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RESEARCH ARTICLE

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Hemispheric sensitivity to body stimuli in simple reaction time

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Abstract Previous research indicates that people respond fastest when the motor response is (spatially, functionally, anatomically, or otherwise) congruent to the visual stimulus. This effect, called ideomotor compatibility, is thought to be expressed in motor areas. Congruence occurs when the stimulus and response share some dimensions in their internal representations. If the ideomotor compatibility hypothesis were true, we would expect facilitation when right hand stimuli are presented to the left hemisphere, or left hand stimuli are presented to the right hemisphere. To address this issue, we conducted a simple reaction time experiment with lateralized targets. Participants were instructed to press a button as soon as a target was observed. The target stimulus was a left hand, a right hand, or a neutral control. Each hemisphere showed faster responses to contralateral hand stimuli as compared with ipsilateral hand stimuli, consistent with the ideomotor compatibility hypothesis. The results support an automatic and implicit processing of visual stimuli within motor representations even when no recognition of, or decision about, the stimulus is necessary.

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Abbreviations LVF: Left visual field · RVF: Right visual field · VF: Visual field

Introduction

Over a hundred years ago, James (1890) posited a relationship between observed and executed action. He called his idea "ideomotor action" and postulated that "watching" oneself make a movement created a movement "image" which was stored together with the proprioceptive information received from action execution. The motor "image" is then invoked whenever one thinks of a movement. Since then, several researchers have expanded on this idea (Greenwald 1970; Prinz 1997; Brass et al. 2001; Iacoboni et al. 2001; Knuf et al. 2001; Craighero et al. 2002; Vogt et al. 2003). Neurological support for these theories has recently been established by the "observation–execution matching system," or the mirror neuron system, where the same neuron was found to be active to the visual, auditory, and motor component of a given action (Gallese et al. 1996; Kohler et al. 2002).

The robustness of the interaction between sensory and motor areas was supported in a recent paper that examined the effects of compatible and incompatible body stimuli in a simple reaction time paradigm. Here, Brass and his colleagues asked participants to execute finger movements in response to compatible or incompatible visual stimuli (a finger tap or a finger lift). Although compatibility effects are not normally observed in simple reaction time tasks, Brass et al.'s study revealed that compatible body stimuli facilitated reaction times. In a follow-up experiment, Brass et al. found that compatible stimuli which are not biological did not show the same effect (Brass et al. 2001).

In the current study, we asked whether the ideomotor action model applies to each hemisphere separately. Can we observe ideomotor compatibility effects in each hemisphere in a simple reaction time task, where no recognition of the stimulus is necessary? If so, this would strongly support the concept of automaticity for processing body parts. It would add to Brass and his colleagues' findings by showing for the first time that body processing is implicit within each hemisphere and extends to the laterality of the effector. Specifically, (1) Does the pattern of facilitation follow the pattern of motor control? That is, in a simple reaction time paradigm, would we see facilitation for trials where right hand stimuli are presented to the right visual field (RVF)/left hemisphere and for trials where left hand stimuli are presented to the left visual field (LVF)/right hemisphere? This result would support the conclusion that such effects rely on the contralateral hemisphere's motor representations (“hemifield compatibility hypothesis”). (2) Would there be a specific facilitation when the laterality of the stimulus hand and the laterality of the response hand were the same? That is, would responses be fastest when one sees a right hand stimulus and responds with the right hand, and when one sees a left hand stimulus and responds with the left hand? We will refer to this hypothesis as the “effector compatibility hypothesis.”

To answer these questions we used a lateralized simple reaction time paradigm with two types of stimuli: left and right hand images (the experimental stimuli), and a scrambled photo of the right hand (the control stimulus). We predicted that hand stimuli would facilitate reaction times as compared to control stimuli. We further predicted that when the RVF/left hemisphere is presented with a right hand stimulus, responses would be facilitated, as they would be when the LVF/right hemisphere is presented with a left hand stimulus.

To understand facilitation in the specific effector (“the effector compatibility hypothesis”), we asked participants to respond using their left or right hand separately in different blocks. We predicted that right hand responses would be facilitated when the participant viewed a right hand stimulus and left hand responses would be facilitated when the participant viewed a left hand stimulus.

If we were to find that responses were fastest when right hands were presented to the RVF and left hands to the LVF, could it be due to a spatial compatibility effect between visual and proprioceptive information? That is, could our effect be due to the participant's own right hand being in their right side and their left hand being in their left side rather than reflecting a hemispheric effect? To control such visuo-proprioceptive compatibility effects, for half the trials we asked participants to cross their hands when making responses.

It is known that trial-to-trial neighborhood effects occur in behavioral laterality experiments and that they mitigate the development of uniform strategies and effects due to particular independent variables (Iacoboni et al. 1997; Weekes et al. 1999). Consequently, we chose to block stimulus type (hand, control) and response hand condition (left, right; crossed, uncrossed). Changes in laterality effects due to repetition of the same stimulus within block are known to asymptote after the second occurrence and are thus not likely to differ between two blocks that contain different large numbers of a particular stimulus type. The number of intervening trials between two repetitions over a stimulus condition does not effect the repetition effect (Weems and Zaidel 2005). Therefore, repetition effects do not seem to pose a problem when blocking stimuli.

Methods

Participants

Sixteen healthy UCLA undergraduate students (8 men and 8 women), naïve to the aims of the study, volunteered to participate for course credit. All participants were strongly right-handed as determined by a modified Edinburgh Handedness Inventory (Oldfield 1971). All participants reported normal or corrected-to-normal vision in both eyes and no history or evidence of neurological insult.

Stimuli

Three different equiluminant stimuli were used. Two were digital color photos taken of one person's left and a right hand, depicted in the same position as the participant's hand would be placed on the response keypad. Both of these hand stimuli were of the participant's own view of their hand (as opposed to a mirror view). The third stimulus was a scrambled photo of the right hand stimulus (Fig. 1).

Fig. 1 Stimuli presented to participants. **a** Left hand stimulus. **b** Control stimulus. **c** Right hand stimulus

Design and procedure

Participants were seated at a distance of 22 in. from a high-resolution monitor, with their chins in a chinrest and eyes focused on a fixation cross in the middle of the computer screen. MacProbe, computer software designed by Dr. Steve Hunt for the Macintosh, was used to present the stimuli and to record responses. Participants were familiarized with the different stimuli prior to the experiment. To minimize the carry-over effects of hand stimuli on control stimuli, participants viewed hand stimuli or neutral stimuli in separate blocks. All blocks were counterbalanced across participants. Within the hand stimuli blocks, left and right hand stimuli were presented randomly. Stimuli were flashed for 45 ms at random to either side of the fixation cross, with each stimulus type appearing equally often on each side. A tone preceded each stimulus presentation, with the interval between the tone and the stimulus randomly varying between 495 and 2,505 ms. Participants were asked to unimanually press a button on a response box as soon as they saw the visual stimulus on either side of the fixation cross.

We also manipulated within-subjects the side of space in which the motor response was made. The participant's hands were placed 6 in. apart from each other. In half of the blocks, participants responded with their arms naturally outstretched in front, on the response keys, while in the other half of the blocks they crossed their arms over to the opposite side of space. Hence, participants completed four different response conditions in separate blocks (right hand natural, left hand natural, right hand crossed, left hand crossed). This created a total of eight experimental blocks for each participant (four blocked response hand conditions, two blocked stimuli sets). The order of the blocks was counterbalanced across participants.

Eighty trials were presented in each block, making a total of 640 trials altogether for each participant. Throughout the experiment, the experimenter inspected the participant for eye movements and often reminded the participants to focus their eyes on the fixation cross. The study concluded with a questionnaire asking participants how well they felt they were able to focus on the fixation cross. Since inspection revealed adequate fixation control and all participants reported adequate ability to fixate on the cross throughout the experiment, none were excluded from the analysis.

Data analysis

Data from all participants were submitted to analyses of variance (ANOVA) with latency as the dependent variable. A significant interaction between stimulus type (left hand, right hand) and visual field (VF; LVF, RVF) would demonstrate a hemifield compatibility effect. Further, an interaction between stimulus type and response hand would demonstrate an effector compatibility effect. Further, an interaction between stimulus type, response hand, and VF would suggest that the two compatibility effects are not independent of each other. Consequently, a three-way ANOVA [stimulus type (right hand, left hand, control), VF (RVF, LVF), response hand (right hand, left hand)] was conducted. Further, to test for visuo-proprioceptive compatibility effects, a three-way ANOVA [stimulus type (left hand stimulus, right hand stimulus, control stimulus) × VF (LVF, RVF) × response position (hand uncrossed, hands crossed)] was conducted. Response times that were too fast or slow to be meaningful (under 150 ms or over 400 ms) were excluded from the analysis.

Results

Contrary to our prediction, hand stimuli were not faster than control stimuli; there was no main effect for stimulus type, $F(2,30) = 1.629$, $P > 0.1$. This was true even when left and right hand stimuli were collapsed into a single variable (hand stimuli).

However, we found a significant interaction between hemifield of presentation and stimulus type, $F(1,15) = 7.484$, $P < 0.01$. Supporting the hemifield compatibility hypothesis, responses to right hand stimuli were faster when presented to the RVF/left hemisphere, while left hand stimuli were faster when presented to the LVF/right hemisphere (Fig. 2). A direct means comparison between the left and right hand stimuli in the LVF or RVF revealed that both hemispheres were significantly sensitive to the laterality of the stimulus. We predicted and observed in the RVF/left hemisphere shorter latencies for right hand stimuli as compared to left hand stimuli, $F = 12.719$, $P(\text{one-tailed}) < 0.001$, and in the LVF/right hemisphere shorter latencies for left hand stimuli as compared to right hand stimuli, $F = 3.575$, $P(\text{one-tailed}) < 0.05$. A final comparison showed that right hand stimuli were significantly faster in the RVF than in the LVF, $F = 15.818$, $P(\text{one-tailed}) < 0.0001$. Left hand stimuli showed a similar trend for faster processing in the LVF than in the RVF, $F = 2.19$, $P(\text{one-tailed}) = 0.075$.

As predicted, the position (crossed, uncrossed) of the response hand did not significantly interact with the VF and type of stimulus presented, $F(1,14) = 0.133$, $P > 0.5$. Furthermore, when the data was analyzed only for trials in which participants crossed their arms, the interaction between hemifield of presentation and stimulus type was still significant, $P = 0.05$. This suggests that the visuo-proprioceptive hypothesis is not a viable alternative here. Contrary to the effector compatibility hypothesis, there was no interaction with response hand and stimulus type, $F(2,30) = 0.240$, $P > 0.5$. Thus, reaction times were not quicker when the laterality of the hand matched the laterality of the stimulus. Finally, the three-way interaction between stimulus type, response hand, and

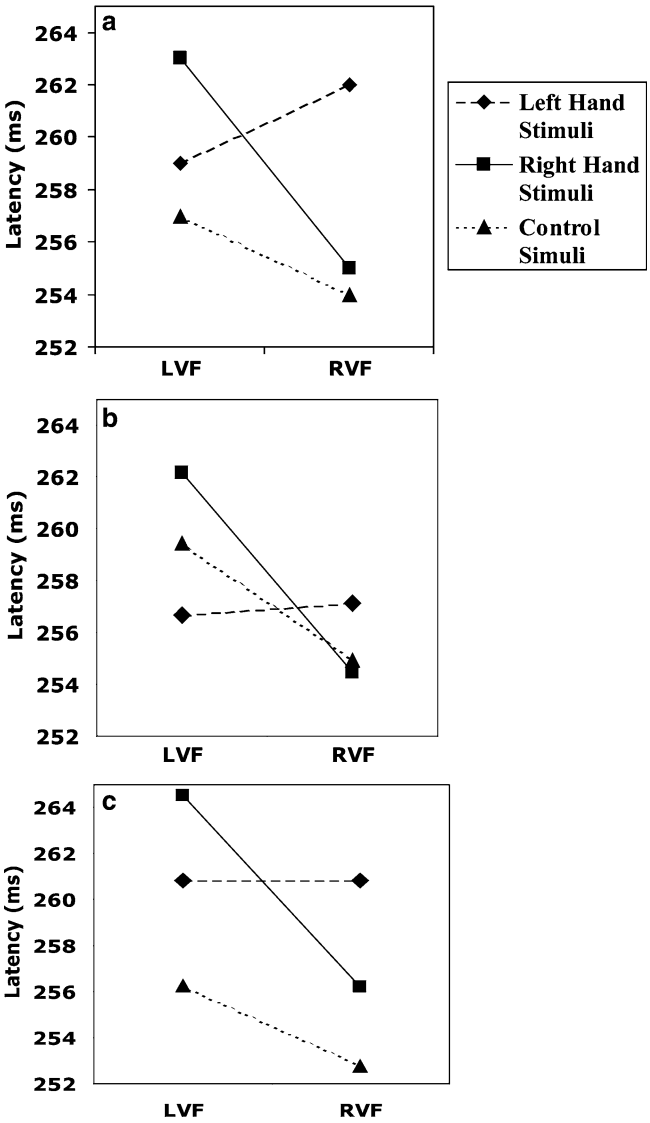

Fig. 2 **a** Overall pattern reaction time pattern for left hand stimuli, right hand stimuli, and control stimuli. Left hand stimuli are responded to faster when presented to the left visual field (LVF), and right hand stimuli are responded to faster when presented to the right visual field (RVF), $P < 0.01$. Right hand stimuli and left hand stimuli significantly differ from each other in both the RVF and the LVF, $P < 0.05$. **b** Reaction times for uncrossed response hand position. **c** Reaction times for crossed response hand positions

VF, was not significant [$F(1,14) = 1.4$, $P > 0.1$], suggesting that there is no evidence for an interaction between the two ideomotor compatibility effects. However, for greater clarity of the effect, in Fig. 2 we graph response times separately for crossed and uncrossed positions as well as the overall pattern. This figure indicates that during the more natural uncrossed position, reaction times for the control stimulus are between those of the contralateral and ipsilateral hand stimuli. Reaction times to all stimulus types are shown in Table 1.

Table 1 Mean reaction times separated by response hand, response hand position, and stimulus type

Response hand position	Response hand	Stimulus	VF	Reaction time
Crossed	lh	lstim	LVF	259
Crossed	lh	lstim	RVF	269
Crossed	lh	neutral	LVF	259
Crossed	lh	neutral	RVF	254
Crossed	lh	rstim	LVF	264
Crossed	lh	rstim	RVF	257
Crossed	rh	lstim	LVF	263
Crossed	rh	lstim	RVF	260
Crossed	rh	neutral	LVF	253
Crossed	rh	neutral	RVF	251
Crossed	rh	rstim	LVF	265
Crossed	rh	rstim	RVF	255
Uncrossed	lh	lstim	LVF	263
Uncrossed	lh	lstim	RVF	256
Uncrossed	lh	neutral	LVF	263
Uncrossed	lh	neutral	RVF	253
Uncrossed	lh	rstim	LVF	266
Uncrossed	lh	rstim	RVF	257
Uncrossed	rh	lstim	LVF	251
Uncrossed	rh	lstim	RVF	259
Uncrossed	rh	neutral	LVF	256
Uncrossed	rh	neutral	RVF	257
Uncrossed	rh	rstim	LVF	258
Uncrossed	rh	rstim	RVF	252

Discussion

This study addressed hemispheric sensitivity for hand stimuli in facilitating motor responses. Our study indicates, for the first time, that ideomotor compatibility is maintained within each cerebral hemisphere in simple reaction time. However, before we discuss this specific hemispheric effect, we discuss first the general effect of hand stimuli as compared to control stimuli.

In contrast with the ideomotor compatibility hypothesis, we did not find that the combined hand stimuli facilitated unimanual reaction times as compared to control stimuli. One possibility is that the ideomotor action system may be most sensitive to naturalistic stimuli, like the moving hand stimuli used by Brass et al. (2001). Another possibility is that the system may be sensitive to the goal of an action, which was not represented in our stimuli. Unlike a study completed by Craighero et al. (2002) where participants were shown the final position of the hand and motor facilitation to these stimuli was observed, our experimental stimulus was in the initial position of the required response, before participants pressed the response button. Thus, our stimuli did not contain a visible representation of the action goal. In a recent fMRI study, the representation of the action goal showed increased activity in motor areas as compared to conditions where no goal was visible (Koski et al. 2002). Thus, it may be that a representation for the goal may be essential to showing facilitation relative to neutral stimuli.

Alternatively, it is known that simple reaction time experiments are sensitive to a great deal of variability, including intertrial variability, intersubject variability, and interblock variability (Iacoboni and Zaidel 2000). It is therefore possible that the difference we see here between the control blocks and the other stimuli is simply a reflection of interblock variability, which is a consequence of the simple reaction time paradigm. Finally, as Fig. 2b and c indicates, in the uncrossed, natural response hand position, reaction times to control stimuli are between the other two hand stimuli. In this natural response position, there appears to be a facilitation (especially in the LVF) for the contralateral hand stimuli and an inhibition for ipsilateral hand stimuli as compared to control stimuli. In the unnatural, crossed response position, there is an overall inhibition for hand stimuli due to the hand position itself, which may interfere with processing of hand stimuli but not with processing of control stimuli. At the same time, the facilitation/inhibition for the two types of hand stimuli is still observed for this condition. While further studies are needed to better understand the effects that response hand position may have on ideomotor compatibility, this data does seem to indicate that under normal response positions, responses to control stimuli are between those to ipsilateral and contralateral hand stimuli.

With regards to the hemifield compatibility effect, we did find that each hemisphere was more sensitive to the hand stimulus for which it has the most extensive representation. Response times were fastest when right hand stimuli were presented to the RVF/left hemisphere and left hand stimuli were presented to the LVF/right hemisphere. This contralateral bias is reminiscent of representations in the motor cortices, where each hemisphere has representation predominantly for the contralateral side of the body. Thus it may indicate that in this task, the stimuli are largely processed in motor areas. In fact, previous brain imaging studies have shown that processing body stimuli activates corresponding motor areas. In tasks where participants were explicitly asked to report whether they were viewing a left or right hand, activations were found in motor areas including the SMA, premotor cortex, striatum, and cerebellum (Parsons and Fox 1998). However, unlike the latter study, in the current study participants were not asked to make any decision about the stimulus. Hence our results indicate that it is not only explicit processing of body stimuli but also implicit processing that may activate motor areas.

We should however note that contralateral motor representation is also found in posterior parietal areas (Desmurget et al. 1999). Thus, it is also possible that facilitation is occurring in these areas, as part of the dorsal stream for motor planning. Finally, some visual areas are also known to respond to body parts, such as the extrastriate body area (EBA) (Downing et al. 2001). Although we cannot rule out an effect at the visual level, the imaging data seem to show a right lateralization of EBA, whereas our data are more bilateral. It is thus unlikely that the effect observed here is mediated by the EBA.

As Fig. 2 shows, there is no significant difference in reaction times between contralateral hand stimuli and control stimuli in each hemifield. Instead, reaction times to ipsilateral hand stimuli are significantly slower than to the other stimuli. This result may be interpreted in two ways. The first interpretation is that body parts in general, as complex stimuli, are slower to process than control stimuli. Our effect would then represent facilitation to contralateral hand stimuli in each hemisphere, which make reaction times to contralateral hands more similar to control stimuli. The second interpretation posits no difference in speed of processing between body parts and control stimuli. Instead, responses to ipsilateral hand stimuli are slowed down due to an inhibition in processing these stimuli.

Both of these interpretations may be due to each hemisphere having better representation for the contralateral side of the body as compared to the ipsilateral side of the body, resulting in faster processing of contralateral body parts. In this view, inhibition may be a transcallosal effect, with the contralateral hemisphere inhibiting activity in the ipsilateral hemisphere. In fact a previous imaging study shows that transcallosal inhibition occurs during simple finger movements (Allison et al. 2000). Further research is needed, however, to better understand which process (facilitation or inhibition of body stimuli) is actually occurring.

Our results do not support the effector compatibility hypothesis; we did not find that right hand responses were faster when right hand stimuli were presented and left hand responses were faster when left hand stimuli were presented. Thus, while there may be a general facilitation for contralateral hand stimuli, this effect is independent of which hand is used to make the action. Facilitation in motor areas appears to be a general effect, not specific to the motor effector being used. That is, facilitation may occur in sensorimotor areas involved in processing body parts while a specific activation of the left of right hand at the level of the primary motor cortex may not occur. This finding is in line with the absence of primary motor activation in a PET study where participants are asked to explicitly decide the laterality of a hand stimulus (Parsons and Fox 1998). We did not find the participant's own hand position (crossed or uncrossed) to interact with a hemifield compatibility hypothesis. For both response hand positions, left hand stimuli were faster when presented to the LVF and right hand stimuli were faster when presented to the RVF (Fig. 2b, c). Therefore our results do not seem to be affected by a spatio-visual mapping of right hands in the right side of space and left hands in the left side of space, corresponding to the participant's own hand. Given these considerations, we do not believe that our results are an effect of visuo-spatial mapping.

It is possible to argue that the ideomotor compatibility effect generalizes to contralateral body parts other than the hand. This would predict a significant interaction between VF and stimulus type (left foot, right foot) in an experiment that manipulated feet as stimuli. Furthermore consider the response hand advantage when observing congruent compared to incongruent actions in a simple reaction time task. Does this occur because of facilitation to perception (Craighero et al. 2002) or due to facilitation of action execution (Brass et al. 2001)? Given that our ideomotor compatibility effect did not interact with response hand, our data could have suggested the perceptual rather than action execution facilitation. However, our post-hoc ANOVA did show that ideomotor compatibility interacts with response hand and position, supporting the execution interpretation.

Conclusion

Our data support the notion that motor representations may play a role not only in motor but also in sensory processing. It may be that in order to fully process body stimuli, motor representations need to be activated. Since our simple reaction time task did not require participants to make any decision about the visual stimuli, the involvement of body representations in stimulus processing appears to be automatic and implicit. This is best revealed by each hemisphere showing facilitation for the body part stimulus for which it has the best motor control. Furthermore, our results indicate that such hemispheric sensitivity is highly robust, as it is evident even in a simple reaction time paradigm. James's early postulations of motor images and motor outputs being automatically and strongly bound together thus appear to be preserved within each brain hemisphere.

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