Synaesthesia in the normal limb

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SUMMARY

We explored the degree to which vision may alter kinaesthetic perception by asking participants to view their hand through a prism, introducing different horizontal deviations, while trying to align their fingers above and below a thin table. When the visual image of one hand was displaced this overwhelmed kinaesthetic judgements and participants reliably reported that they felt their limbs were aligned, even when they were laterally mis-aligned by as much as 10 cm. This effect, however, was mediated by 'visual capture' and when the task was attempted in a darkened room with limb position indicated by an LED taped to the finger, kinaesthesis dominated and participants reported that the LED seemed to become detached from their finger tip. In both light and dark conditions the finger was clearly visible and only the background detail was extinguished. Hence, in perceiving limb position, it appears that we believe in what we see, rather than in what we feel, when the visual background is rich, and in what we feel when the visual background is sparse.

1. INTRODUCTION

Synaesthesia may be defined as a subjective sensation experienced in one modality when a different modality is stimulated. Quantification of synaesthetic effects has been problematic, but recent research has shown that human amputees obtain a vivid kinaesthetic sensation when limb movement is visually superimposed upon the phantom limb (Ramachandran *et al.* 1995; Ramachandran & Rogers-Ramachandran 1996). This fascinating observation questions the extent to which *felt* position is specified purely by mechano-receptors and highlights the role that vision may play as a kinaesthetic surrogate in human sensation.

Under normal conditions, an isomorphic relationship exists between limb position and visual feedback. Changing visual input through a prism thus leads to predictable errors, where the location of visual objects relative to the limb is misperceived. If active movement of the visually displaced limb is allowed then adaptation will occur (Held 1963). Harris (1963) asked participants to point to visual targets with an unseen hand after an extended period of prism adaptation and demonstrated that kinaesthetic judgments (towards visual targets) were biased. This provided evidence that the alignment between kinaesthesis and visual space may be modified, but not that there was a visually induced change in *felt* position of the hand. To demonstrate the latter effect, it is necessary to provide a reference condition that does not rely upon a visual matching procedure. A seminal example was provided by Rock & Victor (1964) whose experimental participants viewed shapes through a magnifying lens, whilst feeling the shapes with an unseen hand. When they were then visually presented with a set of reference shapes they judged the object size to be larger than it was. This, however, demonstrated that haptic perception had not influenced vision, and not that vision biased haptic perception. In a second test participants felt shapes and still judged the object size to be larger than the target shape, suggesting that vision had indeed biased haptically perceived size. Hay *et al.* (1965) asked participants to view their own hand through a 14° prism and then indicate in which of 30 locations they *felt* their hand to be. Limb position judgments were biased by 8.6° toward the visual displacement, suggesting a bias of the *felt* position of the limb. It is well recognized that vision may dominate over non-visual senses, but the studies of Rock & Victor (1964) and Hay *et al.* (1965) went beyond this to suggest that vision may directly modify somato–sensory judgements within their own perceptual domain. The judgement of size or shape requires abstraction from multiple sources of information and, as such, the bias observed by Rock & Victor (1964) is less surprising than that observed for limb position where there is a direct limb-specific somato–sensory mapping. The conditions necessary to elicit a visual bias of felt limb position are not well defined. Hay

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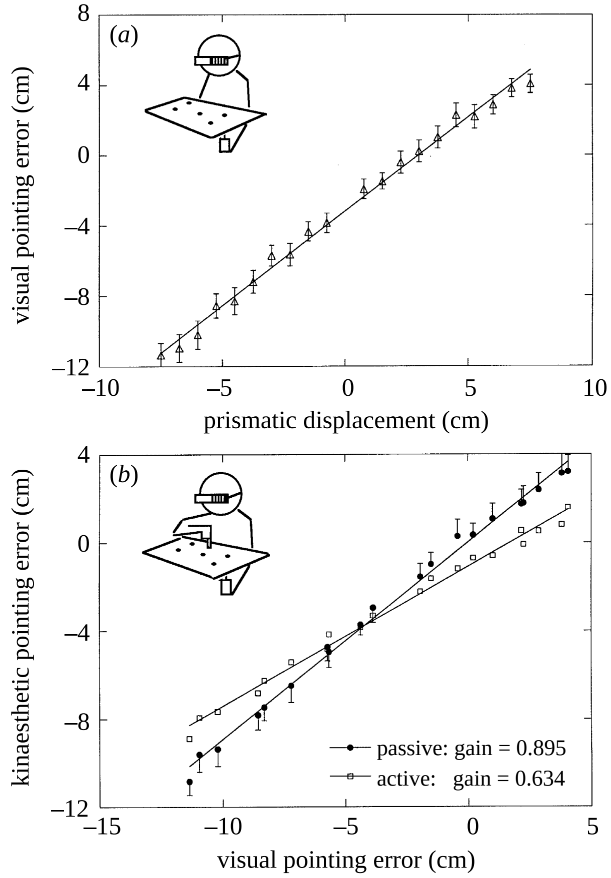

Figure 1. (*a*) The conventional prismatic errors induced in pointing with an unseen hand (under a table), to a set of five targets on top of the table, distributed as shown and viewed monocularly through a Risley prism. Errors are proportional to the degree of displacement. (*b*) Errors in kinaesthetically matching relative finger position, when one finger is below a thin table and the other is above the table and seen through a Risley prism. The kinaesthetic errors (figure 1*b*) are plotted against the pure visual errors (figure 1*a*) to allow an estimate of the transfer. Each symbol represents the mean across 12 participants. For clarity, standard error bars are only displayed for the passive condition, but are equivalent to those for the active condition.

et al. (1965) only tested one visual increment and questions arise as to whether there is a general, linear bias with increasing visual displacements. Both ceiling and floor effects are feasible, whereby some degree of discord may be necessary before a bias is introduced, or the bias may plateau or recede when the visual–kinaesthetic discord is too great. A second issue is that Biguer *et al.* (1988) documented a reciprocal effect, where kinaesthetic inputs from neck vibration produced apparent motion of a stable visual target, presented in a sparse visual environment. Lackner (1988) also reports gross distortions of body image resulting from enhanced kinaesthetic sensation. Hence it is clear that kinaesthesis may sometimes bias other perceptual judgements. We tested the subordinate and dominant role that kinaesthesis may play when it is placed in conflict with visual information in both rich and visually sparse environments.

2. METHODS

(*a*) *Experiment 1*

We used a set of simple pointing tasks to test the effects of visual displacements on kinaesthetic judgements. First, we measured the errors in pointing an unseen finger underneath a table, to prismatically displaced visual locations on the table surface (figure 1*a*). A 'Risley rotating prism' was used to alter the degree of prismatic power. The Risley prism consists of two prisms of equal power that are rotated relative to one another to create a variable degree of horizontal prismatic displacement (over a range of 60 prism dioptres). Vision was displaced to the right or left in 20 randomized steps. Participants were asked to place their finger tips in identical locations above and below the table, but no constraints were placed on how they oriented the rest of their limbs. Pointing accuracy was monitored via electromagnetic sensors attached to both finger tips. This paradigm provided a measure of the normal prismatic error induced when participants match kinaesthesis to vision. We then compared these errors with those occurring when participants pointed their fingers directly at one another, one unseen below a table and one visible (but prismatically displaced) above the table. Two conditions were explored: a passive condition where participants had no feedback about the degree of induced prism; and an active condition where the participants moved their seen hand and therefore gained an indication of the degree of displacement. In the *passive* condition, the participants closed their eyes, the experimenter moved their upper finger to a target location, they then opened their eyes and tried to align their unseen hand. In the *active* condition, they moved their visible hand to the initial target (hence gained some advance knowledge of the direction and degree of visual displacement) and then moved their unseen hand to this location. Twelve participants of normal ophthalmic status (none of whom wore spectacles) took part in the experiments. The participants were volunteers who did not receive payment or credit for participation. Five trials were recorded for each displacement and errors were measured using an electromagnetic tracker (Polhemus Fastrak, USA), with a resolution of 0.01 cm over the target space, providing x, y, z position information, although only errors in the plane of the prism were submitted for further analysis. Proprioceptive drift of the unseen limb (Wann & Ibrahim 1992) was minimized by allowing participants to view their occluded hand between each randomized step.

(*b*) *Experiment 2*

We then repeated the procedure of experiment 1 in a dark, light-sealed room. In the first condition, participants pointed under the table to a red LED that was placed in equivalent positions and a Risley prism was once again used to visually displace the targets. In the second condition, a black glove was placed on the hand above the table, an LED was mounted on the participant's index finger and their finger moved to a set of randomized positions by one of the experimenters. Participants then attempted to match their finger positions (as in experiment 1: passive) while viewing the LED on their index finger through the Risley prism. In both conditions the head was stabilized with a chin rest, the degree of prismatic displacement was varied over a range of 60 prism dioptres in randomized steps and pointing accuracy was monitored electromagnetically. The order of the two conditions was randomized across the six participants and the lights were turned on every 5 min within conditions to offset the effects of dark adaptation.

3. RESULTS

(*a*) *Experiment 1*

Figure 1*a* displays the conventional prismatic errors induced in pointing with the unseen hand to a set of targets viewed monocularly through the Risley prism. Errors are proportional to the degree of displacement (gain = 1.07) and this provides a measure of the commonly observed effect of prismatic displacement on pointing (e.g. Harris 1965). Negative values represent displacement to the left of the target and a leftward constant error of approximately 4 cm (6.5° of visual angle) towards the midline can be observed across all participants.

Figure 1*b* displays errors in kinaesthetically matching relative finger position when one finger is below the table and the other is above the table but seen through the Risley prism. When participants kept their eyes closed the mean error in aligning their fingers was 3.6 cm (s.e. = 0.4), hence kinaesthesis does, on its own, allow quite accurate positioning. When participants completed the same task but viewed their hand through a prism, the finding was that vision completely overwhelmed kinaesthesis. Participants were questioned about their percepts and reliably reported that their fingers *felt* aligned even when the fingers were laterally displaced by as much as 10 cm (16° of visual angle). We calculated gain (ratio of visual displacement to limb displacement) as a measure of the degree to which alignment was biased towards the prismatically displaced visual location. In the *passive* condition, the gain of sensori-motor error was 0.89 (figure 1*b*) indicating that, in the presence of vision, kinaesthesis contributed very little to perceived limb position. The residual input of kinaesthesis (1-gain) ranged from 0.05 to 0.15 across individuals. In the *active* condition, participants had advance knowledge of the degree of displacement when they moved their visible hand; nevertheless, the gain was 0.63, suggesting that vision still dominated kinaesthesis.

(*b*) *Experiment 2*

When the conditions of experiment 1 were repeated in total darkness, the pattern of results was different from experiment 1. Figure 2*a* displays the visual pointing error in the condition directly equivalent to figure 1*a*, but with the room darkened. It may be observed that the participants tended towards a slight overshooting of the visual displacement in the dark and the gain exceeded 1.0. When the second condition of experiment 1 (figure 1*b*) was repeated in the dark, however, visual displacement of the target LED (attached to the index finger) had very little effect. In can be observed from figure 1*a* that, in contrast to figure 1*b*, the gain is only 0.125. Participants reported the experience as rather bizarre and, although they knew that the LED was attached to their finger, some participants stated that it appeared to become ‘detached from my finger’.

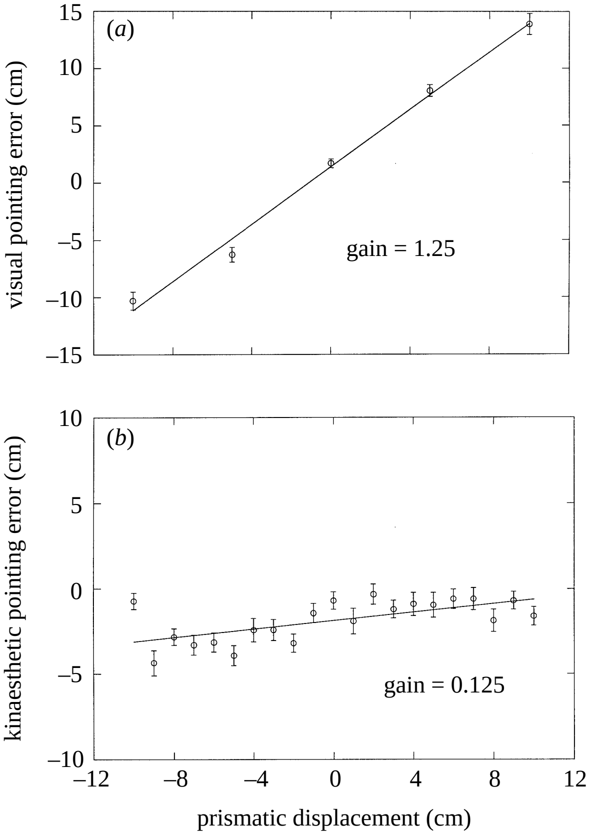

Figure 2. Equivalent conditions to figure 1, performed in a darkened room. (*a*) The prismatic errors induced in pointing with an unseen hand, to an LED on top of the table viewed monocularly through a Risley prism. (*b*) Errors in kinaesthetically matching relative finger position, when an LED is attached to the finger above the table and seen through a Risley prism. Each symbol represents the mean across six participants with standard error bars.

4. DISCUSSION AND CONCLUSION

Our results highlight that although the kinaesthetic system allows accurate perception of limb position in the absence of vision, it may play a relatively minor role when vision is available. The effect of displacing vision of the hand in experiment 1 was that participants reliably reported that they *felt* their limbs were aligned, when limb separation concurred with the degree of prism displacement, even though this was in complete contrast to available kinaesthetic information. This illustrates that vision may provide a primary input for somato–sensory perception.

When the visual environment was made sparse in experiment 2 and participants only saw the LED attached to their finger, then the effect almost disappeared. Participants were then able to match their finger positions reasonably accurately, but reported the strange illusion of seeing the LED floating away from their finger. This latter finding is in general agreement with the findings of Biguer *et al.* (1988), but it also worth noting that our participants were not able to totally ignore the visual displacement and a minor effect of visual displacment is still evident in figure 2*b*.

In both light and dark conditions, the whole visual scene is displaced through a constant angle and visual target position is specified solely by ocular position. Ocular position information appears to be sufficient for relatively accurate pointing (figure 2*a*), but it has a differential effect on felt limb position depending on the lighting conditions (compare figure 1*b* to figure 2*b*). Vision overwhelms kinaesthesis when matching limb position with full view of the hand and table, but in the dark the LED attached to the participant's finger appeared to be detached from their hand. This complements the observations of Biguer *et al.* (1988) and Matin *et al.* (1983) who noted that kinaesthesia biased visual judgments, but only when the room was darkened. Hence vision may induce kinaesthetic illusions, but only when there is a full, well-illuminated, visual environment. When the visual background was dark and sparse, but the finger was still visually salient, participants relied on what they felt rather than what they saw.

Why there should be any cross-sensory bias is an issue of debate. Ramachandran & Rogers-Ramachandran (1996) suggest that their observations with amputees may be amplified examples of a more general phenomenon and our findings would seem to support this proposal. The phantom limb examples may be amplified because there are no kinaesthetic signals from the amputated limb that directly conflict with the visual illusion, and there is also the potential for neural reorganization following amputation (Ramachandran & Rogers-Ramachandran 1996). Our observations, however, suggest that related inter-sensory influences can occur in intact patients, even when there is sensory conflict, but that the influences are also modified by the 'visual capture' observed by Matin *et al.* (1983).

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