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Direction-dependent integration of vision and proprioception in reaching under the influence of the mirror illusion

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Abstract

Recent models of multisensory integration predict differential weighting of information from different sensory modalities in different spatial directions. This direction-dependent weighting account suggests a heavier weighting for vision in the azimuthal (left–right) direction and a heavier weighting for proprioception in the radial (near–far) direction. Visually induced reaching errors, as demonstrated in previous 'mirror illusion' reaching experiments, should therefore be greater under visual-proprioceptive conflict in the azimuthal direction than in the radial direction. We report two experiments designed to investigate the influence of direction-dependent weighting on the visual bias of reaching movements under the influence of a mirror-illusion. In Experiment 1, participants made reaches straight forward, and showed terminal reaching errors that were biased by vision in both directions, but this bias was significantly greater in the azimuthal as compared to the radial direction. In Experiment 2, participants made reaches from right to left, and showed a significant bias only in the azimuthal direction. These results support the direction-dependent weighting of visual and proprioceptive information, with vision relatively more dominant in the azimuthal direction, and proprioception relatively stronger in the radial direction.

Keywords: Multisensory; Phantom limb; Illusion; Hand position; Visuomotor coordination

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1. Introduction

Several sources of information are available when determining hand posture. The brain normally receives input from at least two senses: vision, seeing the hand in a given position; and proprioception, the information coming from muscle and joint receptors. The information available from these two sensory modalities may differ substantially. Vision initially operates in an eye-centred reference frame, and therefore may have different directional-sensitivity compared to proprioception, which initially operates in body-centred coordinates (e.g., centred on the arm and shoulder joints). Several experimental paradigms, such as the "rubber hand illusion" (Botvinick & Cohen, 1998; Ehrsson, Holmes, & Passingham, 2005; Ehrsson, Spence, & Passingham, 2004), and the "mirror illusion" (Holmes, Crozier, & Spence, 2004; Holmes, Snijders, & Spence, in press; Holmes et al., 2005; Ramachandran, Rogers-Ramachandran, & Cobb, 1995) reveal a complex interaction between vision, proprioception, and somatosensation when information from these senses is integrated to perceive arm position and for generating reaching movements.

In the "mirror illusion," a mirror is used to present visual information regarding a participant's "virtual hand" that substitutes for their real but unseen hand which is placed behind the mirror. The mirror illusion can be used to induce systematic reaching and pointing errors for movements made with the unseen hand behind the mirror (Holmes et al., 2004; Holmes & Spence, 2005). The mirror projects visual information regarding the apparent position of the participant's hand that may conflict with proprioceptive information concerning the actual position of the unseen hand. This conflict can influence subsequent reaching movements made with the unseen hand, in that participants make greater terminal reaching errors in the direction predicted by the systematic integration of visual and proprioceptive information concerning hand position. In the absence of a mirror, or when no hand is viewed in a mirror, reaching movements

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with the unseen hand show a lower terminal error. These results indicate the relative dominance of visual input over other sensory information concerning parts of our body seen in a mirror. Some form of "visual bias" therefore appears to influence reaching movements when we receive visual information concerning our body via mirror reflection.

Vision provides information concerning the location of the target, the hand and possibly also the angles of the joints in an eye- or head-centred coordinate system. Proprioception gives information regarding the location of the hand and the joint angles in an intrinsic, body- or bodypart-centred coordinate system. Computing the transformation from one reference frame to the other is required to integrate the two sources of information. This translation may result in errors (noise) that induce extra costs, which may therefore need to be minimised. As well as the dependence on the initial coordinate system of information specifying the position of the *hand* across the sensory modalities, it has also been suggested that the modality of the *target* influences the weighting of the sensory information (Sober & Sabes, 2005). The relative weighting of the component information in the integration process shifts towards the target modality.

Finally, the content and richness of the information is also an important factor in determining the weighting of visual and proprioceptive information. Visual feedback concerning hand position alone has a different, weaker, weighting than visual feedback concerning both hand and arm position together (i.e., visually providing both the hand location and the angles of the arm joints; Sober & Sabes, 2005). The latter results in a heavier weighting of visual information, and thus generates greater movement errors in situations where the visual position feedback conflicts with the true (proprioceptively specified) positional information.

One model of how the brain integrates proprioceptive and visual body position information concerns the direction-dependent weighting of this information (van Beers, Sittig, & Denier van der Gon, 1999; van Beers, van, Wolpert, & Haggard, 2002). The weighting is related to the relative precision of the unimodal information in a given direction. The proprioceptive position sense is more precise (i.e., gives an arm position estimate with lower variability) in the radial direction (i.e., near–far) than in the azimuthal (i.e., left–right) direction.

The experiments described above often used quite simplified visual representations of the hand to indicate its location (e.g., a single spot of light or a geometrical mock-up of an arm, e.g., Sober & Sabes, 2003, 2005; van Beers et al., 1999, 2002). By contrast, a separate line of research concerning the "rubber hand illusion" and the "mirror illusion" suggests that there may be important differences between the effects of visual or multisensory exposure to a real (i.e., mirror reflection) or realistic (i.e., rubber) hand, as compared to a more abstract or neutral exposure object such as a spot of light, a block of wood, or even when compared to a misaligned but realistic looking rubber hand, or to a rubber hand that is stimulated asynchronously or incongruently with respect to the real hand (Austen, Soto-Faraco, Enns, & Kingstone, 2004; Ehrsson et al., 2004, 2005; Holmes et al., in press; Pavani, Spence, & Driver, 2000). Indeed, it appears that even a relatively simple visual cue such as the geometrical representation of an arm can elicit increased visual weighting in determining hand and arm position than a single spot of light (Sober & Sabes, 2005).

The results obtained in rubber-hand and mirror-illusion experiments therefore question whether such simplified representations of the body can be used to provide veridical estimates of visual-proprioceptive integration in normal, everyday behaviours (for example, when we see our body parts in full vision while reaching for an object). In addition, in many of the previous studies of visual-proprioceptive integration in reaching, the participants were not informed of the possible experimental manipulations of the visual feedback of their hand (e.g., see Nielsen, 1963; Sullivan, 1969; Welch, 1972, 1986 for the effects of knowledge of such manipulations on participants' experience, and on the relative weighting of sensory modalities). Explicit trust in the veracity of the visual information may therefore have led participants to neglect the proprioceptive information in cases of visual-proprioceptive conflict, resulting in an overestimation of the relative weighting of visual information in these studies.

In several previous attempts to address these issues, Holmes and colleagues (Holmes & Spence, 2005; Holmes et al., 2004, in press) studied the integration of vision and proprioception in reaching movements using a reflection of a hand in a parasagittally positioned mirror. The rich visual feedback concerning hand position in the mirror led to an increased dependence on visual information as compared to reaches made in the absence of either an image of the hand, or the mirror. These previous mirror experiments, however, manipulated the visual-proprioceptive conflict and measured terminal reaching errors only in the azimuthal, left–right direction of the workspace. According to the direction-dependent weighting account, visual-proprioceptive conflict in the radial direction should therefore be resolved in terms of a stronger weighting of the proprioceptive information, and consequently smaller terminal errors, than in azimuthal conflicts.

Additionally, Holmes and colleagues' experiments (Holmes & Spence, 2005; Holmes et al., 2004, in press) used only a single target location and multiple possible starting positions, distributed along a line perpendicular to the plane of the mirror. This led to a situation in which the distance and direction from the starting position to the target varied with each starting position. There may be an as yet unknown interaction between the starting position and/or the distance of the movement and the direction of the visual-proprioceptive conflict. When participants reached more to the left or the right of the target (i.e., in the azimuthal direction) in the experimental conditions (vision of the hand) than in the control conditions (no vision of the hand), they may actually have been under-reaching to the target—i.e., since the distance and direction of the required reaches were not independently manipulated, it is not certain whether both these factors are affected by the mirror illusion or just the reaching direction as hypothesised (though see Holmes et al., in press, Experiment 5, for initial evidence against this possibility).

We therefore designed two experiments to test a prediction of the direction-dependent weighting model using the mirror-