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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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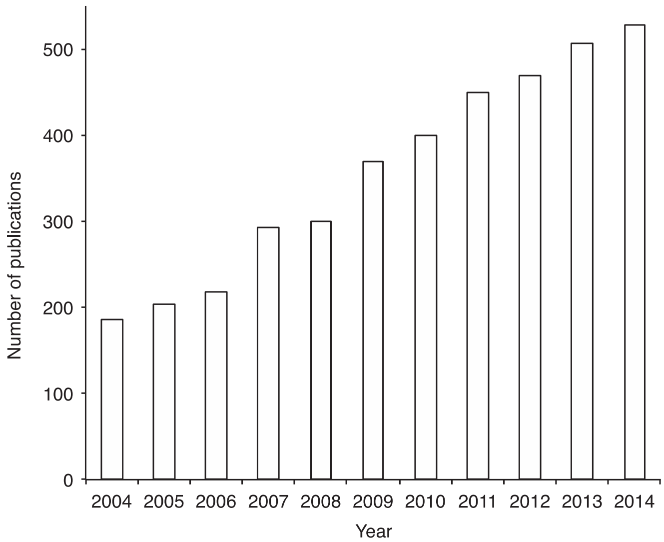

Fig. 1. Number of articles indexed in PUBMED over the last decade that have included the keywords "multisensory", "crossmodal", or "cross-modal" in the title or abstract (see also Murray et al. (2013) and Stein et al. (2010)).

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

[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.

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