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Telling the Right Hand From the Left Hand: Multisensory Integration, Not Motor Imagery, Solves the Problem

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Abstract

Judging the laterality of a hand seen at unanticipated orientations evokes a robust feeling of bodily movement, even though no movement is produced. In two experiments, we tested a novel hypothesis to explain this phenomenon: A hand's laterality is determined via a multisensory binding of the visual representation of the seen hand and a proprioceptive representation of the observer's felt hand, and the felt "movement" is an obligatory aftereffect of intersensory recalibration. Consistent with the predictions implied by such a cross-modal mechanism, our results in Experiment 1 showed that manipulating observers' selective attention can evoke illusory feelings of movement in the "wrong" hand (i.e., the hand whose laterality does not match that of the stimulus). In Experiment 2, these illusions were readily extinguished in conditions in which binding was predicted to fail, a result indicating that cross-modal binding was necessary to produce them. These results are not explained by imagery, a mechanism widely assumed to account for how hand laterality is identified.

Keywords

motor processes, perception, human body, decision making

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The feeling of bodily movement (or motor awareness) is a conscious certification that one is physically performing an action. Surprisingly, judging the laterality of a hand seen at an unanticipated orientation causes people to feel as though they are moving their own hand into the shape and orientation of the seen hand. Despite being illusory, this feeling of movement is closely related to its physically evoked counterpart: Real and illusory feelings of movement seem to be sensitive to the same biomechanical constraints (Ionta & Blanke, 2009; Ionta, Fourkas, Fiorio, & Aglioti, 2007; Parsons, 1987, 1994; Shenton, Schwoebel, & Coslett, 2004), and both have a neural basis in brain systems associated with the planning and execution of physical movement (Bonda, Petrides, Frey, & Evans, 1995; de Lange, Helmich, & Toni, 2006; Kosslyn, DiGirolamo, Thompson, & Alpert, 1998; Parsons et al., 1995). This remarkable phenomenon has presented a long-standing conundrum: What is it about seen hands and the information-processing demands of judging laterality that causes these illusory feelings of movement?

For more than 35 years, this question has been interpreted exclusively on the basis of one concept: *imagery*. Such interpretations draw on a related phenomenon that occurs in mirror/same judgment tasks, in which observers judge whether two unfamiliar objects seen at disparate orientations are identical or mirror reflections of each other. To make this judgment, observers seem to use a *rotate-then-match* scheme, whereby they mentally rotate an image of one object into alignment with an image of the other object before judging whether the two images match (Shepard & Cooper, 1982; Shepard & Metzler, 1971). Because right and left hands are mirror symmetric, Cooper and Shepard (1975) hypothesized that the illusory feelings of movement evoked by hand-laterality judgments might result from a mental rotation process operating on an internal representation of each hand.

The *hand-imagery hypothesis* posits that in hand-laterality judgment tasks, seen hands are represented holistically and are not analyzed at the level of individual features. Consequently, observers' mental images of their own hands have to be spatially transformed (i.e., mentally rotated) into the stimulus's orientation to enable matching. Although this account is widely accepted as an explanation for the illusory feelings of

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movement evoked by hand-laterality judgments (e.g., Barsalou, 2008; Decety & Grezes, 1999; Jeannerod, 2001; Jeannerod & Frak, 1999; Kosslyn, Ganis, & Thompson, 2001; Shepard & Cooper, 1982), its assumption of a holistic hand representation has presented a perplexing paradox.

On each trial in the standard hand-laterality judgment task, participants see a naturalistic image of a hand at a variable picture-plane orientation and judge whether it is a left hand or a right hand. If, as the hand-imagery hypothesis assumes, participants employ the rotate-then-match scheme, then they should have to rotate mental images of their own hands before they can determine the laterality of the seen hand (which is assumed to be represented holistically). The hand-imagery hypothesis predicts that response times (RTs) should systematically increase with the angular disparity between the orientation of the stimulus and a canonical orientation (assumed to be the upright position). Results from hand-laterality judgment tasks are consistent with this prediction, but the obtained RTs have another, unusual property. The function relating change in RT to the orientation of the stimulus is asymmetric: RTs at corresponding clockwise and counterclockwise orientations (relative to the canonical vertical orientation) are not equal, and the asymmetries between RTs for left-hand stimuli at clockwise and counterclockwise orientations are mirror reflections of the asymmetries between RTs for right-hand stimuli at clockwise and counterclockwise orientations (Sekiyama, 1982).

This pattern of results is indicative of a *correct-hand effect*, whereby the stimulus evokes a feeling of movement in the observer's "correct" hand. That is, if the stimulus is an image of a left hand, it evokes a feeling of movement in the observer's left hand, and if the stimulus is an image of a right hand, it evokes a feeling of movement in the observer's right hand; the mirror-reversed RT profiles for left-hand and right-hand stimuli arise from the correspondingly mirror-reversed biomechanical constraints on right-handed and left-handed movements (Parsons, 1987, 1994; Parsons et al., 1995). This pattern of results suggests that a seen hand's laterality is correctly identified before, rather than after, observers execute the mental rotation that the hand-imagery hypothesis predicts should precede identification; in other words, observers seem to execute a *match-then-rotate* scheme, rather than a rotate-then-match scheme.

If a seen hand is represented holistically, as the hand-imagery hypothesis assumes, then mental rotation should be required to determine its laterality. The correct-hand effect rules out this proposed link between imagery and laterality judgments, but it also poses a paradox. If laterality is determined via a feature-based analysis of the hand representation (i.e., without imagery), then why should illusory feelings of movement occur in hand-laterality judgment tasks at all? Researchers have speculated that observers might use simulated hand rotations to confirm their laterality judgments (Gentilucci, Daprati, & Gangitano, 1998; Parsons, 1987, 1994; Sekiyama, 1982), but these speculative accounts have failed to address the conundrum of why a feature-based representation of the seen hand should be linked to illusory movements at all. In this article, we propose a novel resolution of this conundrum: that illusory feelings of movement are generated as an obligatory aftereffect of feature-based analysis of seen hands.

In the hand-laterality judgment task, at the onset of the stimulus, the observer has simultaneous access to sensory representations of hands from different modalities: the visual representation of the seen hand depicted by the stimulus and the proprioceptive representations of the observer's own, felt hands. We hypothesized that observers exploit this multimodal redundancy in hand representations to perceptually identify the seen hand's laterality—a possibility suggested by neurophysiological research (Graziano, 1999; Graziano, Cooke, & Taylor, 2000) and studies on amputees (Funk & Brugger, 2008; Nico, Daprati, Rigal, Parsons, & Sirigu, 2004; Silva et al., 2011).

We assume that cross-modal integration is feature based rather than holistic. Physically producing articulated hand movements requires access to the proprioceptive representation of the hand, its individual digits, and the articulated joints of each digit (i.e., a detailed, part-based spatial representation). Visually guiding such articulations entails a structured representation of the seen hand. For example, when one reaches to grasp an object with a precision grip, the seen positions of the thumb and the index finger have to be paired with the corresponding felt positions of these two digits in order for visual feedback to be translated into digit-specific movement corrections. Apart from its role in the control of movement, an "apples-to-apples" pairing of hand features across modalities is crucial in the face of systematic intersensory discrepancies: Multisensory integration enables the adaptive recalibration of inputs from one sensory modality using reference values from other modalities, a process that can produce pronounced behavioral aftereffects (Harris, 1965; Held, 1965) and perceptual illusions (Botvinick & Cohen, 1998; Ehrsson, Holmes, & Passingham, 2005; Ehrsson, Spence, & Passingham, 2004).

We propose the following account of multisensory laterality identification. On each trial of hand-laterality judgment tasks, the observer automatically pairs features of the seen hand with the corresponding features of each of his or her own, felt hands. The observer evaluates these feature pairings to determine which felt hand is congruent with the seen hand. Evaluation is assumed to be a constraint-satisfaction process rather than a single test across all features of the felt and seen hands to determine whether they match (Botvinick & Cohen, 1998; Pouget, Deneve, & Duhamel, 2002). When the degree of congruence between the seen hand and one of the observer's felt hands exceeds a decision criterion on a critical subset of feature dimensions, the representations of the two hands are *bound* together (Epstein, 1975; Radeau & Bertelson, 1977). Binding automatically initiates a sensorimotor recalibration to resolve conflicts between other feature dimensions of the bound seen and felt hands, such as their discrepant orientations relative to the observer's body. The somatomotor recalibrations to align the bound felt hand with the seen hand are experienced as a feeling of movement. The laterality-judgment response is delayed until these intermodal conflicts are suitably resolved; hence, the RT reflects both the orientation and the laterality of the seen hand, a result consistent with the correct-hand effect.

This *hand-binding hypothesis* predicts that (a) laterality is identified via a cross-modal analysis of a seen hand's features (rather than a holistic hand representation) and (b) the illusory feelings of movement are an aftereffect of cross-modal binding based on this feature-based analysis. We tested these two predictions in Experiments 1 and 2, respectively, by using the asymmetry in RT profiles as an index of the illusory feelings of movement.

Experiment 1

Seen hands are rich in visual detail. The hand-binding hypothesis assumes that visual detail is required only to ensure the extraction and pairing of relevant seen and felt features. For example, the skin covering a hand has visual features, such as color and intricate patterns of lines, that have no direct proprioceptive equivalents (see Fig. 1a). Nonetheless, these visual patterns indirectly specify one pairable feature: the seen hand's orientation in depth—for example, whether the palm or the back of the hand is being viewed. Because digits are flexed toward the palm of the hand rather than toward the back of the hand, the three-dimensional shape of an articulated gesture also specifies the view (i.e., perspective) of the hand independently of the hand's visual patterns.

In Experiment 1, we exploited the critical relationship between shape and the visual patterns in the images of the unarticulated hand gestures shown in Figure 1a. Without these visual patterns, the shapes of these hand images do not convey view information. Because the shapes of the palm-up and palm-down views of the same hand are mirror symmetric, and the palm-up view of one hand has the same shape as the

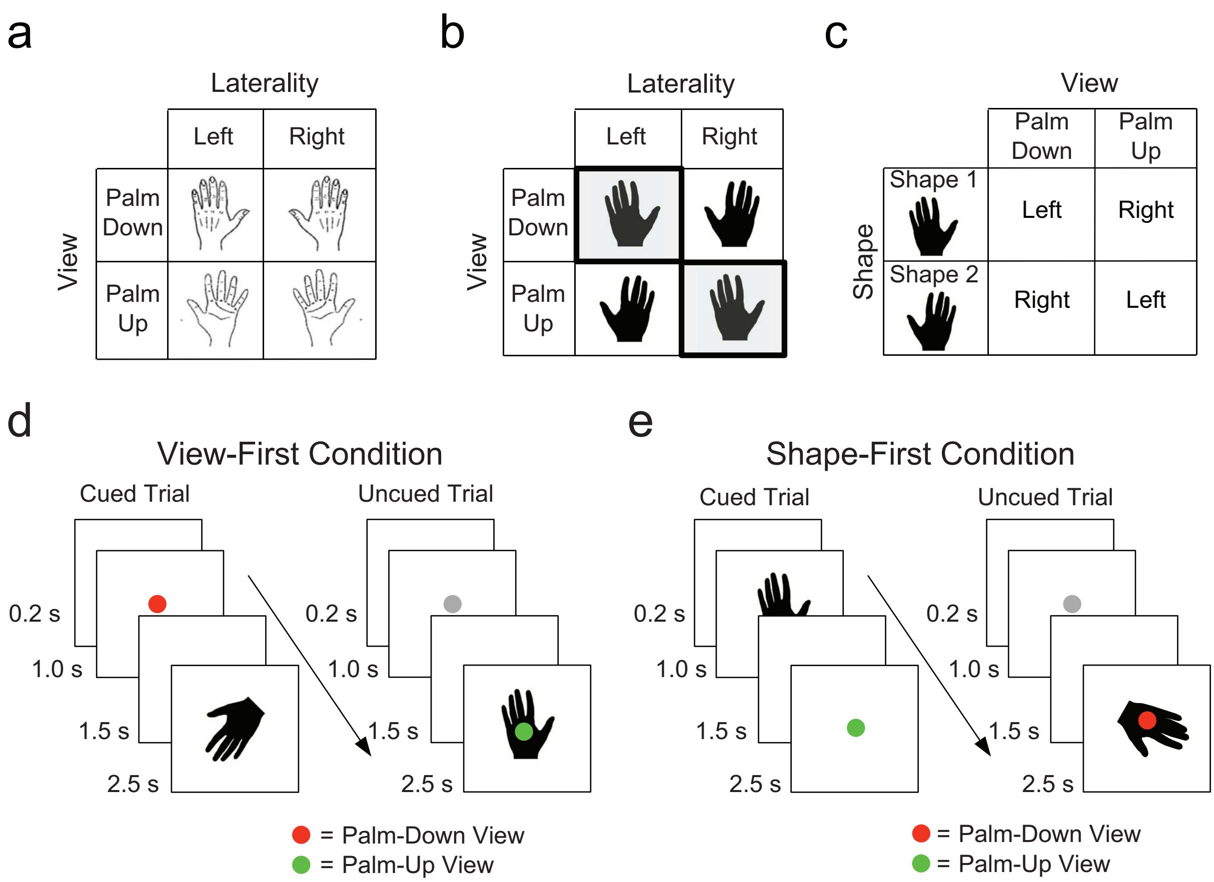

Fig. 1. Explanation of the stimuli and trial sequences in Experiment 1. The visual patterns of hands seen in palm-up and palm-down positions indicate their laterality (a); to create stimuli for our experiment, we used black silhouettes to depict palm-up and palm-down views of left and right hands (b), thereby eliminating the visual patterns that would signal laterality. Note that a right hand and a left hand have the same shape when one is seen from the palm-up perspective and the other is seen from the palm-down perspective (b). Shape and view were treated as independent feature dimensions that, when combined, constrained a seen hand's laterality (c). On cued trials in the view-first condition (d), a blank screen was presented for 0.2 s, followed by a colored dot indicating the view of the forthcoming stimulus. After an interstimulus interval, a hand shape was presented. On uncued trials of this condition (d), after the 0.2-s blank screen, a gray dot was presented, followed by an interstimulus interval and then the presentation of a hand shape with a colored dot indicating its view. On cued trials in the shape-first condition (e), after the 0.2-s blank screen, a hand shape was presented; after an interstimulus interval, a colored dot indicating its view appeared. Uncued trials in this condition (e) were identical to those in the view-first condition. On each trial, participants pressed a response key with their left hand to indicate that the stimulus depicted a left hand or pressed a response key with their right hand to indicate that the stimulus depicted a right hand.

palm-down view of the other hand (diagonals in Fig. 1b), we treated shape (i.e., interdigit positions) and view (i.e., orientation in depth) as independent feature dimensions that, when combined, constrained a hand's laterality: Stimuli that differed on both dimensions had the same laterality (diagonals of Fig. 1c), whereas stimuli that matched on only one dimension had different lateralities (rows and columns of Fig. 1c).

If a seen hand is to be bound to the correct (matching) felt hand, both the shape and the view dimensions of the two hands have to be congruent. This requirement should make the correct-hand effect vulnerable to the influence of attention. Feature pairing requires a heteromodal integrator to receive converging sensory inputs from different modalities (Stein & Meredith, 1993). Therefore, limiting the integrator's access to shape or view information from either sensory modality should affect the accuracy of the binding decision. To test this prediction, we manipulated visual feature-based attention, treating it as a feature-selective gating mechanism.

To equate the visual appearance of all stimuli, we used black silhouettes to depict hand shapes (see Fig. 1c) and signaled the missing visual patterns of each hand with a red or green dot. A red dot indicated a palm-down view of the hand, and a green dot indicated a palm-up view. (Before the experiment began, we trained participants to readily recognize this color-to-view mapping by sticking actual colored dots on their hands.) We modified the standard paradigm of hand-laterality judgment tasks by using these stimuli and varying participants' task set in two independent conditions: a view-first condition (Fig. 1d) and a shape-first condition (Fig. 1e). All participants were assigned to one of the two conditions. During the task, participants' own hands were kept out of sight in a palm-down position.

Each condition consisted of *cued* and *uncued* trials that occurred with (approximately) equal frequency. On the cued trials in the view-first condition (left side of Fig. 1d), participants first saw a colored dot (red or green) indicating the view (palm up or palm down) of the forthcoming test stimulus. After a brief interstimulus interval, a test stimulus depicting one of two hand shapes (without view information) was presented at a variable picture-plane orientation. The two hand shapes are shown in Figure 1c; we refer to the shape shown at the top as Shape 1 and to the shape shown at the bottom as Shape 2. In the shape-first condition, the order of stimulus presentation on cued trials was reversed (left side of Fig. 1e): The advance cue was a hand shape, and the subsequent test stimulus indicated the view of that hand. On the uncued trials in both conditions (right sides of Figs. 1d and 1e), the advance cue (a gray dot) conveyed no information about the view of the hand, and the subsequent test stimulus both depicted the hand shape and contained the colored dot indicating the view.

On each trial, across conditions, participants had to combine view and shape information, whether it was presented serially (i.e., on cued trials) or simultaneously (i.e., on uncued trials), to identify the laterality of the hand. Participants pressed a response key with their left hand to indicate that a stimulus depicted a left hand and pressed a response key with their right hand to indicate that a stimulus depicted a right hand. Stimuli on uncued trials were identical in the shape-first and view-first conditions. Even though shape and view information were presented simultaneously on uncued trials, we assumed that participants would selectively attend to these features in the same sequence in which they were presented on cued trials. Given this assumption, the hand-binding hypothesis makes the following predictions for the uncued trials.

In the view-first condition, view-related intersensory conflicts should be resolved *before* the seen hand and the felt hand are paired on the shape dimension. Therefore, congruence between the seen hand and one of the felt hands on the shape dimension should lead to a correct binding decision for all stimuli. The asymmetric RT profiles for left-hand and right-hand stimuli (irrespective of view and shape) should be mirror reversed, a result consistent with the correct-hand effect.

In the shape-first condition, shape information should be processed before view information. Without view information, a hand shape has ambiguous laterality. However, eliminating view information reduces the number of conflicting cross-modal features. Because the participant's own hand is in a palm-down position, each seen hand shape should be congruent with the shape of a unique felt hand (left column of Fig. 1c). Consequently, the seen hand shape should be bound to this congruent felt hand. Because of this premature binding (i.e., binding that does not incorporate the view dimension), stimuli that have identical shapes but are seen from different views should be bound to the same felt hand, even though these stimuli differ in their laterality (rows of Fig. 1c). Thus, the RT profiles for these stimuli should *not* be mirror reversed, in violation of the correct-hand effect. The resulting *wrong-hand effect* for the palm-up stimuli would not necessarily result in incorrect laterality judgments. When the binding enters awareness, participants can evaluate whether the view of the stimulus corresponds to a palm-down or a palm-up view and can respond accordingly with either the bound hand or the opposite hand.

Method

Subjects. Twenty-four right-handed participants (19 female, 5 male; mean age = 18.9 years, *SD* = 1.2) took part in the experiment in return for course credit. Twelve participants were randomly assigned to each of the two conditions.

Stimuli. Stimuli were generated using MATLAB (The MathWorks, Natick, MA) and the Psychophysics Toolbox (Brainard, 1997) and were displayed at the center of a 32-cm × 42-cm LCD monitor (resolution of 1,152 × 864 pixels) at a viewing distance of 78.5 cm. The hand shapes were bounded by a rectangle subtending approximately 8.8° × 10.3° of visual angle; the colored dots that specified view information had a diameter of 0.7° of visual angle. Hand shapes were presented in three orientations: −120° (counterclockwise orientation), 0° (upright orientation), and +120° (clockwise orientation). These orientations were jittered uniformly and randomly within the range from −5° to +5° on each stimulus presentation.

Trials. Right-hand and left-hand stimuli in palm-up and palm-down views occurred equally often and were each presented equally often at each of the three orientations (17 repetitions on cued trials and 18 repetitions on uncued trials), for a total of 420 trials. A pseudorandom trial ordering specified by a maximum length sequence (Buracas & Boynton, 2002) ensured that the presentation order of the 12 stimulus types was counterbalanced across trials. The time courses for all trial types are shown in Figures 1d and 1e.

Procedure. Participants were instructed to judge on each trial whether the stimulus was a right hand or a left hand. They were told to exploit the advance cue when it was available and to avoid using verbal descriptions of the hand shapes. The importance of speed and accuracy in performing the task was strongly emphasized. Participants sat in a dark room with their heads secured on a chin rest with a head restraint. The computer keyboard participants used to make responses was positioned at the base of the chin rest so that participants could not see their own hands. Participants made responses using the index fingers of their left and right hands. Test stimuli were presented for only 2.5 s; a trial ended at the offset of the test stimulus if no response was made. After making a response, participants received immediate auditory feedback indicating whether it was accurate. Accuracy scores were displayed every 30 trials. Before the main experiment began, participants completed 24 practice trials with the experimenter present.

Results and discussion

Participants whose overall level of accuracy was less than 85% (1 participant in the view-first condition and 2 participants in the shape-first condition) were excluded from analysis. (For the mean level of accuracy for each type of stimulus in the two conditions, see Fig. S1 in the Supplemental Material available online.) For each of the 12 trial types (left- and right-hand stimuli in the palm-up and palm-down views at the three orientations), data for the first two correctly answered trials were excluded from analysis to allow for task-set induction. The harmonic mean of each subject's RTs on the remaining correctly answered trials was used as that subject's RT estimate. Figure 2 shows the mean RT profiles for stimuli with the same shape but different views for the uncued trials in each of the two conditions.

In the view-first condition (Figs. 2a and 2b), the mean RT profiles for all stimuli were asymmetric about the 0° orientation, and the asymmetries for left-hand stimuli were mirror reversals of the asymmetries for right-hand stimuli, irrespective of shape and view. A 3 (orientation: −120°, 0°, 120°) × 2 (view: palm up, palm down) × 2 (shape: 1, 2) repeated measures analysis of variance (ANOVA) confirmed a three-way interaction of orientation, view, and shape, $F(2, 20) = 17.69$, $p < .0001$. There were main effects of orientation, $F(2, 20) = 37.20$, $p < .0001$, and view, $F(1, 10) = 24.50$, $p < .001$. The effect of shape was not statistically significant, $F(1, 10) = 2.64$, $p > .13$. These results are consistent with the correct-hand effect found in previous studies and validate our novel paradigm and stimuli.

In contrast, the RTs in the shape-first condition (Figs. 2c and 2d) did not exhibit the same mirror reversals. The RT profiles were asymmetric about the 0° orientation, but RTs for the palm-up right-hand and left-hand stimuli (dotted lines) exhibit the same asymmetry as the RTs for stimuli depicting palm-down views (solid lines) of the opposite (i.e., wrong) hand. The three-way interaction of orientation, view, and shape in the shape-first condition was not statistically significant, $F(2, 18) = 1.61$, $p > .22$. There were main effects of orientation, $F(2, 18) = 20.55$, $p < .0001$; view, $F(1, 9) = 53.40$, $p < .0001$; and shape, $F(1, 9) = 7.43$, $p = .02$. The only significant interaction was between orientation and shape, $F(2, 18) = 9.40$, $p = 0.002$. These results are consistent with a correct-hand effect for palm-down stimuli and a wrong-hand effect for palm-up stimuli.

The fact that the emergence of the correct-hand effect on the uncued trials depended on which features of the stimuli observers attended to is consistent with a feature-based analysis of the hand representations. If the attentional manipulation had failed, the RT profiles for uncued trials in the view-first and shape-first conditions would have been equivalent, because the stimuli on the uncued trials in the two conditions were identical. Furthermore, if the seen hands in hand-laterality judgment tasks are represented holistically, then attending to shape before view, as participants did in the shape-first condition, should produce illusory feelings of movement in both hands or neither hand, because each shape is compatible with some view of each hand. In this case, the RT asymmetries and their mirror reversals would be eliminated, contrary to the obtained results.

Experiment 2

In this experiment, we turned to the question of why illusory feelings of movement occur at all in the hand-laterality judgment task. According to the hand-binding hypothesis, successful binding is a necessary precondition for the illusory feelings of movement. To test this assumption, we manipulated participants' attention to proprioceptive inputs by requiring them to judge the view of a seen hand shape of known laterality.

On each trial, participants were presented with an advance cue specifying the laterality of the forthcoming test stimulus and the hand the participant should use to respond on that trial; participants were instructed to prepare the cued hand to respond rapidly to the forthcoming test stimulus. After a short delay, a test stimulus depicting only a hand shape was presented; each hand-shape stimulus was presented in one of five possible orientations (–120°, –60°, 0°, 60°, or 120°). Participants judged

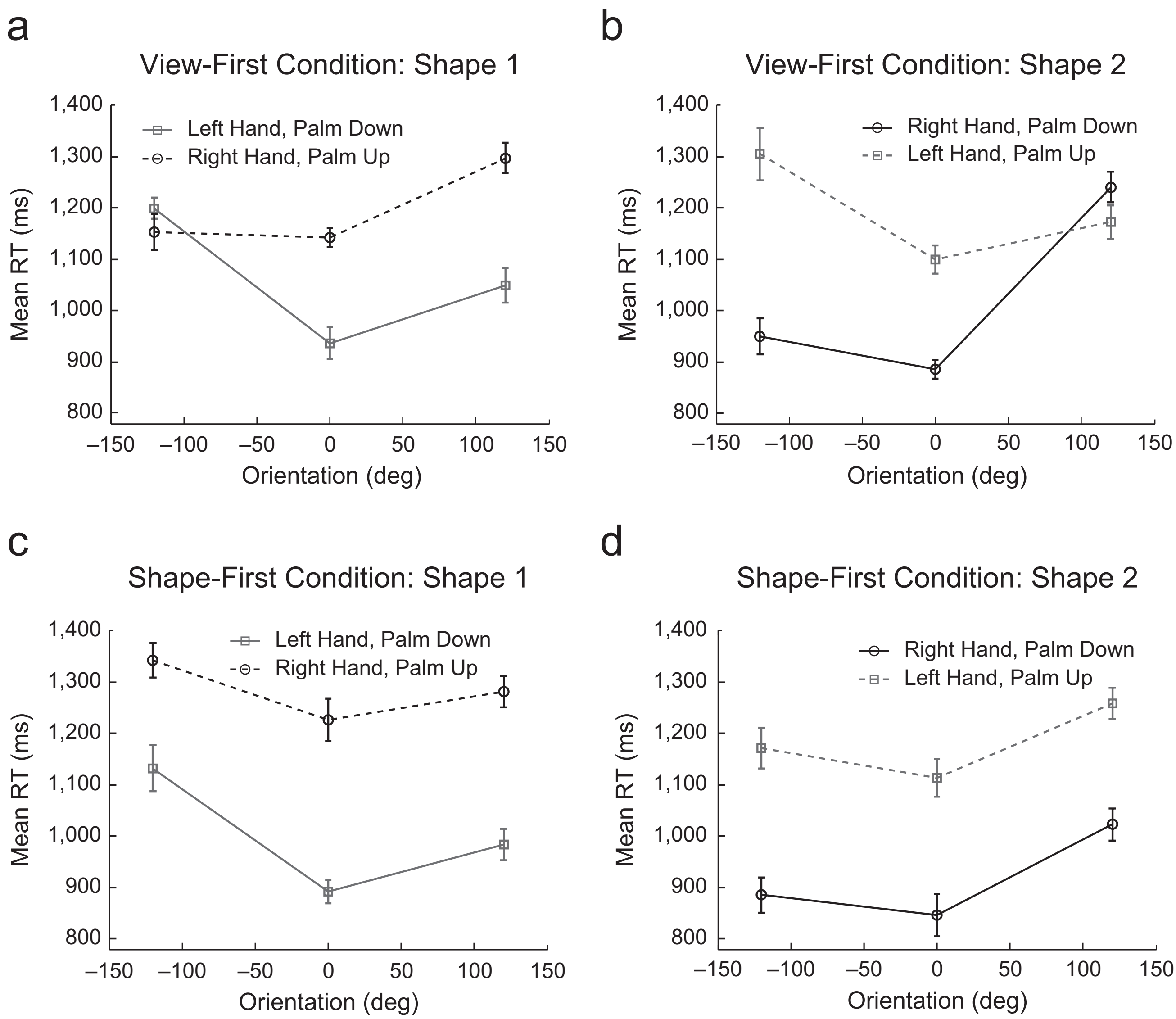

Fig. 2. Results for the uncued trials of Experiment 1. The graphs show mean response times (RTs) for stimuli with the same shape but different views. The graphs in the top row show RTs for (a) Shape 1 and (b) Shape 2 stimuli in the view-first condition, and the graphs in the bottom row show RTs for (c) Shape 1 and (d) Shape 2 stimuli in the shape-first condition. Solid lines indicate RTs for palm-down stimuli, and dashed lines indicate RTs for palm-up stimuli; black lines indicate RTs for right-hand stimuli, and gray lines indicate RTs for left-hand stimuli. Error bars represent within-subjects errors of the mean (Cousineau, 2005).

whether the test stimulus depicted the palm-up or the palm-down view of the hand. Figure 3a shows the time course for right-hand and left-hand trials; Figure 3b shows the relationships among laterality, shape, and view and the five possible stimulus orientations.

We hypothesized that the advance preparation of the response hand would induce observers to selectively attend to that hand's proprioceptive representation while suppressing inputs from the other (nonresponding) hand. According to the hand-binding hypothesis, stimuli with shapes congruent to the palm-down response hand should lead to successful binding, but stimuli with shapes corresponding to the palm-up view of the response hand should not, even though the palm-up stimuli are congruent with the palm-down view of the nonresponding (unattended) hand. Given that successful binding is postulated to be necessary for the subsequent illusory feeling of movement, we expected that the RT profiles for all palm-down stimuli would conform to the characteristic asymmetric-RT signature of illusory feelings of movement, but the RT profiles for all palm-up stimuli, for which binding was predicted to fail, would not.

Method

Subjects. Twelve right-handed participants (9 female, 3 male; mean age = 18.9 years, *SD* = 0.9) took part in this experiment in return for course credit. Six participants were randomly assigned to each of two key-response mappings (described in the next paragraph).

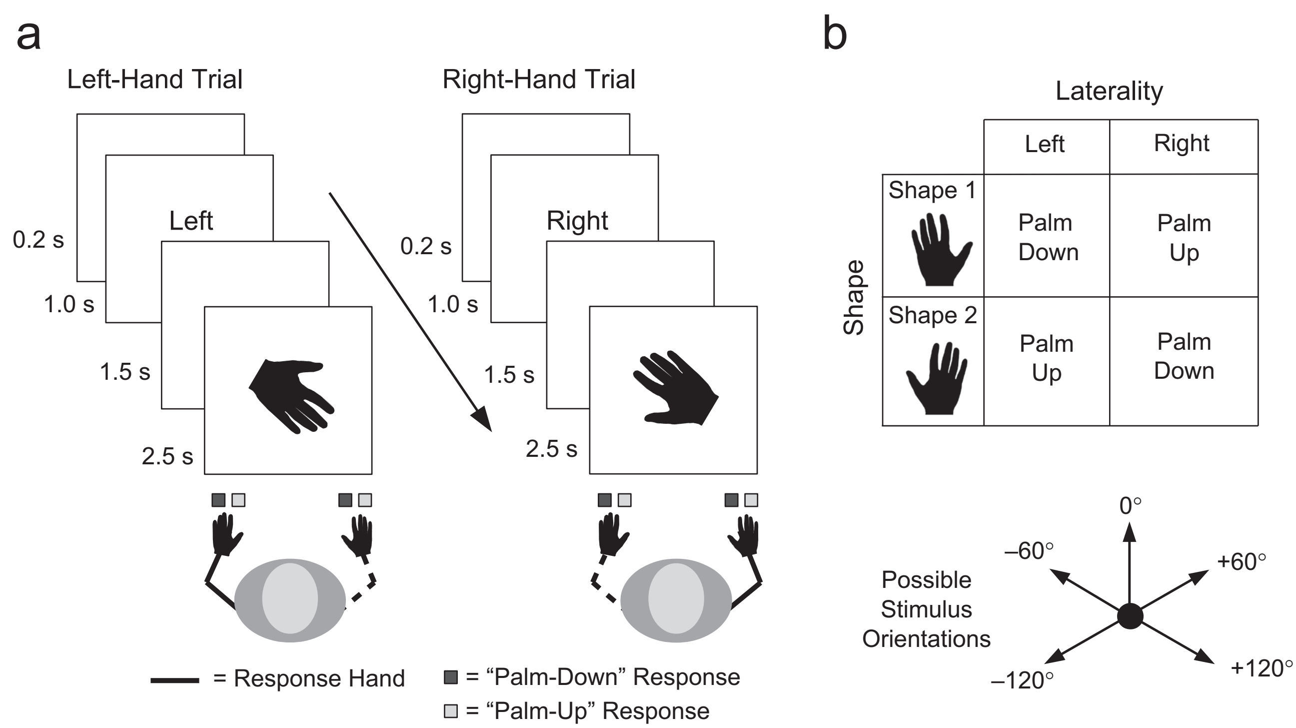

Fig. 3. Trial structure and paradigm for Experiment 2. Examples of left-hand and right-hand trials are shown in (a). On each trial, a 0.2-s blank screen was followed by a 1-s advance cue indicating both the hand the participant should use to respond and the laterality of the hand that would be presented in the test stimulus. After a 1.5-s interstimulus interval, a test stimulus consisting of a silhouette of a hand was presented for 2.5 s. Using the response hand specified by the cue, participants had to press one of two response keys to indicate whether the test stimulus was in a palm-up or palm-down position. The factorial design of the stimuli and their five possible orientations are illustrated in (b).

Stimuli and procedure. Apart from the modifications we have already described, the method and procedure in Experiment 2 were identical to those in Experiment 1. Right-hand and left-hand stimuli in the two hand shapes were presented with equal frequency. Each of these stimuli types was presented at each of the five possible orientations on 20 to 22 trials each, for a total of 420 trials. Participants were instructed to judge whether each stimulus depicted the palm-up or palm-down view of the cued hand. Two side-by-side response keys were assigned to each hand: one key for "palm up" responses and the other for "palm down" responses (see Fig. 3a). Participants made responses by pressing the appropriate key using the index or middle finger of the hand specified by the cue. The assignment of left and right keys to "palm up" and "palm down" responses was counterbalanced across participants. No strategy-related instructions were given.

Results and discussion

Mean RTs for all correctly answered trials were computed as in Experiment 1. (For the mean level of accuracy for each of the trial types, see Fig. S2 in the Supplemental Material.)

Figure 4a shows the mean RTs for stimuli depicting the palm-down views of the right and left hands. As in the laterality judgment task of Experiment 1, the RT profiles for the two hands are mirror reversed. For these palm-down stimuli, the interaction between shape and orientation was significant, $F(4, 44) = 16.35$, $p < .0001$. There was a main effect of orientation, $F(4, 44) = 39.95$, $p < .0001$, but no main effect of shape, $F(1, 11) = 0.09$, $p > .8$.

In striking contrast, the mean RTs for the palm-up stimuli of the right and left hands (see Fig. 4b) did not exhibit the asymmetry characteristic of illusory feelings of hand movement. For these palm-up stimuli, the interaction between shape and orientation was not significant, $F(4, 44) = 0.73$, $p > .5$. There was a main effect of orientation, $F(4, 44) = 30.12$, $p < .0001$, but no main effect of shape, $F(1, 11) = 0.72$, $p > .4$.

If participants had used mental rotation to confirm or disconfirm their laterality judgments, asymmetries should have been present in the RT profiles for both palm-down and palm-up stimuli, contrary to the obtained results. The mirror-reversed RT asymmetries for palm-down stimuli (for which successful binding was predicted) and the lack of such asymmetries in the RT profiles for palm-up stimuli (for which binding was predicted to fail) are consistent with the hand-binding hypothesis, which assumes that illusory feelings of movement are an aftereffect of successful binding. Notably, within the same task, the illusory feelings of movement were present in one condition and absent in another even though there was no variation in participants' reference

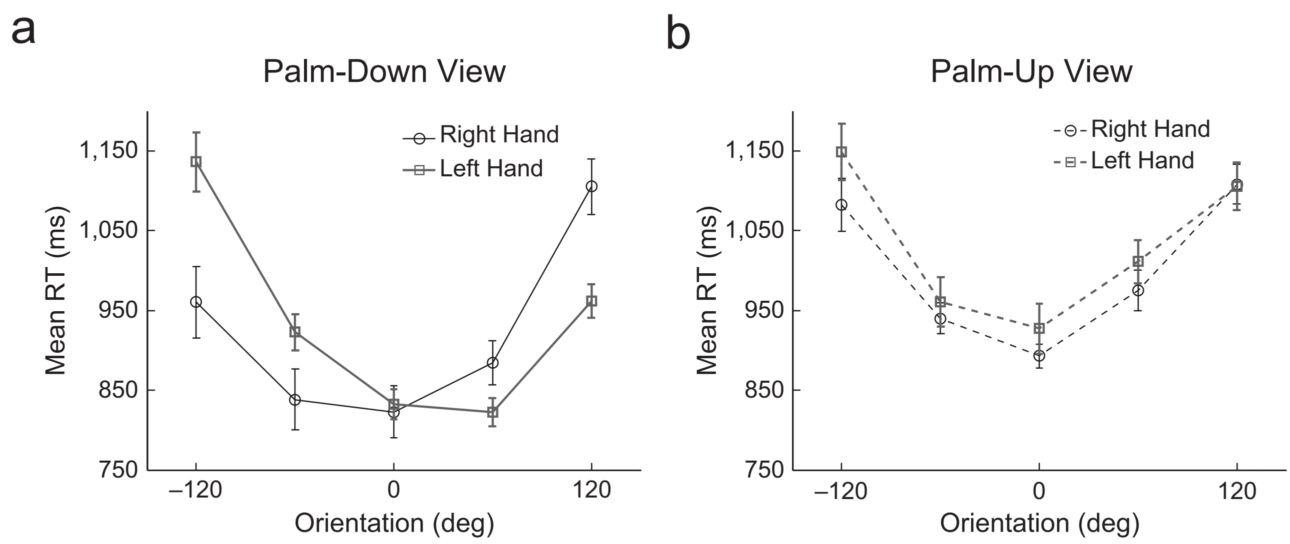

Fig. 4. Results for Experiment 2. The graph in (a) shows mean response times (RTs) for stimuli in the palm-down view as a function of stimulus orientation and hand. The graph in (b) shows mean RTs for stimuli in the palm-up view as a function of stimulus orientation and hand. Error bars represent within-subjects errors of the mean (Cousineau, 2005).

frame (e.g., egocentric vs. allocentric) between conditions (Sirigu & Duhamel, 2001).

General Discussion

Studies of hand-laterality judgment traditionally emphasize the somatomotor basis of the illusory feelings of movement and treat the orientation-dependent RTs as an index of mental rotation. However, judging laterality requires a decision: Is the seen hand a right hand or a left hand? By treating the RT profiles as an index of this decision, we found evidence supporting the hand-binding hypothesis, according to which observers determine a seen hand's laterality by relating the representation of that hand to representations of their own, felt hands via a structured pairing of features across sensory modalities.

Key evidence for the use of a feature-based hand representation in laterality judgments comes from the effect of selective attention on RTs in our two novel variants of the canonical hand-laterality judgment task. This influence of attention is neither predicted nor explained by an account assuming that hand representations are holistic—the critical assumption on which the hypothesized link between the use of mental rotation in mirror/same judgment tasks and the illusory feelings of movement during hand-laterality identification is based. Proprioceptive inputs are known to influence the illusory feelings of movement in hand-laterality judgment tasks (Parsons, 1994; Shenton et al., 2004), but our results indicate that proprioception's role extends to the decision-making process that takes place before the illusory feeling of movement occurs. The emergence of the wrong-hand effect in Experiment 1 depended on the position of the observer's own hands (a palm-down position), and the success or failure of binding in Experiment 2 depended on participants' attention to the state of one of their own hands but not the other. Neither pattern of results indicates that motor representations were involved in the binding decision, contrary to the predictions of the hand-imagery hypothesis.

Multisensory binding in the laterality task is unlike visual-proprioception binding in scenarios involving identification of one's own hand (e.g., scenarios producing the rubber-hand illusion; Costantini & Haggard, 2007; Pavani, Spence, & Driver, 2000; Tsakiris & Haggard, 2005). In those scenarios, the spatial congruence of the positions of seen and felt arms is a critical determinant of cross-modal binding. However, according to the hand-binding hypothesis, cross-modal binding in the laterality task is contingent on (a) the positions of the digits in relation to each other (i.e., shape), rather than the position of the arm relative to the body, and (b) the arm's orientation in depth (i.e., view), rather than its picture-plane orientation. It is possible that these features are weighted more heavily than arm position in the binding decision because of the unreliability of the seen hand's orientation from trial to trial in the laterality task.

In conclusion, the hand-binding hypothesis asserts that the feeling of movement in the hand-laterality judgment task originates from the binding and recalibration of multisensory inputs, rather than from a strategic simulation of motor commands.

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Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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Supplemental Material

Additional supporting information may be found at http://pss.sagepub.com/content/by/supplemental-data

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