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Integrating multisensory information across external and motor-based frames of reference

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ABSTRACT

In the mirror box illusion, participants often report that their hand is located where they see it, even when the position of the reflected hand differs from the actual position of their hand. This illusory shift (an index of multisensory integration) is stronger when the two hands engage in synchronous bimanual movement, in which visual and proprioceptive information is congruent in both motor-based (i.e. coordinate centered on the effector) and external (i.e. coordinates centered on elements external to the effector) frames of reference. To investigate the separate contributions of external and motor-based congruence in multisensory integration, we instructed participants to make synchronous or asynchronous tapping movements in either the same (i.e. both hands palms up) or opposing (palm up, palm down) postures. When in opposing postures, externally congruent movements were incongruent in a motor-based frame of reference, and vice versa. Across three experiments, participants reported more illusory shift and stronger ownership of the viewed hand in the mirror for external versus motor-based congruence trials regardless of motor outflow or motor effort, indicating that information from an externally-based representation is more strongly weighted in multisensory integration. These findings provide evidence that not only information across sensory modalities, but also information regarding crossmodal congruence represented in different spatial frames of reference, is differentially weighted in multisensory integration. We discuss how our findings can be incorporated into current computational models on multisensory integration.

1. Introduction

To form a coherent representation of the body, the brain needs to efficiently and accurately integrate inputs from different sensory modalities. The fundamental role of multisensory integration in body representation can be demonstrated by the mirror box illusion in which careful manipulation of cross-modal congruence can lead to displacements in perceived limb position. To elicit the mirror box illusion, a mirror is placed in the midsagittal plane and an individual places one hand on each side of the mirror. When viewed by the individual, the reflection of the hand in front of the mirror looks like the hand hidden behind the mirror (Ramachandran & Rogers-Ramachandran, 1996). In some studies, the hidden and viewed hands are placed at different distances from the mirror midline, creating a mismatch between the visual (i.e. the hand reflection in the mirror) and proprioceptive (i.e. the actual hidden hand) estimates of the hidden hand. After doing synchronous bimanual movements (e.g. index fingers tapping in-phase), participants made errors when reaching to a target with the hidden hand, as if the hidden hand was felt at the visual reflection instead of

where it actually was located (Holmes, Crozier, & Spence, 2004; Holmes, Snijders, & Spence, 2006; Holmes & Spence, 2005). In addition, participants reported a strong sense of ownership of the hand seen in the mirror (Liu & Medina, 2017; Medina, Khurana, & Coslett, 2015).

These dependent variables (ownership, shifts in perceived limb position and reaching errors) have been used to index multisensory integration under different conditions. For example, the illusion becomes less effective as the distance between the visual and proprioceptive hidden hand estimates increases (Holmes & Spence, 2005; Holmes et al., 2004, 2006; Medina et al., 2015), providing evidence that inputs from multiple modalities are more likely to be integrated if they are spatially close. In addition, making synchronous bimanual movements resulted in more bias of the felt position of the hidden hand towards the visual reflection, and a stronger sense of ownership of the visual reflection than asynchronous movements (e.g. index fingers tapping out-of-phase), indicating increased multisensory integration with more congruence between viewed movements and actual movements (Holmes & Spence, 2005; Medina et al., 2015; see also Fink et al., 1999; Foell, Bekrater-Bodmann, McCabe, & Flor, 2013; McCabe, Haigh,

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Halligan, & Blake, 2005; Otsuru et al., 2014). These findings are consistent with earlier work demonstrating that unimodal inputs are more likely to be integrated if they are spatially and temporally congruent (Meredith, Nemitz, & Stein, 1987; Meredith & Stein, 1986).

Previous studies have manipulated congruence between movements seen in the mirror and movements made by the actual hidden hand (visuomotor congruence) in the mirror box. However, how is congruence defined? For example, there are a number of spatial representations (i.e. neural systems for representing location) of visuomotor information for one's hand, each with its own spatial frame of reference. Positions that are incongruent across modalities in one frame of reference could be congruent in another frame of reference. Consider the simple example of closing one's hand. One frame of reference in which finger movements are encoded is relative to the effector itself, i.e. angles formed by the interphalangeal joints. We will refer to this as a motor-based frame of reference. Evidence that limb movements are represented based on joint angles comes from studies using single-cell recording with non-human primates. For example, when non-human primates grasp objects, the firing rate of some neurons in primary motor cortex are tuned to finger and wrist joint angles (Saleh, Takahashi, Amit, & Hatsopoulos, 2010). However, movements are also represented in external space for the effectors to act on targets (Graziano, 2001). For example, consider a condition in which an individual is grabbing a round ball, suspended in air, from either above or below the ball. In both cases, the hand goes from an open position to one in which the fingers are grasping the ball – the same movement in a motor-based frame of reference. However, the posture of the hand differs for the two movements, resulting in different finger movements in a number of external reference frames (e.g. when above the ball, the fingers move downwards in a gravitational frame of reference; when below the ball, the fingers move upwards in a gravitational frame of reference). Here we use the term external frame of reference to refer to coordinates that are centered on elements external to the effector. The distinction between representations centered on effectors and external space has also been discussed in prior literature (e.g. Brandes, Rezvani, & Heed, 2016; Graziano, 2001; Scott, Sergio, & Kalaska, 1997; Soechting & Flanders, 1989). In addition, studies on goal-directed movements have shown that the relative position between effector and target object can be represented in motor-based and external frames of reference in parallel and is computed as a weighted sum of these spatial representations (Mueller & Fiehler, 2016; Sober & Sabes, 2005; Tagliabue & McIntyre, 2014). When making bimanual movements in the mirror box, movements on the viewed hand (visual information) can be represented in both external and motor-based frames of reference. Similarly, movements of the actual hand (motor information) can also be represented in both frames of reference. With visuomotor information represented in multiple frames of reference, visuomotor congruence could also be calculated in multiple frames of reference during multisensory integration, leading to multiple estimates of visuomotor congruence. The problem faced by the brain is thus efficiently integrating congruence estimates from multiple frames of reference to obtain a unified estimate of visuomotor congruence.

In the current study, we dissociated visuomotor congruence in external and motor-based frames of reference in the mirror box illusion to investigate how information from different types of spatial representations is combined in multisensory integration. In Experiment 1, participants placed their right hand in front of the mirror and their left hand behind the mirror. The hands were placed either in congruent postures (palm down; Fig. 1, upper row), or in opposing postures (palm up versus palm down; Fig. 1, bottom row). Participants tapped the index finger on both hands either motorically synchronously (i.e. flex and extend the metacarpophalangeal joints of each index finger simultaneously) or asynchronously (i.e. flex the joint of one index finger while extending the other index finger). When the hands are in the same posture, motor-based and external visuomotor congruence are yoked (Fig. 1a and b). Critically, motor-based and external

representations are dissociated when the hands are in incongruent postures, such that motor-based congruent movements are in opposing directions in external space (Fig. 1c) and vice versa (Fig. 1d). To examine multisensory integration as a function of congruence across multiple representations, the left and right hands were different distances from the mirror, creating a mismatch between visual and proprioceptive information for the hidden hand.

To index multisensory integration, we measured proprioceptive shift of the hidden (left) hand (i.e. the difference between reported hand position before and after finger tapping in the mirror box) and sense of ownership of the hand viewed in the mirror. Moreover, the visual and proprioceptive inputs differed in hand posture (palm up, palm down) in motor-based and external congruence conditions (Fig. 1c and d). We predicted that multisensory integration would result in changes in perceived hand posture, such that the posture of the hidden hand would be perceived as matching the visual estimate (Ionta, Sforza, Funato, & Blanke, 2013; Liu & Medina, 2017). Therefore, we measured the degree to which the unseen (left) hand is felt as in the same posture as the viewed hand.

Experiment 1 showed that external congruence resulted in more proprioceptive shift than motor-based congruence, indicating that information from different spatial representations, not only different modalities, can be differentially weighted in multisensory integration. In Experiments 2 and 3, we examined whether the relative weighting of information from external or motor-based representations can dynamically change based on the amount of motor outflow and motor effort from a representation in motor-based reference frame. For example, if the participant is making more motor movements, or expending more motor effort, one hypothesis is that information from a motor-based representation will be more strongly weighted. To examine this hypothesis, we increased motor outflow by having participants tap with additional fingers on both hands (Experiment 2), and increased motor effort by adding resistance to the one-finger tapping condition (Experiment 3). Experiments 2 and 3 were also designed to replicate the findings from Experiment 1, in which information from an external representation was more strongly weighted information from a motor-based representation. In summary, we did replicate the findings from Experiment 1, but found no influence of changes in motor outflow or motor effort on these weightings.

2. Experiment 1

Experiment 1 aimed to investigate if visuomotor congruence represented in motor-based and external frames of reference can induce multisensory integration independently, and which representation is more strongly weighted in multisensory integration.

Given evidence that visuomotor information regarding one's limb is ultimately encoded in a motor-based frame of reference (Graziano, 2001; Saleh et al., 2010) for making motor plans, one possibility is that visuomotor congruence is primarily calculated in a motor-based frame of reference, increasing the weight assigned to motor-based representations relative to an external representation. On this assumption, motor-based congruence (with external incongruence) would result in more multisensory integration than external congruence (with motor-based incongruence). Alternatively, given the typical dominance of visual information in multisensory integration (Ernst & Banks, 2002; van Beers, Sittig, & van Der Gon, 1999), along with evidence that vision represents information primarily in external space (Avillac, Deneve, Olivier, Pouget, & Duhamel, 2005; Mechsner, Kerzel, Knoblich, & Prinz, 2001), information from an external representation might be more strongly weighted than information from a motor-based representation. For example, in a similar manipulation with the mirror box, Brandes et al. (2016) found that bimanual motor coordination performance was determined by whether visuomotor information was congruent in an external frame of reference, regardless of visuomotor congruence in motor-based frame of reference (also see Tomatsu & Ohtsuki, 2005). If

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