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Aftereffects of visuomanual prism adaptation in auditory modality: Review and perspectives

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ABSTRACT

Visuomanual prism adaptation (PA), which consists of pointing to visual targets while wearing prisms that shift the visual field, is one of the oldest experimental paradigms used to investigate sensorimotor plasticity. Since the 2000's, a growing scientific interest emerged for the expansion of PA to cognitive functions in several sensory modalities. The present work focused on the aftereffects of PA within the auditory modality. Recent studies showed changes in mental representation of auditory frequencies and a shift of divided auditory attention following PA. Moreover, one study demonstrated benefits of PA in a patient suffering from tinnitus. According to these results, we tried to shed light on the following question: How could this be possible to modulate audition by inducing sensorimotor plasticity with glasses? Based on the literature, we suggest a bottom-up attentional mechanism involving cerebellar, parietal, and temporal structures to explain crossmodal aftereffects of PA. This review opens promising new avenues of research about aftereffects of PA in audition and its implication in the therapeutic field of auditory troubles.

1. What is prism adaptation? Experimental paradigm and aftereffects – main objective of the present review

Have you ever tried to cross the street without using your sense of hearing or sight? This is more difficult than when we have access to all our senses. We are living in a multisensory world, continuously bombarded with sensory inputs from various sources. This quantity of information is simultaneously captured and transmitted to the brain through our seven sensory systems: vision, audition, olfaction, taste, touch, proprioception, and vestibular system. The interaction with our physical and social environment is made possible through these senses which work together to allow us to have more accurate and consistent perception. Faced with receiving a multitude of sensory stimuli, our brain has to decide whether to integrate the stimuli or separate them. This choice is based on the degree of spatial, structural, and temporal congruence of the stimuli from different modalities. Using this disparate and complex multisensory information, our brain manages to build a single and consistent percept of our external world (for reviews see Bolognini et al., 2015; Calvert and Thesen, 2004; de Dieuleveult et al., 2017; Freiherr et al., 2013; Stein and Meredith, 1990). This process, which is named multisensory integration, is crucial for perception, cognition and action (de Dieuleveult et al., 2017). Interactions with our environment highly rely on sensorimotor coordination (i.e., between movements of body segments and information from our static or dynamic external environment; e.g., Porac and Coren, 1981). Accurate multisensory processing facilitates behavioral responses to our environment and in particular enables sensorimotor control to be optimized (for reviews see Bolognini et al., 2015; de Dieuleveult et al., 2017).

Sensorimotor processes involve sensorimotor plasticity, which is defined as our ability to produce appropriate movements in response to environmental (e.g., gravity modulation in astronauts) or body changes (e.g., when growing up). Experimentally, it is possible to induce sensorimotor plasticity by disturbing our senses, for example through the application of dynamic perturbations (e.g., robotic arm: Michel et al., 2018; Coriolis force: Sarlegna et al., 2010) or the use of visuomotor rotation (e.g., Krakauer et al., 2000). One of the oldest experimental paradigms used to study sensorimotor plasticity is visuomanual prism adaptation (PA; Fig. 1; von Helmholtz, 1867, cited in McLaughlin and Webster, 1967), which consists of pointing to visual targets while wearing prisms that shift the visual field laterally in its classic form (Kornheiser, 1976) or vertically (Bonnet, Poulin-Charronnat, Ardonceau, et al., 2022; Bultitude et al., 2012; Martin et al., 2001). PA induces

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a direct sensorimotor and intersensory conflict (Redding et al., 2005) and it can be explained because of changes in vision, proprioception and motor response (Kornheiser, 1976; Welch, 1974; Welch et al., 1974). The experimental paradigm is divided into three phases: before wearing the prism (i.e., before PA; Fig. 1.A.), the pointing movement is correct; during exposure (i.e., during PA; Fig. 1.B.), the pointing movement is shifted in the direction of the optical deviation and is gradually corrected until obtaining a correct pointing movement; after prism removal (i.e., after PA; Fig. 1.C.), the pointing movement is shifted in the opposite direction to the optical deviation (e.g., O'Shea et al., 2014; Redding and Wallace, 2006a; Rossetti et al., 1993; for a review see Fleury et al., 2019). These pointing errors, which are observed after prism removal, are called sensorimotor aftereffects and testify to the successful development of PA (e.g., Michel et al., 2003; for reviews see Prablanc et al., 2020; Redding et al., 2005).

Beyond the sensorimotor framework, PA produces cognitive aftereffects involving mental abilities. Since Colent et al. (2000) pioneer study in healthy participants, over the past 25 years several studies have shown an extension of cognitive aftereffects of PA in this population (for a review see Michel, 2016). PA produces aftereffects in visuospatial representation (i.e., the ability to build a mental map of space; Colent et al., 2000; Fortis et al., 2011; Goedert et al., 2010; Michel and Cruz, 2015; Striemer and Danckert, 2010), spatial attention (Loftus et al., 2009), haptic perception (Girardi et al., 2004), hierarchical processing (i.e., perception of local-level and global-level information; Bultitude and Woods, 2010) and posture (Michel et al., 2003), and in mental scales of spatially valued elements (i.e., the spatial attribute given to an element) such as numbers (Loftus et al., 2008), letters (Nicholls et al., 2008), and auditory frequencies (e.g., Michel et al., 2019). Altogether, PA produces cross-modal cognitive aftereffects involving several sensory systems, which are not directly involved in sensorimotor and intersensory conflict (i.e., vision and proprioception) during PA.

The present paper aimed to review studies showing aftereffects of visuomanual PA in the auditory modality. To meet this challenge, we not only considered auditory modifications in healthy humans but also the therapeutic potential of visuomanual PA for tinnitus patients. For the first time, we address recent issues in exploring cognitive aftereffects of visuomanual PA in audition by considering the visuoauditory interactions, spatial attributes of auditory frequencies and auditory attention. We first briefly present visuoauditory interactions naturally present in humans regardless of PA, to show adaptation of vision observed when audition is impaired (i.e., deaf people) or conversely, how audition adapts when vision is impaired (i.e., visually impaired people). The following sections thus report separately changes in different aspects of the auditory modality after visuomanual PA (i.e., auditory frequency mental representations and auditory attention) and address the therapeutic potential of PA for patients suffering from unilateral tinnitus. We then discuss possible explanations of how aftereffects of visuomanual PA can occur within the auditory modality. In the light of recent results, the present review attempts to provide new insights into how changes in the auditory modality can occur following visuomanual PA and supports the therapeutic potential of PA for unilateral auditory deficits. We conducted an online search in PubMed/MEDLINE and Google Scholar electronic databases for original studies and review articles of relevance in English. Search terms included "prism adaptation", "audition", "auditory modality", "multisensory integration", "auditory spatial attention", and/or "tinnitus". In addition, related papers were manually added through cross-referencing. Given the novelty of the topic and the limited number of studies, the publication date of articles was not a selection criterion.

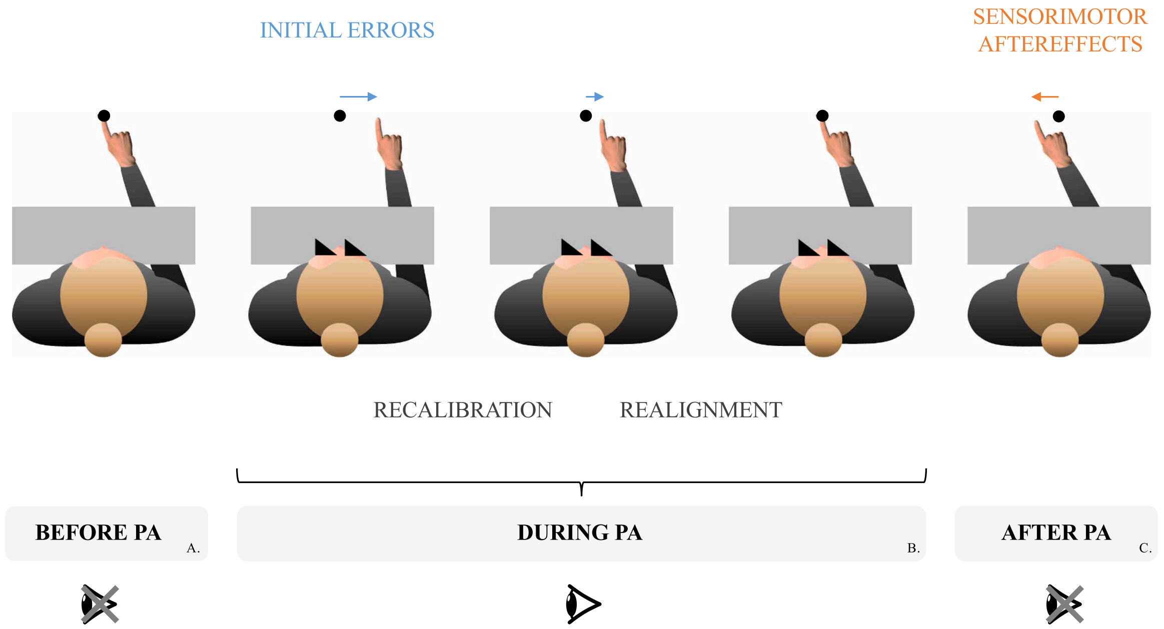

Fig. 1. An example of experimental paradigm of prism adaptation. The black triangles represent rightward optical deviation. PA: Prism adaptation. A. Participants are seated in front of a visual target. A chinrest maintains the head aligned with the trunk and prevents the participants' view of the right hand at the beginning of each pointing movement. Measures before prism adaptation provide a baseline of the sensorimotor performance of participants, who correctly point to the visual target with closed eyes (i.e., open-loop pointing during which targets are shown between each trial but vision is occluded when participants are pointing to visual targets; Prablanc et al., 2020). B. In the illustration, participants wear prismatic glasses deviating the visual field to the right side. Rapid closed-loop (i.e., open eyes) pointing movements are shifted toward the side of the optical deviation (blue arrow), and the motor error reduction occurs during the recalibration. The term 'recalibration' refers to the fast and conscious strategic component of the adaptation, which occurs during the early phase of error reduction involving a corrective motor response. The second phase of the adaptation reduces spatial discordance through the realignment. The term 'realignment', known as the "true" adaptation per se, refers to the slow and automatic adaptative component of the adaptation involving visual and proprioceptive adaptations. C. Following prism removal, participants make open-loop pointing errors in the opposite direction of the optical deviation (orange arrow). These sensorimotor aftereffects testify to the good development of the adaptation. *Adapted from* Rode et al. (2015).

2. Interactions between vision and audition

In everyday life, visual and auditory perceptions coincide relatively precisely and influence each other. In visuoauditory interactions, visual information can reinforce perceptual judgments in auditory perception (Opoku-Baah et al., 2021). A well-known ecological instance of visuoauditory interaction is multimodal speech: when someone speaks to us seeing lip movements facilitates oral comprehension. Recently, the pandemic context associated with mask wearing highlighted the importance of visuoauditory interactions in social exchanges involving verbal language (Opoku-Baah et al., 2021). Another example of these interactions is the improved detection of visual targets in the presence of an auditory cue when the cue and the target are presented on the same side (Buchtel and Butter, 1988). The influences between audition and vision are therefore useful for accurate perception of our environment. However, these interactions sometimes give rise to a sensory conflict, often leading to perceptual transformation commonly referred to as illusions. In an attempt to explain aftereffects of visuomanual PA in the auditory modality, the present section focuses on the natural link between the visual and auditory systems independently of any visuomanual adaptation. Firstly, the main explanations showing how visuoauditory interactions can lead to cross-modal illusions are presented. We then briefly review ways in which one sensory system can adapt when the other is impaired.

2.1. When visuoauditory interactions lead to crossmodal illusions

Cross-modal illusions occur when what we perceive with one modality affects what we experience in another modality. They represent perceptual strategies for dealing with intersensory conflicts in order to give coherence to the ongoing perceptual experience. To keep within the scope of the present review, we focus on two well-known visuoauditory illusions: ventriloquism and the McGurk effect.

Historically, the term “ventriloquism” means “belly talking” (Opoku-Baah et al., 2021). A ventriloquist is able to synchronize her/his speech with the mouth movements of a puppet minimizing her/his own lip movements. This illusion gives the feeling that a puppet is talking to us: it is a visual capture of speech. The low spatial resolution of the auditory system compared to the visual system explains this effect of spatial ventriloquism. While vision provides more accurate information on the location of events, audition is the sense best suited to temporal judgments (Gori, 2015). In that way, sounds can disturb visual perception: when a single visual flash is presented with multiple auditory beeps, participants report seeing multiple flashes (Shams et al., 2000). If the rhythm of the auditory stimulus varies, then the visual stimulus seems to flash according to the rate of the stimuli heard (Gori, 2015). The other well-known illusion involving visuoauditory interactions is the McGurk effect. This perceptual illusion, present in both adults and children, is based on the interference that occurs when an auditory syllable associated with an incongruous visual syllable results in the perception of a new syllable. For instance, when the syllables /ba-ba/ are heard over the lip movements of /ga-ga/, our auditory perception is /da-da/ (McGurk and MacDonald, 1976).

Even though multisensory integration can result in cross-modal illusions, it is a crucial process to interact effectively with the environment. We need to perceive sensory information throughout our sensory systems in order to integrate it and produce correct motor actions in response to the external system. But what happens if a sense is damaged or disturbed? Compared to unaltered sensory systems, an impaired sense can lead to modified multisensory integration with the impaired system being compensated by another. These changes in multisensory integration can result in behavioral adaptations because of a more developed sense (e.g., better auditory abilities in visually impaired people).

2.2. Sensory compensation in visually impaired and deaf people

Visuoauditory interactions can be disrupted naturally or experimentally, and it is well known that when one sense is absent, another can develop more. For example, visually impaired people develop enhanced auditory abilities compared to those with normal vision, this is all the more pronounced when blindness occurs early in life (i.e., up to two years old; Gougoux et al., 2004). The absence of a visual input associated with an increased auditory activity can lead to reorganization of the auditory cortex (i.e., an extension of the auditory cortex and of the tonotopic map; Elbert et al., 2002). As a result, visually impaired people have better auditory localization (Gougoux et al., 2005; Lessard et al., 1998) and pitch discrimination (Gougoux et al., 2004). Enhanced auditory localization can also occur when healthy participants are deprived of light for 90 minutes. Lewald (2007) showed that participants were more accurate in pointing to auditory targets after light deprivation, and they returned to baseline after 180 minutes of re-exposure to light. These results indicate that the pathological or experimental transient absence of vision leads to adaptations within the auditory modality.

This kind of sensory compensation also exists within the visual modality in the absence of auditory perception. Heimler et al. (2017) showed that deaf people had difficulties in ignoring visual distractors when they have to process other sensory information (i.e., tactile). This multisensory interference is more marked when visual stimuli are ipsilateral to the other stimuli to be processed. Another study found that compared to healthy adults, deaf adults perceived an illusion of a double flash of light when a single flash was paired with an irrelevant double somatosensory stimulus (i.e., “air puffs”) delivered next to the eye (Karns et al., 2012). As for blindness, deafness seems to change multisensory integration, including multisensory competition when an irrelevant stimulus must be ignored.

Deprivation of visual or auditory perception has been shown to result in enhanced auditory or visual perception, respectively. This sensory compensation, together with the visuoauditory illusions described above, testify to a strong natural link between the visual and auditory systems. In the following sections, we describe how modifying vision with prism glasses can interfere with auditory perception.

3. Aftereffects of visuomanual prism adaptation on intact auditory frequency mental representation

3.1. Pseudoneglect in auditory frequency mental representation

Auditory frequency mental representation can be defined as our ability to associate pitch (i.e., the attribute of auditory sensation allowing the classification of sounds as low or high, as on a musical scale; Bendor and Wang, 2006) with a spatial feature. Auditory frequencies are mentally represented along horizontal and vertical lines: low auditory frequencies are associated with the left and lower parts of space, whereas high auditory frequencies are associated with the right and higher parts of space (see Fig. 2.a; Lidji et al., 2007; Rusconi et al., 2005, 2006). To test spatial associations of auditory frequencies, Lidji et al. (2007) used stimulus-response compatibility tasks by manipulating the orientation of the response device (i.e., horizontal or vertical), the musical expertise of participants and the task (i.e., instructions and stimuli). Musicians and non-musicians were instructed to indicate if the presented tone was higher or lower than a referent tone by pressing the corresponding key. Participants were faster and more accurate when responding to high auditory frequencies with the right and upper keys, and to low auditory frequencies with the left and lower keys. The authors then used the same experimental paradigm and this time asked participants to make an instrumental timbre judgment. They showed that the vertical spatial association of auditory frequencies (i.e., low frequencies/lower key; high frequencies/higher key) was again present irrespective of musical expertise, whereas the horizontal spatial

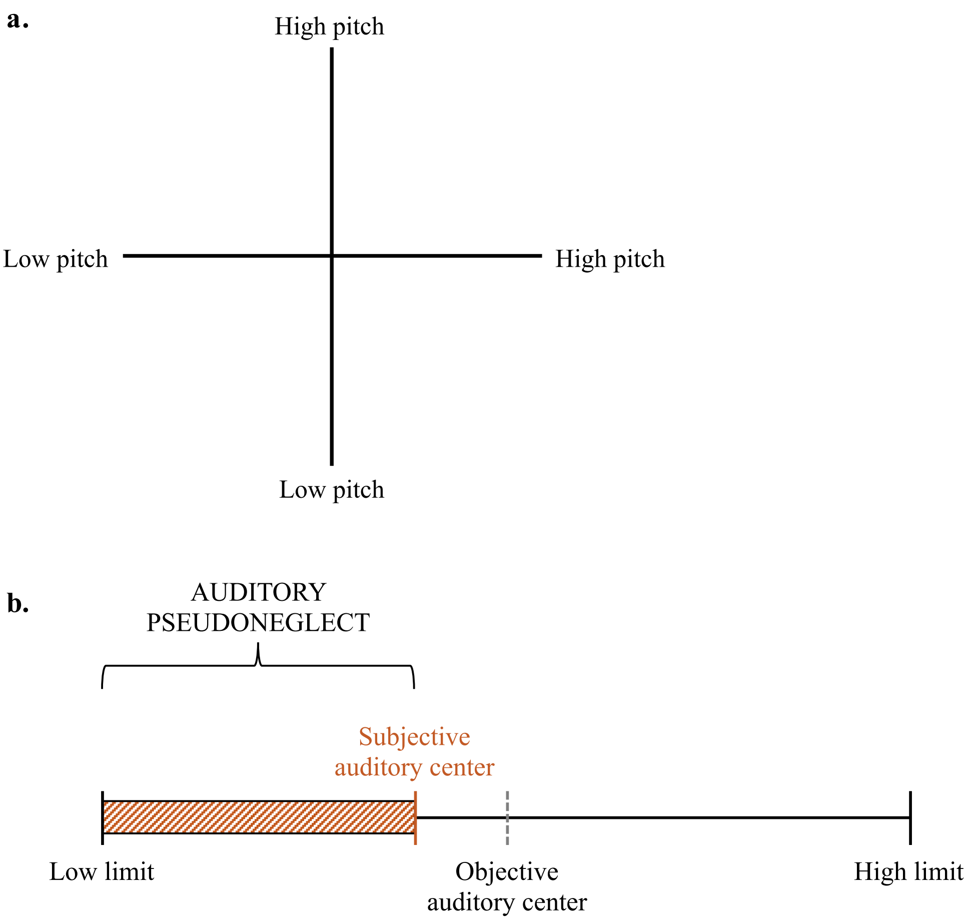

Fig. 2. Auditory frequency mental representation. a. Mental representation of auditory frequencies in the lateral and vertical dimensions. b. Schematical representation of auditory pseudoneglect in an auditory interval bisection judgment task. *The segment represents the auditory interval; the hatched rectangle illustrates the quantity of perceived low frequencies; the subjective center is defined as the auditory center estimated by someone; the objective center corresponds to the real physical auditory center. Adapted from* Michel et al. (2019).

association of auditory frequencies (i.e., low frequencies/left key; high frequencies/right key) was observed only for musicians. In sum, the vertical mental representation of auditory frequencies seems to be automatically activated regardless of musical expertise. In contrast, the horizontal mental representation of auditory frequencies appears to be automatically present in musicians and would occur in nonmusicians only when pitch is task relevant.

This link between auditory frequencies and space was also observed when participants performed a manual line-bisection task (i.e., experimental paradigm used to assess visuospatial representation; Jewell and McCourt, 2000) while being exposed to auditory stimuli. Low auditory frequencies, which are mentally represented to the left side of space, shifted the estimation of the line center toward the left, whereas high auditory frequencies, which are mentally represented to the right side of space, shifted the estimation of the line center toward the right (Ishihara et al., 2013).

Recent studies have shown an auditory representational bias within the mental spatial representation of auditory frequencies in healthy people. Michel et al. (2019) used an innovative auditory interval bisection judgment task, which consisted in playing three pure tones of different auditory frequencies: the first two tones were the limits of the auditory interval and the third was the target auditory frequency (TAF). Participants had to indicate whether the TAF was closer to the first or the second limit of the auditory interval. For half of them, the TAFs were closer to the high limit of the auditory interval and for the other half, they were closer to the low limit of the auditory interval. Michel et al. (2019) measured the percentage of 'low' responses and calculated the subjective auditory center as the frequency for which the participants provided 50 % each of 'low' and 'high' responses. Participants initially perceived more TAFs as being closer to the high than to the low limit of the auditory interval (i.e., percentage of 'low' responses lower than 50 %), and their subjective auditory center was lower than the objective auditory center. Healthy individuals showed a bias directed toward the lower limit of the auditory interval, which is associated with the left and lower parts of space (see Fig. 2.b; Bonnet et al., 2021; Bonnet, Poulin-Charronnat, Ardonceau, et al., 2022; Michel et al., 2019). Michel et al. (2019) named this bias "auditory pseudoneglect" in reference to the pseudoneglect bias observed in visuospatial representation (e.g., Bowers and Heilman, 1980; McCourt and Jewell, 1999) and in the representation of spatially valued elements such as numbers (Loftus et al., 2009). Auditory pseudoneglect was observed in a wide auditory spectrum (1850–4100 Hz), whatever the musical expertise (Bonnet et al., 2021). As previously mentioned, auditory frequencies are associated with a part of space (i.e., spatially valued elements; see Fig. 2.a.). Some spatially valued elements, such as numbers, are supposed to share a common magnitude system in the parietal cortex (e.g., Walsh et al., 2003). An inhibition of the right posterior parietal cortex by repetitive transmagnetic stimulation decreased numerical pseudoneglect (Oliveri et al., 2004). Auditory pseudoneglect could thus be explained, at least in part, by the right hemispheric dominance of the posterior parietal cortex in mental representation of space (e.g., Fink et al., 2000, 2001).

3.2. Changes in auditory frequency mental representation following lateral and vertical visuomanual prism adaptation

Considering naturally present visuoauditory interactions, the spatial attribute of auditory frequencies and the cross-modal nature of aftereffects following visuomanual PA, recent studies have raised questions about changes in the auditory frequency mental representation after visuomanual PA. Michel et al. (2019) were the first to show aftereffects of lateral prism adaptation on mental representation of auditory frequencies. In their study, healthy participants performed the auditory interval bisection judgment task (i.e., indicating whether the TAF was closer to the first or the second limit of an auditory interval; see Section 3.1.) within one auditory interval (700–1300 Hz). They had to give their response by indicating whether the TAF was closer to the first or the second auditory limit without mentioning the pitch (i.e., low or high). The percentage of perceived low auditory frequencies increased in musicians after visuomanual PA to a leftward optical deviation compared to before PA. This result indicated a shift of the subjective auditory center toward the high limit of the auditory interval, which is associated with the right part of space, after leftward visuomanual PA. Similar aftereffects following leftward visuomanual PA were then replicated across a wide auditory spectrum (1850–4100 Hz) in musicians and, for the first time, in non-musicians (1850–3700 Hz; Bonnet et al., 2021). In both these experiments, the instructions were more explicit in terms of pitch compared to Michel et al.'s (2019) previous work. Bonnet et al., (2021) asked participants to indicate whether the TAF was closer to the low or the high limit of the auditory interval by answering 'low' or 'high' during the auditory interval bisection judgment task. Moreover, aftereffects of leftward visuomanual PA were observed in a pseudorandomized presentation of auditory intervals in musicians (auditory spectrum: 1850–4100 Hz). The auditory interval bisection judgment task was then modified to be less difficult for non-musicians by using a blocked trial presentation of auditory intervals and an auditory spectrum of reduced amplitude (1850–3700 Hz). No aftereffects occurred following rightward visuomanual PA regardless the musical expertise or the experimental paradigm used, whereas the easier experimental paradigm strengthened the aftereffects observed after leftward visuomanual PA in non-musicians. Musical training produces plasticity in the auditory network, making it more efficient in auditory processing (Herholz et al., 2008). Compared to non-musicians, the gray matter volume of musicians is higher in the Heschl's gyrus (Gaser and Schlaug, 2003), which is considered as the pitch center (Schneider et al., 2002). Musicians have better pitch perception and they are more sensitive to frequency variations than non-musicians. Altogether, differences in brain structures and pitch discrimination ability between musicians and non-musicians could explain the influence of musical expertise.

As previously mentioned in Section 2.1., the vertical auditory frequency mental representation appears to be more automatic than the horizontal one in non-musicians. Taking this into account, vertical visuomanual PA would thus seem to be more appropriate to modify the auditory frequency mental representation in non-musicians. Nevertheless, the literature about vertical prism adaptation is relatively sparse and only one study has assessed cognitive aftereffects of vertical prism adaptation on auditory mental representation (Bonnet et al., 2022). Non-musician participants performed the same auditory interval bisection judgment task as previously mentioned, within a single auditory interval (724–1330 Hz). The percentage of perceived low auditory frequencies (i.e., 'low' responses) was measured and the subjective auditory center was computed. Visuomanual PA to a downward optical deviation significantly increased the percentage of 'low' responses and shifted the subjective auditory center toward the high limit of the auditory interval that is associated with the higher part of space. Non-musicians perceived more tones as low auditory frequencies, after downward visuomanual PA than before PA. No aftereffects occurred following visuomanual PA to an upward optical deviation (Bonnet et al., 2022).

In sum, leftward and downward visuomanual PA modify the auditory frequency mental representation of healthy individuals by shifting the subjective auditory center toward the high auditory frequencies, which are associated with the right and the high sides of space. Pitch processing (Hyde et al., 2008; Liégeois-chauvel et al., 2001; Zatorre and Belin, 2001), multimodal (Stein and Stanford, 2008) and mental representations (Göbel et al., 2006; Michel, 2016) are lateralized in the right hemisphere. Aftereffects in the auditory frequency mental representation could be due to the ability of visuomanual PA to act on lateralized systems, more specifically on the right dominance in pitch discrimination and auditory frequency mental representation.

4. Aftereffects of prism adaptation on auditory spatial attention

Our sound environment is made up of several sound sources that combine before reaching our ears. Auditory spatial attention plays an important role in auditory source segregation and selection. Allocation of the auditory spatial attention allows us to localize an auditory target of interest. Although the literature on aftereffects of visuomanual PA on auditory spatial attention remains relatively poor, a few studies have shown changes in divided auditory attention and sound source localization.

4.1. The divided auditory attention

4.1.1. Right ear advantage when auditory stimuli are verbal

Divided auditory attention is usually assessed with a dichotic listening task, consisting of presenting two different auditory stimuli simultaneously to the participant, one stimulus to the left ear and the other to the right ear (e.g., Broadbent, 1952; Prete et al., 2018; Westerhausen and Kompus, 2018). In 1967, Kimura was the first researcher to observe a response asymmetry between the left and right ears during dichotic listening of verbal stimuli. This classical auditory asymmetry, which is named right ear advantage (REA; D'Anselmo et al., 2016; Kimura, 1967), can be detected and quantified by measuring the lateralization index (LI; Bellmann et al., 2001). The more positive the LI value, the more marked the auditory asymmetry toward the right ear; conversely, the more negative the LI value, the more marked the asymmetry toward the left ear.

Kimura (1967) explained REA through hemispheric specialization and the relay of information via the auditory nerve, which would be carried out only by the contralateral fibers in a verbal dichotic listening situation. The nerve message perceived in the right ear would reach the left hemisphere more quickly (specialized in verbal stimuli processing; i.e., the left temporal lobe; Michel et al., 1986) compared to the auditory nerve message perceived in the left ear (Kimura, 1967). Complementary to this theory, Kinsbourne (1970) suggested that REA could be due to a preactivation of the left hemisphere during early stages of perceiving verbal stimuli. This preactivation would lead to a specific orientation of attention toward stimuli in the opposite right auditory field. When listening to recognize verbal stimuli, people would activate the left hemisphere in advance and this preactivation would shift attention toward the right (Kinsbourne, 1970).

Perception is considered to be a sequence of information processing steps in which attention has a major function in the efficient processing of stimuli. Attentional modulation could contrast with the initial processing of verbal information. In a verbal dichotic listening task, REA was shown to be present when attention was or was not focused toward the right ear, whereas REA decreased or disappeared when attention was focused toward the left ear (D'Anselmo et al., 2016; Hiscock et al., 1999; Hugdahl et al., 2009). These attentional effects on REA correspond to top-down attention processes (i.e., endogenous attention induced by an individual's intentions, expectations, and experiences; Posner and Peterson, 1990). The bottom-up attention process (i.e., exogenous attention induced by events external to a person; Posner and Peterson,

1990) can also modulate REA. Variations in intensity level of auditory stimuli influenced REA in a non-forced attention paradigm (i.e., without focus on one ear) and in a forced attention paradigm (i.e., with focus on one ear). In a non-forced attention condition, REA increased when the interaural intensity difference (IID) favored the right ear, and it became a left ear advantage when the IID reached 9 dB in favor of the left ear. In a forced attention condition, REA increased or remained present when the IID favored the right or left ear, respectively (for a review, see Hugdahl et al., 2009). REA is therefore naturally present in healthy humans but it is important to note that this advantage is not fixed since it can vary through top-down or bottom-up attentional modulations.

4.1.2. Modulation of auditory divided attention following prism adaptation

The importance of auditory asymmetry in favor of the right ear accounts for the allocation of divided auditory attention in an individual. REA may be intensified in patients suffering from right-hemisphere brain damage such as in neglect patients. Neglect patients fail to orient, report or respond to new stimuli presented to the opposite side of their cerebral lesion (most often in the right temporo-parieto-occipital junction; Halligan et al., 2003; Heilman et al., 2000; Vallar, 1998). Following cerebral lesions in the right hemisphere, neglect patients can have an auditory extinction in their left ear leading to exacerbated REA (Jacquin-Courtois et al., 2010; Tissieres et al., 2017). The first-time modulation of the divided auditory attention following visuomanual PA was shown in neglect patients (Jacquin-Courtois et al., 2010). Before and after exposition to a rightward visuomanual PA, patients performed a verbal dichotic listening test using earphones. Patients were instructed to repeat the words they heard in both ears and their LI was computed. Visuomanual PA to a rightward optical deviation alleviated the auditory extinction by decreasing patients' LI. The divided auditory attention was shifted toward the left ear reducing the initially abnormally high REA of neglect patients. These aftereffects occurred immediately and lasted for two hours after prism removal. However, the LI remained unchanged for patients who were exposed to neutral sham glasses (i.e., control group). The authors argued in favor of a striking cross-modal transfer of visuomanual PA aftereffects to the auditory modality. They suggested that the lateralized remapping of the visuomotor information induced by prism adaptation could modify the orientation of attention in sensory modalities other than those involved during prism exposure (Jacquin-Courtois et al., 2010). Tissieres et al. (2017) showed similar results in neglect patients who improved their performance in dichotic listening following a rightward visuomanual PA. To obtain such beneficial aftereffects in left auditory extinction, the right superior parietal lobule and the posterior part of the temporal lobe has to be spared, and the inputs from the left inferior parietal lobe have to be intact (Tissieres et al., 2017).

Changes in divided auditory attention are not restricted to neglect patients. A recent study demonstrated for the first-time aftereffects of prism adaptation on divided auditory attention in healthy individuals (Bonnet et al., 2022). Participants performed a dichotic listening task before and after leftward or rightward visuomanual PA. They were asked to recall as many words as possible heard by a specific ear indicated by the experimenter. Visuomanual PA to a leftward optical deviation strengthened REA initially present and increased the percentage of correctly recalled words from the right ear. The authors interpreted these new results as attentional aftereffects of prism adaptation on REA, since it has been shown that attentional factors can modulate REA (see Section 4.1.1., Hiscock et al., 1999; Hugdahl et al., 2000). Leftward prism adaptation would increase the LI by shifting divided auditory attention toward the right side (Bonnet et al., 2022). These results reflect cross-modal aftereffects of prism adaptation in audition, which is a sensory modality not involved when sensorimotor prism adaptation develops. They could be related to high-level aftereffects of prism adaptation on spatial attention (Michel, 2006, 2016). It is difficult to dissociate cross-modal and attentional aftereffects because a shift in spatial attention could modify sensory perception in a modality not directly involved during prism exposure, such as the modulation of REA in the auditory modality. It could be assumed that the shift of spatial attention following visuomanual PA could cause cross-modal aftereffects to occur.

To summarize, visuomanual PA can produce changes in the allocation of the divided auditory attention not only in neglect patients but also in healthy individuals. Rightward visuomanual PA rebalances the allocation of auditory spatial attention in neglect by decreasing REA, whereas leftward visuomanual PA produces an increase in REA in healthy individuals. Auditory spatial functions are not restricted to divided auditory attention assessed with dichotic listening task. Studies investigating auditory spatial attention have mainly used a sound localization task. Such research showed a decrease in sound-localization abilities especially when visuospatial attention was impaired, such as in neglect patients (e.g., Matsuo et al., 2020).

4.2. Auditory localization

When a sound source is not exactly behind or in front of our head (i.e., sagittal axis), stimuli coming from this source reach both ears at different times and different intensities. The ear closer to the sound source perceives the auditory stimulus first. Our brain uses this interaural time and intensity difference to determine the localization of a sound source. Abilities to locate sound sources are impaired in neglect patients who misestimate the sound source to the right of the correct source in the left hemispace (Matsuo et al., 2020). Two studies have investigated aftereffects of visuomanual PA in auditory localization in neglect patients (Matsuo et al., 2020; Tissieres et al., 2017). On the one hand, Tissieres et al. (2017) failed to report significant aftereffects and explained this by the complexity of encoding the auditory space at the cortical level. On the other hand, Matsuo et al. (2020) observed significant beneficial aftereffects of rightward visuomanual PA in auditory localization. In the latter study, speakers were installed at patients' ear-height at seven positions (center, 200, 400, and 600 mm to either side of the midline). Neglect patients had to point at the sound source with a laser pointer on a cap with their eyes closed. Visuomanual PA to a rightward optical deviation significantly decreased the localization error in the left hemispace, especially for the speaker positioned 600 mm to the left of the midline. Patients not exposed to visuomanual PA (i.e., control group) continued to mislocalize sound sources after PA (i.e., right shift in the left hemispace). Matsuo et al., (2020) concluded that auditory spatial attention was enhanced after rightward visuomanual PA in neglect patients. The authors proposed assumptions, including an attentional hypothesis in which they assume that spatial mental representations were reacalibrated leading to a redistribution of auditory spatial attention.

Pochopien and Fahle (2017) assessed aftereffects of visuomanual PA in auditory localization using two forms of an auditory-localization task. In one form, participants had to indicate if the auditory stimulus came from the left or the right side while their eyes were closed (i.e., forced choice task without pointing). In the other, participants had to point to the speaker from which the auditory stimulus was emitted. These tasks were performed in the dark, in the light and in the light with head rotation. In the dark, the authors showed expected aftereffects opposite to the optical deviation for both tasks. In the light and in the light with head rotation conditions, they replicated aftereffects opposite to the optical deviation for the pointing task. However, they observed reverse aftereffects (i.e., in the direction of the optical deviation) or no aftereffects for the forced choice task. Pochopien and Fahle (2017) suggested that adaptations in head rotation and proprioception of the arm-hand segment could completely explain the apparently generalized aftereffects in auditory perception. Nevertheless, further studies are needed to explore abilities in auditory localization following visuomanual PA in healthy individuals, while avoiding proprioceptive adaptations of the arm during the localization task.

In sum, visuomanual PA seems to modify abilities in sound source localization, especially for neglect patients who presented strong aftereffects after rightward visuomanual PA. Altogether, studies exploring aftereffects of visuomanual PA on auditory spatial attention (i.e., divided auditory attention and sound source localization) support the extension of cognitive aftereffects within the auditory modality in the healthy population as well as in patients with unilateral neglect symptoms. These issues open a new avenue of research in the therapeutic field for patients suffering from hearing impairments such as unilateral tinnitus.

5. From visuomanual adaptation to auditory aftereffects in tinnitus patients: Initial results and perspectives

5.1. Tinnitus and attention

The word tinnitus comes from the Latin "*tinnire*" (to ring; e.g., Baguley et al., 2013; Han et al., 2021). Tinnitus is an auditory disorder that causes a disturbing sound/noise to be perceived, and it affects between 10 % and 15 % of the world adult population (Baguley et al., 2013; Eggermont and Roberts, 2004). Subjective tinnitus is described as a phantom perception, which is defined as a conscious perception of an auditory sensation in the absence of a corresponding external stimulus (e.g., Lockwood et al., 2002). The sensation of tinnitus only becomes conscious when aberrant neural activity in the primary auditory cortex is linked to a broader cortical level, involving frontal, parietal and limbic areas (de Ridder et al., 2011). Although cochlear abnormalities are thought to be the initial source of tinnitus, the following cascade of neural changes in the central auditory system is more likely to maintain the phantom perception (Baguley et al., 2013). According to de Ridder et al. (2011), maintaining awareness of tinnitus perception is related to an increased activity of the central nervous system that affects the interaction between the limbic and primary auditory cortex.

Tinnitus can be modulated by environmental factors subdivided into soundscape (e.g., silence or noise) and other environmental factors (e.g., weather), as well as by patient-specific factors such as attention, fatigue or stress (Colagrosso et al., 2019). Patients having unilateral tinnitus would automatically orient their attention toward the affected ear, making it difficult for them to divert their attention toward the healthy side. Cuny et al. (2004) showed that when successively presenting a pair of sounds (first sound: S1, second sound: S2) in each ear (i.e., S1 in the right ear followed by S2 in the left ear, and vice versa), the ability to identify the target S2 was better when S2 was presented in the affected ear and S1 in the healthy ear, compared to the opposite condition. These results can be explained by difficulties in attention orientation for tinnitus patients, who automatically shift their attention toward the tinnitus side. It is interesting that this effect was absent in healthy individuals when a unilateral tinnitus was simulated, that is when an auditory stimulus (i.e., a narrow-band noise centered on 4000 Hz) imitating a tinnitus was played in one ear during the sound detection task (Cuny et al., 2004). These results suggest that chronic unilateral tinnitus automatically attracts the patients' attention. The attentional system would be unable to classify the tinnitus signal as irrelevant information, preventing habituation. In another study, selective attention of tinnitus patients was assessed with a Stroop task, which involves the visual presentation of color words that conflict with the color of the ink in which the word is written. Patients suffering from unilateral tinnitus had longer reaction times and a higher error rate than healthy individuals. As the authors explained, tinnitus could consume the attentional resources of patients, thus reducing their selective attention system (Stevens et al., 2007). More recent studies using fMRI, at rest (Kandeepan et al., 2019) or during an auditory attentional task involving non-speech sounds (Husain et al., 2015), showed altered functional connectivity in auditory and non-auditory areas, as well as modified activity in the network involved in top-down attentional orientation compared to healthy individuals (for a review, see Husain, 2016). At a representational level, Bonnet, Poulin-Charronnat, Rossetti, et al. (2022) recently showed sensorimotor and representational biases in a tinnitus patient. The patient pointed toward his affected ear during an open-loop pointing task (i.e., pointing to a sagittal visual target while keeping eyes closed during the movement: sensorimotor bias), and he marked the line center toward his affected ear during a manual line-bisection task (i.e., marking the center of a horizontal line with a pencil while keeping open eyes: representational bias).

In sum, tinnitus patients have a general decrease of attentional resources, probably due to an impaired top-down regulation of irrelevant sensory information caused by the presence of the unilateral phantom sound. Hyperattention directed toward the tinnitus ear seems to exist and it would lead to a deterioration of selective attention and top-down attentional orientation. Since visuospatial representation is modulated by attention (e.g., McCourt and Jewell, 1999; Milner et al., 1992), this attentional imbalance in favor of the tinnitus ear could cause the tinnitus side to be overrepresented. The attentional impact would depend on tinnitus severity: the more the phantom sound/noise is classified as severe by the Subjective Tinnitus Severity Scale (Halford and Anderson, 1991), the more attention is impaired because of the stronger attraction of the tinnitus (Cuny et al., 2004).

5.2. Relieving unilateral tinnitus with visuomanual prism adaptation

In the previous sections, we have detailed innovative results on cognitive aftereffects after visuomanual PA within the auditory modality (see Section 3. and 4.). More precisely, visuomanual PA can rebalance auditory spatial attention in patients with unilateral disorders (i.e., neglect; Section 3.). In a recent case study, Bonnet, Poulin-Charronnat, Rossetti, et al. (2022) investigated aftereffects of visuomanual PA in a patient suffering from a unilateral hearing disorder, i.e., tinnitus in the left ear. The patient participated in three different sessions: neutral glasses (i.e., baseline), prism adaptation to a leftward optical deviation (i.e., toward the affected ear), and prism adaptation to a rightward optical deviation (i.e., toward the unaffected ear). During each session, the patient had to assess the discomfort and the auditory spectrum (i.e., frequency and loudness) of his tinnitus, and he performed an open-loop pointing task (i.e., pointing at a sagittal visual target while keeping eyes closed during the movement: sensorimotor task) and a manual line-bisection task (i.e., marking the center of a horizontal line with a pencil while keeping his eyes open: visuospatial representational task). The three tasks were performed before PA and six times after PA (i.e., six tests at 15-minute intervals). The results showed a decrease in the perceived frequency of the patient tinnitus after prism adaptation to both optical deviations but prism adaptation to a rightward optical deviation (i.e., toward the unaffected side) produced more drastic and durable benefits. Leftward prism adaptation decreased the perceived frequency from 15 min up to 45 min after prism removal, whereas rightward prism adaptation immediately reduced the perceived frequency until the end of the experimental session (i.e., 75 min after prism removal). This frequency decrease made it possible to express tinnitus in frequency ranges that can be easily addressed by audioprosthesists. Another novel result of this case study concerned the representational level. Prism adaptation to a rightward optical deviation (i.e., toward the unaffected side) modulated the visuospatial representation by shifting the estimation of the line center toward the right side (i.e., toward the unaffected ear). However, it is well known in the literature that only leftward prism adaptation modifies visuospatial representation in healthy individuals (e.g., Michel, 2016). Consequently, a specific reaction to visuomanual PA in tinnitus patients can be suggested, namely, that strong aftereffects would occur only after visuomanual PA to an optical deviation toward the affected side.

These results echo those observed in patients suffering from a complex regional pain syndrome (CRPS), which is defined as a chronic disabling pain following peripheral injuries (e.g., fracture or surgery) frequently associated with treatment failure (e.g., Christophe et al., 2016; Marinus et al., 2011; Torta et al., 2016). A few studies have shown that prism adaptation to an optical deviation toward the unaffected side can alleviate phantom pain perception in CRPS sufferers. Through its action on visuospatial attention, visuomanual PA improved the symptoms associated with CRPS by rebalancing the attentional bias initially oriented toward the affected limb (Bultitude and Rafal, 2010; Christophe et al., 2016; Foncelle et al., 2021; Sumitani et al., 2007). Similarities of the aftereffects of visuomanual PA between tinnitus and CRPS patients are not surprising because tinnitus and CRPS share similar characteristics at different levels that are summarized in Table 1. Tinnitus and CRPS are often accompanied by a cortical reorganization in the primary cortex (i.e., the somatosensory cortex for CRPS; the auditory cortex for tinnitus), an altered perception of physical stimuli, a presence of negative emotions, and impaired space representation and sensory perception (Bonnet, Poulin-Charronnat, Rossetti, et al., 2022; for a review see de Ridder et al., 2011). Based on beneficial aftereffects of visuomanual PA in CRPS sufferers (Bultitude and Rafal, 2010; Christophe et al., 2016; Foncelle et al., 2021; Sumitani et al., 2007) and on studies showing an attentional bias in tinnitus patients (Cuny et al., 2004; Husain et al., 2015; Kandeepan et al., 2019; Lima et al., 2020, Bonnet, Poulin-Charronnat, Rossetti, et al. (2022) assumed that how perceived tinnitus frequency was modulated after prism adaptation would depend on the reorientation of attention toward the side opposite to that of tinnitus. This assumption is in accordance with changes in visuospatial representation that can be explained by attentional allocation being rebalanced following visuomanual PA to an optical deviation toward the unaffected side (Bonnet, Poulin-Charronnat, Rossetti, et al., 2022). In CRPS and tinnitus, the beneficial aftereffects occurred toward the same side as the optical deviation used, i.e., toward the unaffected side. In CRPS, the subjective visual straight-ahead has been shown to be abnormally shifted toward the affected side (Sumitani et al., 2007). An abnormal shifted visual straight-ahead could be the cause of an inconsistency between visual and proprioceptive references, leading to a sensorimotor conflict that has been shown to produce pain (McCabe et al., 2005). Since the subjective visual straight ahead has been shown to be shifted in the direction of the optical deviation following PA (for a review: Redding and Wallace, 2006), a visual shift toward the unaffected side after PA to an optical deviation toward the unaffected side would allow to retrieve the visual-proprioceptive coordinative linkage, resulting in congruent sensorimotor feedback loops, and would alleviate phantom perception. On the contrary, a visual shift toward the affected side after PA to an optical deviation toward the affected side would exacerbate the sensorimotor conflict, leading to a maintained and/or an increased phantom perception. Moreover, attentional aftereffects are known to occur in the opposite direction of the optical deviation used, as sensorimotor aftereffects (see Fig. 3). It could be assumed that prism adaptation to an optical deviation toward the unaffected side would shift attention away from the body, removing the initial attentional focus on the phantom side in tinnitus and CRPS patients.

Table 1
Similarities between tinnitus and CRPS.

	Tinnitus	CRPS
Hypersensitivity	Hyperacusis (Møller, 2007b)	Hyperapathy (Møller, 2007b)
Biased attention	Toward the affected ear (Cuny et al., 2004; Husain et al., 2015; Kandeepan et al., 2019; Lima et al., 2020)	Toward the affected limb (Foncelle et al., 2021; Jacquin-Courtois et al., 2012; Sumitani et al., 2007)
Neural plasticity	Auditory cortex (Baguley et al., 2013; de Ridder et al., 2011; Møller, 2007a)	Somatosensory cortex (de Ridder et al., 2011; Møller, 2007a)
Emotion	Depression, anxiety (Tinnitus: de Ridder et al., 2011; Møller, 2007b; CRPS: Shim et al., 2019; Taylor et al., 2021)	
Space representation and sensory perception	Manual line-bisection task: bias toward the affected ear (Bonnet, Poulin-Charronnat, Rossetti, et al., 2022) Open-loop pointing task: sensorimotor bias toward the affected ear (Bonnet, Poulin-Charronnat, Rossetti, et al., 2022)	Visual and proprioceptive straight-ahead: bias toward the affected limb (Foncelle et al., 2021; Sumitani et al., 2007)

This case study provides encouraging preliminary outcomes regarding the benefits of visuomanual PA on tinnitus perception, and it offers several interesting perspectives. The literature on the beneficial aftereffects of visuomanual PA on CRPS is more extensive than that on tinnitus. Several experiments have been performed in patients with CRPS over several days or several weeks with daily (Bultitude and Rafal, 2010; Sumitani et al., 2007) or twice daily (Christophe et al., 2016; Foncelle et al., 2021) prism adaptation sessions. A similar intervention program could be used in tinnitus patients to test beneficial aftereffects of prism adaptation on tinnitus perception. Increasing the number of measurements over several sessions would provide more accurate data on changes in tinnitus parameters (i.e., frequency and loudness).

6. Modifying audition with glasses: How could this be possible?

6.1. Auditory frequency mental representation

Cross-modal aftereffects of visuomanual PA have been observed in sensory modalities other than audition. Girardi et al. (2004) assessed aftereffects of visuomanual PA on haptic modality—requiring haptic (tactile and kinesthetic) exploration of space—in healthy participants. They observed that leftward visuomanual PA shifted the center estimation of a haptically explored center toward the right. The authors explained this result by the action of visuomanual PA on the supramodal representation of space. Other studies have shown aftereffects on mental representation of non-auditory spatially valued elements such as letters and numbers, which are spatially represented along a mental horizontal line in the same way as auditory frequencies (letters: Nicholls and Loftus, 2007; Zorzi et al., 2006; numbers: Göbel et al., 2006; Loftus et al., 2009; Longo and Lourenco, 2007). The sensorimotor realignment achieved throughout visuomanual PA affects these higher-order mental representations. In healthy people, leftward visuomanual PA shifted the estimation of the center of an alphabetical (Nicholls et al., 2008) or numerical interval (Loftus et al., 2008) toward the spatially valued element to the right (e.g., later letters of the alphabet; larger numbers). These results are in line with those observed in auditory frequency mental representation. Leftward visuomanual PA shifts the estimation of the center of an auditory interval toward higher auditory frequencies, which are spatially represented to the right side (see Section 3.1.). Hubbard et al. (2005) suggested that internal numerical representation and visuospatial attention share common parietal areas, and changes in one dimension would lead to changes in another. This is presumably the case for auditory frequencies since multimodal neurons constitute the parietal cortex (Stein and Stanford, 2008). Given that attention modifies the representation of space (e.g., McCourt and Jewell, 1999; Milner et al., 1992), we can assume that the effects of attention modulation extend to the mental representation of spatially valued elements. This assumption matches with the presence of a common magnitude system in the intraparietal sulcus within the parietal cortex, probably involved in perceptual magnitudes such as space, numbers, temporal duration or loudness (Walsh, 2003; for a review, see Winter et al., 2015). This common magnitude system could be defined as a cross-domain shared representation for perceptual dimensions located on a continuous scale of increasing or decreasing magnitude (Winter et al., 2015). Auditory frequencies can be part of the common magnitude system because of their mental representation along continuous horizontal and vertical scales (Lidji et al., 2007; see Section 3.1.1.). The right posterior parietal cortex is dominant in multimodal (Stein and Stanford, 2008) and mental representations (e.g., Göbel et al., 2006). We can thus assume that shifts in auditory mental representation after leftward visuomanual PA could arise due to modulation of the right posterior parietal cortex, which is a core cerebral area involved in prism exposure (Luauté et al., 2009;

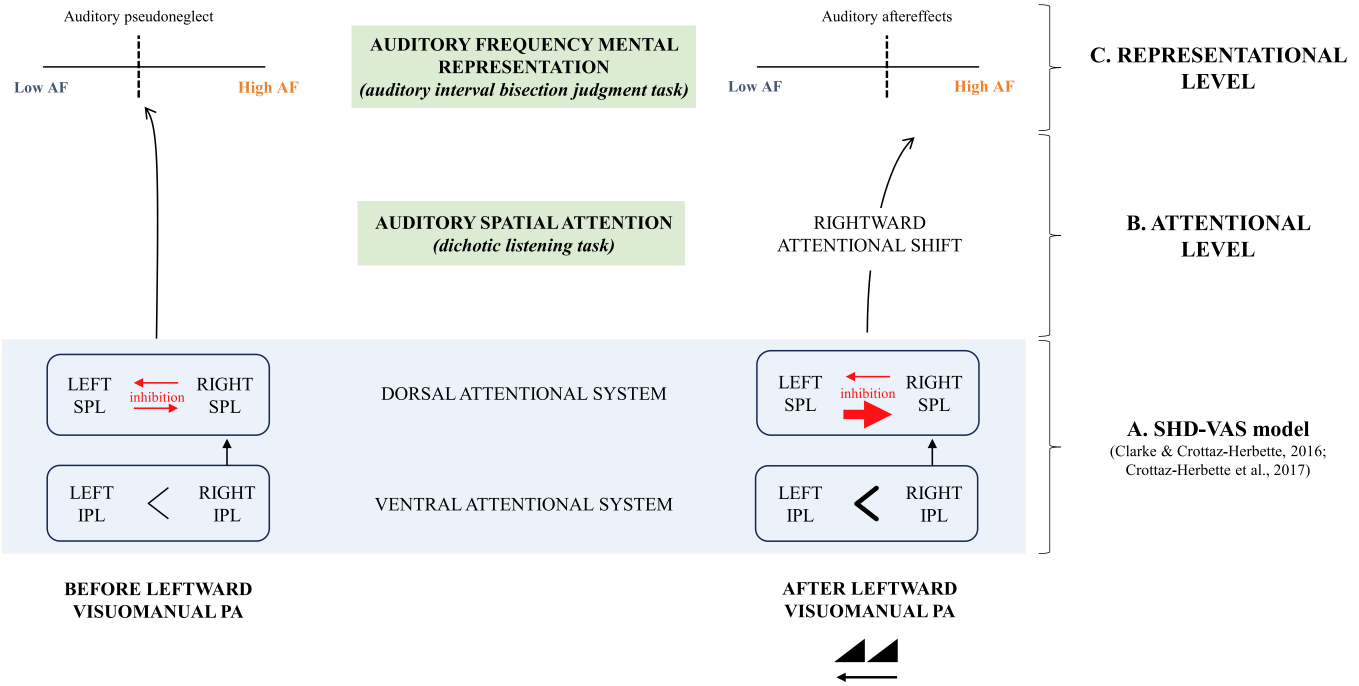

Fig. 3. Schematic representation of hypothetical processes explaining aftereffects within the auditory modality following visuomanual PA in healthy individuals. A. The lower level represents the attentional SHD-VAS model inspired from (Clarke and Crottaz-Herbette, 2016; Crottaz-Herbette et al., 2017). The left part illustrates the right-IPL dominance in the ventral attentional system and the equitable inhibitory interactions between the left and right SPL in the dorsal attentional system. The right part illustrates the increased right-IPL dominance in the ventral attentional system and the increased inhibition of the left SPL on the right SPL following leftward visuomanual PA. B. The middle level represents the rightward attentional shift after leftward visuomanual PA auditory spatial attention (i.e., increased right ear advantage). **C.** The higher level represents the auditory frequency mental representation. The left part illustrates the initial auditory pseudoneglect bias (dotted line) toward low auditory frequencies in the auditory frequency mental representation. The low auditory frequencies are mentally overrepresented (gray writing; i.e., Low AF), and the high auditory frequencies are mentally underrepresented (orange writing; i.e., High AF). The right part of the figure illustrates the shift of the initial pseudoneglect bias (dotted line) toward the high auditory frequencies in the auditory frequency mental representation, following leftward visuomanual PA. The left auditory frequencies are mentally underrepresented (gray writing; i.e., Low AF), and the high auditory frequencies are mentally overrepresented (orange writing; i.e., High AF). *AF: Auditory Frequencies; IPL: Inferior Parietal Lobe; SHD-VAS: shift in hemispheric dominance within the ventral attentional system; SPL: Superior Parietal Lobe. Adapted from* Clarke and Crottaz-Herbette, 2016*;* Crottaz-Herbette et al., 2017.

Panico et al., 2022; Pisella et al., 2006). The right hemisphere also dominates in pitch processing (Liégeois-chauvel et al., 2001; Zatorre and Belin, 2001), especially in the Heschl gyrus (Hyde et al., 2008). The right hemispheric dominance in mental representations and pitch processing, coupled with its strong involvement in visuomanual PA, supports the hypothesis that visuomanual PA acts on lateralized systems. In line with the attentional model proposed by (Clarke and Crottaz-Herbette, 2016; Clarke et al., 2022; Crottaz-Herbette et al., 2017), it can be assumed that visuomanual PA to a leftward optical deviation acts on the right hemispheric dominance in pitch discrimination and auditory mental representation. Prior to visuomanual PA, the right hemispheric dominance in mental representation would lead to a mental overrepresentation of low auditory frequencies (i.e., associated with the left part of space) and a mental underrepresentation of high auditory frequencies (i.e., associated with the right part of space). This mental representational imbalance would be reversed following leftward PA. The rightward attentional shift occurring after a leftward PA would lead to a mental underrepresentation of low auditory frequencies and a mental overrepresentation of high auditory frequencies (see Fig. 3).

6.2. Auditory spatial attention

The increased auditory spatial attention toward the right side after leftward visuomanual PA could be due to changes induced by prism adaptation within the neural networks linked to orientation of attention (Panico et al., 2020). The lateralized remapping of visuomotor information following visuomanual PA can then modify the attention orientation in the auditory modality. According to Pisella et al., (2006), the aftereffects induced by prisms on the cerebellum ipsilateral to the optical deviation interact with the contralateral posterior parietal cortex. Recently, a study showed the key role of the parietal and temporal cortex in the occurrence of aftereffects of visuomanual PA on divided auditory attention (Tissieres et al., 2017). The parietal cortex is involved in orienting of spatial and non-spatial auditory attention (Shomstein and Yantis, 2006), and the temporal cortex is the locus of pitch processing (Hall and Plack, 2009). Based on the existing literature, the aftereffects observed on auditory spatial attention in healthy people can be explained by a bottom-up process involving cerebellar, parietal, and temporal structures.

A recent attentional model has been proposed to explain how visuomanual PA modulates the way attention is allocated (Crottaz-Herbette et al., 2017; for reviews see Clarke and Crottaz-Herbette, 2016; Clarke et al., 2022). The orientation of visuospatial attention depends on two attentional systems (Vossel et al., 2014). The right-lateralized ventral attentional system (VAS) comprises the inferior parietal lobule, the temporoparietal junction, and the superior temporal cortex; the dorsal attentional system (DAS) includes the superior parietal lobule, the intraparietal junction, and the superior frontal cortex (e.g., Corbetta and Shulman, 2002). Clarke and Crottaz-Herbette (2016) proposed a Shift in Hemispheric Dominance within the Ventral Attentional System model (SHD-VAS) in which prism adaptation causes a shuffle of the inferior parietal lobule contralateral to the optical deviation used (Crottaz-Herbette et al., 2017; for reviews see Clarke and Crottaz-Herbette, 2016; Clarke et al., 2022). In healthy people, leftward prism adaptation would strengthen the spatial representation of the right hemispace in the right-hemispheric VAS. This would be followed by changes in the DAS with decreased activity in the right superior parietal lobule and increased activity in the left superior parietal lobule. This imbalance in attentional networks would induce a neglect-like behavior by reorienting attention toward the right side of space (Clarke and Crottaz-Herbette, 2016; Crottaz-Herbette et al., 2017), as observed in dichotic listening (see Fig. 3; Bonnet, Poulin-Charronnat, Vinot, et al., 2022). The proposed SHD-VAS model to explain aftereffects of visuomanual PA on visuospatial attention (for a review see Clarke et al., 2022) might be relevant to explain aftereffects on auditory spatial attention, because both ventral and dorsal attentional systems are involved in this type of attention. This suggestion is supported by some neuroanatomical results. Tissieres et al. (2017) showed that beneficial results in the allocation of auditory spatial attention for neglect patients (i.e., dichotic listening task) needed an intact right DAS and a spared posterior part of the right temporal lobe. We can assume that aftereffects of visuomanual PA on visuospatial attention and auditory spatial attention could be both explained by the same attentional model. Based on this attentional model and according to the results obtained from fMRI studies in tinnitus patients, it can be assumed that the phantom sound could modulate the attentional networks by decreasing activity in regions of the DAS, namely the frontal cortex (Husain, 2016) and the intraparietal sulcus (Husain et al., 2015; Trevis et al., 2016). These changes in cerebral activity could explain the visusospatial representational bias recently observed in a tinnitus sufferer (Bonnet, Poulin-Charronnat, Rossetti, et al., 2022), since the DAS would be involved in auditory attention (Hill and Miller, 2010). Based on the literature, we can suppose that visuomanual PA can change tinnitus perception by acting on the modified DAS of patients. The attention initially focused on the tinnitus side would thus be shifted away from the tinnitus toward the unaffected side. Further studies using methods in neuroanatomic exploration are needed to investigate mechanisms involved in the aftereffects of visuomanual PA in the auditory modality.

7. Conclusion

Visuomanual PA is mostly known as a powerful non-invasive method to alleviate hemineglect (e.g., Jacquin-Courtois et al., 2013; Redding and Wallace, 2006b; Rode et al., 2015; Rossetti et al., 1998), and to produce a neglect-like behavior in healthy people (e.g., Colent et al., 2000; Michel, 2016). Aftereffects of visuomanual PA are cross-modal and occur in unexposed modalities during prism exposure. The present paper reviewed recent interesting results observed in the auditory modality in healthy individuals and in a tinnitus patient. Although we have put forward some assumptions to explain how prism adaptation modulates auditory perception in affected and unaffected ears, future studies are required to understand in detail the underlying mechanisms. This review opens promising new perspectives in the therapeutic field of auditory phantom perception.

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Declaration of Competing Interest

None

Appendix. – Investigations of the aftereffects in the auditory modality following visuomanual prism adaptation

Author	PA	Population	Methods	Results
Michel et al. (2019)	L-PA, R-PA OD: 15°	Healthy M; NM	○ Auditory interval bisection judgment Interval: 700–1300 Hz ○ Use of a chinrest to keep the head aligned to the body axis	Before PA Auditory pseudoneglect toward low AF Following L-PA M: ↑ perceived low AF
Bonnet et al. (2021)	L-PA, R-PA OD: 15°	Healthy M; NM	○ Auditory interval bisection judgment Intervals: 200–800 Hz; 1850–2450 Hz; 3500–4100 Hz Pseudorandomized order ○ Use of a chinrest to keep the head aligned to the body axis	Before PA Auditory pseudoneglect toward low AF for higher auditory intervals (1850–2450 Hz; 3500–4100 Hz)
		Healthy NM	○ Auditory interval bisection judgment Intervals: 600–1200 Hz; 1850–2450 Hz; 3100–3700 Hz Interval-blocked order ○ Use of a chinrest to keep the head aligned to the body axis	Following L-PA M and NM: ○ ↑ perceived low AF ○ shift of the subjective auditory center toward high AF associated with the right side of space
Bonnet et al. (2022)	D-PA, U-PA OD: 15°	Healthy NM	○ Auditory interval bisection judgment Interval: 724–1330 Hz ○ Use of a chinrest to keep the head aligned to the body axis	Before PA Auditory pseudoneglect toward low AF Following L-PA NM: ○ ↑ perceived low AF ○ shift of the subjective auditory center toward high AF associated with the right side of space
Bonnet et al. (2022)	L-PA, R-PA OD: 15°	Healthy	Verbal dichotic listening task; 80 pairs of bisyllabic words; reporting as many words as possible from one ear, for each bloc of 4 pairs	Before PA REA: positive average overall LI Following L-PA ○ ↑ overall percentage of recalled words ○ ↑ percentage of recalled words from the right ear ○ ↑ overall LI
Pochopien and Fahle (2017)	L-PA, OD: 14.5° R-PA, OD: 14.2°	Healthy	Auditory localization task, 3 conditions: ○ In the dark; 7 loudspeakers (−21° to 21°); manual pointing of the sound source; two-alternative forced choice ○ In the light; 7 loudspeakers (−21° to 21°); manual pointing toward the sound source; two-alternative forced choice ○ In the light + head rotation; 7 loudspeakers (−12° to 12°); manual pointing of the sound source; two-alternative forced choice	○ In the dark: aftereffects of visuomanual PA in both manual pointing and forced choice ○ In the light: aftereffects of visuomanual PA in manual pointing (opposite to the OD) and in forced choice (in the direction of the OD) ○ In the light + head rotation: aftereffects of visuomanual PA in manual pointing (opposite to the OD) but no aftereffects in forced choice
Jacquin-Courtois et al. (2010)	R-PA, 10° NL (i.e., sham)	Neglect	Verbal dichotic listening task; 60 pairs of verbal stimuli; reporting words from both ears	Before PA ○ Neglect: High LI and REA, i.e., asymmetry on

(continued on next page)

(*continued*)

Author	PA	Population	Methods	Results
				favor of the right side Following R-PA ○ ↓ overall LI
Tissieres et al. (2017)	R-PA OD: 10°	Neglect	Verbal dichotic listening task; 30 pairs of disyllabic words; reporting both words from both ears Verbal diotic listening task: 30 pairs of words, ITD: 1 ms; reporting both words from both hemispaces Auditory localization task: 60 stimuli; 5 different azimuthal positions; ITD: 0, 0.3, 1 ms, pointing to the source with the right index finger	Verbal dichotic listening task ○ Initial high REA ○ ↓ left auditory extinction after R-PA for responder patients ○ Non-responders have lesions in the SPL, IPS, and the posterior part of the TL on the right hemisphere Verbal diotic listening task ○ No significant aftereffects for the LI after R-PA ○ Descriptive analysis: enhancing of the reporting in the right side for patients with lesions in the SPL, IPS, and BG ○ Descriptive analysis: enhancing of the reporting in the left side for patients with integrity of the SPL, IPS, and BG Auditory localization task ○ No significant aftereffects in sound source localization abilities after R-PA ○ Descriptive analysis: in most patients increase in the rightward spatial bias after R-PA (i.e., deterioration)
Matsuo et al. (2020)	R-PA OD: 10°	Neglect	Sound-localization task: 7 loudspeakers (midline, 200, 400, 600 mm to either side of the midline); rotation of the head toward the sound source to indicate the perceived direction (with a laser)	Before PA ○ Rightward bias in the left part of space ○ Leftward bias in the right part of space Following R-PA ○ ↓ of the rightward bias for the loudspeaker located 600 mm to the left of the midline ○ ↑ of the auditory attention in the left side of space
Bonnet et al. (2022)	L-PA (i.e., toward the affected side) R-PA (i.e., toward the unaffected side) OD: 15°	Tinnitus	Measure of the tinnitus frequency and loudness with the matching method	Loudness: no changes following L-PA and R-PA Frequency: ○ ↓ from 15 min to 45 min after L-PA ○ ↓ immediately after R-PA until the end of the experiment ○ Aftereffects of R-PA longer and stronger than aftereffects of L-PA

AF: Auditory Frequencies; BG: Basal Ganglia; D-PA: Downward Prism Adaptation; IPS: IntraParietal Sulcus; ITD: Interaural Time Difference; LI: Laterality Index; L-PA: Leftward Prism Adaptation; M: Musicians; NM: Nonmusicians; OD: Optical Deviation; REA: Right-Ear Advantage; R-PA: Rightward Prism Adaptation; SPL: Superior Parietal Lobe; TL: Temporal Lobe; U-PA: Upward Prism Adaptation.

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