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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

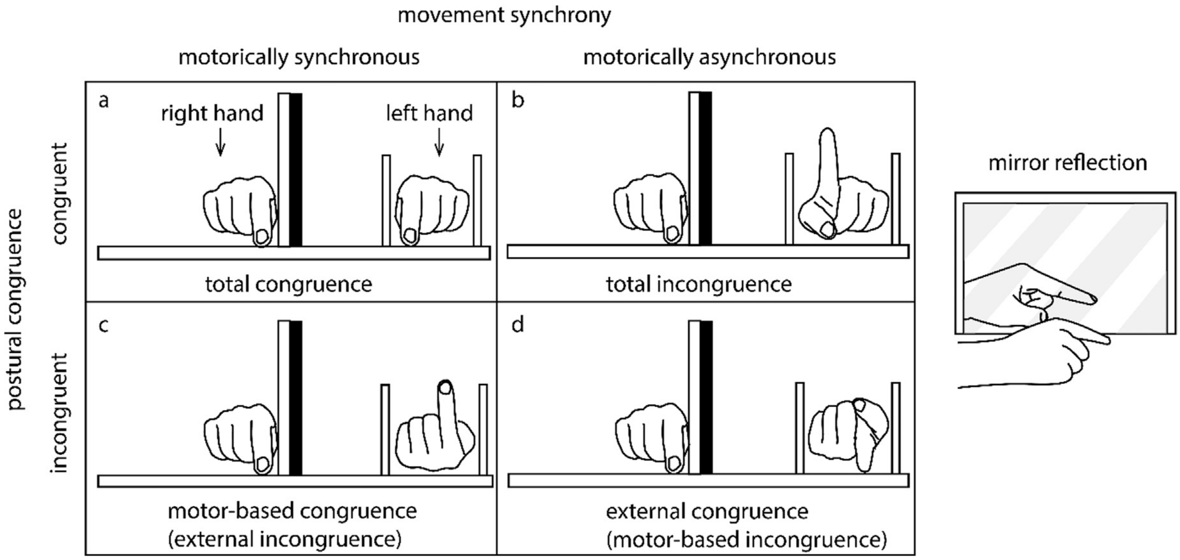

Fig. 1. Left: Front view (facing the participant) of hand posture and movements in the mirror box. Each box represents a trial type in Experiment 1. Participants placed the right hand in front of the mirror and the left hand behind the mirror, with hands in either congruent (palm down) or incongruent postures (unseen left hand palm up and right hand palm down). Two vertically-oriented markers were placed by each side of the left hand to prevent excessive hand displacements during tapping. Participants tapped the index finger on both hands either motorically synchronously or asynchronously. (a) and (b) When the hands were in congruent postures, motor-based and external visuomotor congruence were yoked. (c) and (d) When the hands were in incongruent postures, motor-based congruent visuomotor information was externally incongruent (c), and vice versa (d). Right: Participants viewed the mirror-reflected hand during tapping.

the same manipulation of visuomotor congruence also affects perceived limb location and ownership of the viewed hand, external congruence (with motor-based incongruence) would result in more multisensory integration than motor-based congruence (with external incongruence).

2.1. Methods

2.1.1. Participants

In a pilot version of the study, we tested 24 participants and obtained a large effect size (Cohen's $d > 0.8$) with adequate power ($1 - \beta > 0.8$). Our goal was to test 24 participants. Given that a few participants had problems with the task in piloting (e.g. having difficulty with bimanual coordination in a mirror box), we tested more than 24 participants, assuming some attrition. In total, thirty-one participants (9 male, ages 18–22 years, all right-handed) from the General Psychology participant pool at the University of Delaware were tested. All studies were approved by the University of Delaware Institutional Review Board. All participants signed informed consent forms before the experiment and received course credit as compensation.

2.1.2. Data exclusion

We excluded any participants who were repeatedly observed not looking at the mirror, could not coordinate bimanual tapping in the mirror box, or demonstrated no mirror box illusion (i.e. zero proprioceptive shift) in the total congruence condition. We judged movement coordination by visual inspection. These uncoordinated bimanual movements were characterized by (i) participants tapping at a pace substantially slower than 120 beats per minutes (e.g. at 60 beats per minutes), (ii) the index fingers not moving vertically (e.g. the unseen left index finger was oscillating in random directions), and (iii) the index fingers tapping in random rhythms instead of following the metronome. Two participants were excluded for not looking at the mirror, two were excluded for not perceiving proprioceptive shift in total congruence condition, and two were excluded for being unable to coordinate bimanual tapping, resulting in 25 participants included in the analysis. All original data can be found at https://osf.io/s7wtu/?view_only=c195e4fa0cef4d2d95dd4b29cd48099c.

2.1.3. Apparatus

The mirror box used in the experiments consisted of an acrylic mirror (16″ (40.6 cm) deep × 12″ (30.5 cm) tall) aligned with the participant's midsagittal plane, and a flat wooden base (36″ (91.4 cm) wide × 16″ (40.6 cm) deep). The reflective surface of the mirror faced rightward. Two black curtains hung from each side of the mirror so that participants could not see their forearms. During piloting, quite a few participants had difficulty in freely coordinating bimanual movements with two hands in opposing postures. We therefore had participants tap the index fingers against an upper (7.5″ (19.05 cm) long) and lower (6.5″ (16.51 cm) long) rod, vertically separated by 1.75″ (4.5 cm)). Each pair of rods was attached to a wooden frame (7.5″ (19.1 cm) wide × 3.5″ (8.9 cm) deep × 4.6″ (11.7 cm) height). One wooden frame was placed in front of the mirror with one end of the rods against the mirror, the other frame was placed behind the mirror with the center of the rods 6″ away from the mirror. Both frames were placed with rods perpendicular to the mirror and with the proximal edge 6″ (15.24 cm) relative to the proximal edge of the base of the mirror box. To facilitate limb position responses, a ruler was mounted horizontally above the mirror box, parallel with the body's transverse plane. Given that we were measuring proprioceptive shift, we wanted to ensure that the actual position of the hidden hand did not drift over the course of a trial. Therefore, we placed a vertical marker 1 cm on each side of the hidden left wrist.

2.1.4. Design and procedure

Experiment 1 was a 2 (postural congruence: both hands palm down and the hidden (left) hand palm up, the right hand palm down) × 2 (movement synchrony: motorically synchronous and motorically asynchronous) within-subjects design, leading to four conditions regarding visuomotor congruence in different frames of reference (Fig. 1). Visuomotor information was congruent in both motor-based and external frames of reference in the total congruence condition (Fig. 1a), and was incongruent in both reference frames in the total incongruence condition (Fig. 1b). In the motor-based congruence condition, visuomotor information was congruent in a motor-based reference frame but externally incongruent (Fig. 1c), and vice versa in the external congruence condition (Fig. 1d).

Before the experiment started, participants practiced each type of movement while viewing the movements of the experimenter, with both hands outside the mirror box and in front of the body. During tapping participants made fists with their hands and stretched out the index fingers. To avoid biasing attention, the experimenter simply demonstrated the movements without giving any verbal descriptions. Participants were instructed to tap with the metacarpophalangeal joints while holding the wrists and arms static. The main experiment began after participants demonstrated competence in making the instructed movements.

At the beginning of each trial, participants placed the right index finger 0.5″ (1.27 cm) to the right of the mirror. Next, the experimenter positioned the participant's left index finger 6″ (15.24 cm) to the left of the mirror with the hand in the selected posture (palm up or palm down), with the participant's eyes closed. The index fingers rested on the lower rod of the wooden frame. The right hand and wood frame was then covered with cardboard so that the participant could not see the mirror-reflected hand. The participant then opened his/her eyes and provided an initial, verbal report of the hidden left index finger position using the ruler mounted above the mirror. The cardboard was then removed, and the experimenter demonstrated the movements for the tested condition without giving any verbal descriptions.

For each trial, the participant tapped their index fingers for 60 s to a metronome set at 120 beats per minute, with the index fingers contacting either the upper or lower rod at each beat. During tapping, the participant was instructed to view the mirror-reflection of his/her right hand. Forty-five seconds after tapping onset, participants were asked to verbally report where they felt the unseen (left) index finger was located using the ruler mounted above the mirror box. The ruler was shifted to a different offset after each trial to prevent participants from anchoring to a specific number. After 60 s of tapping were complete, participants responded using a continuous visual analog scale (VAS, ranging from "completely disagree" to "completely agree") to questions (see Appendix A) presented in random order using E-Prime 2.0 (Psychology Software Tools, Inc, Pittsburgh, PA). Five questions were presented to measure perceived ownership of the viewed hand in the mirror. Four questions were taken from prior studies on the rubber hand illusion (Longo, Schüür, Kammers, Tsakiris, & Haggard, 2008) and mirror box illusion (Medina et al., 2015), and one question was newly added to ask whether movements on the viewed hand were felt as the movements on the unseen (left) hand. Cronbach's alpha of the ownership questions was high in all conditions (0.764–0.908), indicating high consistency among the questions. To examine changes in perceived hidden hand posture, we also asked participants whether they perceived their hidden (left) hand and finger in the same posture as seen in the mirror (posture-matching questions). The VAS scales were later transformed to a continuous scale ranging from "0" to "100", with higher scores indicating more agreement with the questions.

Each of the four trial types was presented once with the order randomized for each individual. The total length of each session was approximately 20 min.

2.2. Analyses

Given that bimanual coordination of finger movements with conflicting visual feedback is fairly difficult, some participants were unable to make coordinated movements, whereas the hidden hand of other participants moved. Using visual inspection, we excluded any trials in which movements were not coordinated (two trials) and any trials where the hidden hand moved > 1″ over the course of 60 s (eight trials).

Our four conditions varied, not only based on external versus motor-based visuomotor congruence, but also congruence between the unseen and mirror hand postures. The unseen and mirror hand were in congruent postures (palm down) in the total congruence and total incongruence conditions, but in incongruent postures (hidden hand palm up, mirror hand palm down) in the motor-based and external congruence conditions. Given that postural congruence also influences multisensory integration (e.g. Costantini & Haggard, 2007; Ide, 2013; Liu & Medina, 2017), we compared conditions that were matched for postural congruence, but differed with regards to external/motor-based congruence. First, to examine the overall effect of both motor-based and external congruence on multisensory integration, we compared performance in total congruence versus total incongruence condition. Then, to investigate the relative weighting of motor-based and external representations in multisensory integration, we compared performance on external congruence versus motor-based congruence trials. All external congruence trials were motor-based incongruent, and vice versa.

We analyzed data with linear mixed models using the lmerTest R package (https://cran.r-project.org/web/packages/lmerTest/index.html). lmerTest function applies Satterthwaite approximation when calculating degree of freedom, which takes both sample size and sample variances into account, yielding decimals in some cases. The two levels of each factor were coded as -0.5 and 0.5. Alpha was set to 0.05 for all analyses.

For our dependent variables, proprioceptive shift was calculated as the difference in centimeters between the proprioceptive estimate made before tapping and at 45 s after tapping onset. Positive values indicate shifts towards the visually-defined hand position and negative values shifts away. Greater shifts indicate more multisensory integration. For each participant, perceived ownership of the mirror-reflected hand was calculated by averaging the ratings across the five ownership questions. Higher ratings indicate a greater sense of ownership, which in turn indicates more multisensory integration.

2.3. Results

First, we examined the overall effect of both motor-based and external congruence on multisensory integration on our dependent variables, running linear mixed models with overall congruence (total congruence and total incongruence) as a fixed effect and random intercepts for each participant (Fig. 2a). As expected, total congruence (M = 6.11 cm, SD = 2.45 cm) resulted in significantly more proprioceptive shift than total incongruence (M = 3.59 cm, SD = 2.55 cm), $t(22.0) = 4.03$, $p < .001$. Furthermore, as expected, there was a significantly higher ownership rating in the total congruence (M = 91.1, SD = 8.76) versus total incongruence trials (M = 54.9, SD = 21.7), $t(45) = 7.43$, $p < .001$. These results indicate more multisensory integration when visuomotor information was congruent in both motor-based and external frame of reference versus being incongruent in both frames of reference.

We then investigated the relative contributions of motor-based and external visuomotor congruence to proprioceptive shift (Fig. 2a) and ownership (Fig. 2b), using linear mixed models with selected congruence (motor-based and external congruence) as a fixed effect and a random intercept for each participant. There was significantly more proprioceptive shift in the external congruence (M = 4.17 cm, SD = 2.38 cm) than the motor-based congruence trials (M = 2.45 cm, SD = 3.10 cm), $t(20.7) = 3.34$, $p = .003$. Note that proprioceptive shift was significantly greater than zero in both motor-based congruence, $t(20) = 3.62$, $p = .002$, and external congruence conditions, $t(21) = 8.22$, $p < .001$. These findings provide evidence that while both external and motor-based visuomotor congruence are sufficient for inducing shift in perceived hand position towards the visual estimate, visuomotor congruence in an external frame of reference is more strongly weighted than congruence in a motor-based frame of reference. As for ownership, external congruence (M = 65.5, SD = 23.1) resulted in more ownership than motor-based congruence (M = 51.8, SD = 30.4), although the difference did not reach significance level, $t(21.9) = 1.98$, $p = .061$.

Whereas proprioceptive shift measures changes in perceived position of the limb in external space, here we measured changes in perceived posture of the hidden limb using responses to the hand (Fig. 2c)

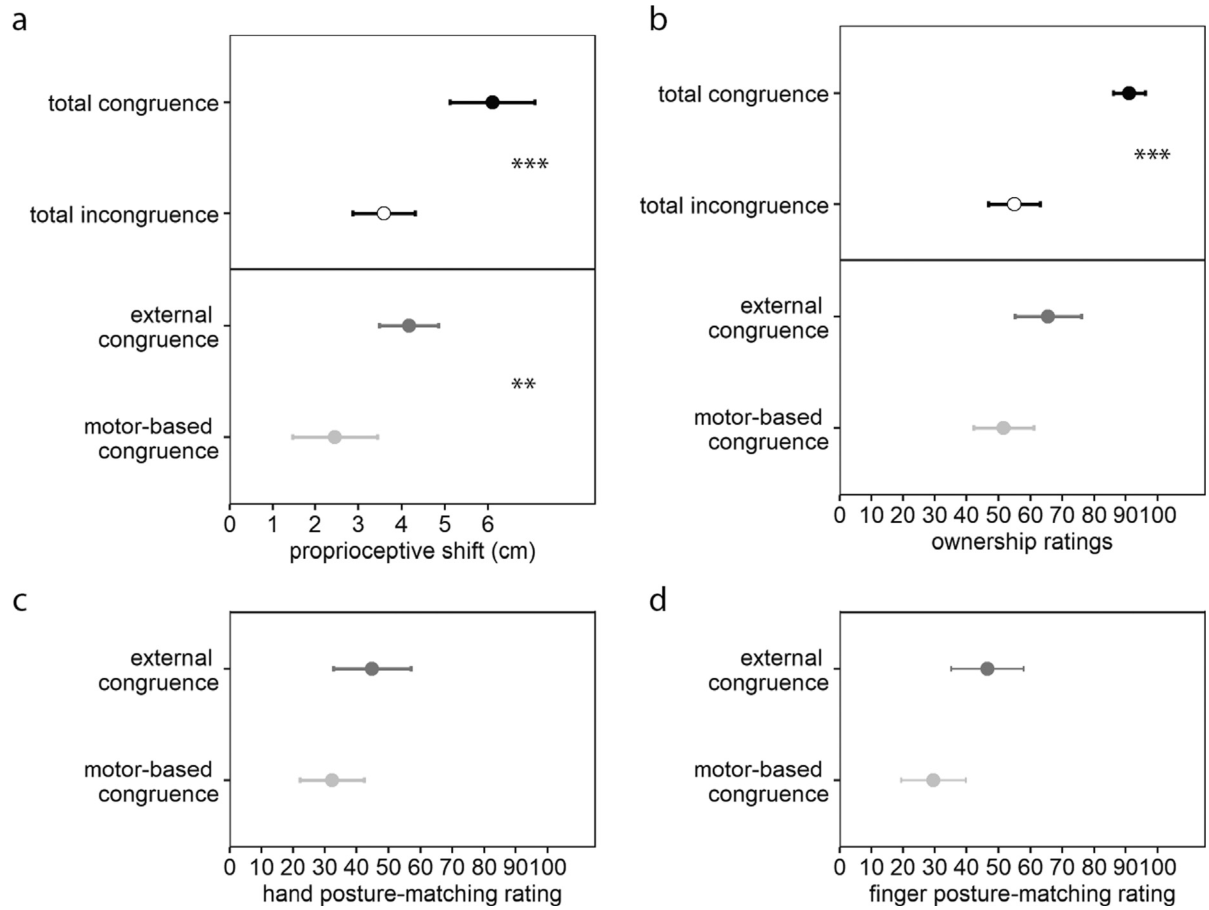

Fig. 2. Results of Experiment 1. (a) Proprioceptive shift. (b) Perceived ownership of the viewed hand. (c) Ratings on the hand posture-matching question. (d) Ratings on the finger posture-matching question. Greater values indicate more multisensory integration. Whenever shown, error bars indicate 95% within-subjects confidence intervals (Cousineau, 2005). **: significance at $p < .01$ level. ***: significance at $p < .001$ level.

and finger (Fig. 2d) posture-matching questions. As the proprioceptive estimate and visual estimate of hand posture differed only in external congruence and motor-based congruence trials (hidden left hand palm up, right hand palm down), we only report results of these trial types. Higher ratings indicate that the hidden limb was reported to be in the same posture with the mirror-reflected limb, thus indicating more multisensory integration.

For both hand and finger posture-matching ratings, we present results from linear mixed models with selected congruence (motor-based and external congruence) as a fixed within-subjects effect and a random intercept for each participant. For the hand posture-matching question, although the rating was higher in the external ($M = 44.9$, $SD = 34.3$) versus motor-based congruence trials ($M = 32.3$, $SD = 32.7$), the difference was not significant, $t(21.1) = 1.47$, $p = .157$. For the finger posture-matching question, ratings in external congruence ($M = 46.6$, $SD = 34.2$) trials higher than motor-based congruence trials ($M = 29.6$, $SD = 31.3$), with the difference being just outside of the typical significance boundary, $t(21.0) = 2.07$, $p = .051$.

In summary, we found significantly more proprioceptive shift in external congruence trials than motor-based congruence trials. Results from ownership and finger and hand posture-matching rating displayed the same trend. These findings provide preliminary evidence that information from representations in an external frame of reference is more strongly weighted than information from a motor-based frame of reference in multisensory integration.

2.4. Discussion

In Experiment 1, we found more proprioceptive shift and ownership of the mirror-reflected hand in total congruence versus total incongruence trials, consistent with the spatial and temporal rule of multisensory integration (Holmes & Spence, 2005; Medina et al., 2015; Meredith & Stein, 1986; Meredith et al., 1987). Importantly, we found more proprioceptive shift in the external versus motor-based congruence conditions, providing evidence that information from an externally-based representation is more strongly weighted than from a motor-based representation. We then did Experiment 2 to replicate and test the effects found in Experiment 1, as well as investigate if relative weighting between external and motor-based representations is affected by the amount of motor outflow in motor-based representations.

3. Experiment 2

Studies of multisensory integration have shown that the relative weighting of information from different modalities can dynamically change based on the precision of information from each modality. For example, when information about the height of an object differed in vision versus haptics, judgments of object height were biased towards the visual estimate. The bias decreased, however, when vision was degraded by introducing noise to the visual input (Ernst & Banks, 2002). Such weighting is statistically optimal in that it maximizes accuracy and minimizes variance in estimates (Alais & Burr, 2004; Deneve, Latham, & Pouget, 2001; Ernst & Banks, 2002; van Beers et al., 1999). Regarding weighting between visuomotor congruence represented in motor-based and external frames of reference, one aspect that could influence the weighting is motor outflow, defined as the number of muscles involved in movement. For example, if a movement involved more motor outflow, this could lead to a stronger weighting of

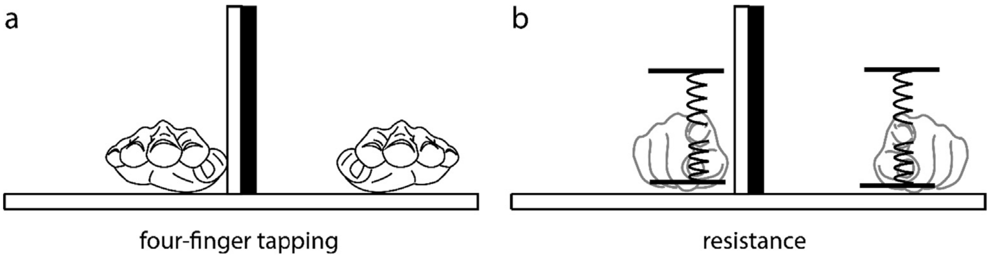

Fig. 3. Illustration of manipulations of (a) Experiment 2 and (b) Experiment 3. (a) Participants tapped with either the index finger or digits 2–5 on both hands in Experiment 2, with the manipulations of hand posture and movement synchrony being the same as Experiment 1. (b) Participants tapped with the index finger on both hands either with resistance from the springs, or without resistance, as with Experiment 1.

information from motor-based as opposed to external representations. In Experiment 2, participants tapped either with their index finger on both hands (index-finger tapping), as with Experiment 1, or with four fingers (digits 2–5, thumb excluded, Fig. 3a) on both hands (four-finger tapping), with the other manipulations the same as Experiment 1. In comparison to tapping the index finger, tapping four fingers on both hands would increase active motor outflow and afferent signals generated by the movements, potentially leading to more attention towards the motor-based representation. The dynamic weighting hypothesis would predict that for index-finger tapping, external visuomotor congruence (with motor-based incongruence) would result in more multisensory integration than motor-based congruence, whereas for four-finger tapping, the advantage of external congruence would decrease or even reverse. Second, if this hypothesis was not supported, we would predict a replication of the Experiment 1 findings – more multisensory integration for externally congruent versus motor-based congruent movements.

3.1. Methods

3.1.1. Participants

We aimed to have adequate power ($1 - \beta = 0.8$) to detect a medium effect size (Cohen's d = 0.5), hence we planned to test 34 participants. Forty-seven participants (15 male, ages 18–20 years, all right-handed), recruited from the General Psychology participant pool at the University of Delaware, took part in the experiment. Two participants were excluded due to experimenter error. Using the same exclusion criteria as in Experiment 1, eight participants were excluded (six participants for poor bimanual coordination in the mirror box, one for not looking at the mirror hand, and one who demonstrated no illusion in the mirror box). As a result, 37 participants were included in the analyses.

3.1.2. Apparatus, design and procedure

The apparatus in Experiment 2 was the same as in Experiment 1. Experiment 2 was a 2 (postural congruence) × 2 (movement synchrony) × 2 (effector type) within-subjects design (see Figs. 1 and 3a). Each of the eight conditions was presented once with the order randomized for each individual. Each experimental session was 40 min.

The procedure of Experiment 2 was the same as Experiment 1 with the following exceptions. To have localization judgments be made closest to the midpoint of the moving fingers, localization judgments and posture-matching ratings were different for the two effector type conditions: index finger for the index-finger tapping condition, and middle finger for the four-finger tapping condition. Second, to ensure that the position of the target fingers was consistent across trials, the right target finger (index finger or middle finger) was 1.5″ right of the mirror midline and the unseen left target finger was 7.5″ left of the mirror midline. Third, although in Experiment 1 trials in which the unseen hand drifted > 1″ were excluded, we wanted to be confident that involuntary drifts within 1″ did not affect our measure of proprioceptive shift. We therefore video recorded all trials and used the recording to measure finger position of the unseen hand before tapping and 45 s after tapping onset.

3.1.3. Analyses

As in Experiment 1, we compared conditions that were matched for postural congruence, but differed with regards to external/motor-based congruency. First, we performed analyses on overall congruence (total congruence and total incongruence) and effector type (index-finger or four-finger tapping). We predicted more multisensory integration in total congruence versus total incongruence for both index-finger and four-finger tapping trials. Next, we performed analyses on selected congruence (motor-based congruence and external congruence) and effector type to test the dynamic weighting hypothesis. Specifically, the dynamic weighting hypothesis would predict an interaction between selected congruence and effector type: in index-finger tapping trials, external congruence would result in more multisensory integration than motor-based congruence, as with Experiment 1. However, the advantage of external congruence would decrease in four-finger tapping trials as a result of increased motor outflow from motor-based representations.

3.2. Results

Overall, we excluded 41 out of 296 trials for the following reasons: the unseen target finger drifted > 1″ (35 trials), incorrect bimanual tapping (four trials), and experimenter error (not video-recorded, two trials). We present main results below, with post hoc analyses of each linear mixed-effect model presented in Supplemental Materials.

First, we report results from linear mixed models with overall congruence (total congruence and total incongruence) and effector type (index-finger and four-finger) as fixed within-subjects effects, and random intercepts for each participant (Fig. 4a). For proprioceptive shift, total congruence (M = 6.69 cm, SD = 3.19 cm) resulted in significantly more proprioceptive shift than total incongruence (M = 4.60 cm, SD = 3.20 cm), $t(92.2) = 3.90$, $p < .001$, with no interaction with effector type, $t(91.1) = 1.7$, $p = .093$. The main effect of effector type was not significant, $t(91.6) = 0.13$, $p = .899$ (index-finger: M = 5.51 cm, SD = 3.72 cm; four-finger: M = 5.58 cm, SD = 3.20 cm). Ownership ratings (Fig. 5a) were consistent with results from the proprioceptive shift data, as total congruence (M = 87.3, SD = 11.7) resulted in a significantly greater sense of ownership than total incongruence (M = 58.9, SD = 23.5), $t(91.95) = 8.9$, $p < .001$, with no interaction with effector type, $t(90.7) = 1.03$, $p = .307$. The main effect of effector type was not significant, $t(91.3) = 1.06$, $p = .290$ (index-finger: M = 70.7, SD = 27.3; four-finger: M = 72.7, SD = 17.0). Overall, these results indicate more multisensory integration for total congruence versus total incongruence regardless of effector type.

To test the dynamic weighting hypothesis, we ran linear mixed models with selected congruence (motor-based and external congruence) and effector type (index-finger and four-finger) as fixed within-subjects effects, and random intercepts for each participant. External congruence (M = 4.10 cm, SD = 3.53 cm) resulted in significantly more proprioceptive shift than motor-based congruence (M = 3.17 cm, SD = 3.10 cm), $t(90.4) = 2.13$, $p = .036$. Importantly, the interaction between selected congruence and effector type was not significant, $t(89.5) = 0.40$, $p = .695$ (Fig. 4b). These findings indicate that the relative weighting between motor-based and externally-based representations is not modulated by motor outflow. The main effect of

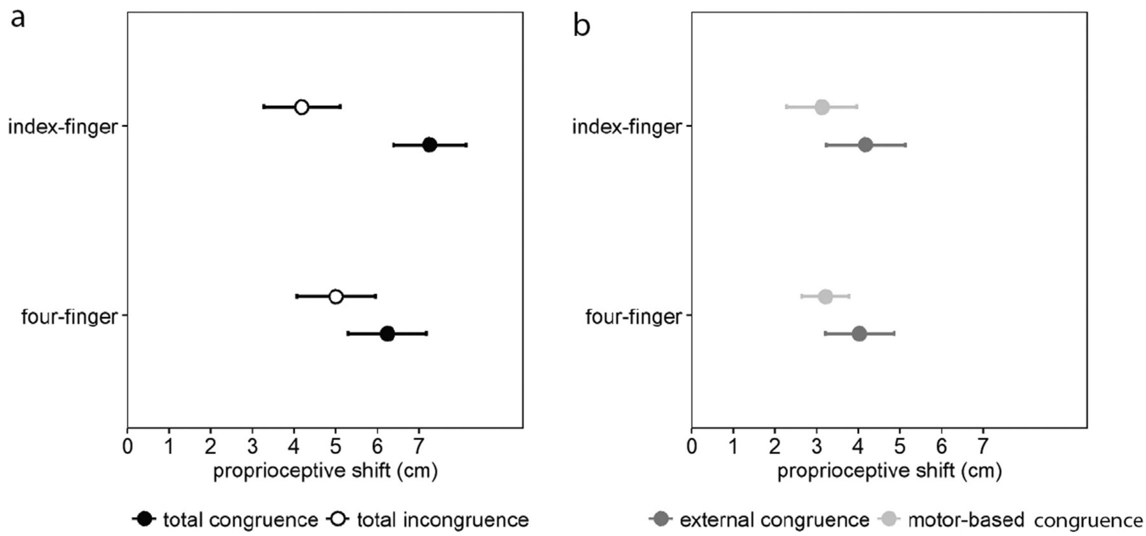

Fig. 4. Results of proprioceptive shift in Experiment 2. (a) Proprioceptive shift from index-finger and four-finger tapping in total congruence (black circles) and total incongruence (white circles) conditions. (b) Proprioceptive shift from index-finger and four-finger tapping in external congruence (dark gray circles) and motor-based congruence (light gray circles) conditions.

effector type was not significant, $t(90.3) = 0.01$, $p = .989$ (index finger: $M = 3.60$ cm, $SD = 3.09$ cm; four-finger: $M = 3.64$ cm, $SD = 2.99$ cm). For ownership ratings (Fig. 5b), external congruence ($M = 63.2$, $SD = 23.9$) resulted in a significantly greater sense of ownership versus motor-based congruence ($M = 50.3$, $SD = 27.6$), $t(90.0) = 3.98$, $p < .001$, with no interaction between selected congruence and effector type, $t(89.1) = 0.01$, $p = .996$. These findings provide evidence that information represented in external frame of reference is more strongly weighted than motor-based frame of reference in multisensory integration, with the relative weighting unaffected by changes in motor outflow. The main effect of effector type was not significant, $t(89.9) = 0.03$, $p = .973$ (index-finger: $M = 57.0$, $SD = 24.0$; four-finger: $M = 56.2$, $SD = 25.2$).

When making bimanual movements with conflicting visual feedback, the hidden hand of some participants involuntarily drifted during tapping. As our measure of proprioceptive shift depends on where the hidden index finger is perceived in space, proprioceptive shift might be undesirably affected by involuntary drift of hand position. Therefore, we performed the same analyses as above, using the difference between the actual position of the finger (from the video recording) and the participant's response as the dependent variable. Accounting for this minimal drift, we found the same effects as above (see Supplemental Materials for results and analyses).

3.2.1. Hand and finger posture-matching questions

As with Experiment 1, only external congruence and motor-based congruence trials are included in these analyses. To test the dynamic weighting hypothesis, we compared posture-matching ratings between motor-based and external congruence trials, and examined whether the difference varied across effector types. For the hand posture-matching question (Fig. 6a), difference between the external ($M = 44.2$, $SD = 31.4$) and motor-based ($M = 33.7$, $SD = 31.3$) congruence conditions was significant, $t(90.4) = 2.69$, $p = .009$. Interaction between selected congruence and effector type was not significant, $t(89.4) = 0.65$, $p = .516$, indicating that the relative weighting was unaffected by changes in motor outflow. The main effect of effector type was not significant, $t(90.3) = 1.09$, $p = .28$ (index-finger: $M = 41.1$, $SD = 32.1$; four-finger: $M = 36.7$, $SD = 27.8$).

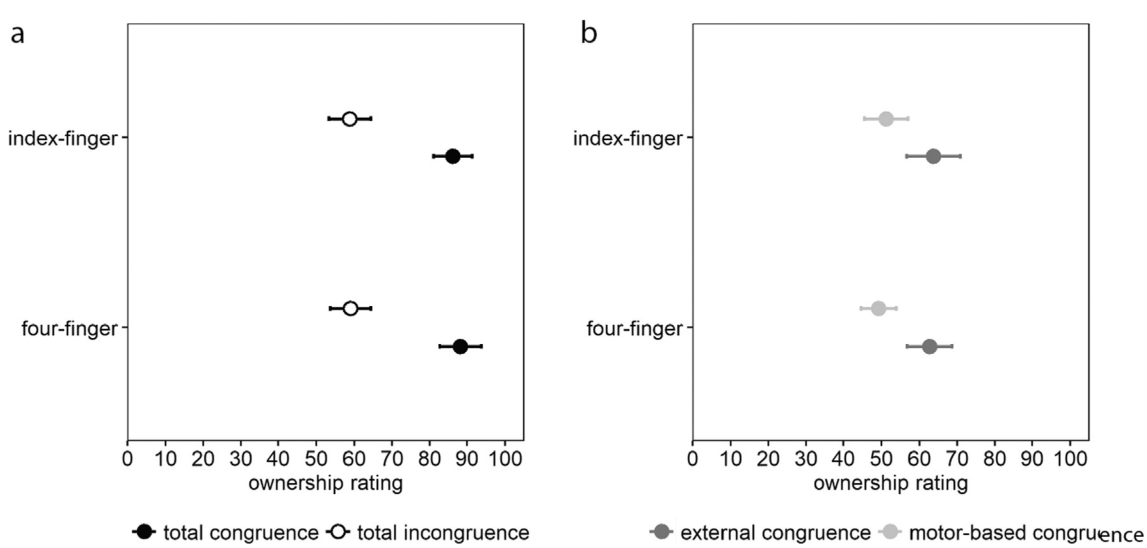

Fig. 5. Results of perceived ownership of the mirror hand in Experiment 2. (a) Ownership ratings from index-finger and four-finger tapping in total congruence (black circles) and total incongruence (white circles) conditions. (b) Ownership ratings from index-finger and four-finger tapping in external congruence (dark gray circles) and motor-based congruence (light gray circles) conditions.

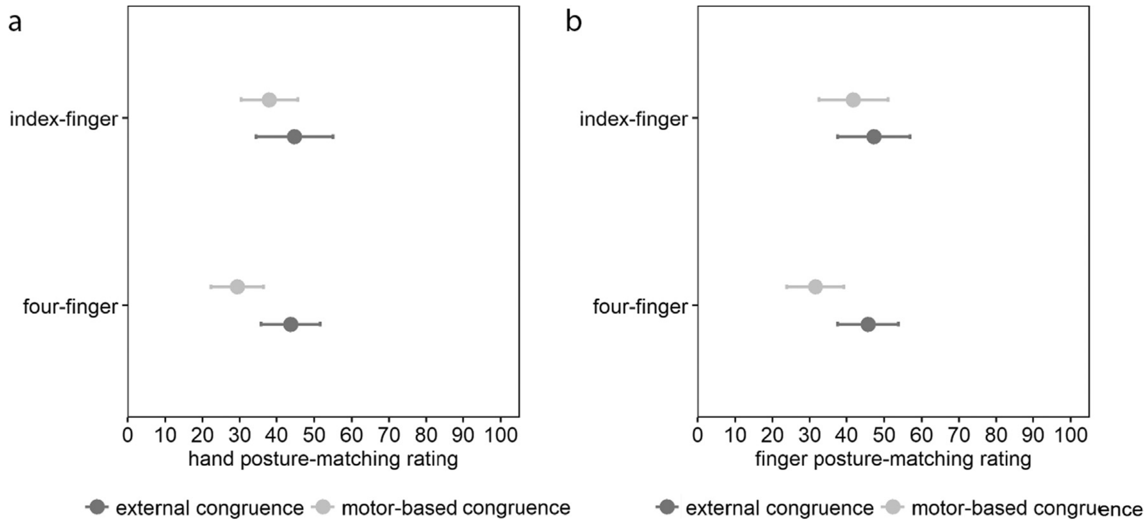

Fig. 6. Results of ratings on the (a) hand and (b) finger posture-matching question in Experiment 2.

For the finger posture-matching question (Fig. 6b), external congruence (M = 46.4, SD = 27.5) resulted in significantly higher ratings than motor-based congruence (M = 36.7, SD = 30.4), $t(91.8) = 2.23$, $p = .028$. Importantly, the interaction between selected congruence and effector type was not significant, $t(90.5) = 0.79$, $p = .434$, consistent with the findings from other dependent variables. The main effect of effector type was not significant, $t(91.6) = 1.18$, $p = .239$ (index-finger: M = 44.3, SD = 31.5; four-finger: M = 38.8, SD = 26.9). These results provide evidence that information from an externally-based representation is more strongly weighted in multisensory integration than information from a motor-based representation, with the relative weighting unaffected by changes in the amount of motor outflow.

3.3. Discussion

In Experiment 2, we manipulated the amount of motor outflow by having participants tap with either one or four fingers to examine whether changes in motor outflow would affect the relative weighting of information from external and motor-based frame of reference. We found more proprioceptive shift, ownership of the mirror-reflected hand, higher finger and hand posture-matching ratings in externally congruent versus motorically congruent trials regardless of index-finger or four-finger tapping. These results confirmed the effects found in Experiment 1, indicating that information from the external representation is more strongly weighted than information from a motor-based representation in multisensory integration, and that this relative weighting is unaffected by the amount of motor outflow.

One possible reason for the lack of a motor outflow effect is that our manipulation of tapping four versus one fingers also changed the number of fingers that are moving in space, potentially increasing the salience of the external representation. The increased salience of external representations then made our manipulation of motor outflow less effective in increasing the weight of information from motor-based representations. To address this, in Experiment 3 we manipulated motor effort, defined by the amount of force excerted by a muscle, without changing salience of external representation, by altering the amount of resistance in this task.

4. Experiment 3

As in Experiment 1, participants tapped with the index finger of both hands only, with two factors varying across trials. First, participants made tapping movements under two resistance conditions. In the *no resistance* condition, participants tapped the index finger between two rods, the same as Experiments 1 and 2. In the *resistance* condition, participants' index fingers were placed between a pair of springs, attached to the top and bottom rod of the apparatus respectively, such that the springs exert resistance on movements in both directions (see Fig. 3b). As a result, participants needed to make more motor effort in the resistance versus no resistance condition. Importantly, the index fingers tapped within the same vertical range in both resistance conditions, keeping the visuomotor information in an *external* frame of reference unchanged. Second, given the robust findings from prior literature and Experiments 1 and 2 demonstrating that total congruence results in more multisensory integration than total incongruence, we only ran external congruence and motor-based congruence trials (see Fig. 1c and d).

Based on results from Experiment 2, we predicted increased multisensory integration in external versus motor-based congruence condition in the no resistance trials. The dynamic weighting hypothesis would predict an increase in multisensory integration in the motor-based versus external congruence trials in the resistance condition.

4.1. Methods

4.1.1. Participants

We aimed to have adequate power ($1 - \beta = 0.8$) to detect a medium effect size (Cohen's $d = 0.5$), hence we planned to test 34 participants. Thirty-nine participants (20 male, ages 18–22 years, all right-handed), recruited from the General Psychology participant pool at the University of Delaware, took part in the experiment. Using the same exclusion criteria as in Experiments 1 and 2, three participants who showed poor bimanual coordination in the mirror box and one participant who was observed not paying attention to the mirror hand were excluded. As a result, 35 participants (17 male) were included in the analyses.

4.1.2. Apparatus, design and procedure

The apparatus in the no resistance condition was the same as Experiment 1 and Experiment 2. In the resistance condition, a different pair of wooden blocks was used. These blocks have the same dimensions as those in the no resistance condition, but each has a pair of springs (length: 49/64″ (1.94 cm), diameter: 27/64″ (1.07 cm)) attached to the upper and low rod respectively. The first coil of each spring is strapped to the rod and pointing to the opposite rod, such that each pair of springs meet in between the rods. One wooden block was placed 0″ to the right of the mirror, with the springs attached at 1.5″ right of the mirror. The other wooden block was positioned with the center of the rods 7.5″ left of the mirror, and the springs are attached at the center of the rod. In all trials, the index finger of the right (seen) hand is placed 1.5″ right of the mirror, and the hidden (left) index finger is placed 7.5″ left of the mirror.

The procedure in the no resistance condition was the same as in Experiment 1. In the resistance condition, participants placed the index fingers between the top and bottom springs, and tapped by pushing the springs. To prevent the fingers from detaching from the springs during tapping, the distal joint of participants' index fingers was strapped with the first coil of the top and bottom springs using medical tape. Participants were instructed to push the spring to the end during tapping to ensure full resistance from the springs and match the spatial range of the movements with the no resistance trials. Participants practiced movements in the resistance condition, and were able to appropriately time their movements in the resistance conditions (as assessed by visual inspection). Each of the four trial types was presented once in a random order. Each experiment session lasted about 25 min.

4.2. Analysis

Given that the hidden (left) hand posture (palm up) and mirror hand posture (palm down) were incongruent in all trials, we performed factorial linear mixed model analyses with selected congruence (external congruence and motor-based congruence) and resistance (resistance, no resistance) as within-subjects effects, and random intercepts for each participant.

4.3. Results

Overall, we excluded 23 out of 140 trials for the following reasons: unseen (left) finger drifted > 1″ (10 trials, 1 resistance trial), incorrected bimanual tapping (including unseen (left) hand rotating to face the body midline, 7), one of the springs detached from the medical tape (3), and experimenter error (3).

For proprioceptive shift, there was a significant main effect of congruence, $t(82.0) = 2.97$, $p = .004$, such that externally congruent movements ($M = 4.09$ cm, $SD = 3.65$ cm) resulted in more proprioceptive shift than motorically congruent movements ($M = 2.34$ cm, $SD = 2.90$ cm; see Fig. 7a). Contrary to the dynamic weighting hypothesis, the interaction of selected congruence and resistance was not significant, $t(83.0) = 0.14$, $p = .887$, indicating that the relative weighting of information from external and motor-based representations was not modulated by the motor effort from motor-based representations. The main effect of resistance was not significant (no resistance: $M = 3.06$ cm, $SD = 3.35$ cm, resistance: $M = 3.27$ cm, $SD = 3.59$ cm), $t(84.2) = 0.27$, $p = .787$.

As with Experiment 2, to account for the possible influence of involuntary finger drifts on proprioceptive shift, we did an additional analysis using the difference between the actual position of the finger (from the video recording) and the participant's response as the dependent variable. We found the same effects when taking into account this involuntary drift (see Supplemental Materials for results and analyses).

For ownership ratings, we only found a main effect of selected congruence, $t(79.6) = 5.84$, $p < .001$, such that external congruence ($M = 68.9$, $SD = 22.5$) resulted in higher ownership ratings than motor-based congruence ($M = 50.9$, $SD = 27.0$, see Fig. 7b). The main effect of resistance (no resistance: $M = 58.5$, $SD = 25.4$, resistance: $M = 60.3$, $SD = 23.9$), $t(80.9) = 0.28$, $p = .782$, and the interaction between selected congruence and resistance, $t(80.2) = 0.74$, $p = .459$, were not significant.

For both the hand (Fig. 7c) and finger (Fig. 7d) posture-matching questions, external congruence (hand: $M = 49.4$, $SD = 30.6$, finger: $M = 57.0$, $SD = 28.6$) resulted in significantly higher ratings than motor-based congruence (hand: $M = 41.0$, $SD = 30.1$, finger: $M = 41.2$, $SD = 30.9$), hand: $t(80.2) = 2.03$, $p = .045$, finger: $t(79.1) = 4.43$, $p < .001$. The main effect of resistance was not significant for both dependent variables, hand: $t(81.7) = 0.83$, $p = .409$, finger: $t(80.3) = 1.35$, $p = .182$ (hand-unresisted: $M = 46.7$, $SD = 33.5$, hand-resisted: $M = 43.7$, $SD = 28.4$, finger-unresisted: $M = 50.8$, $SD = 30.5$, finger-resisted: $M = 47.1$, $SD = 30.7$). The interaction between selected congruence and resistance was not significant, hand: $t(80.9) = 0.36$, $p = .716$, finger: $t(79.6) = 0.23$, $p = .815$.

For the analyses above, we excluded trials in which the hidden (left) index finger drifted > 1″. However, given that the index fingers were strapped with the springs in resistance trials, the hidden index finger was less likely to drift > 1″ than unresisted tapping trials, making our exclusion criterion unbalanced across trial types. In addition, drifts of the hidden index finger would stretch laterally, leading to less resistance in the vertical direction. Taking these factors into account, we did the same analyses with a more stringent exclusion criterion of involuntary drifts (> 0.5″) in resisted tapping trials, keeping the criterion as 1″ for unresisted trials. We found consistent results as above, that for all the dependent variables, external congruence trials resulted in more multisensory integration than motor-based congruence trials, regardless of the resistance condition. These results are presented in the Supplemental Materials.

In summary, for all of our dependent variables, we found significantly more multisensory integration with externally-congruent versus motorically-congruent movements, regardless of whether the movements were resisted or unresisted, i.e. regardless of the amount of motor effort. Importantly, these findings are consistent with Experiments 1 and 2 in general, indicating that information from representations in an external frame of reference is more strongly weighted than in a motor-based frame of reference, regardless of the amount of motor effort. Taken together, the results from both Experiments 2 and 3 demonstrate that the relative weighting of information from an external frame of reference and a motor-based frame of reference is not modulated by the motor outflow or effort represented in motor-based frame of reference.

5. General discussion

Using three experiments, we investigated relative weighting between visuomotor congruence represented in external and motor-based frame of references in multisensory integration. First, we found more multisensory integration, as indexed by proprioceptive shift and perceived ownership of the mirror hand, when visuomotor information was congruent versus incongruent in both external and motor-based frames of reference, consistent with previous findings that inputs from different modalities are more likely to be integrated if they are more similar (Holmes & Spence, 2005; Medina et al., 2015; Meredith & Stein, 1986; Meredith et al., 1987). The observed proprioceptive shift and changes in perceived hand and finger posture were towards the visual estimate of hand position, which is presumably more precise than proprioceptive estimate, consistent with the optimal weighting principle of multisensory integration (Ernst & Banks, 2002; van Beers et al., 1999).

Importantly, our study provided novel evidence regarding the relative weighting of information from external and motor-based representations in calculating visuomotor congruence during multisensory integration. By manipulating postural congruence and movement synchrony in the mirror box, we dissociated external and motor-based visuomotor congruence such that in externally congruent trials, visuomotor information was congruent in an external frame of reference but incongruent in motor-based frame of reference, and vice versa in motor-based congruence trials. We report three major findings. First, either external visuomotor congruence (with motor-based incongruence) or motor-based visuomotor congruence (with external incongruence) is sufficient for inducing multisensory integration. Second, when information from external and motor-based representations

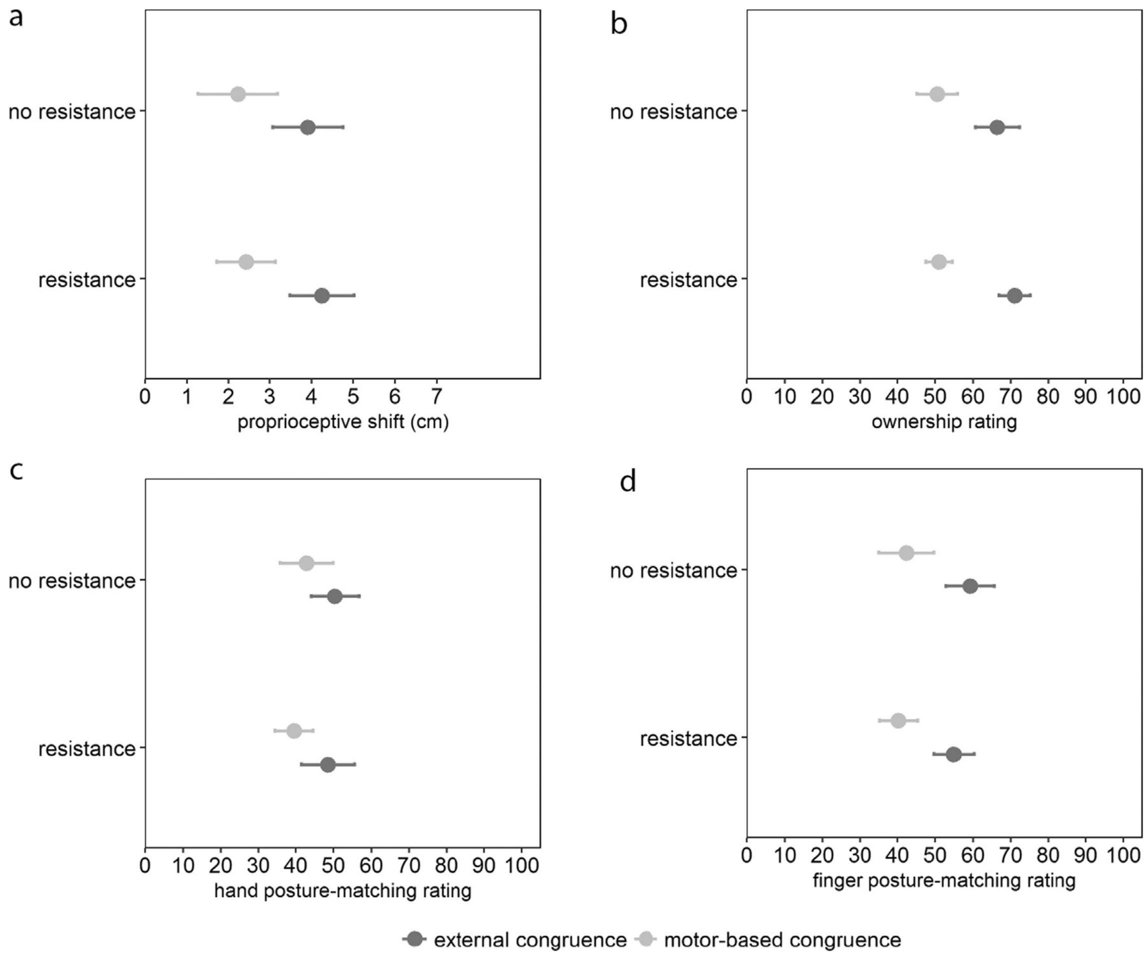

Fig. 7. Results of Experiment 3. (a) Proprioceptive shift. (b) Perceived ownership of the viewed hand. (c) Ratings on the hand posture-matching question. (d) Ratings on the finger posture-matching question. Greater values indicate more multisensory integration.

provide conflicting information regarding visuomotor congruence, more weight is placed on information from the externally-based representation, such that externally congruent trials (with motor-based incongruence) resulted in more multisensory integration than motorically congruent trials (with external incongruence). These effects were found in Experiment 1 and were replicated in Experiment 2 and 3. Finally, the relative weighting between external and motor-based frames of reference is not modulated by motor outflow or effort, as information from an external frame of reference is more strongly weighted regardless of whether participants tapped with one or four fingers (Experiment 2) and regardless of resistance during movement (Experiment 3). Taken together, these findings indicate that visuomotor information is represented in multiple frames of reference for multisensory integration. As a result, different representations with their own frame of reference have a unique estimate of visuomotor congruence. Given multiple estimates of visuomotor congruence from different representations, information needs to be weighted differentially. We found that information from the externally-based representation is more strongly weighted than the motor-based frame of reference.

Previous models of multisensory integration have focused on the weighting between information from different sensory modalities. For example, the optimal weighting principle proposes that information from different modalities are weighted as a function of their relative precision (Ernst & Banks, 2002; Ernst & Bülthoff, 2004; van Beers et al., 1999). Our results demonstrate that in multisensory integration, not only inputs from different *modalities*, but also information from representations with different *frames of reference*, is differentially weighted. We propose a possible mechanism for how information from multiple representations is integrated, utilizing causal inference models for multisensory integration (e.g. Körding et al., 2007; Shams & Beierholm, 2010). In these models, the system first estimates the likelihood that inputs from different modalities are caused by the same source. Inputs that are more similar to each other are more likely to be considered as representing a common cause and be integrated into a unified percept. The causal inference model has also been used to explain embodiment observed in various body illusions (Kilteni, Maselli, Kording, & Slater, 2015; Samad, Chung, & Shams, 2015).

In prior studies of multisensory integration, the similarity between inputs from different modalities, and thus the likelihood of a common cause, is calculated based on a single frame of reference. We propose that instead of calculating the overall likelihood all in one step, the likelihood of observing the current visual and motor information in *each* frame of reference is calculated separately. For example, in external congruence trials, the likelihood that visual and motor information is observed as congruent in external frame of reference ($P_{external}$(common cause)) from externally-based representations and in motor-based frame of reference ($P_{motor\text{-}based}$(common cause)) from motor-based representations is calculated. We found that information from an external representation is more strongly weighted that information from a motor-based representation. Therefore, the overall likelihood $P_{overall}$(common cause), which reflects the overall visuomotor congruence, should be calculated as a weighted sum of likelihood from external and motor-based frames of reference: $P_{overall}$(common cause) = $w_eP_{external}$(common cause) + $w_mP_{motor\text{-}based}$(common cause), where w_e and w_m represent the weight placed on information from external and motor-based frame of reference respectively. This allows for causal inference models to integrate information from multiple spatial representations, differentially weighting information – not just from specific modalities – but from specific representations.

Why would information from an external frame of reference be more strongly weighted than information from a motor-based frame of reference (i.e. $w_e > w_m$), regardless of motor outflow or effort? Prior studies have shown that information about movements in external space, instead of motor-based information centered on muscles or joints, dominates movement coordination (Brandes et al., 2016; Heed & Röder, 2014; Mechsner et al., 2001). For example, in a bimanual finger oscillation task, movements are typically more coordinated when the movements are symmetric (the index fingers simultaneously move towards or away from the body midline) versus parallel (the index fingers move simultaneously in the same direction in external space). Mechsner et al. (2001) instructed participants to do this task with the hands in opposing postures (palm up vs. palm down), such that when the homologous muscles on both hands are co-activated (bimanual symmetry in a motor-based frame of reference), movements were asymmetric in an external frame of reference, and vice versa. They found that bimanual coordination was influenced by bimanual symmetry in an external frame of reference, regardless of symmetry in a motor-based frame of reference, indicating a dominant role of external information in movement regulation. The authors speculated that voluntary actions are encoded as simple perceptual goals, with "perceptual goals" encoded in external space. Given prior evidence, we speculate that movements are preferentially encoded in an external frame of reference, presumably because individuals rely more on vision to monitor movements and visual processes take place in an external frame of reference (Brandes et al., 2016). Our study provides novel evidence that this weighting towards external representations occurs, not only for motor tasks, but also in multisensory integration.

In contrast to our findings, a previous study on the rubber hand illusion found that an internal somatotopic frame of reference (or hand-centered frame of reference) is more strongly weighted than an external frame of reference in visuotactile integration (Costantini & Haggard, 2007, see also Holle, McLatchie, Maurer, & Ward, 2011; Ide, 2013). Based on the results, the authors concluded that "the rubber hand illusion depends on a pre-existing body representation, with its own frame of reference, distinct from external spatial representation" (Costantini & Haggard, 2007). We speculate that the more strongly weighted representation depends on the modality of sensory inputs. Visuomotor information might be primarily represented in an external frame of reference, as movements are typically guided by vision. Visuotactile information, on the other hand, might be processed differently given its passive nature. In the rubber hand illusion, when seeing the rubber hand stroked and passively feeling strokes on the actual hand, without knowing the actual source of the felt strokes, the individual needs to infer if the viewed strokes are the causes of the felt strokes. To do this, and to judge if the rubber hand is his own hand, the individual needs to compare the viewed strokes and the rubber hand relative to his own body, which involves referencing a self-specific, somatotopic frame of reference. As a result, information from a somatotopic frame of reference may be more likely to dominate visuotactile integration.

Our findings of parallel and weighted representations in external and motor-based frames of reference are consistent with a framework proposed from studies on goal-directed movements (Mueller & Fiehler, 2016; Sober & Sabes, 2005; Tagliabue & McIntyre, 2014). In goal-directed movements (e.g. reaching), accurately computing movement vector (i.e. direction and distance) from the hand to the target object is crucial. In an example discussed in Tagliabue and Mclntyre's (2014), an individual is striking a nail held in the left hand with a hammer held in the right hand. In this situation, the movement vector from the hammer to the nail can be computed from visual information in an external frame of reference (external vector), or from proprioceptive information of the two hands in motor-based frame of reference (motor-based vector). The framework proposes that the brain minimizes errors in movement vector by weighting the external vector and motor-based vectors. This framework thus shares the major point with our study that spatial representations with different frames of reference are processed in parallel with a weighting mechanism. However, in the framework of goal-directed movements, representation in each frame of reference is unimodal (e.g. visual information is represented in external frame of reference), and information represented in each frame of reference is a unimodal estimate of movement vector. In our study, representation in each frame of reference is multisensory (i.e. visuomotor congruence), and information represented in each frame of reference is an estimate of *how congruent* visual and motor information is. We thus provide novel evidence that not only unimodal estimates, but also congruence between unimodal estimates, is represented and weighted across multiple frames of reference in multisensory integration.

In summary, we used the mirror box illusion to investigate the relative weighting of external and motor-based frames of reference in calculating visuomotor congruence during multisensory integration. We found external congruence resulted in more multisensory integration than motor-based congruence, regardless of motor outflow and effort from a motor-based frame of reference. These findings provided evidence that external congruence plays a dominant role in calculating visuomotor congruence in multisensory integration.

Author contributions

All authors developed the study question and designed the experiments. Y. Liu performed data collection, analyses and prepared the manuscript draft. J. Medina supervised data analyses and provided critical revisions to the manuscript. All authors approved the final version of the manuscript.

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Appendix A

Ownership questions

1. It felt as though the hand in the mirror is my left hand.
2. It seemed like the hand in the mirror was part of my body.
3. It seemed like I was looking directly at my own left hand.
4. It seemed like my left hand was in the same location as the hand in the mirror.
5. It felt like the movements of the fingers I viewed were the movements I felt on my left hand.

Hand posture-matching question

6. It felt as though my left hand was palm down.

Finger posture-matching question

7. It felt as though the index finger/fingers on my left hand were palm down.

Appendix B. Supplementary material

As mentioned in the main text, additional analyses and results are presented in a supplemental file. In addition, all of the raw data in this manuscript can be found on the Open Science Framework, see https://osf.io/s7wtu/?view_only=c195e4fa0cef4d2d95dd4b29cd48099c. Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.cognition.2018.01.005.

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