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Multisensory interactions in the depth plane in front and rear space: A review

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ABSTRACT

In this review, we evaluate the neurophysiological, neuropsychological, and psychophysical evidence relevant to the claim that multisensory information is processed differently depending on the region of space in which it happens to be presented. We discuss how the majority of studies of multisensory interactions in the depth plane that have been conducted to date have focused on visuotactile and audiotactile interactions in frontal peripersonal space and underline the importance of such multisensory interactions in defining peripersonal space. Based on our review of studies of multisensory interactions in depth, we question the extent to which peri- and extra-personal space (both frontal and rear) are characterized by differences in multisensory interactions (as evidenced by multisensory stimuli producing a different behavioral outcome as compared to unisensory stimulation). In addition to providing an overview of studies of multisensory interactions in different regions of space, our goal in writing this review has been to demonstrate that the various kinds of multisensory interactions that have been documented may follow very similar organizing principles. Multisensory interactions in depth that involve tactile stimuli are constrained by the fact that such stimuli typically need to contact the skin surface. Therefore, depth-related preferences of multisensory interactions involving touch can largely be explained in terms of their spatial alignment in depth and their alignment with the body. As yet, no such depth-related asymmetry has been observed in the case of audiovisual interactions. We therefore suggest that the spatial boundary of peripersonal space and the enhanced audiotactile and visuotactile interactions that occur in peripersonal space can be explained in terms of the particular spatial alignment of stimuli from different modalities with the body and that they likely reflect the result of prior multisensory experience.

1. Introduction

Traditionally, researchers have tended to study the spatial senses (e.g., vision, audition, and touch/proprioception) in isolation from one another.[1] That said, the last few decades have seen something of an explosion of interest in the topic of multisensory perception (see Fig. 1). Much of this interest has been inspired by neurophysiological studies documenting the existence of neurons in animals such as macaques and cats that are responsive to stimuli from more than one sensory modality (e.g., Bruce et al., 1981; Meredith et al., 1987; Meredith and Stein, 1986; see Stein and Meredith (1993) and Stein and Stanford (2008), for reviews). What is more, on closer inspection, many of these neurons have been found to have interesting (that is, non-linear) response properties.

In many cases, the relative and/or absolute spatial location from which the stimuli in the different sensory modalities were presented has proven to be important in terms of determining the kinds of multisensory interactions (and neuronal response properties) that have been reported. So, for example, neurophysiological research has demonstrated that in those situations in which the auditory and visual receptive fields (RFs) of a bimodal neuron overlap, multisensory response enhancement primarily occurs when the auditory and visual stimuli are spatially aligned. When a pair of stimuli is spatially misaligned (as when visual and auditory stimuli are presented from different azimuthal positions), and, for example, the visual stimulus is presented just *outside* of the visual RF of a bimodal neuron while the auditory stimulus is presented *within* the auditory RF of the bimodal neuron, multisensory

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[1] Largely ignoring the chemical senses (of smell and taste) altogether, as we will do here.

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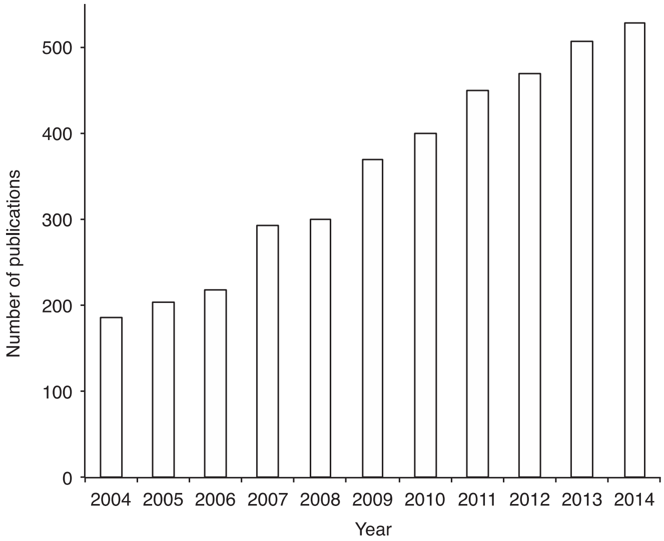

Fig. 1. Number of articles indexed in PUBMED over the last decade that have included the keywords "multisensory", "crossmodal", or "cross-modal" in the title or abstract (see also Murray et al. (2013) and Stein et al. (2010)).

response depression typically ensues (Stein and Meredith, 1990). The relation between the azimuthal alignment of stimuli and the strength of any multisensory interactions that are documented is commonly referred to as "the spatial rule" (e.g., Holmes and Spence, 2005).

In humans, however, the available evidence suggests that this rule is very much task-dependent. That is, the spatial rule is more often observed to modulate performance in those tasks that are in some sense spatial as compared to those tasks in which the spatial location of the stimuli is entirely task-irrelevant to the task being performed (see Spence (2013), for a review). In other words, the principles of multisensory integration that have often been observed in neurophysiological studies in (typically anaesthetized) animals cannot always necessarily readily be observed in behavioral studies in awake humans.

Varying the distance in depth between multisensory stimuli and the observer has also been shown to modulate the responsiveness of at least certain bimodal neurons. So, for example, some (pericutaneous) neurons in the macaque only appear to respond to somatosensory stimuli delivered to the body surface and to visual stimuli presented from a location that lies within reach, but not to the very same visual stimuli when presented beyond the animal's direct reach (e.g., Graziano and Gross, 1994; Rizzolatti et al., 1981). A similar distance-dependent boundary has also been observed in the responsiveness of trimodal neurons with auditory stimuli that were presented from close to, vs. further away from, the animal's head (Graziano et al., 1999). Such results therefore suggest that the spatial alignment of stimuli presented in different sensory modalities in terms of their depth may be just as important as their alignment in azimuthal space when it comes to evoking a response from this type of neuron.

The scientific data would indeed appear to suggest that different regions of space are coded differently by the brain (Previc, 1990, 1998), but this does not seem to be reflected in the way in which we subjectively experience the world around us, namely as a seamless whole. Given this rather curious disconnect, it would seem sensible to try and gain a further understanding of multisensory perception in depth. The importance of investigating multisensory interactions in different regions of space becomes all the more apparent when one considers the enormous amounts of multisensory information that we receive from different locations (e.g., distances beyond the reach of peripersonal space) and which we perceive on a daily basis. We may not think about it, but during the daily drive to work, for example, the most crucial sensory information necessary to drive safely comes from frontal extrapersonal space. Although we also receive sensory information from peripersonal space (e.g., think only of the dashboard lights and alerts, tactile stimulation from the driving seat, steering wheel, and feedback from the gas, break, and clutch pedal), sensory information from frontal and rear extrapersonal space (the latter seen via the rearview mirror, or else perhaps heard) is crucial in terms of our ability to navigate successfully through the environment[2] (see Previc (2000), for an example of applying knowledge about 3-D spatial information processing to the design of aircraft controls; see Spence and Ho (2008) and Ho and Spence (2009), for the application of knowledge of multisensory processing to the design of warning signals in the context of driving). It is currently unclear, however, under which circumstances sensory information from the different senses interact in terms of their spatial (mis)alignment in depth and/or any differences in their lateral position.

Although the investigation of the multisensory interactions taking place in depth has received a growing amount of research attention in recent years, the majority of studies have tended to look at multisensory interactions in two-dimensional (2-D) space (that is, experimenters have mostly varied only the azimuth and, on occasion, the elevation of the stimuli, while keeping their distance from the observer fixed; e.g., Frens et al., 1995; Stevenson et al., 2012; Ten Brink et al., 2014). In fact, in one oft-cited edited volume on the topic of crossmodal space and crossmodal attention (Spence and Driver, 2004), variations in depth rarely get mentioned at all. On those occasions where the authors do talk about variations in depth, it is mainly in the context of the coding of peripersonal space (e.g., in the context of tool-use, and distance-dependent extinction).

In this review, we evaluate the growing body of cognitive neuroscience research that has documented the nature, and peculiarities, associated with multisensory interactions in depth in front and rear space. Below, we review studies of both crossmodal spatial attention and of multisensory integration[3] (see Spence and Driver (2004)). We compare and contrast the results of those studies that have presented their experimental stimuli in both peripersonal and extrapersonal frontal space, as well as in those more recently-discovered regions, referred to as near (peripersonal), and far (extrapersonal) rear space (see Occelli et al. (2011), for a review). According to the definition adopted here, peripersonal

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[2] Given that some visual RFs in (stationary) monkeys have been observed to extend in depth as the speed of an approaching visual stimulus increased (Fogassi et al., 1996), one could argue that an extension of RFs in depth may also depend on the speed of movement with which humans move through their environment. This might result in an increase in the extent of peripersonal space and the observed multisensory interactions in this region (see Section 3).

[3] Although the difference between these two phenomena is undoubtedly a topic of keen scientific debate (see, for example, McDonald et al. (2001) and Spence (2010, pp. 183–184)), differences in the timing of the stimuli presented to different sensory modalities could potentially be used to differentiate between these two processes. So, for example, the most pronounced exogenous spatial cuing effects have typically been demonstrated with cue-target onset asynchronies (SOAs) of between 50 and 200 ms, whereas multisensory integration is often most pronounced with close temporal proximity (e.g., centered roughly on physical synchrony). Thus, multisensory interactions occurring with stimulus intervals of 50–100 ms, say, could therefore easily be explained in terms of both multisensory integration and crossmodal exogenous shifts of spatial attention (for more on the interaction between exogenous attention and multisensory integration see, for example, Vroomen et al. (2001), Santangelo and Spence (2007), Spence and Santangelo (2009), and Van der Stoep et al. (in press). While we most certainly agree that it is important to try to disentangle these empirical phenomena, we feel that discussing studies of both multisensory integration and exogenous crossmodal attention provides relevant insights in terms of the understanding of multisensory interactions and the boundaries in depth in front and rear space.

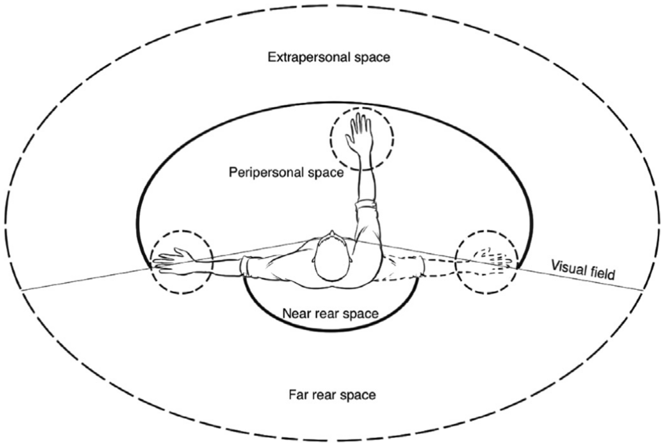

Fig. 2. Bird's-eye view of the different regions of space discussed in this review. The dashed circles around the hands represent just one of the various body-part related regions of multisensory frontal peripersonal space that have been documented in monkeys (e.g., Rizzolatti et al., 1981).

space can be defined as the space directly surrounding different parts of the body as defined by receptive fields of bimodal and trimodal neurons (Rizzolatti et al., 1981), and extrapersonal space as being the space that is further away from the body (Previc, 1998). In most of the studies that have investigated multisensory interactions involving the tactile modality, peripersonal space is referred to as the space that is reachable (e.g., Occelli et al., 2011). In such studies, tactile stimuli are often delivered to the hands while the other parts of the skin surface are largely ignored (although a small number of studies have presented tactile stimuli to, for example, the earlobes, cheeks, abdomen, feet, or shin, see for example Schicke et al. (2009), Wan et al. (2014), and Ho and Spence (2014); see Gallace and Spence (2014), for a review). It is important to note that similar body-related regions of space have been observed for other parts of the body than the hands, such as the head, trunk, and arms (e.g., Fogassi et al., 1996; Graziano and Gross, 1994). When it comes to rear peripersonal space, we refer to the region lying directly behind the head and shoulders of the observer and extending out to a distance of approximately ~20–30 cm from the body. Beyond this lies the region known as rear extrapersonal space (see Fig. 2 for a bird's-eye view of the putatively functionally distinct regions of space that will be discussed in this review). Furthermore, we will also cover the differences and similarities in multisensory interactions that have now been observed between stimuli that are presented in either the same or different regions of space.

We start by discussing those studies that have investigated visuotactile and audiotactile interactions in frontal peripersonal space and the flexibility of the extent of the peripersonal boundary. Given that tactile perception is fixed to the body, most observations of stronger audio- or visuo-tactile interactions in peripersonal space can be explained by the particular spatial alignment of unimodal stimuli in depth (i.e., alignment with the body in the case of multisensory interactions involving touch). No such asymmetry in depth would be expected for audiovisual interactions. Therefore, in order to gain a fuller understanding of the multisensory interactions that occur in the different regions of space, we also discuss those audiovisual interactions that have been documented in frontal peripersonal and extrapersonal space. Lastly, we also discuss those multisensory interactions that have been reported in rear space. We conclude by summarizing our observations and suggesting a number of key principles that may help to define and understand multisensory interactions in depth in front and rear space.

2. Visuotactile and audiotactile interactions in frontal peripersonal space

The special role of the space directly adjacent to the body in terms of those multisensory interactions involving the stimulation of the skin (especially visuotactile and audiotactile interactions) would seem to have been inspired in large part by the results of those neurophysiological studies documenting the existence of bimodal and trimodal neurons in macaques that specifically respond to stimuli presented close to the body, but not to those stimuli that happen to be presented further from the body (see, for example, Canzoneri et al. (2012), Farnè and Làdavas (2002), Graziano and Gross (1994), Graziano et al. (1999), and Rizzolatti et al. (1981)). As for the functions of such enhanced multisensory interactions in this region of space, the integration of visual/auditory, proprioceptive, and somatosensory stimuli appear to contribute to the efficient guidance of actions and defensive behaviors in response to those stimuli/events that are observed in peripersonal space (see Holmes and Spence (2004), for a review; De Paepe et al., 2014).

2.1. Neuropsychological studies of visuotactile and audiotactile interactions in peripersonal space

Support for the importance of audiotactile and visuotactile multisensory interactions in defining peripersonal space has come from neurophysiological studies. Neuropsychological evidence appears to support the notion that space is divided into several separable (or distinct) regions. For example, deficits in the orienting of visuospatial attention in peripersonal space have been observed after brain damage, while visuospatial orienting in extrapersonal space remains intact (or vice versa, e.g., Aimola et al., 2012; Halligan and Marshall, 1991; Van der Stoep et al., 2013). The results of studies of audiotactile extinction also point to a similar conclusion; Namely, that differences in audiotactile extinction have been observed in right brain-damaged patients when auditory stimuli are presented from either close to, or further away from, the patient in either frontal or rear space (Farnè and Làdavas, 2002). Audiotactile extinction was significantly more pronounced under those conditions in which the auditory stimuli were presented closer to the patient[4] (that is, from peripersonal space; see, for example, Làdavas et al. (1998), for similar results with visuotactile extinction). Additionally, differences in the magnitude of crossmodal extinction between near and far space were found to be larger for those audiotactile stimuli that were presented in rear space as compared to those that were presented in frontal space. Taken together, then, these results would appear to suggest that both audiotactile and visuotactile interactions are especially pronounced in the space directly surrounding the body.

2.2. Psychophysiological studies of visuotactile and audiotactile interactions in peripersonal space in healthy individuals

Given the clear distinction between peripersonal and extrapersonal space documented in both neurophysiological and neuropsychological studies, it would seem plausible to suggest that such a border might also influence the kinds of crossmodal and multisensory *behavioral* effects that are seen in healthy individuals under the appropriate experimental conditions. Relevant to this notion, Canzoneri et al. (2012) presented dynamic auditory stimuli that simulated the approach or receding of a sound source using a pair of loudspeakers: one sound source was positioned in

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[4] Importantly, this result could not be explained in terms of any differences in the sound pressure level of the auditory stimuli.

peripersonal space (close to the hand), while the other was placed in extrapersonal space (~100 cm from the participant). The tactile targets in this study were presented to the participant's right hand at various times relative to the approaching or receding sound.

Canzoneri et al.'s (2012) results demonstrated the existence of a boundary in space. In particular, the participants in this study responded most rapidly to the tactile targets when the simulated sound location was situated close to their hand as compared to when it appeared to be further away. Similar results have also been reported when it comes to those multisensory interactions taking place between vision and touch (Gray and Tan, 2002), and when measuring motor evoked potentials in response to an approaching visual stimulus (Makin et al., 2009).[5] It would therefore seem that both dynamic auditory and visual stimuli that give the impression of approaching an observer's body are especially efficient in terms of enhancing an observer's responses to tactile stimulation presented to the body surface (Makin et al., 2007).

3. The flexibility of the extent of frontal peripersonal space

The border between peripersonal and extrapersonal space that can be defined by the strength of visuotactile and audiotactile interactions appears to be modified depending on the position of the body in space. So, for example, consider a study of audiotactile interactions with tactile stimulation of the hand. Responses are generally faster when the hand is placed near a sound source as compared to when the stimulated hand is moved away from it (e.g., Serino et al., 2011; but see Zampini et al. (2007) and Kennett and Driver (2014)). Such results are in line with the idea that unimodal RFs of bimodal neurons can shift with the position of, for example, the hand, the arm, or the rotation of the head (e.g., Fogassi et al., 1996; Graziano and Gross, 1994).

To date, many studies have demonstrated that peripersonal space can be extended or projected simply by modulating the area that an individual can reach by means of, say, the use of a tool (e.g., Holmes et al., 2004; see Spence (2011), for a review). The results of a large number of such tool-use studies now indicate that visuotactile spatial interactions can also be observed at a distance that would normally be considered to fall outside the bounds of peripersonal space following tool-use (e.g., Bassolino et al., 2010; Canzoneri et al., 2013; Farnè et al., 2005; Holmes et al., 2007; Longo and Lourenco, 2006). The flexible properties of peripersonal space have also been demonstrated in neuropsychological research. So, for example, those patients who exhibit visuospatial neglect for stimuli presented in peripersonal space may well display a similar deficit in extrapersonal space following the use of a stick to perform a particular task, but not, interestingly, when using a laser pointer (e.g., Berti and Frassinetti, 2000; see also Pegna et al. (2001) and Maravita et al. (2001)). The observations of changes in distance-based multisensory interactions after tool-use fit well with the observation of RF changes of bimodal neurons in the macaque (Iriki et al., 1996). It was shown that the visual RFs of bimodal visuotactile neurons in the macaque cover a larger region of space surrounding the body after tool-use as compared to before tool-use (but see Holmes and Spence (2004), for a critical note).

Furthermore, it has now been demonstrated that social interactions can also modulate the boundary of peripersonal space (e.g., Heed et al., 2010; Teneggi et al., 2013). So, for example, in one study, Teneggi et al. reported that the speed with which their participants were able to detect a tactile stimulus presented to their right cheek was dependent on the perceived location of a simulated approaching auditory stimulus. When the auditory stimulus was perceived as being closer to the cheek, the participants' vocal responses to tactile stimulation of the right cheek were faster as compared to when the auditory stimulus was perceived as being further away (using an experimental paradigm similar to that used by Canzoneri et al. (2012)). The critical region within which approaching auditory stimuli facilitated the participants' detection of tactile stimuli (when compared to auditory stimuli perceived at a more distant location) was decreased in the presence of an actor who was standing close to the far loudspeaker. With the actor present, the boundary of peripersonal space appeared to move closer to the participant as compared to when a mannequin (i.e., a human-like doll) was placed close to the far loudspeaker instead. In another experiment, Teneggi et al. went on to show that depending on whether or not the actor was cooperating with the participant in an economic game, the border of peripersonal space either extended to incorporate the space surrounding the actor (in the cooperative condition) or not (in the non-cooperative condition). Fig. 3 shows the shift in the time point of a simulated approaching auditory stimulus at which audiotactile interactions start to decrease RTs to tactile targets.

In most of the studies in which the boundary of peripersonal space has been investigated, the participants remained static and the stimuli were either static or dynamic (e.g., perceived to approach or recede from the participant). There are, however, reasons to believe that the speed at which humans move through the environment may also modulate the effective boundary of peripersonal space. In a neurophysiological study by Fogassi et al. (1996), the extent of the RF of a certain type of neuron (i.e., "somatocentered" neurons) in terms of their distance from the observer (i.e., a monkey) was observed to depend on the velocity of an approaching visual stimulus (that is, increasing the velocity of the visual stimulus increased the extent of the RF in depth for certain neurons). It would be interesting here to investigate whether an extension of peripersonal space could be observed with moving observers who approach static stimuli at different speeds.

Another way in which the space that is currently reachable can

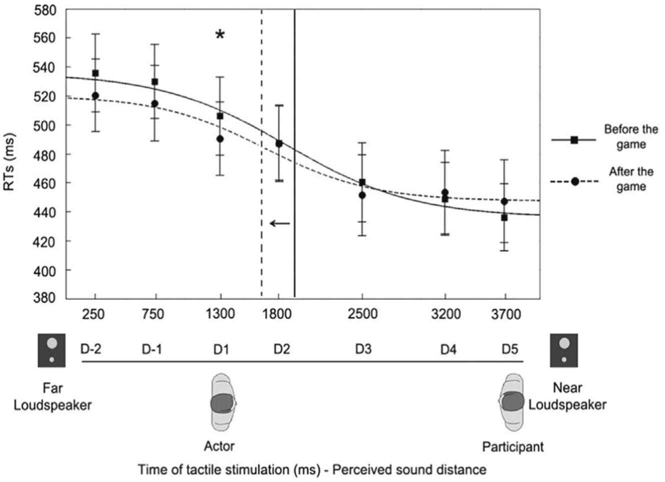

Fig. 3. Vocal RTs as a function of the perceived distance of an approaching sound before (filled squares, solid line) and after (filled circles, dashed line) playing an economic game with a cooperative actor. The time until tactile stimulation is shown on the *x*-axis. Low values correspond with a sound that was far from the body whereas high values correspond with a sound that was close to the body. The boundary of peripersonal space (solid vertical line) shifted towards the actor after the game (dashed vertical line; taken from Teneggi et al. (2013), with permission).

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[5] Whereas in these latter studies dynamic stimuli approached or receded from a static observer, the improvement of visual movement detection by congruent auditory motion signals during simulated self-motion would appear to suggest that multisensory (audiovisual) interactions can also be observed during self-motion (Calabro et al., 2011).

be manipulated is by placing a (transparent) barrier (e.g., a window) in front of an individual, which effectively reduces the reachable space, but not the visible space. One might expect that knowing that a body part cannot be reached by a visual stimulus ought to decrease the extent of the peripersonal space border and the distance at which audiotactile and visuotactile interactions are especially efficient in evoking a rapid response. Knowing that an approaching visual stimulus will collide with a barrier in front of you instead of with your body may serve to reduce anxiety for the physical consequences of approaching visual stimuli, and therefore reduce attention to threat-related stimuli (see Eysenck et al. (2007), for the influence of anxiety on attention). Interestingly, many animals maintain a certain distance between themselves and other animals (or objects; i.e., “flight distance”, see Hediger (1955) and Sommer (1959); “personal space”, e.g., Felipe and Sommer, 1966). The distance that an animal maintains between itself and other animals (or objects) depends on the perceived threat of the other animals (i.e., preserving a smaller distance from other individuals from the same species, while maintaining a larger distance from predators). The distance of the boundary of peripersonal space from an observer varies between individuals. In one recent study, the size of the hand-blink reflex (HBR) was investigated with electrical stimulation of the wrist while participants were instructed to hold their hand at different distances from their face. An increase in the hand-blink reflex was observed as the hand got closer to the participant's face (Sambo and Iannetti, 2013). An increase in the HBR with decreasing distance was taken as a measure of peripersonal space. Interestingly, the differences in the size of the peripersonal space between participants in this case were related to variability in trait anxiety (Eysenck et al., 2007). Although Sambo and Iannetti (2013) observed a relation between the size of defensive peripersonal space and trait anxiety, they did not find a relation between claustrophobic fear and defensive peripersonal space. Interestingly, a relation between peripersonal space and claustrophobic fear was observed when the magnitude of pseudo-neglect was used as a measure of peripersonal space (Lourenco et al., 2011). When indicating the center of a horizontal line, neurologically healthy individuals normally show a slight leftward bias called pseudo-neglect. This bias changes into a rightward bias as the distance between the line and the observer increases (Longo and Lourenco, 2006, 2007). The slope of the change from a leftward into a rightward bias as the distance between the line and the observer increases can be taken to represent the extent of peripersonal space. Shallower slopes indicate a larger peripersonal space and steep slopes represent a smaller peripersonal space. Individual differences in peripersonal space, as indicated by the slope of the bisection bias, were related to claustrophobic fear (Lourenco et al., 2011).

Some evidence for the idea that peripersonal space may contract by modulating the reachable space comes from a neurophysiological study by Caggiano et al. (2009). These researchers found that some mirror neurons (that is, neurons that are responsive to both the performance and viewing of goal-directed actions) responded when the monkey viewed goal-directed actions that were performed outside reachable space, whereas others responded selectively to goal-directed actions performed within reach (see also section 3.3). Crucially, when a transparent barrier was placed in front of the monkey, those neurons that had previously responded to goal-directed actions that were performed within the animal's peripersonal space did not respond anymore to the viewing of goal-directed actions that were performed at the same distance from the monkey but behind a transparent barrier. Thus, when the border changed the previously reachable space of the monkey to non-reachable space, the “periperisonal” mirror neurons did not respond anymore (see also Costantini et al. (2010), for similar behavioral effects in humans). Furthermore, those neurons that previously responded to the viewing of actions in extrapersonal space now responded to those actions that were performed in non-reachable peripersonal space (behind the transparent barrier). These results suggest that it was the currently reachable space that was important in evoking a response in these “extrapersonal” and “peripersonal” mirror neurons.

In humans, however, studies of the influence of a barrier between stimuli from different modalities on multisensory interactions have shown different results. For example, Farnè et al. (2003) reported that the strength of visuotactile extinction in brain-damaged patients was not modulated by the presence of a transparent barrier between the visual and tactile stimuli. Similarly, the size of the visuotactile crossmodal congruency effect was not found to be influenced by the presence of a transparent barrier between the visual and tactile stimuli in Kitagawa and Spence's (2005) study using the crossmodal congruency task. It remains to be seen whether different experimental paradigms may be more sensitive in terms of capturing the influence of a transparent barrier on multisensory interactions. One thing to note about these studies is that the transparent barrier did not separate or create different regions of space in terms of depth. It would therefore be interesting to see if, and how, visuotactile interactions are modulated by the presence vs. absence of a transparent border (e.g., a window or windscreen) between visual and tactile stimuli placed at slightly different distances from the observer (much like when we look out a window and see, for example, a clueless pigeon flying towards us).

This approach has been used in a study of affordances in (virtual) peripersonal and extrapersonal space (Costantini et al., 2010). In this study participants had to perform reaching movements to a virtual mug that afforded either a left or a right precision grip. Before the presentation of the mug, a hand was shown indicating a left or a right hand precision grip (the instruction stimulus). Participants' movement onset times after the presentation of the mug were shorter when the instruction stimulus was congruent with the orientation of the mug (e.g., a left precision grip and a mug with the handle on the left), compared to when it was incongruent. This congruency effect was dependent on the perceived distance of the mug. The congruency effect was present when the mug was presented in peripersonal space, but not when it was presented in extrapersonal space. Placing a transparent border in front of the mug in peripersonal space was shown to remove this congruency effect. In a later study, the congruency effect was also shown to be present in extrapersonal (or non-reachable) space when the mug was within the reachable space of an avatar (Costantini et al., 2010; see also Cardellicchio et al. (2011)). Although these studies of affordances do not directly relate to multisensory interactions in peripersonal and extrapersonal space, they do provide information on the interaction between the body and objects in the environment, the role of the distance between objects and the observer, and predictions about possible interactions with the environment.

3.1. *Spatio-temporal properties of visuotactile and audiotactile interactions in peripersonal space*

The specific spatio-temporal properties of dynamic stimuli can also influence the strength of the multisensory interactions that are observed. For example, when using dynamic (i.e., moving) visual stimuli that are seen to approach or recede from the participant's own body, information concerning time-to-contact can be used to predict when the detection of sensory information will be fastest (e.g., Canzoneri et al., 2012; Gray and Tan, 2002; Teneggi et al., 2013). When visual stimuli approach the body at a certain speed, predictions concerning the location of a tactile stimulus in

3-D space can be made (e.g., when and where contact with the body is expected), thus enhancing the speed with which stimuli at the expected time and location are processed relative to other times and locations. Similar results have now also been observed in a study of visuotactile interactions (Kandula et al., 2015). In the latter experiment, movies of an arm reaching out to the left or right cheek of participants were presented prior to the onset of a tactile target that was presented to their left or the right cheek. Tactile targets were presented at different interstimulus intervals, either earlier, at the same time as, or later than the moment at which contact with the face was expected based on the speed of the reaching movement that was presented in the movie. The participants had to detect tactile targets that were presented to either the left or right cheek. As expected, responses to the tactile targets were fastest in the on-time condition.

In a follow-up experiment, this effect was found to depend on the time-to-contact information that could be derived from the movie of the moving arm (i.e., playing the reaching movie in reverse did not elicit an effect of SOA or spatial congruency). Such findings underline the importance of considering the relation between the temporal and spatial properties of multisensory stimulus presentation when trying to understand the dynamic multisensory interactions that, by now, have been documented in 3-D space.

3.2. *Multisensory interactions involving mirror-reflected stimuli in peri- and extrapersonal space*

The use of mirror-reflected stimuli in the investigation of multisensory interactions in peripersonal and extrapersonal space has also provided some interesting insights in terms of multisensory perception in the depth space. For example, Maravita et al. (2002) studied visuotactile congruency effects with stimuli that appeared to be presented in extrapersonal space. In one condition the stimuli were presented in peripersonal space but mirror-reflected to make them visually appear in extrapersonal space. In another condition the stimuli were presented physically in extrapersonal space at the same location that could be seen in the mirror reflection. A schematic side view of their setup is shown in Fig. 4. Visuotactile congruency effects were shown to be significantly larger when the visuotactile stimuli were observed through a mirror and were known to be coming from peripersonal space as compared to when they were presented in extrapersonal space without the aid of a mirror. The results of this study have now been replicated in a more recent EEG study (Sambo and Forster, 2011). In the latter study, Sambo and Forster investigated visuotactile interactions in peripersonal space, with stimuli that were viewed through a mirror and thus appeared to be presented in extrapersonal space. This condition was then compared with the results from one of their earlier studies (Sambo and Forster, 2009) in which the stimuli were presented in extrapersonal space without the aid of a mirror. The researchers observed that the lateral spatial alignment between visual and tactile stimuli modulated the ERPs recorded over the somatosensory cortex in the mirror condition, but not in the extrapersonal condition. Such results would therefore appear to suggest that the known position of mirror-reflected stimuli is more important than their visually perceived position in depth in terms of modulating multisensory spatial interactions. Once again, this result can be interpreted in terms of the spatial alignment in depth of visuotactile stimuli, but here in terms of the known rather than the perceived spatial locations in the depth space.

3.3. *On the nature of the boundary of peripersonal space*

Although the previously-mentioned observations, of stronger visuotactile and audiotactile interactions in peripersonal space as compared to when the component stimuli are presented from different locations in space, are usually taken to suggest that peripersonal space has a boundary defined by such multisensory interactions, it is important to note that these findings might simply reflect the importance of the particular spatial (mis)alignment of stimuli in depth in modulating these interactions (i.e., perhaps limited by the 3-D spatial RF size of neurons). Given that tactile perception is inherently bound to the body, the stronger multisensory interactions involving touch in peripersonal space require stimuli from different modalities to not only be aligned at any particular depth (presenting visuotactile stimuli in extrapersonal space is not meaningful), but specifically to be aligned with the body (or extensions of the body in the case of tool-use). It

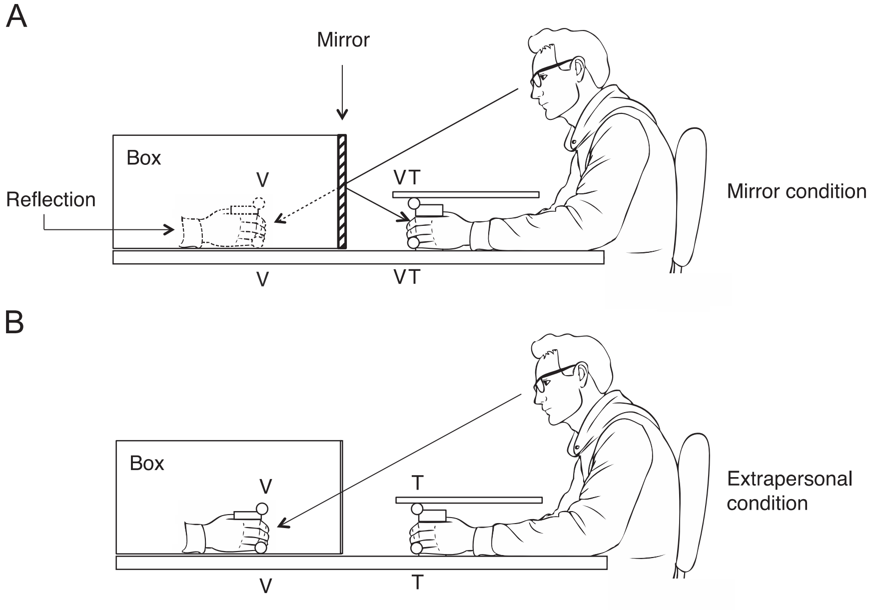

Fig. 4. Schematic side view of the setup used in the study by Maravita et al. (2002). Panel A shows the mirror condition, and panel B show the real extrapersonal condition. LEDs are indicated with a "V", and vibrotactile stimulators with a "T".

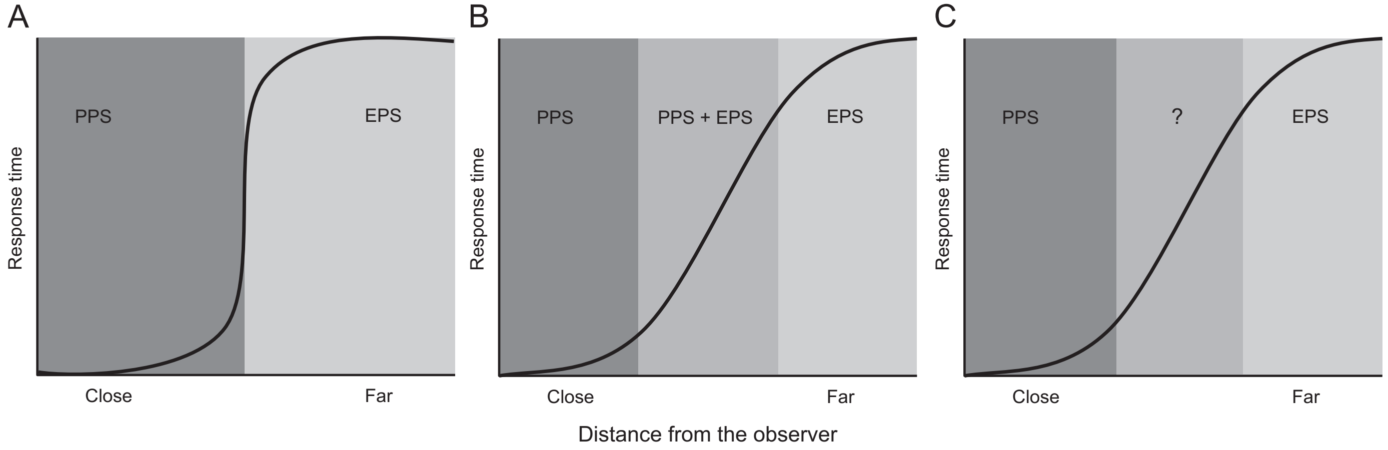

Fig. 5. The putative existence of a border between peripersonal space (PPS) and extrapersonal space (EPS) might be taken to predict that visuotactile or audiotactile interactions would be stronger in peripersonal space. It can be imagined that this border might be relatively sharp (A) or else more gradual (B). Thinking more hypothetically, one might even consider whether there is a region of space that is included in the representation of both PPS and EPS (PPS + EPS in panel B), or a region that is not specifically included in either a PPS or EPP representation of space ("?", panel C).

may be interesting to investigate the relation between the distance separating the unisensory component stimuli in depth and the strength of multisensory interactions involving touch. One can depict this relation as a steep curve with a sudden change in the strength of the interaction when a certain distance has been passed, or as a more gradual one (and if so, over what distance does this change occur). Alternatively, different spatial representation mechanisms may redundantly code stimuli presented within a narrow overlapping field at a border between peripersonal and extrapersonal space (similar to the suggested bilateral representation of a small part of the central visual field, e.g., Bunt et al., 1977; Luo et al., 2011; see Fig. 5 for an overview of the proposed shapes of the peripersonal border).

Canzoneri et al.'s (2012) results may be taken to suggest that the presentation of sensory information from slightly beyond the border of peripersonal space does not result in a sudden absence of all audiotactile interactions. Rather, there is a more gradual decline in the strength of any interactions that are observed, as demonstrated by a gradual increase in RTs. This effect would appear to be most pronounced for those sounds that are perceived to be approaching the participant, and less for those sounds that appear to recede from the participant. The observation of a gradual decline in RT with increasing distance between the unimodal components is in line with the idea that the border of peripersonal space is not a sharp one, but perhaps a (somewhat steep) gradient, suggesting that different neural mechanisms that code peripersonal and extrapersonal space may partly code the same region of space. Similar results have also been observed using the rubber-hand illusion (Lloyd, 2007). The strength of the illusion decreases as the distance between the rubber-hand and the participants' own hand increased with a significant decrease in the strength of the illusion for distances between the rubber hand and the participants' hand larger than ~30 cm (see also Sambo and Iannetti (2013)).

Neurophysiological evidence in support of the idea of there being an overlap in the coding of peri- and extrapersonal space comes from a study by Caggiano et al. (2009). These researchers observed groups of mirror neurons (that is, neurons that are responsive to both the performance and viewing of goal-directed actions) that were responsive to viewing actions performed at different distances from the animal. They reported that while certain neurons that they recorded from were responsive to those actions that were seen in peripersonal space, others were responsive to those actions seen in extrapersonal space. Some of the neurons were responsive to the viewing of actions in both regions of space.

Some hints concerning the nature of the border between peripersonal and extrapersonal space may also be found in a study by Gabbard et al. (2007) in which the participants had to estimate the border of the space that was reachable to them. Visual targets were presented at several distances in both peripersonal and extrapersonal space while the participants responded as to whether they thought that they would have been able to reach the visual stimulus or not. The results revealed that estimation errors peaked at the border of reachable space and declined at larger distances. Speculatively, these results might be seen as fitting in with the idea of overlapping spatial representations of peripersonal (reachable) and extrapersonal (non-reachable) space (see Fig. 5B). In this situation, objects that are presented within the peripersonal space only region (dark gray region Fig. 5B) are clearly reachable and objects that are presented only in extrapersonal space are clearly not reachable (light gray region Fig. 5B). A small region of space surrounding the end of peripersonal space and the beginning of extrapersonal space (medium gray region Fig. 5B) may, however, lead to a larger variation in reach estimates as these objects are coded both as within reach (within peripersonal space) and out of reach (extrapersonal space) and therefore to more errors (see also Bourgeois et al. (2014)).

When thinking about the neuronal mechanisms that may give rise to the border in peripersonal space, studies such as Rizzolatti et al. (1981) immediately spring to mind. In this now-classic study, the researchers demonstrated that some bimodal neurons (pericutaneous and distant peripersonal neurons) were only responsive to those visual stimuli that were presented from within the animal's peripersonal space. Another type of neuron was found to be sensitive to those visual stimuli that were presented both far from and near to the animal (i.e., the distance at which stimuli were presented did not modulate neuronal responses in a systematic manner). Bearing such observations in mind, the visuotactile interactions that are documented in peripersonal space may also depend largely on overlapping RFs, in terms of their sensitivity to the depth from which stimuli are presented. Perhaps visuotactile integration depends on the coding of peripersonal space by bimodal neurons, whereas visuotactile interactions involving visual stimuli that are presented from further away from the observer would undoubtedly still occur, but would simply fail to meet the criterion for integration (that criterion being that multisensory responses should be different from the best of the unimodal responses; e.g., see Stein et al. (2004, p. 32)).

As mentioned before, several studies have shown that distinct brain regions are involved in the processing of sensory information from different regions of space, but we usually do not perceive depth as a dichotomous entity. Drawing a distinction between the space that is reachable and that which is not would appear to be useful in terms of the possible (motor) interactions with the environment and the perception of stimuli that are somehow relevant in terms of their proximity to the body of the observer (in either a positive or negative way). In terms of perceiving and localizing stimuli, and performing fine-grained motor actions, however, a continuous representation of space would seem to make more sense. Interestingly, the existence of these two different spatial representations (dichotomous vs. continuous) has also been supported by the results of several behavioral studies. For example, the results of the sound localization in depth experiment in the study by Canzoneri et al. (2012, Fig. 1B) and Teneggi et al. (2013, Fig. S1)) indicate that participants perceive the location of simulated approaching or receding unimodal auditory stimuli in terms of a spatial continuum in depth. During audiotactile stimulation, however, RTs showed a somewhat steeper decrease at a certain distance from the observer, indicative of there being some kind of boundary in peripersonal space. Such a border was not observed when audiovisual stimuli were used (see Teneggi et al. (2013, Supplementary information)), underlining the idea that those multisensory interactions that involve tactile stimulation may display a (dichotomous) border for peripersonal space (again, perhaps, due to the asymmetric nature of tactile perception).

As should by now be evident, studying multisensory interactions in peripersonal space in isolation is probably not all that informative when it comes to thinking about multisensory interactions in the depth space more generally. For that, one needs to compare the studies of multisensory interactions that have been documented in response to stimuli presented in other modalities (audiovisual), in other regions of space (e.g., extrapersonal space), or at least presented from varying depths.

4. Interim summary

Summarizing what we have seen thus far, a growing number of studies have provided evidence demonstrating the abundant multisensory interactions that take place between those auditory, visual, and tactile stimuli that happen to be presented within reachable space. The results of those studies in which the spatial alignment of the stimuli has been varied in the depth plane would appear to suggest that visuotactile and audiotactile multisensory interactions become more pronounced (as indicated by faster RTs) when the stimuli are aligned in terms of their distance from the (extended) body. In most of those studies in which visuotactile and audiotactile interactions were more pronounced in peripersonal as compared to extrapersonal space, the spatial alignment of the stimuli in the depth plane has also been varied. Such findings may therefore also be interpreted in terms of a reduction in multisensory integration as the distance between the component stimuli is increased. Something like this was also hinted at by Sambo and Forster (2009, p. 1556) when they stated that: *"…these results show that the spatial relationship between visual and tactile stimuli modulate early ERPs, with enhanced amplitudes for tactile stimuli coupled with visual stimuli delivered near the site of tactile stimulation (i.e., perihand space) compared to ERPs obtained when visual stimuli are presented at a different location in peripersonal or extrapersonal space, as one would predict according to the spatial rule of multisensory integration"*. To further explore the role of spatial alignment in multisensory interactions in the depth space, we will now discuss audiovisual interactions in frontal peri- and extrapersonal space.

5. Studies that have focused on audiovisual interactions in frontal peri- and extrapersonal space

As shown in the previous sections of this review, the results of neurophysiological, neuropsychological, and psychophysical studies converge on the suggestion that the space directly surrounding the body (i.e., peripersonal space) and the space that lies just beyond reach is represented differently by the brain when looking at visuotactile and audiotactile interactions (e.g., Caggiano et al., 2009; see Makin et al. (2008), for a review). Given such a distinction, it is remarkable that so little attention has been paid to those multisensory interactions that also take place in extrapersonal space. Indeed, the focus on multisensory interactions in depth thus far has been almost exclusively on uncovering the nature of visuotactile and audiotactile interactions in peripersonal space. If the spatial rule were to apply in the depth plane, as it has repeatedly been shown to apply in the horizontal and vertical planes (at least when the participant's task is in some sense spatial; see Spence (2013)), it can be used to explain the asymmetry of multisensory interactions in depth that involved tactile stimulation. Given that tactile perception is inherently about those stimuli/events that happen to be situated on the observer's skin, spatial alignment in depth (more specifically, spatial alignment with the body) is required for certain multisensory interactions to occur. For purely audiovisual interactions no such an asymmetry would be expected, as the perception of auditory and visual stimuli is not constrained by the distance between the stimuli and the body.

5.1. *Spatial properties of audiovisual interactions in peripersonal and extrapersonal space*

Given that visual and auditory stimuli can be perceived from both close to and far from the observer, we believe that it will be interesting in future research to investigate whether audiovisual interactions are more pronounced in a certain region of space or more or less equal for different regions of space. For example, whereas auditory and visual information may be dominant in extrapersonal space, visual, somatosensory, and vestibular information may be dominant in peripersonal space (Previc, 1998). In their recent study of crossmodal exogenous attention in 3-D space, Van der Stoep et al. (2014a) demonstrated that the presentation of spatially non-predictive auditory cues gave rise to an enhancement in the detection of visual targets at cued as compared to uncued distances (relative to the observer; see Ngo and Spence (2010), for similar findings during visual search). These results can be interpreted in terms of a shift of the participant's exogenous crossmodal spatial attention in the depth plane. The participants in this particular study had to make up/down judgments concerning the elevation of visual targets that were presented on the left or the right of a fixation cross in either peripersonal or extrapersonal space (see Fig. 6 for a bird's-eye view of the experimental setup). An exogenous auditory cue was presented from one of four locations prior to the onset of a visual target presented near left, near right, far left, or far right. The cues could therefore either be valid or invalid in terms of their laterality, and in terms of their depth.

Van der Stoep et al.'s (2014a) results indicated that lateralized spatial cuing effects were only documented when the cue and target were presented from the same depth (see Fig. 7 for a summary of the results). Interestingly, the magnitude of this effect did not appear to differ between those targets that were presented in peripersonal as compared to extrapersonal space. Fig. 7 shows the mean RTs in each cuing condition for those targets presented in peripersonal as compared to extrapersonal space. In addition to showing that crossmodal exogenous attentional cuing can operate

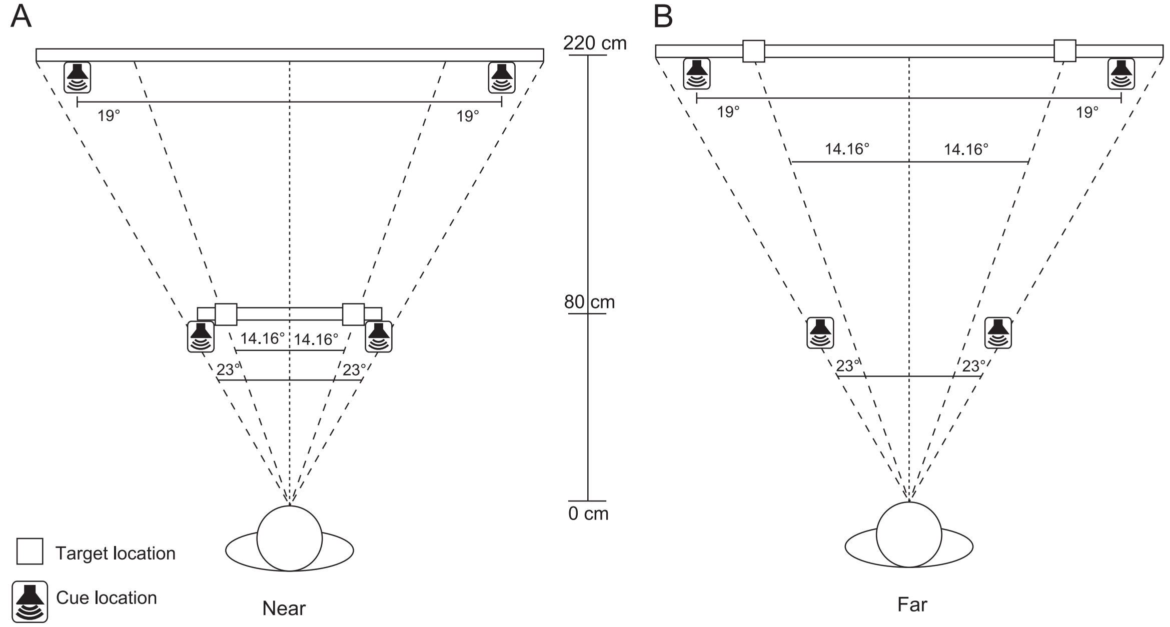

Fig. 6. Panel A shows a bird's-eye view of the experimental setup in the condition in which visual targets were presented in peripersonal space. Panel B shows the setup for targets presented in extrapersonal space [taken from Van der Stoep et al. (2014a), with permission].

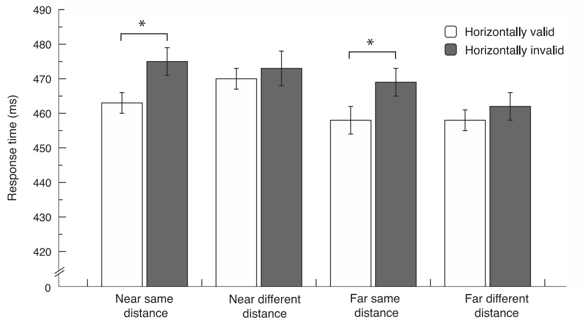

Fig. 7. RTs to visual targets following the presentation of either a valid or invalid lateral cue at the same or a different distance in near and far space. Significant lateral cuing effects were only ever observed when the cue and the target were presented at the same distance (the asterisk indicates a significant difference, $p < .005$). Error bars represent standard errors of the mean with between-subject variance removed [data taken from Van der Stoep et al. (2014a), with permission].

in the depth plane, these results also show that, at least for crossmodal audiovisual exogenous spatial attention, there are no differences in terms of whether both of the stimuli are presented in peripersonal as compared to extrapersonal space. These results therefore do not support a distinction between peripersonal and extrapersonal space as defined by the strength of audiovisual interactions. Instead, they can be taken to suggest that auditory and visual RFs are defined in terms of their responsiveness to stimuli in 3-D space (azimuth, elevation, and depth).

Another recent study provided support for the idea that there might be more pronounced audiovisual interactions in extrapersonal as compared to peripersonal space (Van der Stoep et al., Submitted for publication; also see Previc (1998)). The participants in this particular study had to detect auditory, visual, and audiovisual stimuli that were presented in either peripersonal or extrapersonal space. There were four conditions in the experiment: One condition in which the stimuli were presented in peripersonal space (with a certain intensity), a condition in which the same stimuli were presented from a greater distance and were therefore of a lower intensity (stimuli were not corrected for visual angle and intensity), a condition in which the same stimuli were presented from a greater distance but were corrected for visual angle and intensity, and lastly a condition in which the stimuli were presented in peripersonal space but with the same decrease in intensity as the stimuli presented at a larger distance without correcting for intensity and visual angle (see Fig. 8A for an overview of the conditions). The results revealed that a decrease in intensity that was related to an increase in distance from the observer (presentation in extrapersonal space) enhanced audiovisual integration, whereas the same decrease in intensity for stimuli that were presented in peripersonal space did not result in an increase in multisensory integration (see Fig. 8B).

These results can therefore be taken to suggest that audiovisual interactions may be stronger in extrapersonal as compared to peripersonal space. The amount of audiovisual integration was, however, similar in both regions of space in a condition in which the stimuli were corrected for visual angle and sound pressure level. One could argue that these results reflect a preference of the brain to integrate weak auditory and visual stimuli that are presented at large distances relative to weaker stimuli presented from closer to the observer. Speculatively, this preference might be the result of the multisensory experience that stimulus intensity usually decreases as a function of increasing distance (i.e., increasing distance is lawfully related to decreasing retinal image size and perceived auditory and visual intensity).

Although the previously-mentioned studies on audiovisual interactions in peripersonal and extrapersonal space indicated that audiovisual interactions between those stimuli presented at different distances in the space in front of the observer do not necessarily demonstrate any asymmetric effects in depth, one might have expected that differences in multisensory interactions would occur as the distance at which stimuli are presented increased, given that differences in the arrival time of visual and auditory stimuli will also increase (see Spence and Squire (2003)).

5.2. Temporal properties of audiovisual interactions in peripersonal and extrapersonal space

Given that the temporal relation between auditory and visual information depends on the distance from which the stimuli are presented, any resulting differences in arrival times may influence

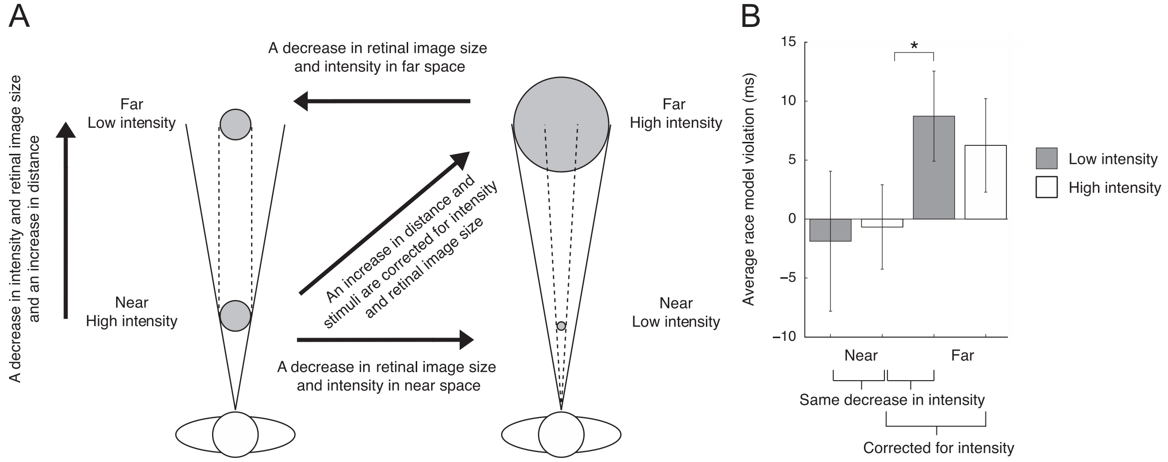

Fig. 8. Left panel: a schematic overview of the conditions that were used in Van der Stoep et al.'s (Submitted for publication) study. Right panel: the average amount of race model violation in each condition. The critical difference between the Near High and the Far Low condition was significant ($p < .05$). Error bars represent standard errors of the mean and contain between-subject variance [data taken from Van der Stoep et al. (Submitted for publication), with permission].

the strength of audiovisual interactions between stimuli presented from different distances. Sugita and Suzuki (2003) investigated whether the point of subjective equality for visual and auditory stimuli (that were presented by means of headphones) depended on the perceived depth of the visual stimulus (see also Engel and Dougherty (1971)). In this case, the participants were explicitly instructed to imagine that the visual stimulus was the source of both the light and the sound. Increasing the distance of the visual stimulus increased the auditory delay that was necessary for subjective simultaneity for stimuli that were presented from distances up to ~20 m.

In a later study of the relation between subjective temporal alignment and the depth at which audiovisual stimuli were presented, Alais and Carlile (2005) investigated the influence of the direct-to-reverberant energy ratio on audiovisual distance perception. This is the ratio between the energy of a sound source that is perceived directly, and the energy that is perceived by means of the reflections in enclosed reverberant environments (Bronkhorst and Houtgast, 1999). The results showed that this ratio was crucial in determining the perceived distance of a sound source and the time delay that was required for participants to judge whether a visual stimulus was aligned temporally (i.e., synchronous) with auditory stimuli that were presented from different simulated distances (also see Gardner (1968)). As in the study by Sugita and Suzuki, the delay that was needed for temporal alignment between the auditory and visual stimuli scaled with approximately the speed of sound (3.43 ms/m) for distances up to 20 m. These results suggests that human observers are able to judge whether the auditory and visual components of an audiovisual stimulus are co-located in terms of their distance from the observer by using multisensory experience-based estimations of differences in arrival times (see also Silva et al. (2013)). However, this effect appears to depend primarily upon strategies in which differences in arrival time are explicitly taken into account (e.g., Alais and Carlile, 2005; Arnold et al., 2005; Kopinska and Harris, 2004; Harris et al., 2010; Lewald and Guski, 2004; Stone et al., 2001). No correction for differences in arrival times was observed when participants judged perceptual simultaneity without taking the distance of the stimuli into account (see Ichikawa (2009), for unisensory visual temporal order judgments with stimuli spatially misaligned in depth).

Based on these results, it could be argued that humans may especially benefit from audiovisual integration when stimuli are presented at distances beyond 20 m as the correct determination of auditory distance becomes increasingly difficult to ascertain. On the other hand, one could argue that visual perception will be dominant at certain distances (Agganis et al., 2010; Kitagawa and Ichihara, 2002), thus reducing any audiovisual integration that is observed merely to the level of statistical facilitation (Miller, 1982, 1986; Raab, 1962).

Taken together, the results of those studies of audiovisual interactions in peripersonal and extrapersonal space suggest that these interactions are not stronger at a certain distance from the observer. This notion is in line with the idea that asymmetric effects of multisensory interactions in depth depend both on spatial alignment of the unimodal component stimuli in depth and the nature of the sensory modalities that are involved. Auditory and visual perception is not constrained by the distance at which stimuli are presented, as is tactile perception. Consequently, audiovisual interactions do not show the same asymmetric effects as audiotactile and visuotactile interactions. In that sense, multisensory interactions involving touch are distinct from purely audiovisual interactions, as the tactile component requires contact with the body. Thus, multisensory interactions involving touch may be especially pronounced close to the body, given that spatial alignment in depth will always require that all unimodal component stimuli be presented in peripersonal space in alignment with the body.

Although these studies do provide information concerning the multisensory interactions taking place in frontal space, it is important to remember that multisensory interactions can also occur between stimuli that are presented in the space behind the observer. Therefore, in order to gain a fuller understanding of multisensory interactions in depth, those multisensory interactions that take place in rear space also need to be addressed.

6. Rear peripersonal and extrapersonal space

The area of space behind the observer, rear space, cannot be seen directly, and therefore provides an interesting opportunity to investigate those interactions taking place between auditory and somatosensory information. Auditory perception covers the full 360° of space around an observer, whereas somatosensory perception covers the entire body surface (and thus covering 360° of (near) space).

6.1. *Audiotactile interactions in rear space*

The distinction between peripersonal and extrapersonal space can also be made when it comes to the space behind an observer.

Indeed, the results of neurophysiological (Graziano et al., 1999) and neuropsychological studies (Farnè and Làdavas, 2002) have clearly shown that audiotactile spatial interactions are more pronounced in near rear space. Graziano et al. (1999) observed that multisensory neurons in the macaque were especially responsive to auditory stimuli that were presented close to the head. In humans, differences between rear peripersonal and rear extrapersonal space have been observed in those patients exhibiting audiotactile extinction (Farnè and Làdavas, 2002). Audiotactile extinction was stronger for auditory stimuli that were presented in rear peripersonal (or near) space compared to rear extrapersonal (or far) space. Similar results have since been obtained in healthy participants. For example, Kitagawa et al. (2005) reported that auditory distractors (white noise bursts) that were presented in rear peripersonal space (~20 cm) caused a greater distractor effect for tactile targets compared to auditory distractors presented in rear extrapersonal space (~70 cm). Importantly, these differences could not be explained in terms of differences in sound pressure level or localizability.

Whereas several studies have shown the importance of spatial alignment for the occurrence of multisensory integration, the spatial alignment of audiotactile stimuli in depth in peripersonal space (i.e., front vs. rear peripersonal space) has been shown not to influence the amount of audiotactile integration (Zampini et al., 2007). Zampini et al. suggested that this is perhaps the result of the large auditory RFs of auditory-somatosensory neurons, making the spatial alignment between auditory and tactile information less relevant for integration to occur (but see Tajadura-Jiménez et al. (2009)). However, influences of spatial alignment on multisensory integration have mainly been observed in studies where the spatial locations of stimuli were somehow relevant to the participant's task (Spence, 2013). Given that the task was to detect stimuli in either the auditory or somatosensory modality, it cannot be ruled out that spatial modulation of audio-somatosensory integration is possible.

A study of the Colavita effect[6] with audiotactile stimuli that were presented in front and rear space revealed an effect of lateral spatial alignment in rear space (i.e., stimuli presented from the same vs. opposite side; Occelli et al., 2010). Furthermore, this effect was only present when auditory stimuli consisted of white noise bursts as compared to pure tones. Compared to pure tones, complex sounds involve more frequencies and therefore they generally allow for better localization (e.g., Frens et al., 1995) and perhaps as a result also better multisensory binding based on the spatial location of stimuli (e.g., Occelli et al., 2010). Furthermore, given that complex sounds are so much more like ecologically valid sounds, humans may have much more multisensory experience with this type of sounds shaping the way in which the brain responds to multisensory stimulation. Interestingly, the difference between the strength of multisensory interactions with complex sounds and pure tones was especially pronounced in rear space (e.g., Occelli et al., 2010; also see Farnè and Làdavas (2002)). Auditory dominance in rear space could cause audiotactile interactions to be more sensitive to differences in the localizability of sounds.

6.2. *Audiovisual and visuotactile interactions in front and rear space*

When thinking of multisensory interactions in rear space, perhaps audiovisual interactions do not readily come to mind, given that we can often not see the space behind us. Nevertheless, some researchers have investigated audiovisual interactions in both front and rear space. For instance, using a simulated driving task, Ho and Spence (2005) demonstrated that auditory exogenous and auditory endogenous spatial cues presented in front of, or behind, participants were able to decrease detection times of visual events that occurred at the cued location. The visual target behind the participants was visible through a mirror, providing ways to see visual targets that were presented in rear space. In a later study, using a similar setup, auditory spatial cues were shown to facilitate visual target discrimination at the same location (valid vs. invalid in front/rear space), whereas tactile spatial cues did not evoke any such effect (Ho et al., 2006; but see Ho et al. (2005)). Among others, the lack of an effect of vibrotactile cues was suggested to be the result of less spatial alignment between cue and target. Vibrotactile cues were presented at the front or the back of the torso of participants, but visual targets were presented in the space on the rear left, 70 cm behind participants. In contrast, auditory cues were presented from the same location as the visual event in rear space (in left rear space 70 cm from the body of the participant).

Mirror reflected visual stimuli presented in rear space have also been used in some studies of visuospatial neglect (Ramachandran et al., 1999; Viaud-Delmon et al., 2007). Interestingly, it has been observed that some patients with left visuospatial neglect in frontal space do not neglect visual stimuli presented in rear space but that are seen through a mirror in frontal space. Although these findings do not provide information on multisensory interactions in rear space, they do provide evidence that attentional orienting can be specifically impaired in frontal space with intact attentional orienting in rear space. This further underlines the idea that rear space is a spatial region that is distinct from other regions of space.

Taken together, then, these results indicate that audiotactile, visuotactile, and audiovisual interactions can also occur in rear space, and again indicate that a distinction between (rear) peripersonal and extrapersonal space can be observed, possibly mediated by the spatial alignment of stimuli in terms of their distance from the observer in rear space.

7. Differences between multisensory interactions involving touch and audiovisual interactions

So far, we have demonstrated that depth related asymmetries in multisensory interactions that occur between different modalities can be explained by the spatial alignment of the unisensory component stimuli in depth and spatial alignment with the body. This may not be so surprising when thinking of the observation of, for example, bimodal, visuotactile neurons with visual RFs that are sensitive to visual stimulation within a certain distance (i.e., depth) from the tactile RF (e.g., Fogassi et al., 1996; Graziano et al., 1999). Although audiovisual interactions and multisensory interactions involving the tactile modality may be explained by differences in the particular spatial alignment of unimodal stimuli in depth, these multisensory interactions also differ in several ways that are determined by the particularities of each sensory modality.

Auditory, visual, and tactile stimuli are initially all encoded in different references frames: auditory stimuli are encoded in a head-centered reference frame, visual stimuli in an eye-centered or retinotopic reference frame, and tactile stimuli in a limb/body-part centered reference frame (see Cohen and Andersen (2002) and Spence and Driver (2004), for reviews). The spatial alignment of stimuli from different sensory modalities can only be determined if the spatial location of these stimuli can be compared in a common reference frame. Interestingly, a target location that

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[6] In a typical study of the Colavita effect, participants have to report the modality of unimodal (e.g., visual and auditory) and bimodal (e.g., audiovisual) stimuli and often report a certain modality more than the others (e.g., more reports of visual than of auditory or audiovisual stimuli; see Spence et al. (2011), for a review).

is initially encoded in one reference frame can be transformed into a different reference frame (e.g., the location of an auditory stimulus location that is encoded in a head-centered reference frame may be transformed into an eye-centered reference frame by means of intermediate-reference-frames; Avillac et al., 2005). With multisensory interactions between auditory and visual stimuli, such reference frame transformations need to take both head and eye-movements into account. When one sensory modality is dominant in a certain brain region (e.g., touch in the ventral intraparietal area, VIP) the reference frame of the other modality is often transformed to that of the dominant modality (Avillac et al., 2005). In line with this idea is the observation of visual RFs of bimodal visuotactile neurons that shift with the position of the hand (e.g., Fogassi et al., 1996; Graziano et al., 1997), anchoring vision to the body (see Avillac et al. (2005, p. 947), for examples with different modalities).

Multisensory interactions involving touch are thus different from audiovisual interactions because they always involve stimulation or prediction of stimulation of the body. The importance of knowing what and when something touches the body seems especially relevant for interaction with the environment and staying out of harm's way (see Section 3.1). However, a clear distinction between the importance of audiovisual interactions on the one hand and audiotactile or visuotactile interactions on the other in spatial processing seems a bit artificial, given that auditory, visual, and tactile information are generally continuously presented to us in our daily lives. In the future, it could be interesting to examine the influence of the spatial alignment of different unimodal component stimuli in depth on the interaction between audition, vision, and touch to investigate the degree to which the spatial alignment of each of these unimodal components contribute to enhanced multisensory (trimodal) interactions in peripersonal space.

8. Conclusions

The importance of studying multisensory interactions in 3-D space is finally starting to be recognized by more researchers. Still, it is evident that research on multisensory interactions that takes the distance at which stimuli are presented into account is still lacking. The majority of studies of multisensory interactions in the depth plane have focused on their distinct nature in peripersonal space. Multisensory interactions between pairs of stimuli that include the tactile modality are often found to be strongest when the stimuli are all presented from within peripersonal space as compared to when the component stimuli are presented from different regions of space. In sum, these asymmetrical spatial effects can be explained by the particular spatial alignment of the unimodal component stimuli, and the fact that tactile perception is limited to body. This means that for multisensory interactions involving touch spatial alignment in depth inevitably requires spatial alignment with the body.

We are generally only able to perceive tactile stimulation when the source of stimulation is presented on, or from, the body (see Spence (2011), for a review; using a tool could be considered to lead to tactile perception in extrapersonal space, but this will always be mediated by, for example, mechanoreceptors in the skin). The nature of certain multisensory interactions in peripersonal space may therefore be attributable to the asymmetry in being able to perceive information presented from different distances. Indeed, studies on active tool use that increase reachable space have revealed similar visuotactile interactions for stimuli that are presented at distances normally considered as extrapersonal space.

Second, a closer look at the multisensory interactions that have been documented in studies concerning multisensory processing in frontal peripersonal, frontal extrapersonal, rear peripersonal, and rear extrapersonal space makes it evident that the majority of the asymmetries in multisensory interactions in the depth plane can be explained in terms of spatial alignment/misalignment in depth/lateral space. Furthermore, multisensory interactions between those sensory modalities that do not require stimulation in close proximity of the body should not be asymmetric in terms of the distance from which these stimuli are presented. This was indeed the finding of a recent study by Van der Stoep et al. (2014a). Although the spatial alignment in depth did affect the presence of a crossmodal cuing effect, this effect did not differ for visual targets that were presented in near as compared to far space. Table 1 provides an overview of the multisensory interactions that are observed in the regions of space and the modulatory factors that were discussed in this review and shows clearly how audiotactile and visuotactile interactions are constrained by the fact that tactile perception is inherently close to the body. This seems to provide an explanation for differences between peripersonal and extrapersonal space both in front of and behind the observer.

It seems as though the importance of visuotactile and audiotactile interactions in peripersonal space has so far mainly been explained in rather non-specific terms concerning their relevance in dealing with interactions with the environment close to the observer. Although these explanations clearly make sense, they do not provide a clear mechanism that underlies the special role of such interactions in peripersonal space.

Given the important role of multisensory experience with the environment in the development of multisensory spatial interactions (Wallace and Stein, 1997, 2001, 2007), it may be relevant to consider the role of depth in the development of multisensory spatial interactions. Sources of tactile stimulation are normally located on the body, which provides an opportunity for the body to build a coherent multisensory spatial representation, perhaps calibrating the sensory systems of audition, touch, proprioception, and vision, through their interactions in depth space (see Graziano et al. (1997, p. 2289)). This may result in multisensory interactions that are sensitive not only to the horizontal and lateral spatial alignment of sensory information but also to their spatial alignment in depth. In contrast with this idea is the seemingly asymmetrical effect of spatial alignment on audiotactile interactions that has recently been documented when stimuli are presented in frontal as compared to *rear peripersonal* space (see Occelli et al.

Table 1
Observed multisensory interactions within each region of space and modulatory factors.

	Frontal space		Rear space	
	Peripersonal space	Extrapersonal space	Near space	Far space
Observed Multisensory interactions	VT, AT, AV	AV, VT	AT	AV
Modulatory factors	Lateral space, depth, social context, anxiety	Lateral space, depth	Lateral space, depth	Lateral space, depth, stimulus intensity

V=Visual, T=Tactile, A=Auditory.

(2011), for a review). Whereas the relative spatial alignment in the horizontal (or azimuthal) plane of auditory and tactile stimuli does not seem to be very important when it comes to studying audiotactile interactions in *frontal peripersonal* space (but see Farnè and Làdavas (2002) and Spence et al. (1998)), it seems crucial for such interactions when the very same stimuli are presented in *rear peripersonal* space. This may, in part, be the result of the dominance of vision in frontal space, making spatial alignment of audiotactile stimuli in frontal space less important for multisensory interactions as compared to spatial alignment of audiotactile stimuli in rear space.

The distance from the body at which multisensory interactions involving the tactile modality are enhanced may depend on the body part that is stimulated (something that has also been suggested by Tajadura-Jiménez et al. (2009)). Although audiotactile interactions seem to be more pronounced with the tactile stimulation of the head compared to the hands (Tajadura-Jiménez et al., 2009), it is still unclear how the spatial alignment between audiotactile and visuotactile stimuli influences multisensory interactions with tactile stimulation of different body parts (perhaps RF sizes around certain body parts allow for a larger distance between the unimodal component stimuli while still resulting in multisensory interactions/integration, see, for example, Teramoto et al. (2013)).

Besides the role of the spatial alignment of stimuli presented in depth in terms of modulating multisensory interactions, there may also be a role for spatial attention. For instance, one could argue that spatial attention is more focused in conditions of spatial alignment or better captured as compared to when stimuli are presented from different positions (see Spence (2010)). It remains to be seen what the relative contribution of attention is to the processing of multisensory information in such a complex spatial environment (e.g., Alsius et al., 2007; Fairhall and Macaluso, 2009; Talsma et al., 2007; Talsma and Woldorff, 2005; Van der Stoep et al., in press; see Koelewijn et al. (2010) and Talsma et al. (2010), for reviews).

To conclude, it would seem important to take several factors into account when investigating multisensory interactions with a focus on either peripersonal or extrapersonal space. The spatial alignment in depth of stimuli presented in different modalities (more specifically spatial alignment with the body in the case of multisensory interactions involving touch), the distribution of attention in depth, and the asymmetric nature of multisensory interactions involving the tactile modality may all contribute to the behavioral effects that arise from such multisensory interactions.

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