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The influence of embodiment on multisensory integration using the mirror box illusion

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ABSTRACT

We examined the relationship between subcomponents of embodiment and multisensory integration using a mirror box illusion. The participants' left hand was positioned against the mirror, while their right hidden hand was positioned 12″, 6″, or 0″ from the mirror – creating a conflict between visual and proprioceptive estimates of limb position in some conditions. After synchronous tapping, asynchronous tapping, or no movement of both hands, participants gave position estimates for the hidden limb and filled out a brief embodiment questionnaire. We found a relationship between different subcomponents of embodiment and illusory displacement towards the visual estimate. Illusory visual displacement was positively correlated with feelings of deafference in the asynchronous and no movement conditions, whereas it was positive correlated with ratings of visual capture and limb ownership in the synchronous and no movement conditions. These results provide evidence for dissociable contributions of different aspects of embodiment to multisensory integration.

1. Introduction

In representing body position, information from different primary senses are integrated, resulting in a single estimate of limb position. To determine the mechanisms by which multisensory information is integrated, various researchers have studied how the brain resolves discrepancies between senses. For example, viewing a limb while wearing prism glasses with a mild (10–20 deg) lateral displacement introduces a difference between visual and proprioceptive information regarding limb position. After viewing for a short period of time, individuals will feel as if their limb is in the same location as the shifted visual image ("visual capture", Hay, Pick, & Ikeda, 1965; Tastevin, 1937; Welch & Warren, 1980), providing initial evidence for a strong weighting of visual information in multisensory integration.

Studies of multisensory integration have elegantly shown that the contributions of vision and proprioception to position estimates are weighted based on the relative spatial precision of each input (Ernst & Bulthoff, 2004; van Beers, Sittig, & Denier van der Gon, 1999b; van Beers, Wolpert, & Haggard, 2002). However, there is another factor that may influence weighting processes in multisensory integration – our sense of **embodiment**. Here, embodiment refers to the subjective experience of having one's own body. Longo, Schuur, Kammers, Tsakiris, and Haggard (2008) attempted to identify different aspects of embodiment using the rubber hand illusion (Botvinick & Cohen, 1998). In the rubber hand illusion, simultaneous

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stroking of the participant's own hidden hand and a viewed rubber hand results in the rubber hand feeling like their own hand, thus embodying the rubber hand in some manner. Using a principal components analysis (PCA) on questionnaire responses to different aspects of the rubber hand illusion, Longo and colleagues found four major components for the rubber hand illusion during the synchronous stroking condition – embodiment of the rubber hand, loss of their own hand, movement, and affect. The embodiment component further dissociated into three subcomponents; ownership (the sense that the rubber hand was part of one's own body), location (the sense that the rubber hand was in the same location as one's own hand) and agency (the sense of control over the rubber hand). This study provided a starting point for further examinations of embodiment and its relationship to cognitive and phenomenological processes.

Interestingly, our sense of embodiment can be altered by multisensory conflict. In the previous study, Longo et al. (2008) also analyzed questionnaire responses during asynchronous stroking in the rubber hand illusion. Although this is often considered as simply a control condition for the synchronous stroking condition, asynchronous stroking is not neutral as it creates multisensory incongruence between visual and tactile inputs. Along with the factors previously reported for synchronous stroking, the principal components analysis for asynchronous stroking discovered an additional component – **deafference**. This component included responses in which participants reported that their real hand felt numb, less vivid, and had a "pins and needles" sensation.

Similar sensations have been reported during multisensory incongruence in the mirror box illusion (Ramachandran, Rogers-Ramachandran, & Stewart, 1992). In a typical mirror box experiment, a mirror is placed perpendicular to the trunk midline of the individual (in the sagittal plane), with one limb on each side of the mirror. When viewed by the participant, the reflection of the left arm in the mirror looks like the participant's right arm, as the visual image is in the typical space where the right hand would be, and has the same chirality as the participant's own right hand. However, since the participant does not actually see his/her own hidden limb, the experimenter can manipulate the congruence between visual and proprioceptive information to examine multisensory integration. When both the hidden limb and viewed reflection are moved congruently, there is a strong sense of ownership and visual capture. However, introducing incongruencies between visual information (from the reflected limb) and proprioception and motor information (from the hidden limb) can result in a variety of abnormal sensations. For example, McCabe, Haigh, Halligan, and Blake (2005) asked participants to make bimanual movements (flexion and extension of the forearm or lower leg, coordinated or out of phase) with the limbs separated by either a whiteboard or a mirror. When participants made out-of-phase movements while viewing the mirrored limb, creating a strong intersensory mismatch between visual and proprioceptive/motor information, participants reported various sensory phenomena in the hidden limb, including tingling sensations, weight changes in the hidden limb, a perceived decrease in hidden limb temperature, and (in some cases) perception of an additional limb (see also Fink et al., 1999; Foell, Bekrater-Bodmann, McCabe, & Flor, 2013; Jackson & Zangwill, 1952; Tajadura-Jimenez, Longo, Coleman, & Tsakiris, 2012; Wasaka & Kakigi, 2012). In both the rubber hand and mirror box illusions, multisensory incongruence regarding the body leads to changes in the subjective experience of one's own body.

In this study, we examined the relationship between measures of embodiment and estimates of limb position while manipulating multisensory conflict using a mirror box paradigm similar to one used by Holmes and colleagues (Holmes, Crozier, & Spence, 2004; Holmes & Spence, 2005b). In a series of experiments, they instructed participants to reach to unseen targets while manipulating the spatial congruency between the mirror reflection and the actual position of their right hand, and found that reach endpoints were biased by the viewed position of the hand. They examined the effect of multisensory congruence on limb position estimates by measuring reach endpoints after synchronous movement of both hands (bimanual, in phase tapping of each index finger), no hand movement, and asynchronous out of phase tapping of both hands (Holmes, Snijders, & Spence, 2006; Experiment 4). They found that the visual bias was strongest in the synchronous condition, followed by the no movement condition, with the asynchronous condition resulting in the least visual bias. These results provided evidence that increased multisensory congruence leads to stronger weighting of visual information in limb position estimates. However, along with altering multisensory congruence, synchronous movement may also result in changes in feelings of embodiment towards the mirrored hand, which may also influence multisensory integration processes.

To examine the role of embodiment in multisensory integration, we also asked participants to tap both hands synchronously (increased sense of ownership), asynchronously (increased sense of deafference), or to make no movements in a mirror box, manipulating the spatial discrepancy between viewed and actual limb position. First, we examined whether differences in multisensory congruence influenced the relative weighting of visual or proprioceptive information in position estimation. Consistent with previous findings (Holmes et al., 2006), we predicted that the temporal congruence across modalities in the synchronous tapping condition would lead to more effective visual capture and result in increased bias towards the perceived visual position of the limb, whereas decreased temporal synchrony in the asynchronous tapping condition would result in more bias towards the proprioceptive estimate. Second, extensive variance has been observed across individuals in visual capture (Welch & Warren, 1980). We examined whether differences in measures of embodiment across individuals predict the effectiveness of visual capture in the mirror box illusion. As each movement condition has the same multisensory congruence across individuals, we predicted that differences in position estimates across individuals are tied to their own subjective sense of embodiment during the illusion. Therefore, we examined the relationship between subjective responses on an embodiment questionnaire and objective estimates of limb position within each movement condition.