity with parietal areas during sensorimotor tasks (reaching and grasping; Hutchison & Gallivan, 2018). While functional connectivity between hand and tool selective LOTC and IPS has been shown to correlate with distal hand and tool preferring regions respectively (Amaral et al., 2021).

More recent research has expanded on simply functional connectivity studies by employing effective connectivity analyses such as dynamic causal modelling (DCM; Friston et al., 2003). DCM allows researchers to assess the presence and direction of connectivity between ROIs during experimental tasks. For instance, Malfatti and Turella (2021) used DCM to investigate connectivity between pMTG, aIPS and PMv during pantomimed grasp-to-move and grasp-to-use movements. They found evidence of bidirectional connectivity between all three regions which was modulated by the grasp to use condition. Specifically, grasp-to-use increased bidirectional connectivity between pMTG and PMv, while connectivity between aIPS and the other two regions was reduced (Malfatti & Turella, 2021). Further research has found that bidirectional effective connectivity between V1, LOTC, IPS, SMG and IFG is modulated by tool manipulation judgements (Kleineberg et al., 2018). The connectivity here was strengthened in the posterior to anterior direction and weakened in the reverse direction. Conceptual judgements of tools on the other hand only appeared to modulate connectivity between early visual regions and the FG (Kleineberg et al., 2018). In sum, bidirectional connections between the ventral, VD and DD streams appear to subserve tool related action execution and processing.

Our findings corroborate Binkofski and Buxbaum's (2013) two action streams model to an extent. For instance, SMG and pMTG are considered to be in the VD 'Use' stream, responsible for storing learned manipulation knowledge of tools (Binkofski & Buxbaum, 2013; Buxbaum, 2017). In Experiment 3 we found that both SMG and pMTG contain representations of tool use actions in both from both viewing tool images and pantomiming their use. I would argue that these are based on stored 'learned' representations in line with a manipulation-based approach to tool use proposed by Buxbaum (2017). Specifically, participants pantomimed tool use actions in response to a presented word and therefore had to retrieve knowledge about how to use a tool rather than relying on structural properties to engage in technical reasoning to interact with the object, as has been argued in a reasoning-based approach to tool use (Osiurak et al., 2020; Osiurak & Badets, 2016).

Interestingly, while no significant difference in tool use action decoding was observed between the view and pantomime tasks in pMTG, decoding of tool use actions in SMG was significantly higher for pantomime than for view. Firstly, significant decoding in pMTG of tool use actions provides further evidence that this region represents information beyond semantic and conceptual knowledge of tools as proposed by Lewis (2006). However, as we observed significantly higher decoding in SMG in the pantomime, compared to the view task, it is possible that SMG stores learned manipulation knowledge for the purpose of executing the movements. Interestingly, our searchlight revealed overlapping representations of tool use actions from viewing and pantomime in pMTG, but not SMG. This provides further evidence that the pMTG plays a crucial role in tool manipulation knowledge for the purpose of both perception and action, whereas the representations in SMG may be more specific to the behavioural output. Recently, the reciprocal connections between pMTG and IPL have been proposed to support the manipulation knowledge associated with tools (Lesourd et al., 2021). Therefore, assessing how effective connectivity between pMTG and SMG is modulated by execution of tool use actions could be a logical next step in investigating the contributions of the VD stream to tool use. Future research could also measure connectivity in information shared across brain regions. For instance, recent MVPA developments have involved multivariate connectivity which can help provide insight into the transformation of representations in stages over time (Anzellotti & Coutanche, 2018; Ju & Bassett, 2020). It would be particularly interesting to investigate how representations in pMTG and SMG, as well as the distinct hand and tool networks represent information to support functional actions with tools.

Interestingly, while the two action systems model proposes that the DD 'Grasp' stream is responsible for processing structural features of objects for the online control of actions towards objects, we observed significant decoding of tool use actions from simply viewing images, as well as when pantomiming their use in the absence of visual feedback. This could seem contrary to the two-action systems model given that structural features of objects were not available during pantomiming, and we controlled our objects entered in to the MVPA pairs for grip type (i.e. the structural information related to tools; precision versus power). However, our findings here support the theory of affordances (Gibson, 1979), that upon viewing manipulable objects, we automatically perceive the actions associated with them. Our findings show that representations of the specific 'use' action (i.e. rotate or squeeze) with the tool are automatically evoked in DD regions from simply viewing images. Therefore, we provide evidence that learned 'Use' information may also be represented in DD 'Grasp' regions. Put together, our findings provide further support for the two-action systems model, specifically by highlighting a role of pMTG and IPL in the representation of actions associated with tools. These representations appear to be of learned, stored interactions with tools. These regions were not highlighted in the TVSH (Milner & Goodale, 1992).

5.5. Is dementia a good model for assessing dorsal stream deficits?

Assessing the deficits associated with dorsal visual stream damage is a powerful method of inferring causal roles of dorsal visual stream regions in aspects of cognition and behaviour. Much of the research providing neuropsychological evidence for the TVSH thus far is limited in its ability to generalise to a larger group due to limited sample sizes and differing locations and extent of lesions. Therefore, we aimed to assess dorsal visual stream function in a larger clinical group with functional and structural differences in a key region of the dorsal visual stream, the PPC.

In Experiments 4 and 5 (Chapter 4), we assessed performance using a double-step reaching paradigm known to recruit the PPC (Pisella et al., 2000), in healthy older adults and in a clinical group with MCI and AD. Here, we found that the clinical group took significantly longer than healthy age-matched controls to initiate and execute their movements, and to make corrections in response to target jumps. We extended on these findings by also including a visuomotor task where participants had to rely on visual information presented in an egocentric reference frame, or an allocentric reference frame, to complete the task. Here, we also found that participants in the clinical group took longer to initiate and execute their reach movements in both conditions. Despite this, participants in the clinical group did not significantly differ from controls in terms of their end-point error, possibly indicative of a speed-accuracy trade off. Interestingly, the visuomotor task requiring representation of space in an allocentric reference frame was the only task that correlated with measures of cognitive decline.

Of course, in the absence of neuroimaging data, it is impossible to draw conclusions as to the specific contributions of AD related pathology to the behavioural impairments we observed. I would hypothesise that the allocentric planning deficits which correlated with overall performance on the ACE-III were associated with AD-related pathology in the precuneus and posterior cingulate. These regions have previously been implicated in the transformation of information from allocentric to egocentric coordinates (Derbie et al., 2021; Tu et al., 2015, 2017), and are also thought to be regions affected at an early stage of AD (Gordon et al., 2018; Jacobs, Visser, et al., 2012). To test this hypothesis, future studies could investigate performance using voxel-based morphometry (VBM) to investigate whether behaviour correlates with grey matter integrity in these regions. Moreover, performance could be correlated with white matter integrity obtained from diffusion tensor imaging (DTI) to assess whether this allocentric to egocentric transformation deficit is a result of reduced structural connectivity between regions. Previous research has found that AD is associated with lower white matter integrity in a number of white matter tracts and this predicts worse visuomotor performance (Rogojin et al., 2019).

Future research could further assess performance on our visuomotor paradigms in different populations. As discussed in Chapter 4, performance on similar tasks have been shown to discriminate between AD and bvFTD. It would also be interesting to investigate performance in those with posterior cortical atrophy (PCA). PCA is a rare form of dementia characterised by progressive visual impairment but preserved visual acuity and is associated with degeneration in the occipital and parietal lobes (Benson et al., 1988; Crutch et al., 2012). Most often, PCA is caused by underlying AD pathology in posterior areas of the cortex, but relatively unaffected hippocampal regions, however other causes, such as Lewy body dementia and cortico-basal degeneration have also been noted in the literature (Crutch et al., 2017; Renner et al., 2004; Schott & Crutch, 2019). PCA has been associated with characteristics of Balint's syndrome, including optic ataxia (Yerstein et al., 2021). Given these more specific areas of atrophy and deficits, individuals with PCA may therefore be more ideal candidates for investigations into dorsal visual stream functioning. I would hypothesise that those with PCA perform significantly worse than those with AD in the double-step online correction paradigm, as well as in the egocentric reaching task due to their more posterior cortical damage.

While our results showed that allocentric performance correlated with cognitive decline using the ACE-III, it is important to note that several patients with an MCI diagnosis actually performed worse overall than those with an AD diagnosis (see Figure 4.7). This raises some questions about the validity of the diagnoses in our clinical group. The prevalence of dementia has steadily increased over the years, however, diagnosis of AD has been shown to differ between regions of the UK. Interestingly, the prevalence and treatment of dementia in Scotland is higher than that in England (Cooper et al., 2016; Donegan et al., 2017). This is possibly due to differing clinical guidelines between the countries and more diagnoses in primary compared to secondary care in Scotland (Cooper et al., 2016). This was reflected in our research which was carried out in conjunction with the University of Edinburgh. We found higher instances of MCI recruited from the Norfolk and Norwich Hospital, and higher instances of AD recruited in Edinburgh. Therefore, the geographical differences in diagnoses should be considered. It is unclear from the present data whether the differences in visuomotor performance are specifically a result of AD pathology, or of cognitive decline associated with MCI. However, this does highlight the importance of developing neuropsychological tools for assessment of dementia which can be used in clinical settings throughout the United Kingdom to provide more streamlined diagnoses.

Overall, the impaired visuomotor performance we observed in AD and MCI could be characteristic of a specific dorsal visual stream impairment, or more widespread cortical degeneration. Without neuroimaging to corroborate our findings, it is not possible to infer whether using an AD clinical group is a suitable model to assess dorsal visual stream functioning. It would be interesting to assess dorsal visual stream functioning using our tasks in those with PCA, although the prevalence of PCA is much lower, accounting for approximately 5-13% of early-onset dementia diagnoses (Koedam et al., 2010). Despite this, given the more posterior degeneration, and spared hippocampal areas, it would be possible to gain more insight into the function of the dorsal visual stream.

Moreover, possible dorsal visual stream damage can contribute to planning and execution deficits in portable iPad-based reaching tasks involving online corrections, egocentric and allocentric reaching. Allocentric reaching, however, was shown to be particularly sensitive to overall cognitive decline. This may be a deficit in the transformation of information subserved by the ventral stream in allocentric coordinates, to egocentric coordinates subserved by the dorsal visual stream.

5.6. Limitations and Future Directions

In Experiments 1-3, participants viewed images of tools carefully matched for low level features, which are impossible to reach and grasp. Tool images are a commonly used proxy for real tools in behavioural studies (e.g. Goslin et al., 2012; Kostov & Janyan, 2020; Saccone et al., 2016; Tucker & Ellis, 1998), and in neuroimaging (e.g. Bracci et al., 2011; Chao & Martin, 2000; Chen et al., 2018; Matić et al., 2020). However, the processing of real tools compared to 2D images of tools has been shown to differ at a neural level (Brandi et al., 2014; Freud et al., 2018; Króliczak et al., 2007; Snow et al., 2011; for a review, see Snow & Culham, 2021). Moreover, behavioural research has shown that 3D graspable objects are more readily detected than their 2D image counterparts (Korisky & Mudrik, 2021). This perceptual advantage has been attributed to a stronger activation of affordances. For instance, EEG research has shown that real objects increase the strength and duration of activation in visuomotor regions compared to matched images (Marini et al., 2019). This real object advantage is attenuated when the objects are presented behind a barrier, and thus not actionable, which suggests that affordances due to the ability to interact with the object are elicited stronger for real compared to 2D objects (Fairchild et al., 2021). It is therefore possible that our graspable object and tool stimuli in these experiments were not representative of their real-world counterparts. Given that we did not observe a handle compatibility effect in response to objects presented in the central VF, any activation of affordances may have been attenuated due to the inability to grasp the object.

Some researchers have incorporated virtual reality (VR) into the handle based SRC paradigm and replicated affordance effects (e.g. Joy et al., 2022; Lai et al., 2023). VR allows for the presentation of well-controlled stimuli while providing a more life-like scenario. However, while the observation of handle compatibility effects in VR is promising, there still remain key differences between VR and real-world environments in terms of depth cues and the lack of haptic information (Harris et al., 2019). Additionally, perception about the size of familiar objects has been shown to be more heavily influenced by expectations, than visual information in VR (Rzepka et al., 2022). Therefore, the next logical step would be to investigate the handle compatibility effect in response to 3D objects, carefully matched for low-level perceptual features such as colour and size. Various task manipulations can be included, such as manipulating the mode of response (keyboard press versus grasping vs pointing), the possibility for interaction (in front of versus behind a screen), and the suitability for interaction (upper versus lower VF). This would aid an understanding of the perceptual attributes required to elicit an affordance and provide evidence in more ecologically valid contexts.

In terms of Experiment 3, despite the difficulties in presenting 3D objects in the scanner, a number of researchers have developed methods to allow for 3D object presentation in fMRI environments (e.g. Brandi et al., 2014; Hermsdörfer et al., 2007; Knights et al., 2021). In the future, it would be interesting to investigate responses to viewing and using 3D tools. It is possible that decoding tool use actions in DD regions would be significantly improved if the object presented was fully graspable, even from passively viewing. Moreover, it is possible that differences in decoding between hand- and tool- selective cortices would become more salient. In particular, tool-selective IPS and LOTC may represent tool use actions when actions are performed with the tool in hand, in line with previous findings that tool-selective pMTG can discriminate upcoming movements with the tool in hand (Gallivan et al., 2013). In a similar vein, previous research in our lab has found that hand-selective IPS and LOTC represent how to grasp a tool correctly for its use (Knights et al., 2021). However, here participants simply executed precision grips towards the tool handle or functional end. Building on from this, it would be interesting to use a similar typicality paradigm where participants execute the tool use action, either typically or atypically. Again, I would hypothesise that tool-selective regions would be more likely to represent tool use typicality with actions performed with the tool in hand. While hand-selective regions may represent hand actions associated with tools, when this is extended to using a tool, it is possible that the mechanical actions associated with the tool become more salient, and thus more likely to be also represented in tool preferring brain regions.

Despite this, presenting highly controlled 3D objects in the scanner and requiring participants to execute hand movements while reducing head motion as much as possible is still problematic in terms of its ecological validity. Another method which could be employed in tool use paradigms while mitigating motion artefacts is through using functional near-infrared spectroscopy (fNIRS). fNIRS measures changes in blood oxygenation levels using near-infrared light, and its performance is comparable to fMRI tasks in naturalistic environments (Noah et al., 2015). A particular advantage of fNIRS is its increased resilience to motion artifacts which enables individuals to engage in more naturalistic behaviours without the constrains of the MRI environment (Piper et al., 2014). fNIRS also has a higher temporal, but lower spatial, resolution compared to fMRI. Given that it is highly portable, this also increases the feasibility of assessing brain activity in response to task performance in older adults and individuals with neurodegenerative disease.

It could be argued that the task we employed in Experiments 1 and 2 were not strictly a demonstration of how perception can influence action. For instance, while the colour judgements depend purely on the objects' low-level perceptual properties, we cannot rule out the possibility that orientation judgements required some level of imagining interactions with the object. It is possible that to judge an object's orientation as upright or inverted required participants to imagine interacting with the object to make the correct judgement. Interestingly, neuropsychological research has identified a phenomenon known as agnosia for object orientation (Turnbull et al., 1995, 1997). This has been characterised by an intact ability to recognise objects, but not their orientation and is associated with lesions in the right parietal lobe. Consistent with this, neuroimaging research has shown that dorsal stream regions are sensitive to object orientation (Valyear et al., 2006). A recent review of neuropsychological and behavioural studies on orientation processing has suggested that, following object recognition, information about object orientation is incorporated following transforming the object representation into an external spatial reference frame (Harris, 2024), possibly mediated by the dorsal stream. Therefore, it is possible that our perceptual task was not entirely independent of an action component. Future studies investigating the compatibility effect could use previous more conceptual judgements. Indeed, previous handle compatibility studies have used judgements which involve classing whether the object belongs in a kitchen or shed (Goslin et al., 2012; Lien et al., 2014; Saccone et al., 2016; Symes et al., 2005).

We also cannot rule out this possibility in our Experiment 3. As participants completed both viewing and pantomiming in consecutive runs, it is possible that the actions associated with tools were more salient even in the view task. Although we counterbalanced run orders, all participants would have viewed tool images in a run following a pantomime run. Therefore, we cannot rule out that carryover effects increased activity (or reduced activity due to adaptation), or neural patterns of activation in response to viewing tools in the dorsal visual stream. This may have explained our significant decoding for tool use actions in the dorsal stream in response to object viewing. Future studies should ensure that the time course is controlled for, however it would have also been interesting to see if there was an effect of time (i.e. run number) on activity in dorsal stream regions. This could have been conducted separately in view and pantomime runs.

To bridge the gap between the three projects I have conducted, it would be interesting to fully investigate the effect of ageing and neurodegeneration on tool use and processing. Interestingly, recent fMRI research has shown that 3D tool use activates similar networks between young and old adults, however greater activation is observed in older adults during tool use planning (Seifert et al., 2023). This could suggest that older adults place a greater emphasis on planning tool use movements compared to relying on online control. However, research assessing reaching and grasping movements in older adults shows that they rely more heavily on visual information during the movement to maintain accuracy (Coats & Wann, 2011; Rossit & Harvey, 2008; Runnarong et al., 2019). Therefore, it is possible that different mechanisms are at play when it comes to incorporating learned motor sequences with objects (i.e. tool use). Understanding how ageing affects tool use at a behavioural and neural level would aid in the development of aids for older adults. For instance, products such as kitchen utensils, for example with larger handles for an ‘easy grip’, have been developed specifically for older adults. However, a further understanding would allow for improvement in these product designs. A recent review has also highlighted that apraxia severity may be associated with AD severity (Vakkila & Jehkonen, 2023). Therefore, further research into tool use mechanisms and how ageing and AD affects tool use would be of particular importance given that we use tools often in everyday life.

5.7. Concluding Remarks

Overall, this thesis has highlighted the tight link between perception in action behaviourally, at a neural level, and through deficits that occur due to neurodegeneration. Specifically, I have highlighted that simply viewing objects elicits affordances, but only when objects are presented in the hemifield specialised for action. Moreover, at a neural level, these affordances (i.e., how we use a tool) are represented in the dorsal stream even when passively viewing tools. However, I have also highlighted the importance of the ventral visual stream in contributing to tool use actions, even during pantomime, in the absence of any visual feedback of the tool and hand. Moreover, I have shown that individuals with MCI and AD (typically associated with memory decline), show evidence of dorsal visual stream deficits. However, the severity of these deficits is less extreme than those with pure dorsal visual stream lesions. Interestingly, however, I have also shown how performance in a task thought to be primarily driven by the ventral stream (allocentric reaching), but also involving the dorsal stream, may be particularly sensitive to cognitive decline associated with AD. Put together, this research highlights the importance of collaborations between the ventral and dorsal visual streams for the effective guidance of skilled actions.

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