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Principles governing the effects of sensory loss on human abilities: An integrative review

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ABSTRACT

Blindness or deafness can significantly influence sensory abilities in intact modalities, affecting communication, orientation and navigation. Explanations for why certain abilities are enhanced and others degraded include: crossmodal cortical reorganization enhances abilities by providing additional neural processing resources; and sensory processing is impaired for tasks where calibration from the normally intact sense is required for good performance. However, these explanations are often specific to tasks or modalities, not accounting for why task-dependent enhancement or degradation are observed. This paper investigates whether sensory systems operate according to a theoretical framework comprising seven general principles (the perceptual restructuring hypothesis) spanning the various modalities. These principles predict whether an ability will be enhanced or degraded following sensory loss. Evidence from a wide range of studies is discussed, to assess the validity of the principles across different combinations of impaired sensory modalities (deafness or blindness) and intact modalities (vision, audition, touch, olfaction). It is concluded that sensory systems do operate broadly according to the principles of the framework, but with some exceptions.

1. Introduction

Information from the senses is combined in order to generate and maintain a multimodal percept of the world. The primary senses are vision (sight), audition (hearing), touch, olfaction (smell), and gustation (taste). When a primary sensory modality is lost or absent from birth, such as in the case of blindness or deafness, abilities based on the remaining intact senses can be substantially affected, including communication, orientation and navigation. The change in ability is often beneficial, such as enhanced auditory localization abilities for blind individuals (Lessard et al., 1998) or significantly better peripheral visual sensitivity for deaf individuals (Neville and Lawson, 1987). However, some abilities can be impaired, for example the poorer judgments of distance to single sound sources for blind people than for sighted individuals (Kolarik et al., 2017a), or degraded temporal tactile discrimination (Bolognini et al., 2012) or temporal visual production and reproduction abilities (Kowalska and Szelag, 2006) for deaf individuals.

A number of explanations have been put forward to account for differences in abilities in the intact modalities associated with sensory loss, and there have been previous attempts at establishing general organizational principles that determine whether sensory loss in one modality is associated with better or worse performance in another modality. These attempts have often invoked cortical reorganization mechanisms (for a review, see Bell et al., 2019). One example is the proposal that supramodal features or functions that are shared across senses, such as the perception of stimulus movement, are likely to involve beneficial crossmodal recruitment, whereas modality-specific features such as color processing do not benefit from such recruitment (Lomber et al., 2010). Improvements in some abilities may result from the positive effects of crossmodal cortical reorganization, whereby cortical regions made redundant by loss of a sense are recruited to process information from an intact modality (Collignon et al., 2009; Voss and Zatorre, 2012b). This is linked with the idea of "neural recycling," according to which brain areas deprived of sensory input can learn new functions (Bell et al., 2019), and "revised neural recycling theory," whereby sensory-independent task specialization was proposed to be a principle determining brain reorganization (Amedi et al., 2017).

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It has also been proposed that cross-modal plasticity and skill learning share common mechanisms, which has led to attempts to develop a unified model for explaining plasticity and skill acquisition following sensory deprivation (Park and Fine, 2024). Intensive training of the intact senses associated with sensory loss has also been proposed as an explanation for why abilities in the intact senses are often enhanced (Voss, 2011). Rice (1970) argued that both training and compensatory processes such as cortical reorganization were the drivers behind improvements in abilities in intact sensory modalities associated with loss in one modality. The degree to which the observed outcomes depend upon structural or chemical brain changes as opposed to training and experience continues to be a contentious issue (Makin and Krakauer, 2023; Norman et al., 2021, 2024; Teng and Whitney, 2011; Voss, 2011). In the case of deafness, it has been proposed that a redistribution of attention to the visual periphery results in enhanced performance for some spatial tasks (Bavelier et al., 2006).

Poorer sensory abilities in intact modalities associated with loss in another modality have often been explained using the concept of crossmodal calibration, based on the idea that information from one sense is necessary to calibrate another (Axelrod, 1959; Jones, 1975). Two seemingly incompatible general hypotheses have been proposed to account for the effects of sensory loss in one modality on performance in another modality. When applied to the effects of vision loss on auditory abilities, the perceptual deficiency hypothesis is that the loss of visual calibration information degrades auditory spatial abilities (Axelrod, 1959; Jones, 1975). The compensation hypothesis is that visual loss results in greater reliance on audition, which, in combination with compensatory processes, such as recruitment of visual brain areas for auditory processing, results in enhanced auditory abilities (Rice, 1970).

Despite previous attempts to explain the effects of sensory loss and establish general organizational principles determining behavioral changes, there is a need for a more global, comprehensive explanation for the effects of sensory loss. For example, crossmodal reorganization might explain why blindness is associated with enhanced spatial performance for certain tasks in the auditory modality (Collignon et al., 2009; Voss and Zatorre, 2012b). However, crossmodal reorganization might also be expected to lead to enhanced temporal visual abilities following deafness, whereas the evidence suggests that these abilities are instead degraded for deaf individuals (Amadeo et al., 2019; Kowalska and Szelag, 2006; Zhang et al., 2020). The application of the perceptual deficiency and compensation hypotheses was found to be somewhat ad hoc when interpreting findings in the literature on auditory abilities following vision loss (Kolarik et al., 2021). If degraded auditory abilities were found, the perceptual deficiency hypothesis was invoked, whereas if enhanced abilities were found, the compensation hypothesis was invoked. It was often not clear why one hypothesis but not the other should apply to a given auditory ability, diminishing the explanatory value and empirical importance of the hypotheses.

To address these issues, a theoretical framework originally based on a set of nine governing principles was developed to predict whether a specific auditory ability would be enhanced or degraded following blindness or partial visual loss (Kolarik et al., 2021). These principles together comprise the perceptual restructuring hypothesis, which is described in more detail below. The perceptual restructuring hypothesis was developed to account for why certain auditory abilities were enhanced following blindness, while others were degraded. It brings together the previously incompatible perceptual deficiency hypothesis and the compensation hypothesis within a common framework. The aim of the current paper was to investigate whether the principles of the perceptual restructuring hypothesis, reduced to seven principles in this paper, can be generalized to other configurations of sensory loss, for example whether they correctly predict whether different visual abilities are enhanced or degraded following deafness, and whether they can be generalized to other domains, such as the thermal domain. In addition, the study was intended to assess whether some sensory systems might not generally follow the framework of these principles, and another set of principles might apply.

The effects of sensory loss have been reviewed in a number of papers (Bavelier et al., 2006; Bell et al., 2019; Collignon et al., 2009; Frasnelli et al., 2011; Kolarik et al., 2021; Mitchell and Maslin, 2007; Voss, 2016; Voss et al., 2010; Voss and Zatorre, 2012b). Intramodal plasticity has been proposed as a contributor to the mediation of behavioral changes following sensory loss (Bottari et al., 2011; Elbert et al., 2002; Huber et al., 2019; Smittenaar et al., 2016; Stevens and Weaver, 2009). The measurement of crossmodal activity has also been a significant development in the field, and previous reviews have often primarily focused on brain plasticity and cortical changes. However, it has proved difficult to derive general principles due to the often variable severity and etiology of different sensory losses and difficulties associated with recruiting individuals with sensory loss, sometimes leading to small sample sizes. Inconsistencies across the literature might also be due to differences in the criteria used to select individuals with sensory loss and controls, as well as different experimental procedures (Stevens and Neville, 2006). The current paper widens the scope and range of the reviewed articles, to encompass studies such as those investigating identification of fear from the smell of sweat and thermal change discrimination by the blind, and visual temporal bisection abilities of the deaf, and interprets the results within the framework of the perceptual restructuring hypothesis.

In summary, the main aim of this paper was to assess whether the principles of the perceptual restructuring hypothesis, previously applied only to the effects of visual loss on hearing abilities in humans (Kolarik et al., 2021), can be extended to account more generally for the findings of studies investigating (but not limited to) the visual, tactile, olfactory and gustatory abilities of blind and deaf individuals. Other abilities are also reviewed, such as thermal change discrimination, heat pain thresholds, and spatial imagery in blind people.

2. Material and methods

Our literature review and synthesis consisted of two steps. Step 1 involved defining generalized principles that describe whether enhancement or degradation occurs in the intact senses. Step 2 involved a literature search for studies investigating the effects of sensory loss on abilities in the intact senses. It was then determined whether the findings of the identified studies were consistent or inconsistent with the principles, followed by summarizing and synthesizing the results. We report how we determined our sample size, data exclusions (if any), and all measures in the study.

2.1. Step 1: generalized principles that determine if enhancement or degradation occurs in the intact senses, in the event of sensory loss

The principles underlying the perceptual restructuring hypothesis are listed below. The principles are broadly similar to those described by Kolarik et al. (2021) to account for changes in auditory abilities following visual loss, except that principles P2 and P3 from Kolarik et al. (2021) have been combined within a single principle, and principles P4 and P5 have also been combined. As mentioned by Kolarik et al. (2021), the principles may not apply in every circumstance, but they gave appropriate predictions for the majority of studies reviewed by Kolarik, et al. (2021). To make the principles applicable to a range of sensory modalities, the wording was modified (e.g. “blindness” was changed to “sensory loss”). Each principle is denoted by P and a number, to more easily match the principles to the sensory abilities described later.

P1. . *Complexity.* For changes in ability (for better or worse) to occur as a result of sensory loss, the task must be complex. This principle means that for very simple tasks, such as detection of a stimulus under conditions of minimal uncertainty (when measuring an absolute threshold), a loss of one sensory modality should not affect performance involving other modalities.

Basic sensory thresholds are limited by peripheral processes and the resolution afforded by biological "hardware," and plasticity is unlikely to affect performance for such thresholds. For example, auditory absolute thresholds may be limited by internal noise related to blood flow and by limitations of the active mechanical amplification provided by the outer hair cells in the cochlea (Moore, 2012).

P2. . *Detection of changes*. The ability to detect small changes in stimuli is usually improved by sensory loss in another modality when the task only requires detection of a change and not judgment of the direction or magnitude of the change.

Consider as an example vibration-change detection. The participant might be required to detect a "deviant" stimulus embedded within a series of "standard" stimuli, and judgment of the direction of change (rising or falling rate of vibration) is not required.

P3. . *Identifying the direction of change.* When the task is to identify the direction of a change, Enhancement will occur when the sensory cues involved change monotonically with the attribute to be judged or when the relationship between the sensory cues and the attribute to be judged has been learned; otherwise degradation will occur.

A sensory cue is defined as a physical quantity that changes in a systematic way with the subjective attribute that is being judged. Examples of monotonic cues are: the frequency of a sinewave when the attribute being judged is pitch; and changes in the angle subtended by a visual stimulus at the eye when the attribute being judged is the direction of movement of the visual stimulus towards or away from the observer. An example of a non-monotonic cue is the complex spectral change produced by changes of the elevation of a sound source relative to the listener.

P4. . *Calibration requiring cues from the absent modality.* Sensory loss results in degraded performance when lack of requisite calibration information from the absent modality leads to a less precise mapping of sensory cues to the quantity to be judged or to an imprecise internal spatial or temporal representation.

Calibration refers to using information from a high-precision modality to "fine tune" information from a modality that provides less accurate/precise information. For example, the visual system usually provides detailed spatial information that may be used to calibrate auditory judgments of distance. Such visual information cannot be used by early-blind individuals, leading to the prediction of poorer performance for early-blind participants compared to sighted controls for judgments of absolute auditory distance.

An internal representation, sometimes referred to as a "metric" (Aggius-Vella et al., 2019, 2020), describes a mapping between physical cues and an internal representation of space. For example, a normally sighted listener may form an internal representation of the azimuth of an external sound source by processing "raw" spatial cues including ITD (interaural time difference), interaural level difference (ILD), and pinna cues, and the spatial relations between them, using the visual signal for calibration.

P5. . *Mapping using cues from intact modalities.* Sensory loss leads to enhanced performance for tasks that require a mapping of cues when the cues can be mapped/calibrated without the absent modality. Otherwise, degradation will occur.

As an example of cues that can be calibrated, consider the localization of sounds in azimuth. The mapping of interaural level difference (ILD) and interaural time difference (ITD) cues to azimuth may be learned without visual information, by reaching out and touching sound-producing objects at various azimuths.

P6. . *Experience and practice.* Prolonged experience and practice using sensory cues leads to superior performance in the intact modalities.

P7. . *Age of onset*. Changes in sensory ability in the intact modalities are greater the earlier in life that a major sense is lost, partly because brain plasticity tends to decrease with increasing age, and partly because early loss is associated with greater experience with and reliance on the intact modalities. This principle can be applied to studies that compared a group with early-onset sensory loss with a group with late-onset loss.

For each of the studies that were identified for inclusion in the review, the findings were reviewed in the context of the seven principles. The text in the following sections reviews and links studies investigating various sensory abilities in the literature that are enhanced or degraded by the loss of a sense and describes whether the findings are consistent with P1-7. Where significant differences were observed between participants with sensory loss and controls, the studies, the tasks involved and experimental groups, and their findings are listed in Tables 1–6, and marked regarding whether the findings were consistent or inconsistent with the principles that applied to each study (note that studies with null results are not included in the summary tables). In the main text, P7 is mentioned only where studies contrast performance for participant groups with early- and late-onset sensory loss.

2.2. Step 2: preferred reporting items for integrative review and literature search

The framework was intended to be as broad as possible, covering different sensory abilities and forms of sensory loss. Identified studies were included in the integrative review if they tested human abilities in the intact senses using age-matched groups of individuals with sensory losses and controls. We note that the criteria for what constitutes early-onset loss vary substantially across studies. This can make it difficult to draw conclusions regarding the effects of early- vs. late-onset loss. For example, the criterion used by Gougoux et al. (2005) was early-onset loss occurring at 14 years or less, whereas the criterion used by Veraart and Wanet-Defalque (1987) was loss occurring at 3 years or less. In an attempt to address this, in the current study the criterion for early-onset loss was taken as loss occurring at 5 years of age or less, to match several previous studies (Kolarik et al., 2013b, 2017b; Lewald, 2002), and a previous review of the effects of blindness on auditory abilities (Kolarik et al., 2021). Where a different criterion is specified by the authors of a study, the main text reports the definition used by the authors. The sample sizes were determined by the authors of the relevant studies and were reported for each study. Animal studies were excluded.

The findings of the studies identified in the literature were organized and summarized according to domain of sensory loss (deafness, blindness), the intact sensory modality studied (visual, auditory, haptic, olfactory, gustatory, thermal), and effect of sensory loss (enhanced or degraded). Studies in the literature previously reviewed by Kolarik et al. (2021) that investigated the effect of blindness on auditory abilities in the context of the perceptual restructuring hypothesis were excluded from the literature search, but the findings from Kolarik et al. (2021) are summarized in Table 3. Both spatial and non-spatial abilities were included. In line with the research objectives of identifying studies that were consistent or inconsistent with P1 of the perceptual restructuring hypothesis, searches were first screened to identify studies that tested basic perceptual thresholds, regardless of whether or not significant differences were found. Following this, to identify studies that were consistent or inconsistent with P2-7, inclusion was restricted to studies where significant differences in performance were found, as these principles are concerned with the direction of significant changes (enhancement or degradation) relative to controls for individuals with sensory losses. Studies were grouped according to the domain of sensory loss and intact sensory ability.

We used the guidelines of the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) Statement (Moher et al., 2009) as the basis for the selection process of the papers that were included in the review (Fig. 1). The American Psychological Association

Table 1

Outcomes of studies reporting significantly enhanced or degraded visual abilities following deafness. Column 1 shows the type of task, column 2 lists the authors of the studies, and column 3 shows whether performance was significantly enhanced or degraded compared to that for normally hearing controls. C and I (column 4) indicate whether the results are consistent or inconsistent with the principles. Column 5 indicates whether the group showing significant differences from controls had early or late-onset deafness or a mix. Unless a different definition is mentioned in the text, early-onset refers to loss before 5 years of age, while late-onset refers to loss after 5 years. Where a different definition is specified by an asterisk, the main text gives the definition used by the authors. Column 6 (Participants) shows the groups (including final number of participants following any exclusions) tested in each study. P refers to the principle numbers involved with each task. RT refers to reaction time. ED and LD refer to Early Deaf and Late Deaf respectively. HS refers to Hearing Signers. Dys refers to dyslexic. C refers to Controls.

Visual task	Study	Effect of deafness		Onset	Participants
Target detection RT P1–2	Parasnis and Samar (1985)	Enhanced	C	Early	20 ED, 20 C
	Hong Loke and Song (1991)	Enhanced	C	Early	20 ED, 19 C
	Colmenero et al. (2004)	Enhanced	C	Mix	17 ED/LD, 27 C
	Bottari et al. (2010)	Enhanced	C	Early	11 ED, 11 C
	Heimler and Pavani (2014)	Enhanced	C	Early	8 ED, 12 C
Temporal order judgment RT P1–2	Nava et al. (2008)	Enhanced	C	Early	10 ED, 22 C
Temporal synchronization P1–3	Iversen et al. (2015a)	Enhanced	C	Early	23 ED, 22 C
Temporal discrimination P1–2	Heming and Brown (2005)	Degraded	I	Early	10 ED, 10 C
Motion detection P1–3	Dittmar et al. (1982)	Enhanced	C	Early	20 ED, 50 C
	Neville and Lawson (1987)	Enhanced	C	Early	12 ED, 12 C
	Stevens and Neville (2006)	Enhanced	C	Early	17 ED, 15 Dys, 9 C
	Buckley et al. (2010)	Enhanced	C	Early	13 ED, 13 C
	Hauthal et al. (2013)	Enhanced	C	Early*	14 ED, 14 C
	Shiell et al. (2014)	Enhanced	C	Early	16 ED, 20 C
Flash-lag-illusion reduction P1, 3	Amadeo et al. (2022)	Enhanced	C	Early	13 ED, 18 C
Lipreading P1, 5–6	Bernstein et al. (2000)	Enhanced	C	Early	72 ED, 96 C
	Mohammed et al. (2005)	Enhanced	C	Early	29 ED, 29 C
	Auer and Bernstein (2007)	Enhanced	C	Early	112 ED, 220 C
Facial feature recognition P1–3, 6	McCullough and Emmorey (1997)	Enhanced	C	Early	30 ED, 30 C
Visual attention P1–2, 6	Bosworth and Dobkins (2002)	Enhanced	C	Early	16 ED, 10 HS, 15 C
	Rothpletz et al. (2003)	Degraded	I	Early	10 ED, 10 C
Eriksen flanker task accuracy P1–2, 6	Sladen et al. (2005)	Enhanced	C	Early	10 ED, 10 C
Eriksen flanker task RT P1–2, 6	Sladen et al. (2005)	Degraded	I	Early	10 ED, 10 C
Search P1–2	Stivalet et al. (1998)	Enhanced	C	Early	12 ED, 12 C
	Rettenbach et al. (1999)	Enhanced	C	Early	8 ED, 8 C
Temporal bisection P1, 4	Amadeo et al. (2019)	Degraded	C	Mix	17 ED/LD, 17 C
	Zhang et al. (2020)	Degraded	C	Not reported	16 ED/LD, 16 C
Temporal production/ reproduction P1, 4	Kowalska and Szelag (2006)	Degraded	C	Early	16 ED, 16 C
Visual/motor temporal order discrim P1–2, 4	Vercillo and Jiang (2017)	Degraded	C	Early	9 ED, 11 C

PsycInfo database and Google Scholar were accessed on or before the 29th of June 2023, covering publications from 1900.

3. Transparency and openness

The current study was not preregistered. The data and study materials used in the review are available online from the American Psychological Association PsycInfo database and Google Scholar, and a full listing of the journal articles utilized during database searches and screening is available at https://osf.io/w2pjk/files/osfstorage. Google Scholar uses a 256 character limit for searches, and automatically searches for synonyms. As a result, the Google Scholar search was restricted to the following keywords: 'deafness,' 'blindness,' 'cross-modal,' 'neural plasticity,' 'tactile,' and 'olfactory.' The PsycInfo database search involved screening the PsycArticles citation index using the OR function with the same keywords as used for the Google Scholar search.

4. Results

4.1. Visual abilities for which deafness is associated with enhancement

4.1.1. Enhanced reaction times for visual spatial detection and discrimination, lateralization, temporal order and tempo matching by deaf individuals

Evidence has suggested that for visual abilities to become enhanced by deafness, the task must be complex, consistent with P1. Reviews by Pavani and Bottari (2012) and Frasnelli et al. (2011) concluded that most evidence supported the idea that visual perceptual thresholds for a variety of simple tasks were neither enhanced nor degraded as a result of deafness. Deaf individuals and hearing controls showed comparable contrast sensitivity (Finney and Dobkins, 2001; Stevens and Neville, 2006), brightness discrimination (Bross, 1979), visual sensitivity to motion (Bosworth and Dobkins, 1999; Brozinsky and Bavelier, 2004), visual acuity (Codina et al., 2011), and visual temporal perceptual thresholds, including visual flicker frequency thresholds (Bross and Sauerwein, 1980; Poizner and Tallal, 1987) and temporal order thresholds (Nava et al., 2008).

Although lack of auditory information at an early age can adversely affect the development of language and cognitive abilities (see Quittner et al., 2004), there is evidence that certain visual abilities can be enhanced by deafness. For a review, see Pavani and Bottari (2012). Often, enhanced abilities are observed for stimuli presented in the visual periphery, probably because this is a spatial region where tasks tend to be more difficult due to the decrease in visual acuity with increasing eccentricity (Strasburger et al., 2011). However, factors other than difficulty have been proposed. For example, auditory and visual modalities may interact most strongly in peripheral regions. A lack of auditory

Table 2
As for Table 1, but for studies reporting significantly enhanced or degraded haptic abilities following deafness.

Haptic task	Study	Effect of deafness		Early or late-onset, or a mix	Participants
Vibration change detection P1–2	Levänen and Hamdorf (2001)	Enhanced	C	Early	6 ED, 6 C
Identify emotions in music P1–2	Sharp et al. (2020)	Enhanced	C	Early	10 ED, 10 C
Vibration detection & spatial acuity P1–2	Schiff and Dytell (1972)	Enhanced	I/C	Not reported	179 ED/LD, 121 C
Vibration detection P1–2	Frenzel et al. (2012)	Degraded	I	Early	29 ED, 99 C
Spatial acuity P1–2	Frenzel et al. (2012)	Degraded	I	Early	39 ED, 151 C
Spatial orientation acuity P1–2	Pellegrino et al. (2020)	Degraded	I	Early	69 ED, 99 C
Temporal discrimination P1–2	Heming and Brown (2005)	Degraded	I	Early	10 ED, 10 C
	Bolognini et al. (2012)	Degraded	I	Early	9 ED, 9 C
	Papagno et al. (2016)	Degraded	I	Early	7 ED, 14 C

input could lead to effects specific to the eccentricities that are strongly crossmodal. Effects in the periphery have also been observed for auditory tasks performed by blind individuals (Chen et al., 2006). However, it is sometimes difficult to compare results across studies because working definitions of the visual and auditory periphery tend to differ. In the visual domain, stimuli located more than approximately 20° from the mid-sagittal plane are typically considered to be in the periphery (e.g. Hong Loke and Song, 1991), while in the auditory domain stimuli located at an azimuth exceeding approximately 45° (e.g. Chen et al., 2006) are typically considered as in the periphery.

Parasnis and Samar (1985) reported faster reaction times for a congenitally deaf group than for hearing controls for a visual lateralization task involving an informative cue stimulus (arrow pointing left or right) or a neutral cue (plus sign), followed by a target stimulus (black circle) located left or right. Participants were asked to report whether the target was located to the left or right. In valid trials, the target was presented on the side shown by the arrow, and on invalid trials the target was presented on the opposite side to that shown by the arrow. There were two conditions. In one, the foveal load condition, five distractors (crosses) that were to be ignored were presented with the target. In the other, no-load condition, no distractor crosses were present. Deaf participants responded significantly faster in invalid trials in the foveal load condition, suggesting that deaf individuals are more flexible than hearing individuals at reorienting their attention to different areas of the visual field when distracting visual information is present. This result is consistent with the findings of Bosworth and Dobkins (2002), who used a direction-of-motion discrimination task to investigate visual spatial attention. They found that selective attention was significantly better for early-onset deaf participants than for hearing controls when attending to a stimulus presented in the periphery.

Hong Loke and Song (1991) tested the visual detection abilities of young-adult early-onset deaf and hearing control participants for stimuli presented in the central and peripheral visual fields. In each trial, a random number was presented in the middle of the screen, followed by an asterisk presented either centrally or peripherally. Participants were required to press the space bar as soon as they detected the asterisk and then type the number that was presented. Although there was no significant difference in response time between groups for stimuli presented in the central visual field, deaf participants showed significantly shorter response times than hearing controls for stimuli presented in the periphery.

Colmenero et al. (2004) tested a mix of early- and late-onset deaf participants and hearing controls in a visual task involving spatial orienting. Alphanumeric characters were presented on a computer screen to the left and right of a fixation cross. A vertical mark appearing over the left or right character served as a cue. Participants were required to detect the target, indicated by an “O” over the character. Reaction times for detecting the target were significantly faster for the deaf group than for the controls. Similar findings were reported by Bottari et al. (2010), who tested early-onset deaf individuals and hearing controls with visual targets that randomly appeared in either central or peripheral locations on a computer screen. The deaf participants detected the targets on average 44 ms faster than the hearing controls, independent of the location of the target.

Heimler and Pavani (2014) measured response times for early-onset deaf individuals and hearing controls in detecting visual stimuli or tactile stimuli delivered to one of four possible locations, either on their left or right arms (in peripheral vision where spatial acuity was low), or left or right index fingers (in central vision where spatial acuity was high). Deaf participants had significantly shorter reaction times to the visual stimuli for both central and peripheral stimuli, but there was no significant difference between the groups for tactile stimuli.

Nava et al. (2008) obtained visual temporal order judgments for early-onset deaf participants and hearing controls. Two successive visual stimuli were presented at different eccentricities on a computer screen, and participants had to judge their temporal order. Accuracy, Just-Noticeable-Difference (JND), and Point of Subjective Equality measurements were similar for the two groups, indicating that temporal order judgments were not affected by deafness. However, the deaf participants responded significantly more quickly than the controls when the first stimulus was the more peripheral.

Iversen et al. (2015a) tested groups of early-onset deaf participants and hearing controls in a task where participants had to tap their finger in synchrony with a series of visual flashes presented at a steady tempo. The deaf participants tapped significantly more closely in time to the flashes than the hearing group.

Not all studies have shown enhanced visual temporal discrimination abilities for deaf people. Heming and Brown (2005) assessed tactile and visual temporal discrimination for early-onset deaf and hearing groups. For the visual task, participants were presented with pairs of light flashes that had to be judged as simultaneous or non-simultaneous. The tactile task and results are described later in this paper. The onset asynchrony of the first and second lights was adjusted based on the previous response. Visual temporal thresholds were significantly higher for the deaf group than for the control group. However, as pointed out by Moallem et al. (2010), performance for this task would have been affected by the response criterion of the participant due to the subjective nature of participant’s simultaneity judgments (this is also mentioned below in the context of tactile temporal order judgments made by deaf individuals).

Overall, the finding that deafness results in shorter reaction and detection times for visually presented stimuli in relatively complex tasks is consistent with P1 (*complexity*), P2 (*detection of changes*), and P3 (*identifying the direction of change*).

4.1.2. *Enhanced visual motion perception and detection by deaf individuals*

Dittmar et al. (1982) tested early-onset deaf participants and hearing controls in a visual vigilance task. Participants watched a visual display with a moving bar of light for 45 minutes, and had to detect occasional increases in the magnitude of the horizontal movement of the bar. The deaf group showed significantly higher detection rates than the hearing controls.

Neville and Lawson (1987) showed that congenitally deaf participants had greater accuracy and faster reaction times than hearing controls when judging visual motion direction in the periphery. Stevens and Neville (2006) also compared visual motion processing for

Table 3
Spatial and non-spatial auditory abilities that are significantly enhanced or degraded by blindness. EB and LB refer to Early Blind and Late Blind, respectively. RV refers to Residual Vision, and SR refers to Sight Recovered after a long period of blindness. NE and EE refer to Expert and Non-Expert Echolocators, respectively. AVL refers to Acquired Vestibular Loss. Adapted and expanded from Table 1 and 2 in Kolarik et al. (2021). Note that P2/P3 and P4/P5 in that paper have been combined in the current paper.

Spatial auditory task	Study	Effect of blindness		Early or late-onset, or a mix	Participants
Localization in azimuth P1–3, 5, 7					
[Binaural]	Rice (1969)	Enhanced	C	Early	6 EB, 8 C
[Binaural]	Muchnik et al. (1991)	Enhanced	C	Early	20 EB, 20 C
[Monaural]	Lessard et al. (1998)	Enhanced	C	Early	8 EB, 3RV, 36 C
[Binaural]	Röder et al. (1999)	Enhanced	C	Early	8 EB, 8 C
[Binaural]	Voss et al. (2004)	Enhanced	C	Early (<11 yrs) and Late (>16 yrs)	14 EB, 9 LB, 10 C
[Monaural]	Voss et al. (2011)	Enhanced	C	Early and Late	12 EB, 6 LB, 7 C
[Monaural]	Voss et al. (2015)	Enhanced	C	Early	11 EB, 12 C
[Binaural]	Després et al. (2005)	Enhanced	C	Early	7 EB, 13 C
[Monaural]	Doucet et al. (2005)	Enhanced	C	Mix	10 EB/LB, 5 C
[Monaural]	Gougoux et al. (2005)	Enhanced	C	Mix	12 EB/LB, 7 C
[Binaural]	Yabe and Kaga (2005)	Enhanced	C	Early and Late	14 EB, 9 LB, 14 RV, 10 C
[Binaural]	Fieger et al. (2006)	Enhanced	C	Late	9 LB, 9 C
[Binaural]	Chen et al. (2006)	Enhanced	C	Early	15 EB, 18 C
[Binaural]	Feierabend et al. (2019)	Degraded	I	Mix	9 EB/LB, 18 C
[Binaural/Monaural]	Finocchietti et al. (2023)	Enhanced	C	Early	8 EB, 8 C
Echolocation P1–2, 6					
Discrimination of object material, size, distance	Kellogg (1962)	Enhanced	C	Late	2 LB, 2 C
Object detection and location	Rice (1969)	Enhanced	C	Early	6 EB, 8 C
Walking parallel to a wall	Strelow and Brabyn (1982)	Enhanced	C	Mix	8 EB/LB, 14 C
Object shape or texture discrimination	Hausfeld et al. (1982)	Enhanced	C	Early	Expt 4 1 EB; C Expts 1 + 2 18, Expt 3 45
Object localization accuracy	Schenkman and Nilsson (2010)	Enhanced	C	Mix	10 EB/LB, 10 C
	Schenkman and Nilsson (2011)	Enhanced	C	Mix	12 EB/LB, 25 C
Spatial acuity	Teng and Whitney (2011)	Enhanced	C	Early	1 EB EE, 11 C
ILD and ITD sensitivity	Nilsson and Schenkman (2016)	Enhanced	C	Mix	23 EB/LB, 23 C
Detection of echoes in trains of noise bursts	Schenkman et al. (2016)	Enhanced	C	Mix	12 EB/LB, 26 C
Obstacle detection range and circumvention	Kolarik et al. (2017b)	Enhanced	C	Early	8 EB NE, 1 EB EE, 10 C
Relative distance judgements P1–3	Ashmead, et al. (1998)	Enhanced	C	Mix	35 EB/LB, 18 C
	Voss et al. (2004)	Enhanced	C	Early (<11 yrs) and Late (>16 yrs)	14 EB, 9 LB, 10 C
	Kolarik, et al. (2013a)	Enhanced	C	Mix	5 EB/LB, 10 C
Motion discrimination P1–2, 7	Schiff and Oldak (1990)	Enhanced	C	Early	6 EB, 60 C
	Lewald (2013)	Enhanced	C, I	Early and Late	7 EB, 7 LB, 14 C
	Jiang et al. (2014)	Enhanced	C	Early	7 EB, 7 C
	Jiang et al. (2016)	Enhanced	C	Early	7 EB, 4 LB, 1 SR, 11 C
	Park and Fine (2023)	Enhanced	C	Early	8 EB, 8 C
Self-localization P6	Després, et al. (2005)	Enhanced	C	Early	7 EB, 13 C
Auditory selective spatial attention P1–2	Collignon et al. (2006)	Enhanced	C	Early	8 EB, 8 C
Bimodal divided spatial attention P1–2	Kujala et al. (1997)	Enhanced	C	Early	9 EB, 18 C
	Collignon et al. (2006)	Enhanced	C	Early	8 EB, 8 C
Absolute distance judgement	Wanet and Veraart (1985)				
…in far space P1, 4, 7	Wanet and Veraart (1985)	Degraded	C	Early	6 EB, 5LB, 19 C
	Macé et al. (2012)	Degraded	C	Early	8 EB, 9 C
	Kolarik, et al. (2013b)	Degraded	C	Early	5 EB, 6 C
…in near space P1, 5	Kolarik, et al. (2017a)	Degraded	C	Early	10 EB, 11 C
	Pardhan et al. (2024)	Degraded	C	Early	24 ERV, 10 LRV, 18 C
	Lombera et al. (2022)	Enhanced	C	Mix	19 EB/LB, 19 C
Elevation P1, 3–4	Zwiers, et al. (2001)	Degraded	C	Early	6 EB, 7 C
	Lewald (2002)	Degraded	C	Early	6 EB, 10 C
Azimuth bisection P1, 4					
[Binaural]	Gori et al. (2014)	Degraded	C	Early	9 EB, 27 C
[Binaural]	Vercillo et al. (2015)	Degraded	C	Early	6 EB NE, 3 EB EE, 11 C
[Binaural]	Vercillo et al. (2016)	Degraded	C	Early	8 EB, 29 C
[Binaural]	Campus et al. (2019)	Degraded	C	Early	16 EB, 16 C
[Binaural]	Finocchietti et al. (2023)	Degraded	C	Early	8 EB, 8 C
[Monaural]	Finocchietti et al. (2023)	Enhanced	I	Early	8 EB, 8 C
Auditory encoding and movement reproduction P1, 3–4, 7	Finocchietti et al. (2015)	Degraded	C	Early	12 EB, 8 LB, 20 C
Audio-spatial memory P1, 4	Setti et al. (2022a)	Degraded	C	Early	12 EB, 12 C
	Setti et al. (2022b)	Degraded	C	Early	9 EB, 9 C
Inferential navigation P1, 4, 7					
	Herman et al. (1983)	Degraded	C	Early	12 EB, 11 blindfolded C, 11 non-blindfolded C
	Rieser et al. (1986)	Degraded	C	Early	6 EB, 6 LB, 6 C

(*continued on next page*)

Table 3 (*continued*)

Spatial auditory task	Study	Effect of blindness		Early or late-onset, or a mix	Participants
	Veraart and Wanet-Defalque (1987)	Degraded	C	Early	3 EB, 3 LB, 10 C
	Seemungal et al. (2007)	Degraded	C	Early	6 EB, 2 AVL, 12 C
	Gori et al. (2017)	Degraded	C	Early	7 EB, 3 LB, 10 C
Road crossing decisions using sound P1, 4	Guth, et al. (2013)	Degraded	C	Mix	10 EB/LB, 9 C
	Hassan (2012)	Degraded	C	Not reported	10 EB/LB, 12 C
Non-spatial auditory task					
Pitch perception P1–2, 7	Witkin et al. (1968)	Enhanced	C	Early	25 EB, 28 C
	Gougoux et al. (2004)	Enhanced	C	Early	7 EB, 7 LB, 12 C
	Rokem and Ahissar (2009)	Enhanced	C	Early	16 EB, 16 C
	Chen et al. (2006)	Degraded (slower)	I	Early	15 EB, 17 C
	Wan et al. (2010)	Enhanced	C	Early(<13 yrs)	11 EB congenital, 11 EB (1–13 yrs), 11 LB> 14 years, 33 C
	Voss and Zatorre (2012a)	Enhanced	C	Early	14 EB, 13 LB, 19 C
	Arnaud et al. (2018)	Enhanced	C	Early	15 EB, 15 C
Pitch-timbre categorization P1–2, 7	Wan et al. (2010)	Enhanced	C	Early(<13 yrs)	11 EB congenital, 11 EB (1–13 yrs), 11 LB> 14 years, 33 C
Transposed melody discrimination P1–2, 7	Voss and Zatorre (2012a)	Enhanced	C	Early	14 EB, 13 LB, 19 C
Speech perception P1–2	Niemeyer and Starlinger (1981)	Enhanced	C	Early	18 EB, 18 C
	Lucas (1984)	Enhanced	C	Early	10 EB, 10 C
	Muchnik et al. (1991)	Enhanced	C	Early	16 EB, 10 C
	Röder et al. (2003)	Enhanced	C	Early	12 EB, 14 C
	Hugdahl et al. (2004)	Enhanced	C	Early	14 EB, 129 C
	Rokem and Ahissar (2009)	Enhanced	C	Early	16 EB, 16 C
	Ménard et al. (2009)	Enhanced	C	Early	12 EB, 12 C
	Klinge et al. (2010)	Enhanced	C	Early	10 EB, 10 C
	Dietrich et al. (2013)	Enhanced	C	Mix	14 EB/LB, 12 C
	Föcker et al. (2012)	Enhanced	C	Early	13 EB, 13 C
Lexical tone, vowel, and consonant discrimination P1–2	Feng et al. (2019)	Enhanced	C	Early	12 EB, 12 C
Temporal resolution P1–2	Muchnik et al. (1991)	Enhanced	C	Early	20 EB (10 congenital, 10 “acquired”), 10 C
Rhythm discrimination P1–2	Zhang et al., (2019)	Enhanced	C	Early	18 EB, 28 C
Learning non-metrical rhythms P1–2	Carrara-Augustenborg and Schultz (2019)	Enhanced	C	Early	8 EB, 8 C
Learning metrical rhythms P1–2	Carrara-Augustenborg and Schultz (2019)	Degraded	I	Early	9 EB, 9 C
Beat detection P1–2	Lerens et al. (2014)	Enhanced	C	Early	14 EB, 14 C
	Araneda et al. (2021)	Enhanced	C	Early	12 EB, 12 C
Voice recognition P1–2	Bull et al. (1983)	Enhanced	C	Mix	92 EB/LB, 72 C
Auditory attention P1–2	Liotti et al. (1998)	Enhanced	C	Early	12 EB, 12 C
Bimodal divided attention P1–2	Collignon et al. (2006)	Enhanced	C	Early	8 EB, 8 C
	Kujala et al. (1997)	Enhanced	C	Early	9 EB, 18 C
Auditory memory P1, 6	Röder and Rösler (2003)	Enhanced	C	Early and late	20 EB, 20 LB, 24 C
Verbal memory P1, 6	Röder et al. (2001)	Enhanced	C	Early	11 EB, 11 C
	Amedi et al. (2003)	Enhanced	C	Early	10 EB, 7 C
Temporal order judgments P1–2	Stevens and Weaver (2005)	Enhanced	C	Early	13 EB, 21 C
Dichotic & temporal sequencing P1–2	Bae et al. (2022)	Enhanced	C	Early	23 EB, 22 C
Duration discrimination P1–2	Van der Lubbe et al. (2010)	Enhanced	C	Early(<7 years)	12 EB, 12 C
Backward masking P1–2	Stevens and Weaver (2005)	Enhanced	C	Early	13 EB, 21 C

normal-hearing controls and congenitally deaf participants. The task involved pressing a button when a light point moving from any direction toward the center of vision was detected in the visual periphery in one eye. Deaf participants performed significantly better than controls. Enhanced motion processing for congenitally deaf participants compared to hearing controls was also reported in a study that employed a similar task but involved both eyes (Buckley et al., 2010).

Hauthal et al. (2013) tested normally hearing controls and early-onset deaf participants (all lost their hearing before age 5 years, except for one participant whose deafness onset was at age 6 years) in visual movement perception tasks. In a movement localization task, participants fixated a central cross, and two dot patterns were simultaneously presented leftwards and rightwards of the cross. In each trial, only one set of dots moved. The participants were required to identify whether the left or right dot pattern was moving. Performance did not differ significantly across the groups, although a left visual field advantage (indicated by faster reaction times) was reported for the deaf group only. In a direction of motion task, dot patterns were also presented leftwards and rightwards of a fixation cross, but the dots on both sides were moving, with one pattern moving diagonally upwards and the other pattern moving horizontally. Participants were required to identify the pattern that was moving diagonally. For small angular differences between the horizontally and diagonally moving patterns, the deaf participants’ reaction times were significantly shorter than those for sighted controls, indicative of an advantage of deaf individuals in judging small differences in the direction of visual movement.

Shiell et al. (2014) tested an early-onset deaf group and a hearing control group in a visual motion-detection task. Participants were

Table 4
As Table 3, but for studies reporting significantly enhanced or degraded haptic abilities associated with blindness. BR refers to Braille Readers, and NBR refers to Non Braille Readers. EDB refers to Early Deafblind participants.

Haptic task	Study	Effect of blindness		Early or late-onset, or a mix	Participants
Orientation discrimination P1–2, 6	Van Boven et al. (2000)	Enhanced	C	Early*	15 EB, 15 C
	Goldreich and Kanics (2003)	Enhanced	C	Mix	43 EB/LB, 47 C
	Chebat et al. (2007)	Enhanced	C	Early	15 EB, 25 C
	Jednoróg and Grabowska (2008)	Enhanced	C	Early	14 EB BR, 14 RV BR, 12 RV NBR, 14 C
	Wong et al. (2011)	Enhanced	C	Mix	28 EB/LB, 55 C
	Gori et al. (2010)	Degraded	I	Early	18 EB, 40 C
	Norman and Bartholomew (2011)	Enhanced	C	Early* /Late	6 Congenital, 5 onset< 14, 5 onset> 14, 16 C
	Frenzel et al. (2012)	Enhanced	C	Not reported	57 EB/LB, 151 C
Angle discrimination task P1–2, 7	Alary et al. (2008)	Enhanced	C	Early	14 EB/LB, 15 C
Texture discrimination P1–2	Alary et al. (2009)	Enhanced	C	Mix	16 EB/LB, 17 C
Size discrimination P1–2	Sunanto and Nakata (1998)	Enhanced	C	Not reported	5 EB/LB, 5 C
	Gori et al. (2010)	Enhanced	C	Early	18 EB, 35 C
Raised letter working memory P1, 6	Bliss et al. (2004)	Enhanced	C	Mix	21 EB/LB, 16 C
Gap/length discrimination, and line orientation P1–2	Stevens et al. (1996)	Enhanced	C	Not reported	69 EB/LB, 69 C
Shape discrimination P1–2	Norman and Bartholomew (2011)	Enhanced	C	Early* /Late	6 Congenital, 5 onset< 14, 5 onset> 14, 16 C
Grating detection P1–2	Goldreich and Kanics (2006)	Enhanced	C	Mix	37 EB/LB, 47 C
Tactile acuity: dot patterns P1–2	Legge et al. (2008)	Enhanced	C	Mix	49 EB/LB BR, 83 NBR C
Tactile acuity: Landolt rings P1–2	Legge et al. (2008)	Enhanced	C	Mix	22 EB/LB BR, 19 C
Temporal order judgment P1–2, 7	Röder et al. (2004)	Enhanced	C	Early	10 EB, 5 LB, 13 C blindfolded, 12 not blindfolded
Duration discrimination P1–2	Van der Lubbe et al. (2010)	Enhanced	C	Early(<7 years)	12 EB, 12 C
Mental rotation P1, 4, 7	Millar (1976)	Degraded	C	Early*	36 EB, 36 C
	Marmor and Zaback (1976)	Degraded	C	Early	16 EB, 16 LB, 16 C
	Pasqualotto and Newell (2007)	Degraded	C	Early	10 EB, 12 LB, 10 C
	Postma et al. (2008)	Degraded	C	Early	13 EB, 17 LB, 16 C
Object recognition P1, 4	Lederman et al. (1990)	Degraded	C	Early	7 EB, 7 C
	Bhirud et al. (2016)	Enhanced	I	Early	30 EB, 30 C
Line bisection P1, 4	Cattaneo et al. (2011)	Degraded	C	Early	17 EB, 18 C
	Cattaneo et al. (2018)	Degraded	C	Early	11 EB, 8 EDB, 25 ED, 25 C

Table 5
As Table 1, but for studies reporting significantly enhanced or degraded olfactory abilities following blindness or deafness.

Olfactory task	Study	Sensory loss and effect		Early or late-onset, or a mix	Participants
Odor thresholds P1	Guducu et al. (2016)	Deafness, degraded	I	Early	14 EB, 13 ED, 10 C
	Beaulieu-Lefebvre et al. (2011)	Blindness, enhanced	I	Early	11 EB, 14 C
	Çomoğlu et al. (2015)	Blindness, enhanced	I	Early and late	17 EB, 16 LB, 33 C
Discrimination P1–2	Cuevas et al. (2009)	Blindness, enhanced	C	Early	13 EB, 13 C
	Rombaux et al. (2010)	Blindness, enhanced	C	Early	10 EB, 10 C
	Renier et al. (2013)	Blindness, enhanced	C	Early	10 EB, 10 C
	Çomoğlu et al. (2015)	Blindness, enhanced	C	Early and late	17 EB, 16 LB, 33 C
Odor identification P1–2	Rosenbluth et al. (2000)	Blindness, enhanced	C	Early	30 EB, 30 C
	Wakefield et al. (2004)	Blindness, enhanced	C	Early	32 EB, 5 LB, 14 RV, 32 C
	Cuevas et al. (2009)	Blindness, enhanced	C	Early	13 EB, 13 C
	Rombaux et al. (2010)	Blindness, enhanced	C	Early	10 EB, 10 C
	Renier et al. (2013)	Blindness, enhanced	C	Early	10 EB, 10 C
	Gagnon et al. (2015)	Blindness, enhanced	C	Early	12 EB, 14 C
	Manescu et al. (2018)	Blindness, degraded	I	Early	12 EB, 12 C
Awareness P1–2, 6	Beaulieu-Lefebvre et al. (2011)	Blindness, enhanced	C	Early	11 EB, 14 C
Emotion identification P1–2	Iversen et al. (2015b)	Blindness, enhanced	C	Early	14 EB, 14 C

presented with pairs of sinusoidal gratings, one randomly moving and the other static. Participants were asked to report which of the two was moving. A staircase method was used to determine the lowest movement speed that could be detected. Thresholds were significantly lower for the deaf group.

When a brief static visual stimulus (a flash) is presented in spatial alignment with a moving visual stimulus, participants often report that the flash stimulus is slightly offset from the moving stimulus. For example, if the moving stimulus goes from left to right, the flash appears slightly to the left of the moving stimulus. This is called the flash-lag illusion (FLI). Amadeo et al. (2022) reported that the magnitude of the FLI was smaller for early-deaf individuals than for sighted controls. In other words, the deaf participants perceived the stimuli more veridically.

The literature reviewed above indicating that deaf people have significantly better visual motion perception than hearing controls in somewhat complex tasks is in line with P1 (*complexity*), P2 (*detection of changes*), and P3 (*identifying the direction of change*).

4.1.3. *Enhanced lipreading, face perception, visual attention, and search ability for deaf individuals*

Lipreading (generally referred to as speechreading in the literature) refers to the ability to perceive speech using visual information about the talker, either alone or combined with auditory information. Here we focus on studies of speechreading using visual information alone. Bernstein et al. (2000) tested early-onset deaf individuals and hearing controls in a task involving identification of consonant-vowel nonsense syllables and words, both in isolation and in full sentences. Accuracy

Table 6
As Table 1, but for studies reporting significantly altered performance for thermal and gustatory tasks following blindness or deafness. A refers to Anosmic.

Thermal/ gustatory task	Study	Type of sensory loss and effect		Early or late-onset, or a mix	Participants
Heat pain sensitivity P1–2, 7	Slimani et al. (2013)	Blindness, enhanced	C	Early	11 EB, 15 C (Italian); 18 EB, 18 C (Danish)
	Slimani et al. (2014)	Blindness, enhanced	C	Early	23 EB, 12 LB, 48 C
Thermal change detection P1–2	Slimani et al. (2015)	Blindness, enhanced	C	Early	11 EB, 11 C
Auditory temperature discrim P1–2	Oleszkiewicz et al. (2023b)	Blindness, enhanced	C	Early/ Late	50 EB, 51 LB, 99 C
Auditory bubbliness discrim P1–2	Oleszkiewicz et al. (2023b)	Blindness, enhanced	C	Early	50 EB, 51 LB, 99 C
	Oleszkiewicz et al. (2023b)	Anosmia, enhanced	C	Not reported	101 A, 100 C
Gustatory identification P1–2	Oleszkiewicz et al. (2023a)	Blindness, enhanced	C	Early	49 EB, 51 LB, 99 C
	Oleszkiewicz et al. (2023a)	Deafness, degraded	I	Early	74 ED, 100 C

was greater for the deaf group. This finding was supported by the results of Auer Jr and Bernstein (2007), who reported enhanced speechreading for early-onset deaf participants using much larger groups of participants. Mohammed et al. (2005) tested early-onset deaf and hearing groups using the Test of Adult Speechreading (TAS). Participants watched a video of a talker producing a word, a sentence or connected speech. They were then presented with a choice of pictures and were required to match the speech segment to the picture. The deaf group performed significantly more accurately than the hearing controls. For the deaf group only, the ability to detect visual motion coherence in random-dot kinematograms was significantly positively correlated with speechreading ability. This may link to the findings described above of enhanced visual motion perception following deafness (Neville and Lawson, 1987; Stevens and Neville, 2006).

In summary, these findings are in line with the idea that deaf individuals have more extensive experience of, practice with, and reliance on visual speech cues than hearing controls, leading to enhanced speechreading abilities. This is consistent with P1 (*complexity*), P5 (*mapping using cues from intact modalities*) and P6 (*experience and practice*), on the assumption that deaf individuals learned the associations between phonetic information and the complex movements of the lips and jaw obtained visually and used audiomotor associations for calibration. Audiomotor associations are derived from the correspondence between changes in auditory information and self-controlled motor movements. Deaf individuals can reproduce the motor movements that generate speech, which might help in speechreading.

Deaf individuals and those who use sign language rely primarily on visual information to extract emotional and social information about the talker, while hearing individuals obtain that information partly from the speaker's voice (Mitchell and Maslin, 2007). McCullough and Emmorey (1997) tested deaf participants with sign language experience (age of onset not reported, but participants were described as prelingually deaf) and hearing groups with and without sign language experience, in a facial feature discrimination task. Participants were presented with a target face and then, after a few seconds, they were presented with a pair of faces. One face matched the target, while the other differed from the target in a single feature (eyes, nose or mouth). Deaf participants were significantly more accurate than the other groups at detecting mouth alterations only. The authors suggested that the advantage of the deaf group may be linked to speechreading experience, rather than experience with discriminating American Sign Language facial grammatical expressions.

Abilities that involve visual attention also tend to be affected by

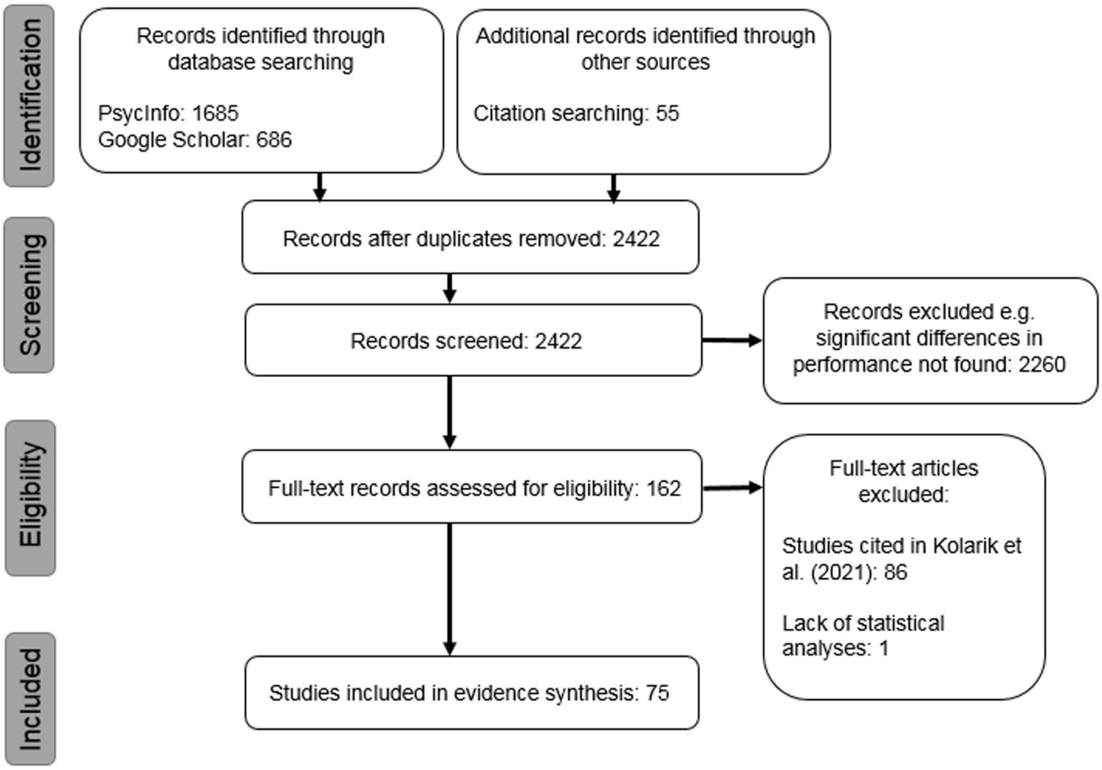

Fig. 1. Flow of process for selecting studies included in the research synthesis.

deafness, as shown for tasks where increased accuracy comes at the cost of longer reaction times. Sladen et al. (2005) tested hearing and early-onset deaf participants using the Eriksen flanker task. Participants were visually presented with target letters flanked by similar or dissimilar letters (all letters were either H or N) and responded using one button when a target H was presented and another button when a target N was presented. In contrast to the findings of the studies described above that showed significantly faster reaction times for deaf individuals than for hearing controls (Bottari et al., 2010; Colmenero et al., 2004; Heimler and Pavani, 2014; Hong Loke and Song, 1991; Neville and Lawson, 1987; Parasnis and Samar, 1985), reaction times were significantly longer for the deaf group than for the hearing group, although errors were significantly greater for the hearing group. The authors suggested that the longer reaction times of the deaf participants were due to this group utilizing their visual resources more carefully, resulting in fewer errors, as proposed previously by Rothpletz et al. (2003), who also tested early-onset deaf and hearing participants using a visual attention task. Rothpletz et al. (2003) asked participants to turn their heads towards a target light positioned at various eccentricities either in the presence of a distractor light or without a distractor. The deaf group showed significantly longer reaction times for single targets presented in the near periphery and for targets in the presence of a distractor. The authors suggested that the longer reaction times may be indicative of deaf participants responding more deliberately than controls in a visually distracting environment so as to achieve higher accuracy. However, accuracy was not measured in this study.

Stivalet et al. (1998) tested congenitally deaf participants and hearing controls in a visual search task. Participants were presented with visual arrays consisting of single “Q” targets embedded within “O” stimuli, or vice versa. For “O” targets, slopes for search time plotted against number of letters were significantly shallower for deaf than for hearing participants, indicating more efficient visual search by the deaf group. The results are notable in that visual processing enhancement following deafness was observed in the central visual field for this difficult task, whereas enhancement has more often been restricted to peripheral visual processing (Lomber et al., 2010; Neville and Lawson, 1987; Stevens and Neville, 2006).

The results of Stivalet et al. (1998) were confirmed for groups of early-onset deaf adults and hearing controls by Rettenbach et al. (1999), who tested participants in texture segmentation and visual search tasks in conditions with and without attentional load. Rettenbach et al. (1999) suggested that enhanced visual abilities as a result of deafness only developed later in life, since deaf children and adolescents did not show this enhancement, instead showing longer reaction times than hearing controls.

These findings are, for the most part, consistent with P1 (*complexity*), P2 (*detection of changes*), P3 (*identifying the direction of change*), and P6 (*experience and practice*).

4.2. *Visual abilities that are degraded as a result of deafness*

4.2.1. *Degraded visual complex temporal representations in deaf individuals*

Amadeo et al. (2019) showed that the ability to construct complex temporal representations using vision was impaired for a mix of early- and late-onset deaf participants. Groups of deaf participants and hearing controls performed temporal and spatial bisection tasks. Three stimuli were visually presented, and the task was to report whether the second stimulus was closer to the first or the third stimulus in terms of either temporal or spatial position. Thresholds were calculated using the standard deviation of cumulative Gaussian functions fitted to the data. The deaf group showed significantly higher temporal bisection thresholds than controls. There was no significant difference between groups for the spatial bisection task. Zhang et al. (2020) also showed that visual temporal bisection was significantly poorer for deaf individuals than for hearing individuals.

Kowalska and Szelag (2006) tested the ability of congenitally deaf adolescents and hearing controls to produce and reproduce various durations of visually presented stimuli. A green rectangle was presented on a screen and participants had either to terminate the stimulus using a response button when the duration was judged to be the same as a previously presented stimulus lasting between 1 and 5.5 s (reproduction) or to terminate the stimulus after a pre-specified duration between 1 and 6 s (production). The deaf group showed significantly poorer performance than controls for both reproduction and production tasks, overestimating the duration of shorter stimuli and underestimating the duration of longer stimuli.

Vercillo and Jiang (2017) tested early-onset deaf and hearing participants in a temporal-order discrimination task involving a motor action and a visually presented stimulus. On each trial participants pressed a key after a fixation cross disappeared from a screen. A white circle was presented at various times after the cross disappeared and participants were required to judge whether the circle was presented before or after the key was pressed. Significantly higher temporal-order JNDs were reported for the deaf than for the hearing participants, suggesting a role of auditory information in calibrating motor-sensory timing.

The findings suggest that deafness results in a reduced ability to construct or accurately reproduce complex temporal representations in the visual domain, probably due to the absence of auditory information to calibrate visual temporal information, consistent with P4 (*calibration requiring cues from the absent modality*).

4.3. *Summary of the effects of deafness on visual abilities*

Table 1 summarizes the results of studies showing enhanced and degraded visual abilities for deaf individuals, and whether the findings are consistent (C) or inconsistent (I) with the principles of the perceptual restructuring hypothesis. Although the majority of findings are consistent, there are some inconsistencies for visual attention reaction times (Rothpletz et al., 2003; Sladen et al., 2005) and temporal discrimination (Heming and Brown, 2005). However, for the tasks involving visual attention, increased accuracy came at the cost of slower reaction times, which may be linked to more deliberate responses by deaf individuals, underpinned by more careful use of visual resources. Hence, these findings are not indicative of degraded visual attention *per se* as a result of deafness. Rather, they indicate that deafness results in a redistribution of attention to the visual periphery, so that peripheral visual attention is heightened (Bavelier et al., 2006; Dye et al., 2007). Although deaf individuals might have performed better if they had focused attentional resources, redistribution of attentional resources might be beneficial in avoiding loss of visual information regarding the surrounding environment, even when that information is unrelated to the task at hand (Mitchell and Maslin, 2007). As mentioned above, the results of Heming and Brown (2005) are hard to interpret owing to the subjective nature of the simultaneity protocol used in that study (Moallem et al., 2010).

4.4. *Haptic abilities that are enhanced as a result of deafness*

4.4.1. *Enhanced haptic change detection and emotion recognition by deaf individuals*

While many studies have investigated the effects of deafness on visual abilities, fewer have assessed the haptic abilities of deaf individuals. Schiff and Dytell (1972) tested young deaf and hearing controls (age 7.5–19.5 years, age of onset not reported) using a range of haptic perception tasks, including measurement of vibrotactile sensitivity, two-point thresholds, gap-detection involving a haptic version of the Landolt-C test, roughness discrimination using four grades of sandpaper, pattern discrimination, and object and letter identification. Two-point thresholds were measured by touching either the tip of the index finger or the palm with two points of an instrument, or only one point, with varying distances between the two points. Participants were required to report if they felt one or two points. Performance was significantly better (thresholds were lower) for the deaf than for the hearing participants for the vibrotactile sensitivity (inconsistent with P1) and two-point tasks only. The results of Chakravarty (1968) also suggest better haptic spatial discrimination abilities for deaf than for hearing children, but due to lack of statistical analyses it is unclear whether the difference was significant.

Levänen and Hamdorf (2001) investigated tactile sensitivity for congenitally deaf participants and normally hearing controls. Participants held a plastic tube that vibrated with constant amplitude. Participants were asked to judge whether a test stimulus of adjustable vibration frequency (160–250 Hz) had a higher or lower frequency than a 200-Hz reference stimulus. A change-detection task was also performed, involving detection of a 180-Hz deviant stimulus within a series of 250-Hz standard stimuli. Deaf participants were significantly better than hearing controls at the change-detection task, but there was no significant difference in frequency discrimination between the groups. The results suggest that deaf individuals have enhanced tactile sensitivity in detecting sudden changes (P2), such as vibrations resulting from loud noises, that the authors proposed might compensate for the lack of auditory information about important or dangerous local events.

Sharp et al. (2020) tested congenitally deaf individuals and hearing controls in their abilities to haptically identify emotions in music. A vibrating glove was used to convey melodies intended to evoke either happiness, sadness, fear/threat, or peacefulness. The deaf group were significantly more accurate than the controls at identifying happiness only.

In summary, the findings for change-detection and emotion recognition tasks in deaf individuals are broadly consistent with P1 (*complexity*), and P2 (*detection of changes*).

4.5. Haptic abilities that are degraded as a result of deafness

4.5.1. Degraded haptic vibration detection and spatial acuity, and temporal discrimination for deaf individuals

Frenzel et al. (2012) tested young congenitally deaf participants (age 14–20 years) and age-matched hearing controls using a grating orientation task (GOT) that required identification of the orientation of a single grooved surface. The threshold for detecting sinusoidal vibration applied to the finger was also measured. Both vibration detection thresholds and tactile acuity were significantly poorer for the deaf group.

Pellegrino et al. (2020) showed that early-deaf individuals demonstrated impaired performance on a tactile spatial acuity task. Square-wave gratings were cut into plastic domes and applied to either the tongue or finger. They were oriented either parallel or perpendicular to the long axis of the tongue/finger (these were the only available response options), and the participants reported the orientation by holding up one finger for "parallel," or two fingers for "perpendicular," using the hand not being tested. Acuity thresholds were measured using a staircase method that varied groove width according to the participant's response. Early and late-onset blind, early-onset deaf, and control groups were tested. Deaf participants had higher thresholds (worse performance) for the task at the finger only. No other group differences were observed.

Heming and Brown (2005) assessed the tactile and visual temporal discrimination abilities of early-onset deaf participants and hearing controls. Participants had to report whether pairs of tactile stimuli presented to the index and middle fingers were simultaneous or sequential. The stimulus onset-asynchrony of the first and second stimuli was adjusted based on the previous response. Thresholds were higher (i.e. performance was worse) for the deaf group than for the controls for both tactile and visual tasks. However, the thresholds may have been affected by the response criterion of the participant (as was the case for the visual discrimination task). Moallem et al. (2010) tested early-onset deaf participants and hearing controls in a tactile temporal order resolution task that used objective methods and separated sensitivity from response bias, in which stimuli were presented to the thumb and index finger and participants responded by reporting which of the two locations had the earlier onset, or which of the two had the later offset. No significant differences were observed between groups.

Bolognini et al. (2012) tested congenitally deaf and hearing groups of participants using tactile temporal and spatial discrimination tasks in which vibratory stimuli were delivered to a participant's index finger. In the temporal task, participants were required to discriminate between longer and shorter intervals. In the spatial task, participants had to discriminate between stimuli that varied in spatial length using stimulators positioned along the finger. Deaf participants performed significantly worse than hearing controls in the temporal task only.

Papagno et al. (2016) tested congenitally deaf, congenitally blind, mixed onset deaf-blind, and normally hearing and sighted control participants on temporal and spatial discrimination tasks using vibratory stimuli applied to both index fingers. Spatial discrimination involved discriminating the spatial length of arrays composed either of three vibrotactile stimulators (a "long" condition), or two stimulators (a "short" condition). Temporal discrimination was tested using two arrays of equal spatial length that differed in the duration of the vibration. In the spatial discrimination task, deaf-blind participants showed significantly better performance than the blind participants, but not than the controls. For the temporal discrimination task, deaf and deaf-blind participants performed significantly worse than controls.

In summary, the findings for haptic vibration detection and spatial acuity, and temporal discrimination by deaf individuals are broadly inconsistent with P1 (*complexity*), and P2 (*detection of changes*).

5. Summary of the effects of deafness on haptic abilities

The results are mixed regarding whether haptic abilities are degraded or enhanced by deafness in a manner consistent with the principles of the perceptual restructuring hypothesis (Table 2). The findings for emotion identification in music (Sharp et al., 2020) are consistent, contrasting results across studies are reported for vibration detection (Frenzel et al., 2012; Levänen and Hamdorf, 2001; Schiff and Dytell, 1972), while findings for spatial orientation acuity (Pellegrino et al., 2020) and temporal discrimination (Bolognini et al., 2012; Heming and Brown, 2005) are inconsistent. However, the findings of Heming and Brown (2005) might have been affected by methodological issues (Moallem et al., 2010). Overall, there are currently too few studies to conclude whether haptic abilities are affected by deafness in ways consistent with the principles of the perceptual restructuring hypothesis. Further work is needed. It has been suggested that more complex and cognitive tasks (such as face discrimination) are needed in order to clearly demonstrate changes in haptic ability following deafness, especially in the context of the cortical reorganization that may underlie enhanced haptic performance (Papagno et al., 2016; Sharp et al., 2020).

5.1. Auditory abilities that are enhanced or degraded as a result of blindness

Previous work on the effect of blindness on auditory abilities, published up to 2020, has been reviewed in a number of papers (Collignon et al., 2009; Voss, 2016; Voss et al., 2010). Kolarik et al. (2021) concluded that most, but not all, of the findings were consistent with the principles of the perceptual restructuring hypothesis (summarized in Table 3). In addition, blind individuals show no significant differences from sighted controls for basic auditory detection or discrimination tasks, such as pure tone detection (Kärnekull et al., 2016; Yabe and Kaga, 2005) or intensity discrimination (Voss and Zatorre, 2012a), consistent with P1 (*complexity*). The reader is referred to Kolarik et al. (2021) for details. An additional summary of recent studies reporting significantly enhanced or degraded auditory abilities following vision loss, published after the review by Kolarik et al. (2021), is presented below, and incorporated into Table 3.

Araneda et al. (2021) presented groups of early-onset blind and sighted control participants with rhythmic or non-rhythmic sequences. Participants had to detect if a rhythmic beat was present in the sequence. Accuracy was significantly higher for the blind group. Enhanced non-spatial abilities for early-onset blind participants were also reported by Bae et al. (2022) for dichotic listening and temporal sequencing tasks.

Setti et al. (2022a) showed that early-onset blind participants showed significantly poorer performance than sighted controls in a task involving the use of internal spatial representations to remember sound source locations. Poorer recall of auditory spatial information stored in memory by early-onset blind participants was also shown in a second study (Setti et al., 2022b).

Finocchietti et al. (2023) tested early-onset blind and sighted controls in an auditory localization task, where participants reported the azimuth of a sound source by pointing, and an auditory bisection task, where three sounds were presented at different azimuths and participants verbally reported if the second sound was closer to the first sound or the third sound. Tasks were performed monaurally (one ear only) or binaurally (with two ears). In the localization task, the blind group performed significantly better than the sighted group for both binaural and monaural conditions. The blind group performed the auditory bisection task significantly more poorly than sighted controls in the binaural listening condition, but significantly better in the monaural condition. The results for the monaural bisection task, which requires a spatial metric, are inconsistent with P4 (*calibration requiring cues from the absent modality*). The superiority of the blind group for this task probably stems from the superior ability of the blind group in the use of monaural spectral cues.

Lombera et al. (2022) tested a mix of early- and late-onset blind participants and a sighted control group in an absolute distance judgement task, using nearby sounds. Blind participants showed significantly less biased responses, suggesting that audio-motor feedback obtained from manipulating nearby sources could be used to calibrate auditory distance perception, consistent with P5 (*mapping using cues from intact modalities*).

Park and Fine (2023) showed that early-blind participants were significantly better able to discriminate the direction of auditory motion (left vs. right) in the presence of background noise than sighted controls.

Pardhan et al. (2024) obtained auditory distance estimates for virtual sound sources presented between 1.2 and 13.8 m from groups of participants with early- or late-onset partial visual loss and sighted controls. Auditory distance estimates were significantly larger for the early but not late-onset participants than for sighted controls. The results are consistent with P1, 4 and 7 and add support to the idea that the principles can apply to changes in ability in response to partial sensory loss as well as full sensory loss.

5.2. Haptic abilities that are enhanced as a result of blindness

A number of haptic abilities are enhanced following full visual loss. The haptic abilities of the blind have been reviewed by Sathian and Stilla (2010), and Voss et al. (2010).

5.2.1. Enhanced haptic orientation discrimination by blind individuals

Van Boven et al. (2000) investigated tactile orientation discrimination for early-onset (6 years or less) blind braille readers and sighted controls using an absolute GOT. Participants were required to identify the orientation (either parallel or at right angles to the long axis of the finger) of single grooved plastic domes that were placed against the skin of a stationary finger. A two-alternative forced-choice task was used to determine the grating orientation threshold, specified as the groove width leading to 75 % correct performance. Performance was significantly better for blind participants, who had a mean grating orientation threshold of 1.04 mm, than for sighted controls, who had a mean threshold of 1.46 mm.

Enhanced tactile acuity was also reported for a mix of early- and late-onset blind participants by Goldreich and Kanics (2003) utilizing a GOT. On each trial, two successive gratings with identical groove width were presented to a stationary finger. One grating was oriented with the grooves parallel to the finger axis, and the other with grooves transverse to the finger axis. Participants reported the order of groove orientation presentation. Groove widths ranged from 0.25 to 3.10 mm. Performance was significantly better for the blind group, independent of the level of vision present during childhood (whether or not light perception was present) or Braille reading ability.

Chebat et al. (2007) compared tactile orientation identification for stimuli applied to the tongue for early-blind and sighted controls. Stimuli were delivered using the Tongue Display Unit, a sensory substitution device (SSD) that uses a camera to observe the scene and converts the optical information into electro-tactile information presented to the tongue. All participants were blindfolded and stimuli consisting of Snellen E letters were shown to the camera in various orientations. The participant had to report the orientation of the letter, and progressively smaller letters were presented if correct responses were given. The threshold was taken as the smallest letter size for which the orientation could be identified at a level above chance. However, there was a limit to the smallest letter size that the device could present. This limit was reached by 31 % of blind participants but only 8 % of sighted controls, and this difference was significant, indicating better performance of the blind participants.

Jednoróg and Grabowska (2008) examined performance for a coarse texture task and a GOT for early-blind braille readers, low-vision participants (braille readers and non-braille readers), and sighted non-braille readers. Performance of the GOT is likely related to shape discrimination but is dissimilar to reading Braille, allowing tactile ability to be measured independently of possible haptic training effects specific to practice using Braille (Jednoróg and Grabowska, 2008). In the coarse texture task, two surfaces covered with sandpaper were presented, and the participant had to report if the surfaces had the same or different grade of sandpaper coarseness. Braille readers performed significantly better than low-vision non-braille readers for the hand trained in braille reading only, suggesting that specific practice using braille may improve tactile ability. However, performance did not differ significantly for the sighted controls and the other groups. For the GOT, blind participants significantly outperformed low-vision non-Braille readers and sighted controls.

GOT performance for stimuli applied to the lips and fingers was investigated by Wong et al. (2011) for early- and late-blind participants and sighted controls. Their goal was to test two distinct hypotheses: the tactile-experience hypothesis, which holds that the degree of reliance on the sense of touch underlies enhanced tactile acuity (and predicts that blind participants will show enhanced GOT performance for the fingers only and that braille experience would be associated with enhanced haptic acuity), and the visual-deprivation hypothesis, which holds that loss of vision enhances tactile acuity more generally (and predicts that blind participants will show enhanced GOT performance for both fingers and lips). The results were consistent with the predictions of the tactile-experience hypothesis, and in line with P1, 2, and 6 (*experience and practice*).

Norman and Bartholomew (2011) tested three groups of blind participants (congenitally blind, early-blind who lost vision between 1 and 14 years of age, and late-blind who lost their vision after 14 years of age) and sighted controls in a grating orientation discrimination task, and in a 3-D shape discrimination task. While 3-D shape discrimination was significantly better than for controls for the early- and late-onset groups only, grating orientation thresholds were significantly smaller for all three blind groups than for sighted controls.

Frenzel et al. (2012) tested blind (age of onset not reported) and sighted controls using a GOT and a vibration detection task for stimuli presented to the fingertip. The blind participants performed significantly better than the controls for the GOT task, but there were no significant differences between groups for vibration detection thresholds.

Not all studies have shown that blindness leads to enhanced performance for haptic orientation tasks. Gori et al. (2010) measured haptic orientation discrimination thresholds for congenitally blind children and sighted controls with ages ranging from 5 to 19 years, using pairs of tilted bars. Participants reported which of the two bars was slanted more clockwise. The thresholds were significantly higher (by an average factor of 2.2) for the blind children than for the sighted controls. It was suggested that these findings were consistent with predictions based on the hypothesis that a more accurate sense (vision in this case) is needed to calibrate a less accurate sense (haptic). Visual object orientation is directly coded via orientation-selective cells in the primary visual cortex, whereas haptic orientation information is gleaned indirectly using relatively complicated coordinate transforms (Gori et al., 2010). It is unclear why Gori et al. (2010) found degraded haptic orientation discrimination for the blind, while the other studies described above showed enhanced orientation discrimination (Frenzel et al., 2012; Goldreich and Kanics, 2003; Jednoróg and Grabowska, 2008; Norman and Bartholomew, 2011; Van Boven et al., 2000; Wong et al., 2011). It is possible that the differences across studies were due to task differences, since Gori et al. used tilted bars rather than grooved surfaces. Age may also have been a factor, since Gori et al. tested children, whereas the other studies tested adults. It is possible that a long duration of blindness allows the haptic sense to be accurately calibrated even in the absence of visual information. Mixed results for children and adolescents have been reported for the effects of visual loss on hearing abilities (Kolarik et al., 2021). Further work is needed to investigate whether age and the time in life when a sensory loss is acquired influence performance using the intact modalities.

Although some other studies did not show significant differences between blind and sighted groups using a GOT (Alary et al., 2009; Grant et al., 2000), it has been suggested that the lack of group differences in these studies may have been due to the choice of task (passive or active) and/or inappropriate matching of participant age or gender across groups (Voss et al., 2010), or ceiling effects (Alary et al., 2009).

In summary, the majority of the findings regarding enhanced haptic orientation discrimination abilities in blind individuals are consistent with P1 (*complexity*), P2 (*detection of changes*), and P6 (*experience and practice*).

5.2.2. *Enhanced haptic discrimination of angle, texture, size, letter recognition, shape, and duration by blind individuals*

Alary et al. (2008) tested sighted controls and blind participants who lost their sight between birth and 14 years of age, using a tactile angle-discrimination task. Using continuous movements with their right index finger, participants actively explored pairs of surfaces intersecting at different angles and had to identify the pair with the larger angle. Congenitally blind participants showed significantly smaller discrimination thresholds than sighted controls when the whole arm was moved in the task. Unlike the congenitally blind participants, late-onset blind participants did not show any significant difference in performance from sighted controls, consistent with P7 (*age of onset*).

In a follow-up study using the same blind participants and sighted controls (Alary et al., 2008), Alary et al. (2009) investigated performance for several tactile tasks, including discrimination of surface roughness, grating orientation and vibrotactile frequency discrimination. The blind participants performed better than controls only for the discrimination of small changes in surface roughness. Similar performance for the sighted and blind groups for the grating orientation and vibrotactile frequency discrimination tasks was attributed by the authors to ceiling effects. Although enhanced texture discrimination by blind compared to sighted groups was not observed in a previous study of Heller (1989), Alary et al. (2009) suggested that their significant findings may have stemmed from their use of a blind subject pool of fluent braille readers and a larger control group.

It has been reported that haptic size discrimination is enhanced following visual loss (Gori et al., 2010; Sunanto and Nakata, 1998). Sunanto and Nakata (1998) tested blind (age of onset not reported) and blindfolded sighted controls in a haptic height discrimination task. Using a cane, participants explored the heights of pairs of wooden cubes presented in a random order. Pairs consisted of a standard cube of a set height and a comparison cube chosen from a set ranging in height from shorter to taller than the standard. Participants reported whether the second cube presented was taller than, equal to, or shorter than the first cube. Despite there being only five participants in each group, blind participants made significantly more correct judgments than the controls and had shorter exploration times. Gori et al. (2010) compared performance for congenitally blind children and sighted controls (ages ranged from 5 to 19 years) using a size-discrimination task. Participants were asked to handle two successive blocks presented behind a screen and to report which was larger. Thresholds were significantly lower (better) for the blind children than for the controls.

Blindness has been reported to be associated with enhanced performance in a raised-letter *n*-back recognition working memory task (Bliss et al., 2004). In the *n*-back task, a sequence of letters containing target letters was presented and the participant was asked to respond when the letter presented matched the one presented *n* steps back in the sequence (where $n = 0, 1, 2$ or 3). Early- and late-blind groups were tested using a haptic task involving raised letters and Braille. A sighted group was tested using a haptic task involving raised letters and a visual task involving letters shown on a computer screen. The two groups of blind participants performed significantly better than the controls for the haptic raised letters *n*-back task, with no significant difference between early- and late-blind groups. Enhanced memory performance for blind participants may be due to an improved sensory representation of the stimuli. The performance of the blind group with haptic stimuli was similar to that of the sighted group using visual stimuli.

Stevens et al. (1996) tested blind participants (age of onset not reported) and sighted controls, measuring thresholds for the tactile discrimination of spatial gaps, length of lines, and line orientation for stimuli presented to a fingertip or the lip. Blind participants showed significantly lower thresholds than sighted controls for the index finger, but not the lip, for gap discrimination and line orientation, but not line length.

As described above, Norman and Bartholomew (2011) tested three groups of blind participants (congenitally blind, early-blind who lost vision between 1 and 14 years of age, and late-blind who lost their vision after 14 years of age) and sighted controls in a grating orientation discrimination task and in a 3-D shape discrimination task. For the shape discrimination task, the early- and late-blind groups performed significantly better than the sighted controls, whereas performance for the congenitally blind and sighted controls was similar, a result that led the authors to propose that early visual experience was necessary for enhanced 3-D shape discrimination associated with blindness to occur. The lack of a significant difference in shape discrimination for the congenitally blind and sighted controls may have been due to the small number of participants in each group ($n = 6$).

Goldreich and Kanics (2006) tested a mix of early- and late-onset blind participants and sighted controls, estimating the thinnest grooved surface that could be distinguished from a smooth surface using tactile information from a stationary finger. Tactile acuity was found to be better for the blind than for the sighted participants, regardless of the age of onset. Taken together with the findings of previous studies of enhanced grating orientation discrimination among blind participants when the finger was held stationary (Goldreich and Kanics, 2003; Van Boven et al., 2000), the authors suggested that the evidence supported the idea that passive tactile spatial abilities (for tasks where the finger is stationary) were enhanced by blindness. However, the enhancement does not seem to be restricted to passive tasks. Legge et al. (2008) tested a mix of early- and late-onset blind and sighted controls using tactile-acuity charts, where participants actively explored test symbols (dot patterns and Landolt rings), and found that blind participants showed enhanced abilities. Furthermore, unlike sighted controls, whose tactile acuity decreased over the lifespan, blind participants maintained high tactile acuity with increasing age.

Röder et al. (2004) reported that performance on tactile temporal-order judgment tasks was enhanced for early-onset blind individuals. Metallic pins were pressed against the middle fingers of the left and right hand with a range of stimulus onset asynchronies. Participants were asked to indicate which of the two fingers had been stimulated first by raising the index finger of the corresponding hand. Performance was significantly better for congenitally blind participants than for sighted controls and late-blind participants (consistent with P7, *age of onset*). Van der Lubbe et al. (2010) reported that for a tactile duration-discrimination task, performance was significantly better in terms of accuracy and response time for early-blind participants than for sighted controls.

In summary, results showing that blind individuals often have enhanced performance compared with sighted controls for haptic tasks are consistent with P1 (*complexity*) and P2 (*detection of changes*). The finding for some tasks of an advantage only for early-blind participants is consistent with P7 (*age of onset*).

5.3. Haptic abilities that are degraded as a result of blindness

5.3.1. Degraded haptic mental rotation, object identification, line bisection, and parallel-setting by blind individuals

Mental rotation tasks can be used to investigate internal representations and mental imagery for individuals with sensory loss. This provides an opportunity to assess whether abilities are consistent with predictions based on P4 (*calibration requiring cues from the absent modality*), as loss of calibration information from an absent sense may lead to difficulties in generating and maintaining internal representations, also referred to as spatial metrics (Gori et al., 2014; Vercillo et al., 2016, 2015). See Aggius-Vella et al. (2020) for a discussion of the possible strategies involved in using "raw" sensory cues versus spatial metrics to perform spatial perceptual tasks.

Millar (1976) asked early-onset blind (the maximum age of onset was 6 years) and sighted children to mentally rotate a raised, haptically explored line in a clockwise direction, to duplicate the appearance of the line to an observer in another location rotated between 45 and 315° from the initial viewpoint. Performance was assessed by a score from zero to four with higher scores for increased accuracy, where zero indicated that the intended view matched the initial view, and four indicated a completely accurate response. The blind group performed significantly more poorly than the controls. Marmor and Zaback (1976) reported that an early-blind group were significantly slower and made significantly more errors than late-onset blind or sighted control groups in a task requiring judgment of whether pairs of tactile forms were the same or different in orientation, consistent with the combination of P4 (*calibration requiring cues from the absent modality*) and P7 (*age of onset*).

Pasqualotto and Newell (2007) investigated mental rotation and the ability to recognize and update haptic scenes for early-blind and late-blind participants (3 of whom out of 12 had onset between 2 and 5 years of age) and sighted controls. A scene of novel objects was presented using touch and then presented again in the original orientation or rotated. Participants were required to report if they recognized the scene. Overall performance was significantly poorer for the early-blind group than for the late-blind and sighted control groups, and early-blind participants showed an inability to recognize a scene that had been rotated. The authors suggested that the results indicated that visual experience plays an important role in representing and updating spatial scenes, and that the visual system can construct high precision spatial reference frames via which spatial information from the other sensory modalities can be interpreted. These findings link to a study of Noordzij et al. (2007), who investigated mental rotation abilities for early- and late-blind participants and sighted blindfolded controls in a spatial imagery task, where two spoken clock times were presented and participants had to imagine these times on a clock face and to report which time was associated with the largest angle between the clock's hands. The only significant difference between groups was that early-blind participants made significantly more errors than sighted controls. This suggests that the lack of visual calibration information early in life resulted in a degraded ability to compare internally generated spatial representations for the early-blind group. These findings are consistent with P1 (*complexity*), P4 (*calibration requiring cues from the absent modality*), and P7 (*age of onset*).

Postma et al. (2008) reported that early-onset blindness was associated with degraded performance for a haptic parallel-setting task. Groups of early-blind and late-blind participants and sighted controls were tested. The task involved two aluminum bars placed on protractors in front of the participant. The bars could be rotated to different orientations and explored haptically. One bar was set at a reference orientation and the other "test" bar had to be rotated to be parallel to the just-felt reference bar, either with or without a delay. The results showed that overall performance improved significantly for the late-blind and sighted groups only when the parallel-setting action was delayed, which was interpreted as indicative of a beneficial change in spatial representation from an egocentric reference frame to an allocentric frame, for which early visual experience is necessary. In addition, the performance of the early-blind group was more variable than that of the other groups. In a second task where the orientation of a single bar presented haptically was reported verbally by assigning a number of minutes corresponding to the time on an imaginary clock, early- and late-blind participants showed significantly greater errors than the sighted control group. These tasks might depend on well-calibrated internal representations of haptic space. The parallel-setting task might require a representation of the remembered orientation of the reference bar, while in the verbal judgment-of-orientation task, the orientation of the bar might need to be matched to an internal representation of a corresponding time on an imagined clock face. Poorer performance as a result of blindness may indicate the necessity of visual information in calibrating haptic space (P4, *calibration requiring cues from the absent modality*). The significantly degraded performance for the early-onset blind group compared to the late-onset blind group is consistent with P7 (*age of onset*).

Lederman et al. (1990) tested the ability of congenitally blind participants and sighted controls to recognize raised-line drawings of commonly encountered objects, such as a pencil or key. The objects were either two-dimensional or three-dimensional, depending on whether they were depicted with perspective cues, or lines representing edges. The objects were explored haptically and had to be identified. The sighted group was significantly more accurate at identifying the objects, a result that was interpreted by the authors as probably due to the blind participants' inability to use visual imagery to represent the objects. However, the findings are not consistent with those of Bhirud et al. (2016), who investigated tactile object recognition by congenitally blind and sighted groups. Everyday objects, such as a pen or keys, were presented. Participants explored the objects using the tip of their index finger. The blind group identified objects significantly more quickly and more accurately than the sighted group. As noted by Bhirud et al. (2016), the study protocol may have affected performance, since time is required to construct haptic representations of the shapes of objects. It is possible that the differences in findings across studies are due to methodological differences. Bhirud et al. (2016) allowed 30 s to identify as many items as possible from sets of 5 items (3 sets were presented), whereas Lederman et al. (1990) used 1 set of 22 items and allowed 2 minutes of exploration time per item. Taken together, the results of these studies suggest that sighted participants outperform congenitally blind participants in a haptic object recognition task when given sufficient time to construct internal representations of objects. However, further studies are needed to investigate how the duration of object exploration affects performance.

Cattaneo and colleagues presented early-blind and sighted participants with horizontal rods of different lengths and asked them to haptically explore each rod and locate its midpoint (Cattaneo et al., 2011, 2018). Both groups displayed a significant tendency (termed pseudoneglect) to locate the midpoint leftward of the actual midpoint, which was suggested to be due to the dominant role of the right hemisphere in spatial attention. The blind participants showed greater spatial bias than the sighted controls, but this was offset by greater consistency.

In summary, some tasks involving object identification, line bisection, and parallel-setting probably can be performed best using internal spatial representations, and the absence of visual spatial calibration information for blind individuals is often associated with poorer performance on these tasks than for sighted controls. This is consistent with P4 (*calibration requiring cues from the absent modality)*.

6. Summary of the effects of blindness on haptic abilities

Table 4 summarizes findings in the literature regarding the effects of blindness on haptic abilities. Most of the findings are in line with the principles of the perceptual restructuring hypothesis.

6.1. Olfactory abilities that are enhanced or degraded as a result of blindness and deafness

As highlighted by Çomoğlu et al. (2015), olfaction may play an important role for those with sensory impairment in identifying potential sources of danger, such as smoke from fires, toxic chemicals, or decomposing food. Research investigating changes in olfactory abilities associated with loss of another modality, reviewed by Araneda et al. (2016) and Manescu et al. (2018), has shown mixed results. A previous meta-analysis concluded that loss of vision does not lead to changes in odor identification, or discrimination or detection thresholds (Sorokowska et al., 2019b). Basic olfactory measures of chemosensory function, such as odor detection thresholds, have mostly shown no significant differences between blind and sighted individuals (Kärnekull et al., 2016; Smith et al., 1993; Sorokowska et al., 2020), consistent with P1 (*complexity*). However, some studies have reported significantly lower detection thresholds for blind people for olfaction (Beaulieu-Lefebvre et al., 2011; Çomoğlu et al., 2015). Sorokowska et al. (2020) investigated whether blindness or deafness were associated with changes in the ability to detect hazards associated with rotten food, using large group sizes ($n \geq 74$). Odor detection thresholds were found to be similar for blind and sighted individuals and for deaf and hearing individuals. It has been suggested that the differences across studies may be due to the use of different methodologies and/or the lack of a globally standardized methodology for the assessment of olfactory abilities (Çomoğlu et al., 2015). Studies that have reported significant differences in olfactory abilities associated with blindness or deafness are described below.

Beaulieu-Lefebvre et al. (2011) tested congenitally blind participants and sighted controls using a smell battery (the "Sniffin'Sticks" test) that assessed three olfactory abilities: odor detection threshold, odor discrimination and odor identification. Participants were also tested using the Odor Awareness Scale (OAS) questionnaire, which assesses participants' own judgments of their abilities to notice, attend to, or attach importance to odors. Although there were no significant differences between the groups for odor discrimination or odor identification, blind participants had significantly lower odor detection thresholds than sighted controls, inconsistent with P1 (*complexity*). The blind group had significantly higher (better) OAS scores. Taken together, the results suggest greater sensitivity to odors for blind individuals, and that blind individuals have greater olfactory awareness of their surroundings than sighted controls.

Cuevas et al. (2009) assessed odor discrimination, identification and categorization by early-blind participants and sighted controls. In the discrimination task, participants were presented with pairs of bottles that emitted a fragrance and were asked to decide whether the fragrance in the two bottles was the same or different. In the identification task, participants were sequentially presented with 30 odors that had to be named in a free-identification task. Later, participants completed a semantic categorization task where the odors were presented again and had to be classed as fruit, flower, plant or other. In a final multiple-choice identification task, on each trial the participant was presented with one of the previously presented odors and was asked to select which one it was from six possibilities. Scores were significantly higher for the blind than for the sighted participants for all of the tasks. Using the same odor materials as Cuevas et al. (2009), Renier et al. (2013) showed that an early-onset blind group performed significantly better than sighted controls for odor identification, discrimination and categorization. The degree of activation in the right occipital cortex was correlated with performance for the blind group, suggesting a role of what would normally be visual cortex in olfactory processing.

Enhanced olfactory discrimination for early blind individuals was also reported by Rombaux et al. (2010). Blind and sighted control groups were presented with pairs of odors and reported whether they were the same or different. Blind participants showed significantly better performance than the sighted controls.

Using the Sniffin'Sticks test, Çomoğlu et al. (2015) showed that early- and late-onset blind participants showed significantly lower odor detection and discrimination thresholds than sighted controls. There was no significant difference between groups for odor identification. The finding of Çomoğlu et al. of enhanced odor detection thresholds for blind participants is consistent with the finding of Beaulieu-Lefebvre, et al. (2011), but the finding of enhanced odor discrimination is not, despite both studies employing the Sniffin'Sticks test. The finding of Çomoğlu et al. of enhanced odor discrimination for blind participants is consistent with the finding of Cuevas et al. (2009). Çomoğlu et al. (2015) suggested that additional factors, including the subjective nature of the Sniffin' Sticks test, education, environmental conditions, and age might lead to differences across studies. Cuevas et al. (2009) stated that they chose not to use the Sniffin'Sticks test due to concerns regarding possible ceiling effects. Such ceiling effects may have been responsible for the finding of Sorokowska and Oleszkiewicz (2021) of no significant difference between blind and sighted groups for the olfactory identification of unpleasant odors using the Sniffin'Sticks test.

Other studies have reported blindness to be associated with enhanced olfactory identification abilities. Rosenbluth et al. (2000) reported that early-blind children showed significantly better performance than sighted controls in an odor-naming task involving 25 common odors, but there were no differences across groups for odor sensitivity or choosing a correct odor label from a set of four choices. Similarly, Wakefield et al. (2004) found that early-blind children performed significantly better than sighted controls in an odor-naming task, but there was no significant difference between groups for an odor-sensitivity task.

Rombaux et al. (2010) presented early-onset blind participants and sighted controls with 30 odors in a free identification task. For each odor, participants reported the name of the odor if they recognized it. Identification scores were significantly higher for the blind participants than for the controls.

Gagnon et al. (2015) tested the ability of early-onset blind and sighted controls to identify various powdered foods via smell. They then performed a forced-choice task, requiring choice of each odor from four possibilities. Blind participants were significantly faster, but not more accurate, than sighted controls in the free-identification task. The groups did not differ significantly for the forced-choice task.

Other studies have not found that blindness leads to enhanced olfactory identification abilities. Sorokowska and Oleszkiewicz (2019) reported that although participants were able to make olfactory judgments of personality (neuroticism and dominance) and sex based on body odor with above-chance accuracy, performance was similar for early- and late-onset blind and sighted control groups. Manescu et al. (2018) reported that an early-blind group had significantly poorer performance than sighted controls when categorizing wine odors (participant groups were matched regarding wine consumption) and did not display higher olfactory sensitivity. The authors proposed that sighted and blind participants did not have differences in basic olfactory ability and that the differences in odor identification were due to a disadvantage of blind individuals stemming from lack of visual input to support the construction of internal categories of odors corresponding to red, white, and rose wines.

Iversen et al. (2015b) tested the ability of congenitally blind participants and sighted controls to discriminate and identify emotions from pads containing the odor of sweat obtained from people while viewing movies containing emotional scenes involving sexual arousal, disgust, fear, or amusement. A control condition with unused pads that did not involve sweat was included. Although the two groups performed similarly for the discrimination task, for the identification task the blind participants performed significantly above chance for identifying disgust and fear only, whereas the sighted participants performed at chance for all four emotions. Congenitally blind participants were significantly better than sighted controls at identifying fear using samples of male odor.

Guducu et al. (2016) tested congenitally deaf, congenitally blind, and sighted and hearing groups of teenagers. They measured olfactory thresholds, olfactory discrimination, and odor identification, and also analyzed total scores across measures. The deaf group showed significantly poorer thresholds and total scores than the other groups. No significant differences were observed between the blind group and the sighted and hearing groups.

Overall, the findings for enhanced and degraded olfactory abilities for blind or deaf individuals are broadly, but not completely, in line with P1 (*complexity*), P2 (*detection of changes*), and P6 (*experience and practice*).

7. Summary of enhanced and degraded olfactory abilities for blind or deaf individuals

Table 5 summarizes reports of significantly enhanced and degraded olfactory abilities for blind or deaf participants. Overall, the results indicate that blindness is associated with enhanced olfactory discrimination, awareness and identification of odors and emotions. A single study showed that deafness is associated with poorer olfactory thresholds, but further work is needed to draw firm conclusions. Although the findings regarding altered detection thresholds are inconsistent with P1, the number of studies showing significant effects of sensory loss are limited, and some studies have failed to find significant differences between sighted and blind controls for olfactory detection thresholds (Kärnekull et al., 2016; Smith et al., 1993; Sorokowska et al., 2020). More studies are needed to clarify how deafness and/or blindness affect olfactory abilities.

7.1. Thermal and gustatory task performance that is enhanced or degraded as a result of sensory loss

Changes in temperature might be used by some blind individuals as a cue when navigating. For example, the small drop in temperature resulting from an object casting a shadow might indicate the presence of a landmark. Thermal information could also provide useful cues regarding dangerous stimuli in the vicinity (Slimani et al., 2013) and object identity (Slimani et al., 2015). To our knowledge, the effects of deafness on thermal perception abilities have yet to be investigated, but congenital blindness has sometimes been shown to be associated with better discrimination and detection of thermal changes than for sighted controls, as described below.

Slimani et al. (2013) assessed thresholds for detecting increases and decreases in temperature, responses to suprathreshold heat stimuli, and pain thresholds for heat and cold, for congenitally blind participants and sighted controls. Participants also completed the Pain Vigilance and Awareness Questionnaire and the Pain Anxiety Symptoms Scale, to evaluate how they responded to and their attitudes towards painful events. There were no significant differences between the groups for detection thresholds, but the blind participants rated suprathreshold heat stimuli as significantly more painful than sighted participants and had lower heat and cold pain thresholds. Questionnaire data indicated that the blind group paid greater attention to threatening stimuli. The results are consistent with the idea that the lack of visual information regarding potentially dangerous stimuli in the vicinity results in blind people having greater sensitivity to painful thermal stimuli than sighted people. A follow-up study by Slimani et al. (2014) used similar methods to those of Slimani et al. (2013) but also tested late-onset blind individuals, who performed similarly to sighted controls. Enhanced discrimination abilities of the congenitally blind relative to sighted controls were reported for a task where participants were required to detect small temperature increases (Slimani et al., 2015).

Information regarding the temperature and bubbliness of drinks can be provided by auditory cues, as temperature affects the sound absorption properties of the drink, and different magnitudes of carbonation affect sound quality. Using large participant groups, Oleszkiewicz et al. (2023b) investigated the discrimination abilities of early- and late-onset blind, anosmic (individuals with impaired olfaction; age of onset not reported), and control groups listening to samples of water being poured at hot or cold temperatures, and with different levels of carbonation. Recorded pairs of sound samples of liquids being poured were presented, and participants were required to report which of the pair had the higher temperature liquid or was foamier/bubblier than the other. Discrimination accuracy for temperature judgments was significantly better for both blind groups than for controls, but there were no significant differences between the anosmic and control groups. The early-blind and anosmic groups were significantly more accurate at discriminating carbonation than controls, but this was not the case for the late-blind group.

Taken together, the findings are consistent with P1 (*complexity*) and P2 (*detection of changes*), and suggest that early visual deprivation is necessary for hypersensitivity to pain to develop in blind individuals (P7, *age of onset*).

Research on changes in gustatory abilities associated with sensory loss is sparse. Oleszkiewicz et al. (2023a) tested large samples of early- and late-onset blind, and early-onset deaf groups, as well as sighted and hearing control groups, using a taste identification paradigm. Taste sprays were presented at increasing concentration levels, and the participants chose between sweet, sour, salty and bitter taste options. It is not clear what limits performance in this task: the ability to detect the stimuli or the ability to map the chemical signals to the appropriate taste labels at low concentrations. The deaf participants showed significantly poorer performance for all tastes than controls, while the early-blind participants showed significantly higher sensitivity than controls for the salty taste only. Smith et al. (1993) reported no significant difference between sighted untrained controls and a mix of early- and late-onset blind participants in suprathreshold taste identification, intensity, and pleasantness tests. However, trained, sighted controls performed significantly better than the other groups, a finding that is discussed below.

Table 6 summarizes the results of studies of the thermal and gustatory abilities of participants with sensory loss for which significant differences between participants with sensory loss and controls were observed. The results are mostly consistent with the principles of the perceptual restructuring hypothesis. However, too few studies are available for firm conclusions to be drawn.

8. Discussion

8.1. The relationship between crossmodal mechanisms and the principles of the perceptual restructuring hypothesis

8.1.1. Crossmodal reorganization and enhanced sensory abilities (P1-3, 5–7)

There has been extensive work demonstrating that sensory loss leads to crossmodal reorganization of cortical areas that are deprived of sensory input. It has been argued that this brain plasticity is beneficial and underlies enhanced abilities in the intact modalities (changes in neural networks or other elements of brain physiology may underlie P2-3 and 5–6), and, in line with P7, the magnitude of cross-modal plasticity is dependent upon the age of onset of sensory loss (for in-depth discussions, see reviews by Bell et al., 2019; Collignon et al., 2009; Voss, 2019; Voss et al., 2010; Voss and Zatorre, 2012b). For example, for blind people, it has been suggested that recruitment of visual occipital areas to carry out auditory localization tasks may underlie enhanced auditory spatial abilities (Gougoux et al., 2005), or that practice-induced reorganization of visual occipital areas, in the event of vision loss, results in recruitment of these areas in verbal-memory processes (Amedi et al., 2003). In the case of deafness, cortical reorganization has been suggested to be associated with enhanced visual working memory and visual attention (Andin and Holmer, 2022) and enhanced visual localization abilities (Lomber et al., 2010).

There is also limited evidence suggesting that plasticity may occur outside the primary sensory cortices. Codina et al. (2011) investigated whether early-onset deafness affected neural structures responsible for processing vision in the retina and optic nerve head, prior to the visual cortex. Deaf participants showed a significantly larger optic nerve neural rim area than normally hearing controls, and the area was significantly correlated with visual sensitivity.

Overall, the majority of findings suggest that for significant differences in sensory abilities to arise following the loss of a sense, the task has to be complex, in line with P1 (*complexity*), and that for any form of sensory loss basic perceptual thresholds for intact senses mostly do not change following sensory loss in another modality.

In summary, crossmodal reorganization probably plays a significant role in the enhanced visual, haptic, olfactory, thermal and gustatory abilities following blindness or deafness that are summarized in Tables 1–6, and enhanced auditory abilities following blindness summarized in Tables 1–4 in Kolarik et al. (2021). However, for tasks that require calibration using an intact modality, loss of that modality leads to impaired performance. Examples of this are absolute distance judgments by blind individuals (Kolarik et al., 2017a) or visual temporal bisection by the deaf (Amadeo et al., 2019). This concept is encapsulated by P4 (*calibration requiring cues from the absent modality*).

8.1.2. Crossmodal calibration and degraded sensory abilities (P1, 3, 4)

An assumption of the perceptual restructuring hypothesis, as well as other hypotheses involving sensory calibration, such as the perceptual-deficiency hypothesis (Axelrod, 1959; Jones, 1975) and the crossmodal-calibration hypothesis (Gori et al., 2010), is that the senses operate and interact in order to provide the most accurate and precise information for interpreting the world. In general, the findings of the studies reviewed in the current paper support the idea that information from a more accurate sense can be used to calibrate a less accurate sense for specific stimulus dimensions or features (Tables 1 and 4). This is also the case for the effects of blindness on audition, as reviewed by Kolarik et al. (2021) and summarized in Table 3. It has been posited that due to the greater spatial acuity of the visual system, visual information is used to calibrate auditory space (Axelrod, 1959; Jones, 1975), and evidence has supported this assertion for normally sighted individuals (Aggius-Vella et al., 2022). Also, internal representations of auditory space are degraded for blind compared to sighted individuals (Aggius-Vella et al., 2019; Gori et al., 2014; Kolarik et al., 2017a).

Visual spatial acuity is superior to auditory spatial acuity, especially in the central field (Mills, 1958; Perrott and Saberi, 1990) and visual acuity is also superior to haptic acuity (Ernst and Banks, 2002). In environmental conditions where visual cues are unrestricted, visual distance perception is far more accurate and less variable than auditory distance perception (Anderson and Zahorik, 2014; Da Silva, 1985; Kolarik et al., 2016). As a result, in the spatial domain it is likely that visual information is used to calibrate auditory and haptic space and that blindness leads to degraded performance for complex tasks requiring well-calibrated internal representations, such as bisection or mental rotation (see Kolarik et al. 2021 and Table 3 for evidence regarding auditory abilities, and Table 4 for haptic abilities).

In the case of deafness, since visual spatial acuity is superior to auditory and haptic spatial acuity, auditory information is not used to calibrate visual and haptic space, and deafness is not significantly associated with degraded visual or haptic spatial abilities (see Tables 1 and 2, respectively). However, auditory temporal acuity is better than visual temporal acuity (Van Wassenhove, 2009), so it is likely that auditory information is used to calibrate visual temporal representations. There is evidence from a number of studies that hearing shapes temporal perception in both the visual and tactile modalities (Bolognini et al., 2012; Heming and Brown, 2005; Kowalska and Szelag, 2006; Papagno et al., 2016). For deaf people, the performance of tasks requiring complex visual temporal representations, such as bisection and production/reproduction of time intervals, is degraded (see Table 1; note that the performance of temporal tasks not requiring internal representations, such as temporal-order judgements, is in general enhanced rather than degraded by deafness).

In summary, the principles underlying the perceptual restructuring hypothesis predict that sensory abilities in intact modalities that would be enhanced by loss of another sense include those where information from the lost sense is not needed to calibrate the remaining senses. This would be the case for detection tasks, or discrimination tasks where spatial or temporal metrics are not involved and participants could use a strategy of comparing the magnitude/direction of change of “raw” cues, without the need to rely on internal representations of space or time. For example, an auditory relative distance discrimination task does not require an internal representation of where the two sounds are located in space. The task can be performed by reporting which of the two sounds has the greatest overall level, as this corresponds to the closer sound. If a primary sense such as vision is lost, sensorimotor cues from self-motion (e.g. attending to how sound cues change when turning the head or approaching a sound source) might be used as an alternative to vision when calibrating auditory space (Ashmead et al., 1998; Collignon et al., 2009; O’Regan and Noë, 2001). This is encapsulated by P5 (*mapping using cues from intact modalities*). But this does not appear to be sufficient in situations involving more complicated tasks, such as auditory azimuth bisection (Gori et al., 2014; Vercillo et al., 2016) and inferential navigation (Rieser et al., 1986; Seemungal et al., 2007), for which performance is degraded by vision loss. These tasks involve complex auditory spatial representations and visual spatial calibration information appears to play a vital role (for a discussion and review, see Kolarik et al., 2021).

8.1.3. The role of experience and practice (P6) and age of onset (P7)

In general, the evidence supports the propositions that, for tasks that do not require calibration using a missing or lost sense, greater experience and practice with an intact sense is associated with enhanced abilities and that earlier age of onset of sensory loss in one modality leads to greater changes in intact modalities; see Tables 1, 4 and 6 in the current paper, and Tables 1–4 in Kolarik et al. (2021). An example of this is provided by the findings of Wong et al. (2011), who reported that blind participants showed enhanced GOT performance for the fingers but not the lips, suggesting that braille experience was associated with increased haptic acuity. The implications of the findings of Wong et al. (2011) were discussed by Voss (2011), see their Fig. 1), who highlighted the lack of evidence demonstrating that intensive training in isolation results in crossmodal plasticity. Voss (2011) discussed the possible interaction between visual loss, intensive training, crossmodal plasticity and enhanced sensory abilities, which relates to the possible interaction of certain principles of the perceptual restructuring hypotheses. For example, experience and practice (P6) might relate to the age of onset (P7), as degree of plasticity may be age-dependent, being greatest during (mostly early) critical periods (Gori et al., 2010). The extent to which enhancement of certain abilities depends on blindness, plasticity, training and experience and the relationship between them requires further study. There is evidence that for certain auditory abilities, such as echolocation, with practice sighted participants are able to achieve performance approaching or as good as that for some blind participants (Norman et al., 2021; Teng and Whitney, 2011), suggesting that any echolocation advantage for blind participants is not due to blindness per se, but due to practice. Smith et al. (1993) also demonstrated the important role of training, by demonstrating that experienced sighted participants who worked for the Philadelphia Water Department and were trained for the Water Quality Evaluation Panel, scored significantly higher than untrained sighted participants and blind participants in odor detection, odor discrimination, and taste identification assessments.

Although most of the findings in the literature are consistent with the principles of the perceptual restructuring hypothesis, there are several inconsistencies (see Tables 1–6). In part, these might be associated with factors such as subjectivity related to certain perceptual judgments or testing heterogeneous groups with sensory losses. For example, when testing blind people, tactile experience due to proficiency with Braille for some participants but not others might introduce inter-subject variability (Alary et al., 2009). Delays in spatial processing early in development that are associated with sensory loss can sometimes be alleviated by using spatial cues from the intact senses (Kolarik et al., 2021). There can be uncertainty associated with findings related to P3 (*identifying the direction of change*) and P4 (*calibration requiring cues from the absent modality*), as these principles depend on whether individuals are able to learn associations between cues in the intact modalities and judged variables.

8.1.4. *Current issues involving sensory loss research*

There are several potential confounds and issues involving sensory loss research that may affect the findings, including the response mode for behavioral measurement, sign language capabilities in deafness research, and spatial and social independence and mobility. These are discussed next.

The response mode for behavioral measurement can affect performance in sensory loss research. Various tasks that have demonstrated significantly different performance between blind participants and controls have utilized spatially oriented motor responses, such as finger, hand, nose or head pointing or orienting the hands in a certain way (Finocchietti et al., 2015; Vercillo et al., 2018; Voss et al., 2015; Zwiers et al., 2001), or judgments linked to spatial features, such as ‘more clockwise’ (Gori et al., 2010; Millar, 1976), or judging distance in absolute terms (Kolarik et al., 2017a). There is controversy regarding the extent to which such behaviors are typically used by blind people. It has been suggested that differences in performance between blind and sighted individuals may result from differences in goal-directed hand movements, rather than changes in spatial-hearing abilities of the blind (Battal et al., 2020). Response mode might also affect performance in other domains and for different forms of sensory impairment. To establish whether response mode affects behavioral performance, future studies could use various response modes within a single study, such as a pointing task in addition to a psychophysical minimum-audible-angle task (Mills, 1958) that avoids possible confounds due to sensorimotor involvement (Battal et al., 2020).

Sign language abilities, the age of sign language acquisition, and levels of competency may affect task performance in research involving deaf participants. Sign language is a visual language working across central and peripheral visual fields, and it is possible that the degree of expertise with sign language may moderate the effects of visual attention, and potentially also affect motion discrimination and temporal order judgments. There are few studies that have included participant groups to control for potential effects of sign language, e.g. deaf signers, hearing signers, deaf non-signers, and hearing non-signers (Bosworth and Dobkins, 2002; Dye et al., 2009; Fine et al., 2005).

For people who have sensory loss, the degree to which they are independent in their mobility and spatial orientation may also affect performance using intact modalities. Differences in mobility and independence across individuals and groups with sensory loss are a potential confound, as studies most often match groups with sensory loss and controls for age and gender, and sometimes education level (Chen et al., 2006), but the degree of ‘spatial’ independence is rarely controlled for, even though the ability to navigate independently affects plastic changes in brain structure (Maguire et al., 2000). It is possible that these changes also affect social cognition (Montagrin et al., 2018; Rubin et al., 2014; Tavares et al., 2015). To identify potential confounding issues, the degree to which people with sensory loss who take part in research are independent navigators or travelers, and/or are independent in social contexts (i.e., function without the need for guides or interpreters) should be reported, which is not the case for most published research.

8.1.5. *Directions for future study, implications, and applications involving the perceptual restructuring hypothesis*

Overall, the majority of the evidence is consistent with the seven principles of the perceptual restructuring hypothesis. The principles allow predictions to be made regarding abilities in the intact senses that remain to be investigated. For example, humans are able to localize the azimuth of odor sources, which Von Békésy (1964) suggested could be achieved using inter-nostril odor concentration and timing differences, similar to the process of using binaural auditory cues to localize sound sources. Blind and sighted controls have been reported to show similar performance for odor lateralization (judging which nostril was stimulated by an odor), and for angular odor localization, which was measured by the difference, in degrees, between actual odorant position and the judged odorant position (Sorokowska et al., 2019a). However absolute olfactory distance judgements have not yet been assessed for blind individuals. It is predicted that congenital blindness would result in a degraded ability to judge the distance of olfactory sources (P4, 7). Another prediction is that early-onset blindness will significantly increase the accuracy of judging whether a bus or truck is approaching or receding, compared to accuracy for sighted controls or late-onset blind participants (P1, 3, 7).

It is important that people with acquired visual or auditory loss are provided with evidence-based information regarding which abilities will likely change for better or worse following the loss and the magnitude of change that they can expect, so that they can factor this knowledge into their daily and planned activities. Popular beliefs regarding sensory compensation in populations with and without sensory loss do not always align with the evidence (Pieniak et al., 2022). For example, both normal-hearing and hearing-impaired people tend to believe that gustatory abilities are improved following deafness, but Pieniak et al. (2022) and Oleszkiewicz et al. (2023a) showed that deafness instead was associated with poorer taste identification.

The studies described above generally investigated the effects of sensory loss on performance using a single intact modality. However, a more comprehensive investigation of the effects of the loss of a single sense on performance using multiple intact senses (e.g. the effects of blindness on judgment of type of material (e.g. cloth, paper, aluminum foil) made via tearing the material, which would involve hearing, tactile and motor abilities, would provide further insight regarding how the senses interact. It is currently unknown whether the loss of a single sense results in changes in abilities across multiple senses to a similar degree or whether compensation in a particular sense might be lesser or greater than for the other senses. The papers reviewed in the current work also highlight several gaps in the literature. Little work apart from that of Oleszkiewicz et al. (2023a) has investigated the effect of sensory loss on gustation, and research investigating the olfactory abilities of deaf individuals is sparse (see Table 5). Research has generally focused on the effects of blindness and deafness (or both). Research is needed to investigate how tactile, olfactory, and gustatory sensory losses affect the intact senses. It is probable that the principles of the perceptual restructuring hypothesis will be refined to encapsulate new results as further work on sensory loss is conducted.

Studies of hearing loss have generally focused on the effects of full deafness on abilities in the intact senses. More research regarding the effects of partial hearing loss would indicate how the magnitude of hearing loss affects tactile, visual or olfactory abilities. For example, it may be the case that increased magnitude of hearing loss is associated with greater changes in the intact senses, as occurs for audition in the case of partial visual loss (Kolarik et al., 2020). However, this has yet to be investigated. Also, more work is needed to investigate the possible effects of late-onset deafness. Further research contrasting haptic abilities in deaf-blind individuals and those with deafness or blindness only might be useful in determining whether the benefits of crossmodal plasticity increase when additional cerebral resources are available (Voss, 2011), especially in light of the greater reliance on touch of deaf-blind individuals (Papagno et al., 2016). It was recently proposed that vestibular damage, which is prevalent in the deaf population, might play a significant role in visual or tactile task performance by deaf individuals (Moïn-Darbari et al., 2021). Further work is needed to examine this. Finally, the studies reviewed in the current paper have tended to focus on accuracy (e.g. Nava et al., 2008; Neville and Lawson, 1987; Sladen et al., 2005) but variability should be investigated more closely to clarify the effect of sensory loss on abilities in the intact senses.

An area for future research regards the extent to which age affects the degree of plasticity of sensory systems, and how this interacts with the age of onset of sensory loss. An influential approach has involved the necessity of sensory input during critical periods for cross-modal sensory calibration. Critical periods are time-frames of development during which the brain is especially plastic (Gori et al., 2010). Heimler and Amedi (2020) argued that, based on evidence in the literature, brain plasticity decreased as age increased, but plasticity processes could occur across the adult lifespan. Sensory training, for example with sensory substitution devices (Chebat et al., 2007; Kupers et al., 2010; Striem-Amit et al., 2012), might provide a means to restart such processes. Research on this topic would help clarify the relationship between P6 (experience and practice), and P7 (age of onset). There is a need to systematically address these issues for various age groups, including children, for whom there is currently a gap in the literature.

The perceptual restructuring hypothesis could have practical implications for the rehabilitation of people with sensory losses. By predicting and identifying sensory abilities that become degraded following the loss of a major sense, improvements might be made using training, or by using assistive technology that provides various forms of information, or rehabilitative technology that stimulates brain plasticity. Strategies could also be devised to target the abilities that are more likely to get better, in order to exploit them to maximum effect for practical applications in daily life, such as echolocation training for blind people (see Kolarik et al. 2021 for a discussion of the training of auditory abilities in the event of blindness). Practical applications might involve navigation, orientation, or the design of indoor and outdoor environments that provide cues that people with sensory loss are able to use effectively due to their enhanced abilities. Products and experiences could likewise be designed to provide cues to help inform the consumer-based choices of individuals with sensory loss (Oleszkiewicz et al., 2023b).

Future research could utilize computational modelling to investigate how well current models of sensory processing predict behavioral results for control participants and those with sensory loss. For example, the model developed by Moore et al. (2018) and adopted as an ISO standard (ISO 532-3, 2022) provides estimates of two aspects of loudness: a running estimate of the momentary impression of loudness and an estimate of the overall loudness impression of the entire stimulus. These estimates can be used to predict judged distances for the static and dynamic sounds made by blind individuals and sighted controls, which we are currently investigating in our laboratory.

The current paper provides an overview of present knowledge regarding how a wide range of abilities are affected by different forms of sensory loss and provides evidence that broadly supports the seven principles of the framework underlying the perceptual restructuring hypothesis. In most cases, the principles lead to correct predictions as to how visual, auditory, tactile, thermal and gustatory spatial and non-spatial abilities change for the intact senses following early- or late-onset deafness or blindness. The framework may also help to resolve issues associated with contrasting findings in the literature. Currently, the point of view sometimes expressed in the literature is that conclusions regarding whether enhancement or degradation of abilities in an intact modality following sensory loss cannot be reached, due to reports of both occurring depending on the task, for example for tactile processing following deafness (Xiao et al., 2021) or for visual abilities following deafness (Papagno et al., 2016). The current work aims to clarify this issue on the basis of the seven principles, which in most but not all cases give accurate predictions of whether an ability will be enhanced or degraded following sensory loss in another modality.

9. Conclusions

The review shows that, in general, sensory systems operate under a set of common principles that spans modalities and different forms of sensory loss. This comprehensive framework allows interpretation of a wide range of research findings, without requiring recourse to interpretation according to the compensation or perceptual deficiency hypotheses that were previously applied in an ad-hoc manner, depending on whether enhanced or degraded task performance was observed. The following general conclusions can be made. Firstly, the evidence reviewed is broadly in line with the principles underlying the perceptual restructuring hypothesis. For individuals with intact senses, vision is used to calibrate auditory space and haptic space, and audition is used to calibrate visual time representations. For individuals with sensory loss, lack of calibration information from a more accurate sense degrades abilities in the intact modalities when the task would be performed best using internal representations of the external world, either spatial or temporal. This contrasts with discrimination and detection judgments for which internal representations are not required. For such judgments, abilities in the intact modalities are often enhanced following sensory loss, probably due to the beneficial effects of crossmodal plasticity and intensive training. Basic sensory thresholds usually do not change in the intact modalities as a result of sensory loss, although there are some exceptions. The effects of deafness on haptic abilities and the effects of blindness or deafness on thermal and gustatory abilities are mixed regarding consistency with the perceptual restructuring hypothesis, although the relative paucity of studies that have investigated these sensory configurations means that firm conclusions cannot yet be drawn.

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Data availability

Data will be made available on request.

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