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Title: Enhanced integration of multisensory body information by proximity to 'habitual action space'

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Abstract

Previous research suggests integration of visual and somatosensory inputs is enhanced within reaching (peripersonal) space. In such experiments, somatosensory inputs are presented on the body while visual inputs are moved relatively closer to or further from the body. It is unclear, therefore, whether enhanced integration in 'peripersonal space' is truly due to proximity of visual inputs to the body space, or, simply the distance between the inputs (which also affects integration).

Using a modified induction of the rubber hand illusion, here we measured proprioceptive drift as an index of visuo-somatosensory integration when distance between the two inputs was constrained, and absolute distance from the body was varied. Further, we investigated whether integration varies with proximity of inputs to the *habitual* action space of the arm – rather than the actual arm itself.

In Experiment One, integration was enhanced with inputs proximal to habitual action space, and reduced with lateral distance from this space. This was not attributable to an attentional or perceptual bias of external space because the pattern of proprioceptive drift was opposite for left and right hand illusions i.e. consistently maximal at the shoulder of origin (Experiment Two).

We conclude that habitual patterns of action modulate visuo-somatosensory integration. It appears multisensory integration is modulated in locations of space that are functionally relevant for behaviour, whether an actual body part resides within that space or not.

Keywords

Visual; somatosensory; tactile; rubber hand illusion; optimal integration theory; proprioceptive drift; proprioception; peripersonal space; reaching space; visuo-somatosensory integration

Enhanced integration of multisensory body information by proximity to 'habitual action space'

A wide body of research suggests that there is enhanced integration of auditory/ visual stimuli with somatosensory stimuli within the reaching space of the arms, i.e. the *action* or *peripersonal* space (Brozzoli, Pavani, Urquizar, Cardinali, & Farne, 2009; Canzoneri, Magosso, & Serino, 2012; Holmes, Sanabria, Calvert, & Spence, 2007; Holmes & Spence, 2004; Làdavas, Di Pellegrino, Farnè, & Zeloni, 1998; Maravita, Spence, & Driver, 2003; Serino, Canzoneri, & Avenanti, 2011; Teneggi, Canzoneri, Di Pellegrino, & Serino, 2013). For example, a tactile stimulus on the body will be detected faster and more accurately when a visual stimulus is presented at the same bodily location, compared with when the visual stimulus is presented contralaterally or outside reaching space (in *extrapersonal* space) (Spence, Pavani & Driver, 2000; reviewed in Làdavas & Farnè, 2004, Holmes & Spence, 2004, and Làdavas, 2002). Within peripersonal space, other 'integration regions' have been documented around body parts such as the hand (*perihand* space) (in humans, Sambo & Forster, 2009), as well as the head, abdomen and arms (in primates, Fogassi et al., 1996; Graziano, 1999).

These integration regions are thought to exist because of the potential for functional interaction with objects within these spaces (Makin, Holmes, & Zohary, 2007). Supporting this, tool-use studies show the boundary for altered integration can be extended to accommodate a larger 'reaching space' incorporating the area around the tip of a tool that is being used (or has been used) to perform actions (Bassolino, Serino, Ubaldi, & Làdavas, 2010; Canzoneri et al., 2013; Farnè, Iriki, & Làdavas, 2005; Holmes et al., 2007; Iriki, Tanaka, & Iwamura, 1996). Additionally, Brozzoli and colleagues

(2009) demonstrated task-irrelevant visual distractors interfere with the detection of tactile targets if the hand is about to move into the location of the distractors, compared with when the hand is not about to move (as reflected in reaction time changes, see also Brozzoli, Cardinali, Pavani, & Farnè, 2010). This shows the potential for future action in a spatial location modulates sensory integration (Brozzoli et al., 2009). More generally, it also shows that the borders of integration regions are dynamic, that is, the border between peri- and extrapersonal space can be shifted. Finally, it also suggests integration zones may not only exist around actual body parts, but rather around functionally relevant locations of space (related to action) – whether a body part is currently present within that space or not.

Paradigms examining the efficiency of visuo-somatosensory integration have presented the somatosensory stimulus on the body as the visual stimulus is moved further away (Lloyd, 2007; Spence, Pavani, & Driver, 2004). Thus any changes in integration could be interpreted as caused by the visual stimulus crossing beyond the border of the integration region. However, it is known that simple spatial congruency also affects the strength of multisensory integration: that is, the closer two inputs in space, the more efficiently they will be integrated (reviewed in Holmes & Spence, 2005). This means that, in the case of multisensory integration involving a somatosensory stimulus, it is difficult to disambiguate the effects of distance from the integration region (body space explanation) from the pure spatial separation of inputs (relative space explanation). In the current study, we wished to examine the integration of visual and somatosensory hand position information, and whether this varied with respect to the body space. Given the above considerations, we constrained the distance between the two inputs to examine the effect of absolute proximity of sensory inputs to the body (controlling for relative distance).

As a secondary interest, we wished to investigate the idea (alluded to above) that zones of modulated multisensory integration might exist around functionally relevant locations of space, even when an actual body part does not reside therein. Specifically, we aimed to determine whether integration varies with proximity to the 'habitual action space' of the hand, rather than the position of the hand itself. Research using portable motion tracking suggests that, despite the wide range of possible positions, the hand most commonly operates with the elbows at the trunk and the forearms extended at 90º in front of the body i.e. the 'habitual action space' (Howard, Ingram, Körding, & Wolpert, 2009). Research from outside the field of multisensory integration, suggests that habitual patterns of stimulation shape perceptual systems (Ejaz, Hamada, & Diedrichsen, 2015; Howard et al., 2009; Ingram, Kording, Howard, & Wolpert, 2008; Makin, Wilf, Schwartz, & Zohary, 2010; Medina & Rapp, 2014). Within the sphere of multisensory integration, developmental exposure to sensory inputs (Wallace, Perrault Jr., Hairston, & Stein, 2004; Wallace & Stein, 2007) and experience with speech (McGurk & MacDonald, 1976) have been shown to affect perception and processing of audio-visual stimuli. To the best of our knowledge, however, there has been no previous investigation of experience-based effects on visuo-somatosensory integration – particularly with respect to the influences of action in the space surrounding the body. Here, we predicted maximal multisensory integration in the action space because of previous research supporting the role of functional interactions with space in modulating such integration (see above).

To investigate the integration of visual and somatosensory hand-position information we used a modification of the rubber hand illusion induction (RHI). In the RHI, an illusory spatial separation is created between the participants' actual hand and a false visual hand stimulus (Botvinick & Cohen, 1998; Lloyd, 2007; Tsakiris & Haggard, 2005). In the majority of participants, this produces the perception that the actual hand position is closer to the visual hand position after (compared with prior to) the illusion induction, (Botvinick & Cohen, 1998; Holle, McLatchie, Maurer, & Ward, 2011; Rohde, Di Luca, & Ernst, 2011). This change is called proprioceptive 'drift' and is used as a proxy measure for the strength of integration between the somatosensory and visual inputs – where more drift indicates more integration (Rohde et al., 2011). According to the principles of optimal integration theory, this occurs because the visual information is considered more reliable by the central nervous system and therefore is given a greater weighting to influence the final percept (Ernst & Bülthoff, 2004; Lackner & Taublieb, 1984). Therefore, using this paradigm we were able to manipulate explicitly the perceived position of the visuo-somatosensory stimuli with respect to the habitual action space.

In Experiment One, participants were seated at an apparatus that occluded the position of their actual left hand, and were presented with a realistic photo of a hand at one of four spatial locations (see also Dempsey-Jones & Kritikos, 2014). Two hand positions were presented near the habitual action space. In these positions the left hand was located slightly to the left or right of the left shoulder respectively (conditions 'OLS' and 'ILS', for 'Outside' and 'Inside Left Shoulder'). Two further positions were located laterally away from the habitual action space, towards the right shoulder (conditions 'M', for 'Midline' and 'IRS' for 'Inside Right Shoulder') (see Figure 1A & B axis labels). The experimenter placed the participant's actual hand in a position directly adjacent to the hand image (i.e. with a constant 10cm separation). Actual and hand image positions were varied trial-by-trial to include all adjacent combinations of the four possible positions. As stated above, we predicted a systematic reduction of drift as the position of the actual (somatosensory) and seen (visual) hand position information moved away from the habitual action space of the arm. This would result in maximal drift when the left hand was positioned near to the left shoulder (condition OLS). We further predicted a gradient of reduction as the visuo-somatosensory stimuli moved to the right (along an azimuth plane). This result would support a habitual action space explanation of drift modulation (modelled in Figure 1A). The demonstration of a modulation of drift by absolute proximity to the action space would argue against the suggestion that integration differences between extra and peripersonal space are caused by the distance between visual and somatosensory inputs alone (that is, a relative space explanation: modelled in Figure 1B), and would support the modulation of such integration by habitual action.

EXPERIMENT ONE.

Methods

Design

We used a repeated-measures design, with independent variables: Hand Position (four levels: OLS, ILS, M, IRS, more details below) and Time (three levels: baseline, pre-illusion, post-illusion).

Participants

Twenty-one students from the University of Queensland (11 male, 10 female; age, M = 19.3 years, SEM = .55) with normal or corrected to normal vision participated for course credit. Sixteen were right handed and five left handed or ambidextrous by self-report. All participants gave informed consent for participation. Ethical approval for the study was provided by the Behavioural & Social Sciences Ethical Review Committee of the University of Queensland (approval code: 11-PSYCH-PHD-06-JS).

Experimental apparatus

A specialised apparatus was constructed which allowed realistic hand images to be presented in the spatial depth plane of the actual hand, as opposed to a traditional rubber prosthetic hand. The apparatus consisted of three equidistant horizontal shelves (for dimensions see Figure 2). A LCD computer screen was fitted into the top shelf at head height, facing downwards (size, 51 x 33cm; resolution, 1680 x 1050 pixels). The left hand image was presented on this screen and reflected by a mirror set into the middle shelf, at chest height. Participants looked down into the mirror, which made it appear they were looking down at their own left hand through a pane of glass. The height of the chair was adjusted so the participant's arms could rest pronated comfortably on the bottom shelf (the experimental workspace) with their upper arms by their side and their forearms projecting at 90° from the body, parallel with the ground – consistent with the position of the habitual action space (Howard et al., 2009).

Real hand/ hand image positions

The four hand positions were selected for their orientation with respect to major bodily landmarks – primarily the habitual action space and the head. They were positioned 10cm apart, on a straight lateral plane (perpendicular to the mid-sagittal plane) across the bottom shelf of the apparatus, out of sight of the participant (see Figure 2). The spacing of the hand positions was based on pilot work[1] that ensured the hand positions were naturalistic and comfortable to maintain. This decision was based on previous research suggesting extreme joint positions that cause discomfort can reduce proprioceptive position sense (Rossetti, Meckler, & Prablanc, 1994). Lines were drawn on the experimental workspace for each position and used to orient the participant's hand and wrist accordingly. The hand images were taken using a representative pilot participant's hand placed on the experimental apparatus, in each of the four positions (taken from the vantage-point of the middle of the computer screen). This was considered important because relative rotation of the (real or rubber) hand can create a violation between what is seen and felt, and therefore reduce illusion effectiveness due to anatomical implausibility (Costantini & Haggard, 2007).

Footnote[1]. Piloting work consisted of asking a range of participants to sit at the apparatus with their hands in various positions across the experimental workspace (around the habitual action space and across the body, laterally) for a period matching the duration of the illusion induction (60 seconds). Anecdotal self-reports of comfort and ease of holding the position were used to create the final positions. The four positions selected aligned well with body landmarks (midline/ shoulder etc.) of the average participant, across the male and female sample of typical undergraduates (N ≈ 5/ gender). Note: here the location of the 'shoulder' is defined as the edge of the acromion (top part of the shoulder blade, lateral to the clavicle). This point was selected because this is the centre of gravity for the functional midpoint of spino-humeral abduction (Inman, Saunders, & Abbott, 1944).

Positions OLS and ILS ('Outside' and 'Inside Left Shoulder', respectively) were positioned an equal distance (5cm) either side of the left shoulder (OLS: visual angle, 25.73° left of straight-ahead; ORS: 14.56°). Position M ('Midline') was at the body-midline (0°). IRS ('Inside Right Shoulder') was a mirror image of position ILS, on the contralateral side of the body – and was thus, located between the midline and the right shoulder (14.56° right of straight-ahead). The participant's forehead rested against the apparatus and was positioned in line with hand position M. A chin-rest, which extended 15cm above the surface of the middle shelf, was used to ensure the participant's head remained at the correct location and a constant elevation for the duration of the experiment (i.e. midway between the middle and top shelf) (see Figure 2). The subject's unused right hand rested in their lap, which was outside the boundaries of the apparatus and, therefore, not overlapping with the experimental workspace.

All combinations of positions where the actual hand and hand image were at adjacent positions were used. This created six 'raw' illusion conditions: condition OLS-ILS (i.e. in which the illusion shifted felt location from the actual hand position OLS towards the hand image position ILS), condition ILS-ORS, condition ILS-M, condition M-ILS, condition M-IRS, and condition IRS-M (see Table 1A).

For our main spatial comparison, these six raw conditions were collapsed according to the position of the participant's hand to form the four 'actual hand conditions' (OLS, ILS, M, IRS). For example, conditions M-ILS and M-IRS were combined to form M – because for both conditions the hand was at position M (Table 1B). The six raw conditions were also collapsed according to the position of the hand image to form 'hand image conditions' for positions OLS, ILS, M and IRS (Table 1C). This was to test whether the spatial modulation of integration was stronger when conditions were grouped according to actual hand position or hand image position.

Estimation of proprioceptive hand position

Participants estimated the position of the tip of their (hidden) left middle finger using a ruler displayed on the computer monitor (see Figure 2). The fingertip was 25cm from the edge of the apparatus/ screen closest to the participant. The ruler used veridical centimetres (with mm demarcations). It appeared on screen at the same on-screen height and depth as the fingertip (also 25cm from the closest edge of the apparatus). Fifteen different rulers (i.e. starting at different numbers) were used to prevent memory or learning effects. Experimental stimuli were presented with Eprime (Version 2.0, https://www.pstnet.com/). For each hand position judgement, the program randomly selected and presented one ruler on screen. Participants verbally reported the number representing their finger position aloud. This was coded into the computer by the experimenter – allowing the participant's hands to remain still for the duration of the trial.

Modified RHI induction

i. No condition of visuo-proprioceptive disintegration (asynchrony)

In the traditional RHI paradigm, during the spatial displacement of visual and proprioceptive hand information, both the rubber hand and participant's hand are subjected to synchronous tactile input, i.e. 'intermodal matching' (hereafter matching) (Botvinick & Cohen, 1998; Longo, Schüür, Kammers, Tsakiris, & Haggard, 2008; Tsakiris & Haggard, 2005). In their original work, Botvinick and Cohen (1998) suggested visuo-tactile synchrony (resulting from the synchronous brushing) causes a three-way interaction between vision, touch and proprioception, which in turn causes drift and subjective changes. Many studies report a reduction, or attenuation of the illusion under asynchronous stroking conditions (Botvinick & Cohen, 1998; Longo et al., 2008; Tsakiris & Haggard, 2005; Zopf, Savage, & Williams, 2010). Given our interest in the current experiment was not in what arrests (or reduces) visuo-proprioceptive recalibration, but whether the strength of integration is altered under particular conditions, asynchronous conditions were not informative for the central questions of this experiment. That is, our main experimental comparisons rely on comparisons across (synchronous) conditions. In addition previous research suggests that when the real and 'rubber' hand are close together there is no significant difference in illusion outcomes for synchronous and asynchronous conditions (separations of 15cm: Zopf et al., 2010; and 10cm: Preston et al., 2013).

Furthermore, the causative role of tactile synchrony in producing the RHI has now been undermined by results that demonstrate greater illusion in a 'vision-only' condition (with no stroking), compared to synchronous and asynchronous stroking conditions (Rohde et al., 2011). Other studies that demonstrate drift without visuo-tactile matching support this (Durgin, Evans, Dunphy, Klostermann, & Simmons, 2007; Holmes, Snijders, & Spence, 2006). Recent theories now suggest drift may occur simply through the recalibration of proprioceptive information to the false visual information (Rohde et al., 2011). According to this account, illusion attenuation following asynchronous stroking reflects the inhibition of visuo-somatosensory integration caused by the unexpected mismatch between seen and felt tactile inputs (Rohde et al., 2011). That is to say, matching may not cause drift, but conflicting intermodal inputs may disrupt it. For these reasons we did not include a condition of asynchronous stimulation in our modified illusion induction, (see also Dempsey-Jones & Kritikos, 2014).

The causative role of matching is currently unknown, but even if redundant in causing drift, it should not reduce visuo-proprioceptive integration. Subsequently, here we induced synchronous stroking of the actual hand and hand image during the illusion induction, in line with other comparable research. Synchronous visuo-tactile stimulation was applied by brushing the participant's own hand and the hand image in time for a period of 60 seconds, at approximately 1Hz using soft paintbrushes of .5cm diameter. These brushes were affixed to the apparatus to ensure pressure, angle and contact of the brushes remained constant over the experiment duration and across participants.

ii. Inclusion of proprioceptive measures of the illusion only

There are widely reported subjective changes associated with the RHI induction – involving alteration of the psychological ownership and embodiment of the participant's own hand and the rubber hand (Ehrsson, Holmes, & Passingham, 2005; Longo et al., 2008; Tsakiris, Hesse, Boy, Haggard, & Fink, 2007). These have also been documented without intermodal matching (Samad & Shams, 2012). Importantly, the subjective and behavioural (drift) outcomes of the RHI have been shown to be dissociated and are likely supported by separate mechanisms of multisensory integration (Dempsey-Jones & Kritikos, 2014; Holle et al., 2011; Kammers et al., 2008; Rohde et al., 2011). Here we were interested in drift as a measure of integration only (not the psychological experience of ownership/ embodiment). Thus, these subjective changes were not of direct relevance and therefore were not assessed here.

Procedure

The baseline block was conducted first. At the start of each trial, the experimenter placed the participant's left hand in one of the four possible hand positions. All four positions were repeated twice, with order randomised (all randomisation was determined by the experimental software). One ruler (randomly selected from the set of 15) was then presented on the screen, and the participant was made their baseline position estimation. The ruler then disappeared and a 60 second inter-trial interval (ITI) occurred where the screen was blank. Participants were asked to remove their hand from the shelf and place it in their lap, with their unused right hand, during this period.

Following the baseline block, the experimental block began. The six raw illusion conditions were presented twice each (order randomised between-participants). Each raw condition trial commenced with a pre-illusion hand position estimation (procedure as above). Then the left hand image was presented on screen (timed for 60 seconds by the computer). During this time the participant's left hand and the left hand image on the screen were brushed in synchrony by the experimenter (see above for procedure and timing). The hand image then disappeared and participants made their post-illusion estimate. Procedure for hand placement, break and ITI remained the same.

Calculation of hand position measures

For each judgement (baseline, pre-illusion, post-illusion), participants' estimated hand position (from reported ruler value) was subtracted from actual hand position (on the same ruler) to determine the error in cm. We found significant illusion induction in the direction of the hand image in all conditions (i.e. significant change in position estimation from pre- to post-test using Bonferroni corrected within-participants t-tests; results in Supplementary Section One, section B). Subsequent to this, we created a difference score to represent drift magnitude. This difference score was the absolute value of the post- minus pre-illusion values.

Analyses

A within-participants contrast analysis was used to investigate whether there was a spatial modulation of drift. This analysis occurs within the ANOVA but provides a means of assessing whether particular functions (e.g. linear, or other higher-order functions such a cubic or quadratic) provide a significant fit to the data. We used this method to assess whether there was a significant linear change in drift magnitude from hand positions on the left (at the left shoulder) to right (as hand position moved away), as per our hypothesis – first for the six raw conditions[2], and then for the four actual hand conditions.

Additionally, we analysed whether a linear effect of drift occurred for a grouping of the six raw conditions based on the hand image position (as opposed to grouping based on the actual hand position, as above). Presence of a linear effect for the actual hand grouping, but not for the hand image grouping would suggest that the drift effect we identified occurs more as a result of the spatial position of the actual limb (proprioceptive information) than the position of the hand image (visual information).

In sum, the linear modulation of drift was first assessed in the six raw conditions, then in the four actual hand conditions, and finally in the four hand image conditions.

Footnote[2]. The order for the six raw conditions for linear analysis was selected by putting the six conditions into pairs where the actual hand position and hand image position were the inverse of each other (e.g. OLS-ILS and ILS-OLS) from left-to-right. The condition that had the actual participant's hand at the leftmost position was placed at the leftmost side of the condition order (see order in Table 1).

Results

Drift is maximal for hand positions near the habitual action space, decreasing as hand position moves away

To examine the hypothesis of a spatial difference in drift magnitude we first compared all six raw conditions (to give a complete picture of change across all conditions conducted) and then compared the collapsed actual hand conditions (see Table 1B for calculation details).

A one-way ANOVA with contrast analysis demonstrated a significant linear effect representing the differences between the six raw drift conditions, $F(1, 21) = 5.57$, $p = .028$, $\eta^2_p = .21$. Figure 3A below demonstrates the direction of this linear function, where the largest drift magnitude occurred when the hand was in the left-most position (condition OLS-ILS). This drift magnitude reduced as hand position moved towards the right shoulder, with a minimum drift at the right-most position (IRS-M).

A second one-way ANOVA demonstrated a significant linear effect fit to the drift means for the four actual hand positions, $F(1, 21) = 4.37$, $p = .049$, $\eta^2_p = .17$. The direction was consistent with the raw conditions: the illusion induced largest drift when the left hand was in the left-most position (OLS), reducing as the hand moved laterally to the right, with a minimum at IRS (see Figure 3B).

Proprioceptive position modulates spatial visuo-somatosensory integration more than visual position

A one-way ANOVA showed no significant linear (or other) effect for the four hand image condition means, $F(1, 21) = 1.07$, $p = .313$, $\eta^2_p = .05$. Therefore, the spatial effect of drift magnitude was abolished when using a spatial grouping based on hand image position (see Figure 3C). This supports the role of the proprioceptive position in creating the spatial effect documented above.

Experiment One - Discussion

Preliminary evidence for enhanced visuo-somatosensory integration in habitual action space

In this experiment we wished to demonstrate the modulation of visuo-somatosensory integration as a function of the absolute position of the sensory inputs with respect the habitual action space (i.e. action space explanation, Figure 1A). To this end, we held the position between the visual and somatosensory inputs constant – to show that any modulation was not attributable to simple spatial congruence between these inputs, unrelated to the action space position (i.e. relative space explanation, Figure 1B: see Holmes & Spence, 2005). We used proprioceptive drift as a measure of this integration, where larger levels of drift indicate increased integration of visual and somatosensory information about hand position (and lower drift indicates less integration: Rohde et al., 2011).

Concurrently, we were also able to investigate whether functional modulations of multisensory integration can occur as a function of habitual patterns of action and sensory stimulation. Previous studies have suggested that the presence of the actual hand may not be necessary for modulations of integration to occur: for example, tool-use studies (Bassolino et al., 2010; Canzoneri et al., 2013; Farnè et al., 2005; Holmes et al., 2007; Iriki et al., 1996) and studies indicating the plan for action might alter integration in the space into which the arm 'is about to move' (Brozzoli et al., 2010; Brozzoli et al., 2009). To investigate this, we looked at whether drift varied with respect to the habitual action space of the arm: that is, when the hand is approximately aligned with the shoulder of origin (Howard et al., 2009).

Supporting our hypothesis that there would be maximal integration in the habitual action space of the arm, the analysis of drift scores revealed that for the left arm there was a linear spatial modulation of drift. The greatest drift occurred when visuo-proprioceptive recalibration was induced at, or near to, the left shoulder. Drift magnitude decreased steadily from left to right, reaching a minimum for the hand position furthest to the right. This was the case for the six ‘raw’ conditions (see Figure 3A) and the four actual hand position means (see Figure 3B).

The combination of proximity of the actual hand (somatosensory/ proprioceptive hand position cues) and proximity of the hand image (visual hand position information) to the habitual action space alters multisensory integration within this spatial region. We wondered, however, whether the position of the actual hand or the position of the hand image was the more critical factor in driving this spatial effect. That is, the alteration of multisensory integration in action space could result because of the high frequency of proprioceptive interactions with objects within that area, or the frequency of visual targets for action in that area. We assessed the relative modulation of visual and somatosensory inputs on drift by grouping and comparing the actual hand position conditions with the hand image position conditions. We found that when drift values were grouped into four hand image position means (as opposed to actual hand means, above) the spatial effect was no longer significant (see Figure 3C). This supports a proprioceptive basis for the spatial effect we identify here.

Significant drift at all positions and directions tested across the workspace of the arm

Previous investigations of the absolute spatial modulation of multisensory integration have suggested drift does not occur when the real or rubber hand crossed the midline

(Cadieux, Whitworth, & Shore, 2011), or when the rubber hand was more lateral to the body than the real hand (Preston, 2013). It is known, however, that there is significant variation in proprioceptive localisation of the hand across the workspace of the arm (Haggard, Newman, Blundell, & Andrew, 2000; Wilson, Wong, & Gribble, 2010), also see Supplementary Section One, section A for demonstration in our data. We anticipated, therefore, that drift should actually occur for all positions of the hand once this variability in proprioceptive localisation had been accounted for. Subsequently, we used a pre- to post-illusion difference score for hand localisation. Using our error corrected measure we were able to demonstrate significant proprioceptive drift in all conditions. This indicates that irrespective of the direction of the shift or relative position of the hands (real or illusory), the central nervous system integrates visual and proprioceptive hand position information. Indeed, according to models of multisensory integration that detail how integration occurs as a function of the reliability of multisensory inputs, integration should occur across whole workspace of the hand. Optimal integration theory, for example, suggests integration occurs as a function of the reliability of the sensory inputs available (Ernst & Bülthoff, 2004; Fitzpatrick & McCloskey, 1994; Guerraz et al., 2012; Lackner & Taublieb, 1984; van Beers, Sittig, & Dernier van der Gon, 1999). The reliability determines the weighting of each input to the final percept. Thus, in the RHI, felt position shifts from the actual hand location towards the false visual information due to the greater sensitivity and reliability of the visual body position information in this context (Rohde et al., 2011).

Interestingly, considering optimal integration theory could lead to an alternative prediction about how drift should vary across the workspace of the arm. Following this account, it could be predicted that visual information should cause increased bias to the proprioceptive percept when the proprioceptive information is least stable: that is, when the hand is far from the shoulder, and proprioceptive localisation is least accurate and reliable (Wilson et al., 2010). This would mean the hand is least susceptible to illusory displacement when the hand is near the shoulder (Cadieux et al., 2011). However, as we describe, such a pattern is the direct spatial converse of the results we identify here. This is an interesting consideration, and future investigation should investigate the interaction of reliability-based and functional-interaction based modulations of multisensory integration.

As a supplementary analysis we explicitly investigated the distribution and inhomogeneity of variance between-participants, using a measure similar to standard deviation (as a proxy measure to represent the reliability of sensory inputs). We compared the distribution of variance with the distribution of drift magnitude. We found that the distribution of variance scores followed a significantly different pattern to the drift magnitude scores, suggesting that alterations in variance cannot explain the spatial pattern of drift that we present here (see Supplementary Section Two, section B for full analysis and discussion).

Alternative explanation of the spatial drift effect – action space vs. external space hypotheses

Next we performed additional checks to ensure the nature of the spatial effect we had identified was indeed consistent with a habitual action space interpretation. We performed an analysis to determine whether our spatial effect was, in fact, simply caused by baseline error in proprioceptive localisation. To do so, we compared drift scores across hand position conditions that had the same baseline error. Our analysis (presented in Supplementary Section One, section D, for brevity) did not support the suggestion that baseline error caused the spatial modulation of drift we present here. Further, there was no evidence to support a distribution of drift around the midline – an area within which much bimanual hand action occurs. If drift varied with respect to the midline this would have lead to a significant quadratic or cubic function best fitting to our drift data, with the peak/ trough drift value at the midline. As we report, only the linear function fit significantly to the data, both quadratic and cubic functions had a non-significant fit ($p = .347$ and $p = .988$ respectively) – providing evidence against a midline centric account of drift.

Critically, we wished to rule out a second alternative explanation: that a general bias in perception or integration due to the position of the hands in external space (i.e. left vs. right hemispace) caused the drift effect identified in Experiment One. Neurotypical individuals show a general attentional bias towards the right hemispace, associated with a perceptual shift of the subjective straight ahead towards the left hemispace (as seen in line bisection tasks: Bowers & Heilman, 1980; or line cancellation tasks: Vingiano, 1991; and visuo-spatial tasks, Makin, Wilf, Schwartz, & Zohary, 2010; as well as other left-right representational or attentional differences (e.g. in mental imagery, McGeorge, Beschin, Colnaghi, Rusconi & Sala, 2007). Our finding of left-to-right modulation of multisensory integration is consistent with our predictions, but also with increased attention to visuo-proprioceptive stimuli occurring in the left versus right hemispace. That is, the spatial effect we reported could be explained by a left hemispace bias (i.e. an ‘external space account’). This means it is impossible to conclude at this stage whether the modulation of drift we report is due to proximity of the hand to its habitual action space (‘action-space’ account).

To address this issue, in Experiment Two we replicated Experiment One (left-hand induction) with the addition of a mirror image condition (right-hand induction). We predicted distinct linear patterns of drift for the two different hand induction conditions: Specifically, there would be maximal drift when the hand was at the shoulder of origin – resulting in a left-to-right linear effect when using the left hand and a right-to-left effect when using the right hand (modelled in Figure 1C). This would contradict an external-space hypothesis, in which there would be a left-to-right linear drift effect for both hand induction conditions (Figure 1D).

EXPERIMENT TWO.

Methods

Design

We used a mixed design with repeated-measures factors: Hand Position (four levels: described below) and Time (two levels: pre- and post-illusion). Induction-side (i.e. hand used for the RHI) was varied between groups, factor Group: (two levels: left-hand induction, right-hand induction).

Participants

Sixty-six students from the University of Queensland with normal (or corrected to normal) vision participated in the experiment for course credit, all giving informed consent. All procedures were certified for ethical approval, as per Experiment One. There were 36 in the left-hand induction group and 30 in the right-hand group (a larger sample was recruited compared to Experiment One due to the complexity of the mixed factorial design).

The left-hand group consisted of 17 males and 19 females (mean age = 18.5 years, SEM = 0.26; 19 right handed, 16 left handed, and one ambidextrous as assessed by the Edinburgh Handedness Inventory (EHI) (Oldfield, 1971)). The right-hand induction group consisted of 12 males and 18 females (mean age = 19.2, SEM = .49; 17 right-handed and 13 left-handed. Demographics were matched across the two groups, and independent-samples t-tests revealed there were no differences between gender distribution, age or EHI score between groups (.239 < p > .899). Approximate matching across left- and right-handers was done a priori to even out potential differences that may exist in RHI between handedness groups (Niebauer, Aselage, & Schutte, 2002; Ocklenburg, Ruther, Peterburs, Pinnow, & Gunturkun, 2011). Comparing over all groups/conditions together, we found no main effects or interactions between handedness and drift (.347 < p > .932), thus handedness groups were collapsed.

Real hand/ hand image positions

The positions of the hand with respect to the body remained the same in Experiment Two – though in the right hand induction group positions were the mirror image of those used in the left-hand group. From left to right, the positions for the left-hand group were: OLS, ILS, M and IRS (‘Outside’ and ‘Inside Left Shoulder’, ‘Midline’ and ‘Inside Right Shoulder’). From right to left, the positions for the right-hand group were: ORS, IRS, M and ILS (‘Outside’ and ‘Inside Right Shoulder’, ‘Midline’ and ‘Inside Left Shoulder’).

As with Experiment One, participants had their head fixed in a chin-rest at position M. This allowed one hand position either side of the shoulder of origin (i.e. OLS and ILS in the left-hand group, ORS and IRS in the right-hand group). It also allowed one position at the midline (both condition M) and one inside the opposite shoulder (ORS in the left-hand group, OLS in the right) (see Figure 4 below).

Stimuli & procedure

The stimuli, apparatus and procedure were an exact replication of Experiment One (see methods section above).

Analyses

As previously, we found a significant difference between pre- and post-illusion judgements in the direction of the hand image using Bonferroni corrected within-participants t-tests (results in Supplementary Section One, section C), and created difference scores for our main comparisons.

A series of mixed ANOVAs with contrasts analysis were used. This was to determine, first, if there was a significant difference in the linear spatial pattern of drift between the two groups, and second, separate contrasts analyses were used to determine the precise nature of the linear effects and the direction (i.e. left-to-right or right-to-left). Following the results of Experiment One, for brevity this was only conducted on the four actual hand conditions.

Results

Spatial drift effects differ across induction groups

A 2 x 4 mixed ANOVA with factors Group (two levels: left-hand induction, right-hand induction) and Hand Position (four levels: OLS, ILS, M and IRS for the left-hand group and ORS, IRS, M and OLS in the right-hand group) was conducted to determine if spatial effects varied across groups. As predicted, this indicated a significant interaction of Group x Hand Position, $F(1,64) = 9.73$, $p = .003$, $\eta^2_p = .13$. The main effects of Group and Hand Position were not significant, $F(1,64) = 0.29$, $p = .591$, $\eta^2_p = 0.01$ and $F(1,64) = 0.07$, $p = .792$, $\eta^2_p = .01$, respectively. These are not interpreted due to the presence of the significant interaction.

To explore the significant interaction, once again two separate repeated-measures ANOVAs were conducted – allowing analysis of each induction group separately. For the left-hand induction group, there was a significant linear main effect of Hand Position, $F(1,35) = 4.67$, $p = .037$, $\eta^2_p = .12$. For the right-hand group, the linear main effect of Hand Position was also significant, $F(1,29) = 6.39$, $p = .017$, $\eta^2_p = 18$. Mean values indicated that these two spatial effects were in the opposite directions for the two groups. For the left hand induction group, there was greatest drift in the left-most condition (OLS), decreasing to the right, with minimum drift at IRS. Conversely, in the right hand induction group greatest drift was found in the right most condition (ORS), with drift decreasing to the left, reaching a minimum at ILS.

It is possible that while the location of the habitual action space drives the direction of drift, there may be some effect of attentional biases on the shape of the distribution. To investigate this we spatially flipped the right-hand used data so it was in the same orientation as the left-hand used data (i.e. left-to-right distribution, maximal drift at the left side). We then performed the same ANOVA as above. The interaction of Group x Hand Position was non-significant ($F(1,64) = 0.07$, $p = .792$, η2p = .01) indicating that the distributions were the same, suggesting there was no effect of attentional bias to either side of space in altering the shape of the distribution (please see Supplementary Section Two for full analysis, and Figure Supp4 for graphic representation).

Experiment Two – Discussion

In Experiment Two, we asked whether the results of Experiment One truly reflect a modulation of multisensory integration in the habitual action space of the arm (action-space explanation). To support this claim we wished to provide evidence against a general attentional explanation. According an attentional account, the modulation of drift seen in Experiment One could simply be the result of the normal human bias towards the left hemispace (external space explanation) (Bowers & Heilman, 1980; McGeorge et al., 2007; Vingiano, 1991). To distinguish between these accounts, we compared the effect of the induction across left-hand and right-hand induction groups. We predicted distinct patterns of drift magnitude whereby drift was maximal at the shoulder of the hand of origin for both groups (modelled in Figure 1C). That is, maximal drift magnitude with proximity of the hand to the habitual action space. This would rule out the external space prediction, under which maximal drift would be predicted on the left side of space[3] regardless of the hand used for induction, and therefore, the location of the habitual action space (modelled in Figure 1D).

Footnote[3]. Note that an over-representation of the right side of space could also conceivably manifest in greater drift in the right hand side of space (due to increased attention in this location). Importantly, however, according to such an account there would still be no difference in drift distribution depending on the hand used – an outcome refuted by our results.

Supporting the action space hypothesis, in the left-hand group, drift magnitude was greatest for the left-most positions (i.e. near the left shoulder), decreasing towards the right – replicating Experiment One. In the right-hand group, drift magnitude was greatest at the right-most positions (near the right shoulder), decreasing towards the left. Our results, therefore, suggest that within peripersonal space there is a modulation of sensory processing as a result of habitual functional interactions within a spatial location. Enhanced visuo-somatosensory integration in the action space likely results from the large number of habitual hand-eye coordinated movements that occur within this space (Howard et al., 2009) and serves to allow high dexterity and precision in the area of space within which action occurs most regularly.

Following this suggestion, several lines of research suggest that it is the functional properties of space that dictate perception and multisensory integration within these areas. For example, extending space by use of a tool (Bassolino et al., 2010; Canzoneri et al., 2013; Farnè et al., 2005; Holmes et al., 2007) leads to multisensory interactions around the functional tool end similar to those occurring around the hand. This shows the boundary between extra- and peripersonal space is dynamic. That is, there is an extension of peripersonal space to an area that would once have been considered to be outside peripersonal space, due to the possibility for functional interactions within the space (reviewed in Brockmole et al., 2013). The behavioural demonstration of flexible peripersonal space fits with studies suggesting flexible receptive field properties documented in bimodal neurons (Iriki, Tanaka, & Iwamura, 1996; though see comments in Holmes and Spence, 2004). In sum, these studies suggest that the functional properties of space strongly influence the integration of inputs therein, i.e. enhanced integration in reachable space vs. beyond. We extend this to propose that high frequency sampling of one area of space also influences the integration of inputs in this area. Finally, these functional explanations of space also fit with electrophysiological work which suggest various brain circuits that encode space also play a role in the programming of motor activity (i.e. 'spatial pragmatic maps', see review in Rizzolatti, Riggo & Sheliga, 1994).

Limitations

As outlined in the methods section (see section 'Real hand/ hand image positions') the experiments both consisted of two repetitions of the six raw conditions. Due to constraints of the experimental apparatus (the width of the computer screen) and anatomy (hand positions beyond the outermost location OLS and ORS being uncomfortable to hold) we were unable to include two conditions that shift felt position away from these outermost hand positions. Thus, when combining the raw conditions into the four hand position means, the outer conditions contained one raw condition mean each, where the inner positions contained two conditions collapsed. This creates unequal trial numbers, with twice the number of trials in the inner two actual hand position conditions compared to the outermost conditions. This might have improved slightly the reliability of the middle position means. Given the standard error of the mean appears to be quite similar for all position conditions (see Tables 1 & 2), however, we do not believe this significantly compromised the results we document here (also see Supplementary Section Two, section A for results suggesting that variance does not appear affect drift distribution).

Conclusions

In the current study we show that not only can multisensory integration vary as a function of distance from the body or a body part, but we present results that suggest that experience may shape this integration process. Through consistent patterns of functional interaction with space, the hand samples a particular location of the possible action space more frequently than other locations i.e. the habitual action space. This pattern of repetitive action is reflected in the function of our perceptual systems, leading to greater integration of multisensory inputs in this location. The current study extends our knowledge regarding the dynamic nature of the boundaries of multisensory integration regions. Previous research has demonstrated such boundaries exist around the body (e.g. peripersonal space), as well as around individual body-parts (e.g. the perihand space). Our results suggest that these integration zones may not need to be anchored to an actual body part, but may exist for locations of space that are functionally relevant for habitual human behaviour.

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Figure 1. *Graphs representing the possible outcomes of Experiment One* ***(A & B)****. We predicted an absolute modulation of visuo-somatosensory integration in vs. beyond the habitual action space, i.e. a linear decrease in drift from left-to-right (body space explanation)* ***(A)****, as opposed to equal drift across space* ***(B)*** *which would occur if integration only varied as a function of the spatial distance between inputs (relative space explanation). In Experiment Two, the illusion was conducted on the left and right hands separately. We expected to see opposite linear patterns of drift for the two different hand conditions, with maximal drift in the habitual action space (body space explanation) regardless of the hand used* ***(C)****. This would contradict the theory a left-to-right linear effect of drift in Experiment One was caused by a bias to the left hemispace (external space account)* ***(D)****. Condition codes represent the position of the hand with respect to the shoulder of origin (i.e. also the hand upon which the illusion was induced): OLS/ORS – Outside Left/ Right Shoulder respectively, ILS/IRS – Inside Left/Right Shoulder respectively, M – Midline.*

Figure 2. *Diagram of experimental apparatus* ***(top-left panel)****; display of ruler for estimation of hand position* ***(top-right panel)*** *and an example of positioning of the actual hand and hand image for raw condition OLS-ILS ('Outside Left Shoulder-Inside Left Shoulder respectively): i.e. actual hand at position OLS, and illusion shifting felt position towards hand image a position ILS* ***(bottom-right panel)****; and a schematic of the experimental timeline and individual trial timeline* ***(bottom-left panels)****.*

Figure 3. *Analysis of drift magnitude for Experiment One. Points on the lines represent mean drift in each condition, bars represent standard error of the mean (SEM). Condition*

codes represent the position of the hand with respect to the shoulder of origin (i.e. also the hand upon which the illusion was induced): OLS/ORS – Outside Left/ Right Shoulder respectively, ILS/IRS – Inside Left/Right Shoulder respectively, M – Midline. ***(A)*** *The six raw conditions show a significant spatial linear effect of drift, with maximal drift at the left, decreasing with lateral distance towards the right.* ***(B)*** *The same pattern was found when six conditions were collapsed into four conditions to represent actual hand positions.* ***(C)*** *No linear (or other) significant spatial effect of drift magnitude was observed when conditions were collapsed according to hand image position – suggesting the spatial modulation of drift identified (in* ***A*** *and* ***B****) is more due to the proprioceptive position of the limb, than the visual position of the hand image.*

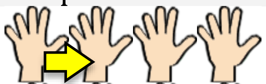
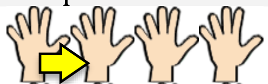
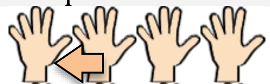
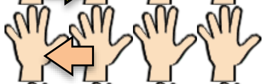
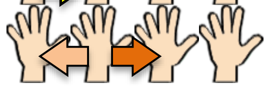
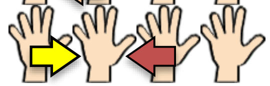
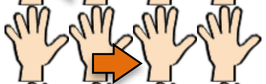
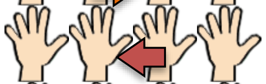
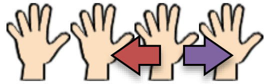
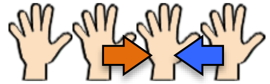
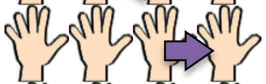
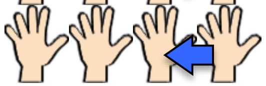
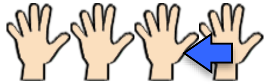
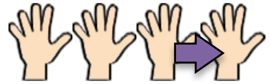
Figure 4. *Drift magnitude scores for the left- and right-hand illusion induction groups* ***(left and right panels respectively)*** *at the four actual hand position conditions. ** indicates statistical significant of the comparison at alpha = .01, ** indicates significance at alpha = .05. Condition codes represent the position of the hand with respect to the shoulder of origin (i.e. also the hand upon which the illusion was induced): OLS/ORS – Outside Left/ Right Shoulder respectively, ILS/IRS – Inside Left/Right Shoulder respectively, M – Midline. A significant difference was found in the distributions of drift magnitude for the two groups, with maximal drift at the shoulder of origin (i.e. the habitual action space). These results, therefore, support the body space explanation of drift magnitude differences and rebutting the alternative 'external space' hypothesis (left to right hemispace bias).*

Table 1. *Data for Experiment One: Pre- and post-illusion hand position estimations (mean & standard error of the mean (SEM)) and calculation of drift magnitude (drift) from these values (absolute value of the post-illusion score minus pre-). This is presented for the six raw conditions* ***(A)****, actual hand conditions* ***(B)*** *and hand image conditions* ***(C)****. See images for a visual representation of the real hand and hand image positions, as well as the direction of illusion in each condition. Condition codes represent the position of the hand with respect to the shoulder of origin (i.e. also the hand upon which the illusion was induced): OLS/ORS – Outside Left/ Right Shoulder respectively, ILS/IRS – Inside Left/Right Shoulder respectively, M – Midline.*

Table 2. *Data for Experiment Two: Pre- and post-illusion hand position estimations (mean & SEM) and calculation of drift magnitude (drift) from these values (absolute value of the post-illusion score minus pre-). This is presented for the six raw conditions* ***(A),*** *actual hand conditions* ***(B)*** *and hand image conditions* ***(C)****. See images for a visual representation of the real hand and hand image positions, as well as the direction of illusion in each condition. Visual representations are presented for the left-hand group induction only, right-hand induction forms a mirror image of these positions. Data for the left-hand group are presented on the left, right-hand group values on the right. Condition codes represent the position of the hand with respect to the shoulder of origin (i.e. also the hand upon which the illusion was induced): OLS/ORS – Outside Left/ Right Shoulder respectively, ILS/IRS – Inside Left/Right Shoulder respectively, M – Midline.*

Table

Table 1

A. Raw conditions					B. Actual hand conditions			C. Hand image conditions		
Condition	Visual representation	Pre-illusion	Post-illusion	Drift	Condition	Visual representation	Drift	Condition	Visual representation	Drift
OLS-ILS		1.25 (0.59)	5.73 (0.75)	**4.48 (0.55)**	OLS		**4.48 (0.55)**	OLS		**4.20 (0.46)**
ILS-OLS		-0.77 (0.67)	-4.98 (0.66)	**4.20 (0.46)**	ILS		**4.13 (0.40)**	ILS		**4.11 (0.54)**
ILS-M		0.84 (0.58)	4.89 (0.80)	**4.05 (0.55)**						
M-ILS		-1.84 (0.31)	-5.59 (0.64)	**3.75 (0.64)**	M		**3.74 (0.56)**	M		**3.76 (0.43)**
M-IRS		-1.34 (0.49)	2.39 (0.89)	**3.73 (0.58)**						
IRS-M		-3.55 (0.56)	-7.02 (0.29)	**3.48 (0.47)**	IRS		**3.48 (0.47)**	IRS		**3.73 (0.58)**

Table

Table 2

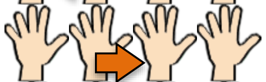
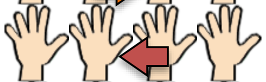
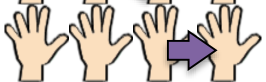
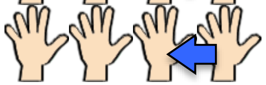
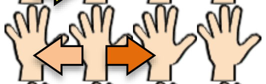
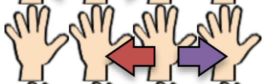
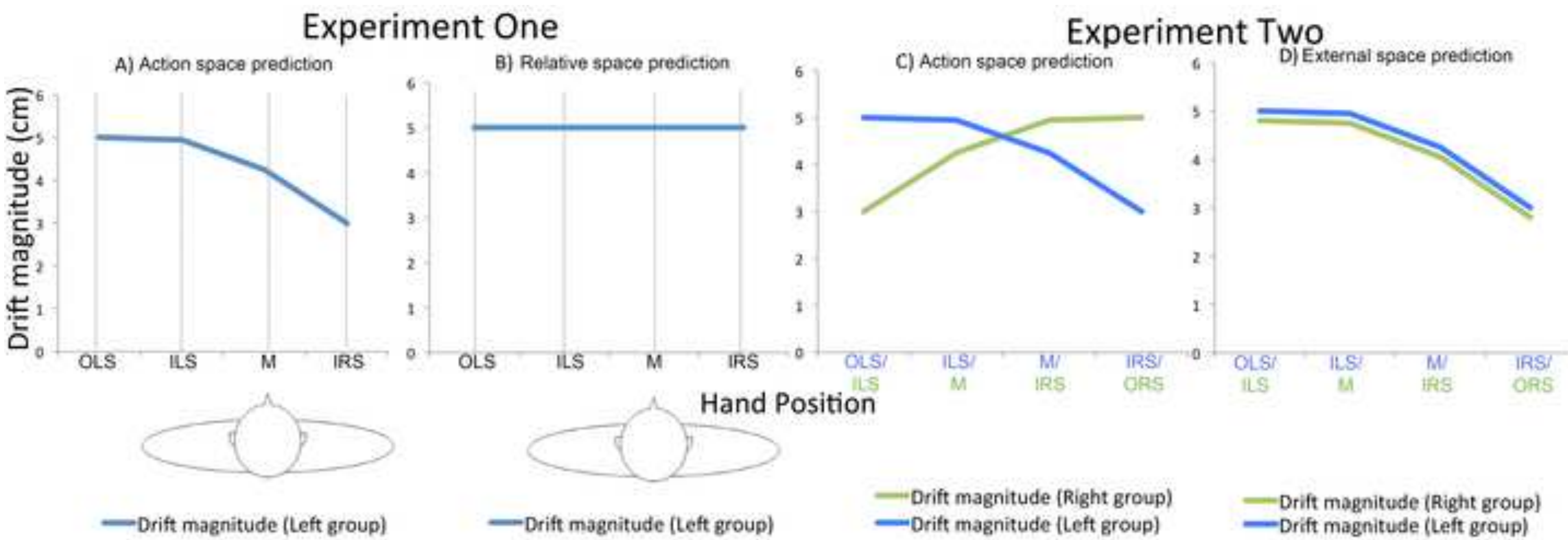
A. Raw conditions								
		Left-hand illusion				Right-hand illusion		
Condition	Visual representation (for left-hand induction, mirror reversed for right-hand induction)	Pre-illusion	Post-illusion	Drift	Condition	Pre-illusion	Post-illusion	Drift
OLS-ILS		1.94 (0.38)	5.78 (0.46)	**3.83 (0.31)**	ORS-IRS	2.46 (0.48)	5.44 (0.51)	**2.98 (0.30)**
ILS-OLS		-0.79 (0.45)	-5.07 (0.55)	**4.28 (0.38)**	IRS-ORS	0.51 (0.40)	-2.75 (0.76)	**3.25 (0.58)**
ILS-M		0.81 (0.37)	4.46 (0.51)	**3.65 (0.43)**	IRS-M	1.00 (0.40)	4.08 (0.48)	**3.08 (0.38)**
M-ILS		-1.29 (0.37)	-4.94 (0.59)	**3.65 (0.44)**	M-IRS	-1.52 (0.41)	-4.92 (0.59)	**3.40 (0.46)**
M-IRS		-0.79 (0.38)	2.83 (0.58)	**3.63 (0.41)**	M-ILS	-0.10 (0.42)	3.80 (0.55)	**3.90 (0.42)**
IRS-M		-3.40 (0.55)	-6.31 (0.54)	**2.90 (0.38)**	ILS-M	-2.71 (0.47)	-6.40 (0.52)	**3.70 (0.36)**

Table 2

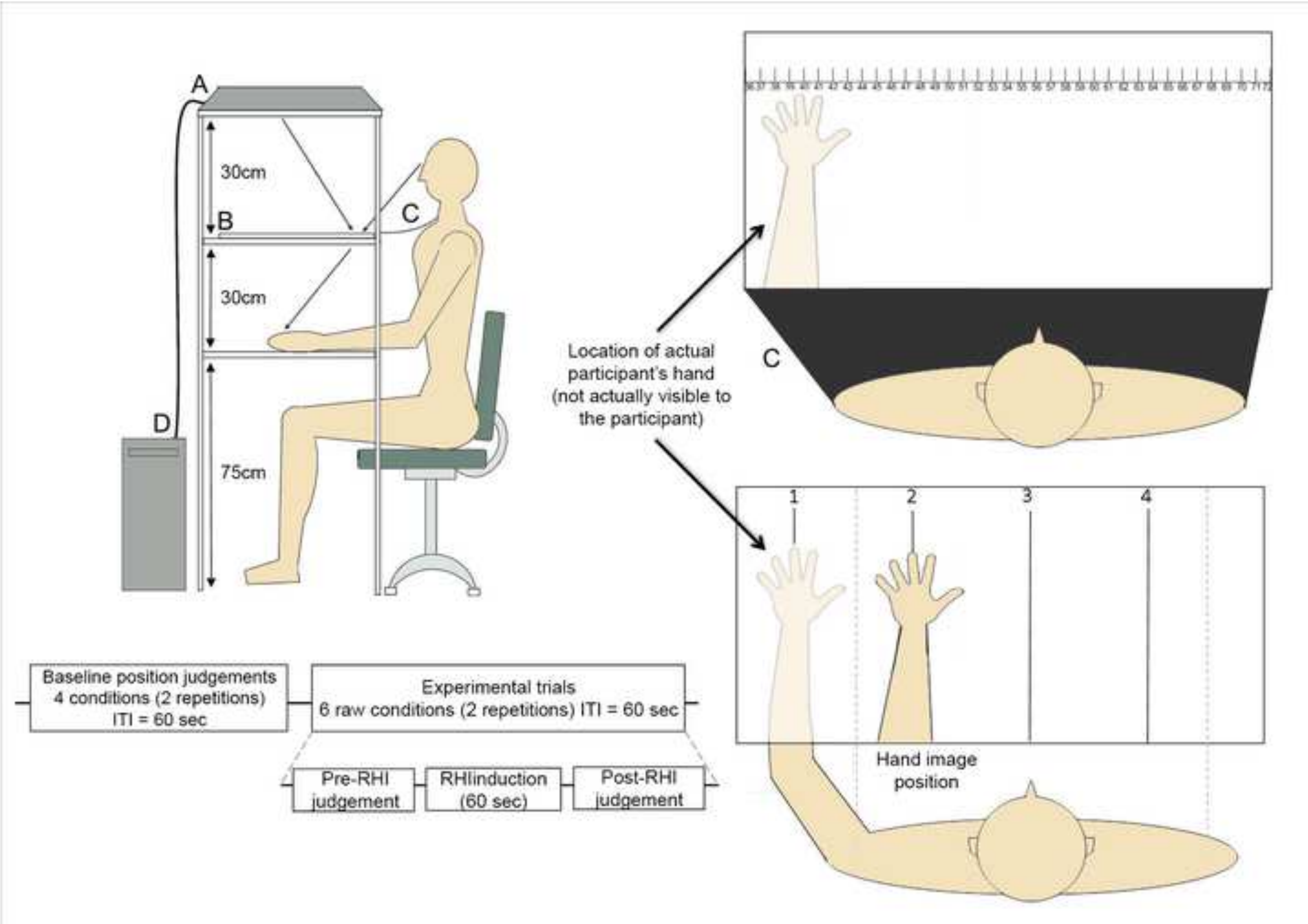
B. Actual hand position conditions								
		Left-hand illusion				Right-hand illusion		
Condition	Visual representation (for left-hand induction, mirror reversed for right-hand induction)	Pre-illusion	Post-illusion	Drift	Condition	Pre-illusion	Post-illusion	Drift
OLS		1.94 (0.38)	5.78 (0.46)	**3.83** **(0.31)**	ORS	2.46 (0.48)	5.44 (0.51)	**2.98** **(0.30)**
ILS		-0.80 (0.41)	-9.53 (0.53)	**3.97** **(0.35)**	IRS	-0.25 (0.40)	-3.41 (0.62)	**3.17** **(0.39)**
M		0.25 (0.38)	7.78 (0.58)	**3.64** **(0.37)**	M	0.71 (0.42)	4.34 (0.57)	**3.65** **(0.34)**
IRS		-3.40 (0.55)	-6.31 (0.54)	**2.90** **(0.38)**	ILS	-2.71 (0.47)	-6.40 (0.52)	**3.70** **(0.36)**

Figure



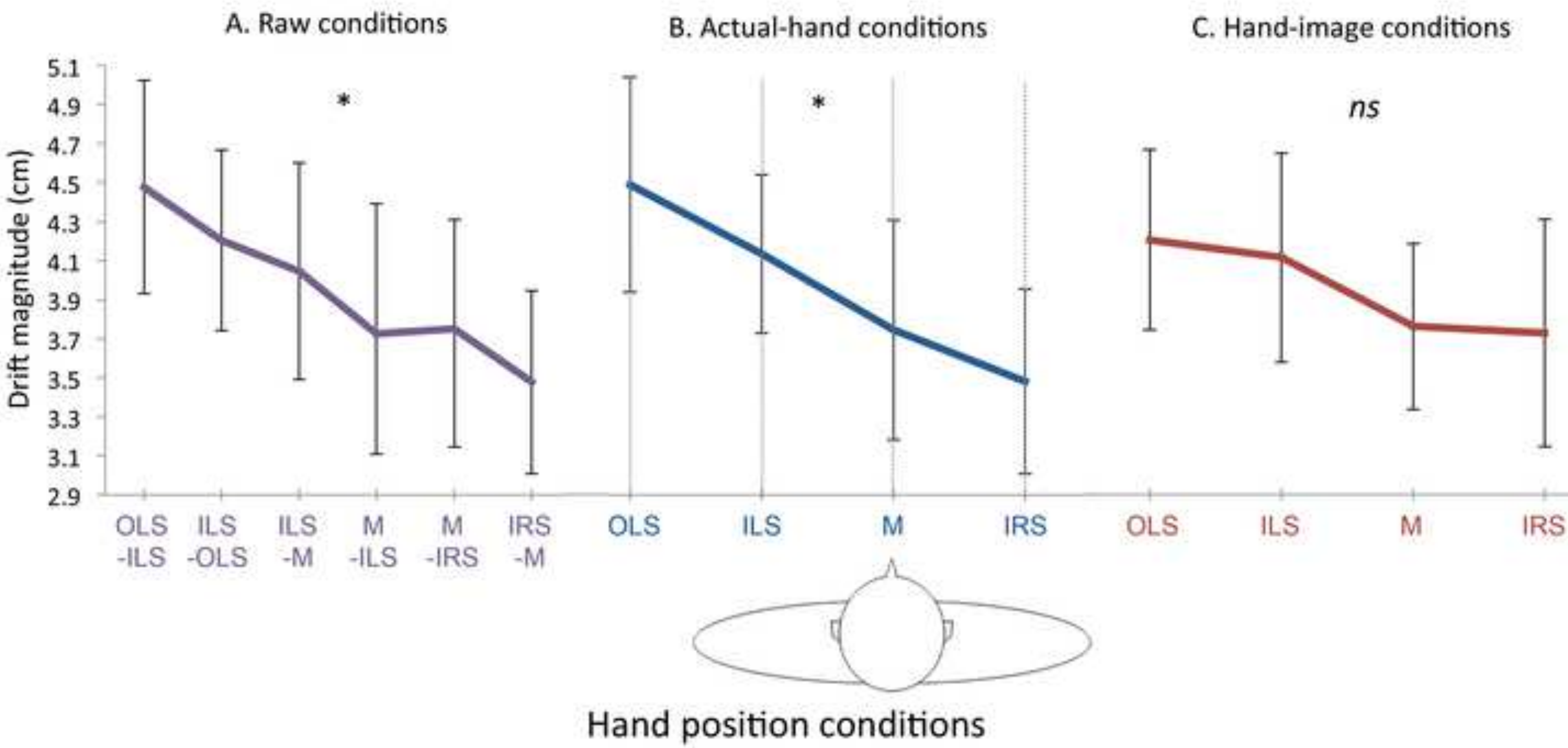
Experiment One
Experiment Two
A) Action space prediction
B) Relative space prediction
C) Action space prediction
D) External space prediction
Drift magnitude (cm)
0
1
2
3
4
5
6
OLS
ILS
M
IRS
OLS/
ILS
ILS/
M
M/
IRS
IRS/
ORS
Hand Position
Drift magnitude (Left group)
Drift magnitude (Right group)

Figure

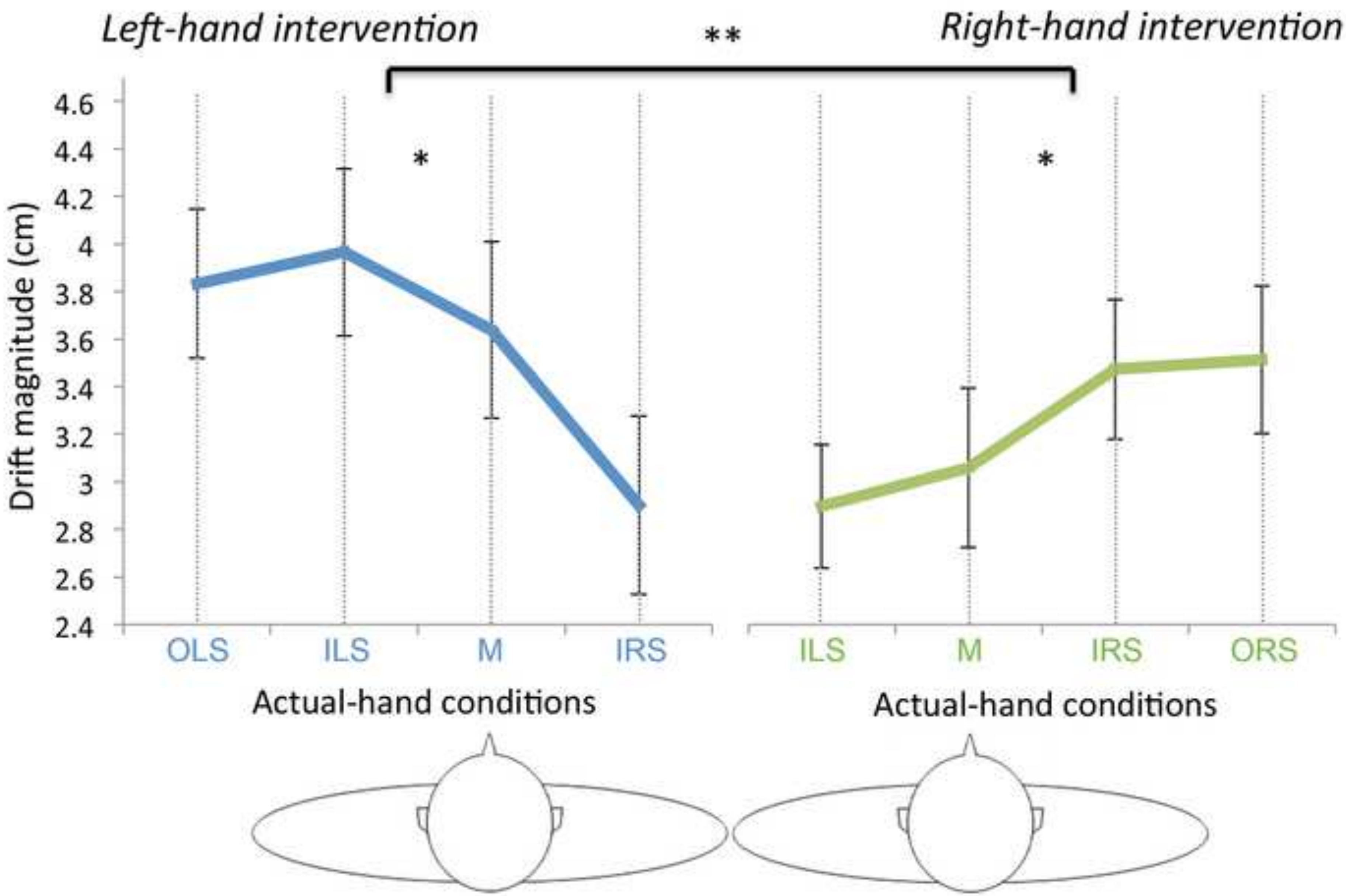


A
B
C
D
30cm
30cm
75cm
Location of actual participant's hand (not actually visible to the participant)
C
1
2
3
4
Hand image position
Baseline position judgements
4 conditions (2 repetitions)
ITI = 60 sec
Experimental trials
6 raw conditions (2 repetitions) ITI = 60 sec
Pre-RHI judgement
RHIinduction (60 sec)
Post-RHI judgement

Figure


A. Raw conditions
B. Actual-hand conditions
C. Hand-image conditions
5.1
4.9
4.7
4.5
4.3
4.1
3.9
3.7
3.5
3.3
3.1
2.9
Drift magnitude (cm)
*
*
ns
OLS -ILS
ILS -OLS
ILS -M
M -ILS
M -IRS
IRS -M
OLS
ILS
M
IRS
OLS
ILS
M
IRS
Hand position conditions

Figure



Left-hand intervention
**
Right-hand intervention
Drift magnitude (cm)
4.6
4.4
4.2
4
3.8
3.6
3.4
3.2
3
2.8
2.6
2.4
*
*
OLS
ILS
M
IRS
ILS
M
IRS
ORS
Actual-hand conditions
Actual-hand conditions