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**EXPERIENCE-BASED PRIMING OF BODY PARTS:
A STUDY OF ACTION IMITATION**

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Abstract:

Two important dimensions of action are the movement and the body part with which the movement is effected. Experiment 1 tested whether automatic imitation is sensitive to the body part dimension of action. We found that hand and foot movements were selectively primed by observation of a corresponding, task-irrelevant effector in motion. Experiment 2 used this body part priming effect to investigate the role of sensorimotor learning in the development of imitation. The results showed that incompatible training, in which observation of hand movements was paired with execution of foot movements and vice versa, led to a greater reduction in body part priming than compatible training, in which subjects experienced typical contingencies between observation and execution of hand and foot movements. These findings are consistent with the assumption that overt behavioral imitation is mediated by the mirror neuron system, which is somatotopically organized. Our results also support the hypothesis that the development of imitation and the mirror neuron system are driven by correlated sensorimotor learning.

Section: Cognitive and behavioral neuroscience

Keywords: Imitation; body part coding; visuomotor priming; mirror neuron system;

1. Introduction

One of the most important findings to emerge from action perception research has been that the observation and the execution of body movements activate a common cortical network. This network, known as the ‘mirror neuron system’, is active when movements are executed without visual feedback, and when the same actions are passively observed (e.g. di Pellegrino et al., 1992; Iacoboni et al., 1999; Raos et al., 2006; for a review see Rizzolatti and Craighero, 2004). Neurons exhibiting ‘mirror’ properties, that is, a close correspondence between the visual input (observed action) and the motor output (performed action) in the neural response, are known to exist in ventral premotor area F5 (e.g. di Pellegrino et al., 1992; Gallese et al., 1996) and inferior parietal lobule area 7b of the macaque (e.g. Fogassi et al., 1998; Gallese et al., 2002), and areas with similar characteristics have been identified in homologous regions in human premotor cortex, often centered on Broca’s area in the inferior frontal gyrus, and parietal areas (e.g. Iacoboni et al., 1999). The present study is concerned with two questions: To what extent does the activity of the mirror neuron system parallel overt, behavioral imitation, and how do we acquire the capacity to map observed onto executed actions?

1.1. The mirror neuron system and imitation

Overt behavioral imitation occurs when one individual, an ‘observer’, copies the body movement of another individual, a ‘model’. More specifically, observation of some dimension of the model’s body movement (e.g. its rate or topography) causes the

observer's behavior to become more like that of the model on the observed dimension (Heyes, 2001, Box 1). For example, when two people, A and B, are in conversation, each tends to imitate the incidental foot-shaking and face-rubbing behavior of the other; the frequency of foot-shaking by A increases when B engages in foot-shaking, but not when B engages in face-rubbing, whereas face-rubbing by A increases when B engages in face-rubbing, but not when B engages in foot-shaking (Chartrand and Bargh, 1999).

Superficially, it is plausible that imitation is mediated by the mirror neuron system. Imitation requires a neural mechanism that can map observed onto executed actions, and the mirror neuron system appears to fulfill that function. Furthermore, the hypothesis that imitation is mediated by the mirror neuron system is supported by evidence that the mirror neuron system, and particularly the inferior frontal gyrus, is more active during imitation than during either observation or execution of actions (e.g. Aziz-Zadeh et al., 2006; Iacoboni et al., 1999; Koski et al., 2003; Nishitani and Hari, 2000; Williams et al., 2006), and is involved in imitation learning (Buccino et al., 2004; Vogt et al., 2007). However, a strong connection between imitation and the mirror neuron system remains to be established. Mirror neurons have been found in monkeys, animals which are apparently incapable of imitation (Rizzolatti, 2005; Visalberghi and Fragaszy, 2001), and greater activation of the mirror neuron system during imitation than during observation alone or execution alone does not show unambiguously that the mirror neuron system mediates imitation. An imitation task involves action observation, action execution, and, critically, matching or translation of observed into executed actions. Therefore, this result may indicate, not that the mirror neuron system translates observed into executed

actions, a distinctively imitative function, but that the effects of observation and execution on the mirror neuron system are additive.

A strong connection between imitation and the mirror neuron system, indicating that the former is mediated by the latter, would be established if it could be shown that a range of action variables have parallel effects on imitation and on the mirror neuron system. Two important variables or dimensions of action are effector and movement (Chaminade et al., 2005; Meltzoff and Moore, 1997). The effector dimension relates to the limb or body part used to perform an action, whereas the movement dimension relates to the topography or trajectory of the effector. For example, to wave at another person, we typically use a hand (effector), and a lateral, parabolic trajectory (movement). Research to date has indicated that movement variables have parallel effects on imitation and the mirror neuron system (e.g. di Pellegrino et al., 1992; Ferrari et al., 2003; Craighero et al., 2002; Puce et al., 2000; Stürmer et al., 2000), but it is not yet known whether the mirror neuron system's sensitivity to effector variables, as indicated by neurological measures, is reflected in overt imitative performance.

Evidence that the mirror neuron system is sensitive to movement type has been provided by studies on both monkeys and humans (e.g. di Pellegrino et al., 1992; Ferrari et al., 2003; Puce et al., 2000). Parallel evidence of behavioral sensitivity to movement type comes from many studies of imitation (Bertenthal et al., 2006; Brass et al., 2000, 2001; Castiello et al., 2002; Chartrand and Bargh, 1999; Craighero et al., 2002; Dimberg et al., 2000; Heyes et al., 2005; Kerzel and Bekkering, 2000; Kilner et al., 2003; Press et

al., 2005; Stanley et al., 2007; Stürmer et al., 2000; Vogt et al., 2003), but is particularly clear in research on ‘automatic imitation’ using stimulus-response compatibility paradigms. For example, when participants have been instructed to make a pre-specified response (e.g. opening their hand) as soon as an observed hand begins to move, they initiate their response movement faster if the observed hand is performing a compatible movement (opening) than if it is performing an incompatible (closing) movement (Heyes et al., 2005; Press et al., 2005; Stürmer et al., 2000). Effects such as this show movement sensitivity in visuomotor priming: an observed action can prime the execution of the same action, but not of a different action, performed with the same body part. The matching of observed and executed movement types that occurs in automatic imitation is not reducible to the effects of either simple or complex spatial compatibility (Press et al., in press; see also Brass et al., 2001; Bertenthal et al., 2006).

Recent studies using neurological measures have shown that the human mirror neuron system is sensitive, not only to movement type, but to effector type: it responds differentially to the observation of different body parts in motion (Buccino et al., 2001; Sakreida et al., 2005; Wheaton et al., 2001; Wheaton et al., 2004). Buccino et al. (2001) and Wheaton et al. (2004) used neuroimaging to demonstrate that hand, foot and mouth actions selectively activate distinct regions of human ventral premotor and parietal cortex. Importantly, Wheaton et al. (2004) showed this somatotopic pattern of activation even when movements were held constant across effectors (opening and closing movements of a hand and a mouth, respectively). These findings indicate that the mirror

neuron system codes the body parts involved in action, but there is no directly corresponding evidence that imitative behavior is sensitive to effector type.

A recent study has shown priming of index finger lifting movements by the observation of a lifting index finger, relative to observation of a lifting middle finger, and vice versa for middle finger lifting movements, even when fingers were in incongruent spatial locations (Bertenthal et al., 2006, Experiment 3b). While this provides some evidence that body part priming in imitative behavior is possible, it does not establish a parallel between imitation and the mirror neuron system because there is, at present, no corresponding evidence that body part coding in the mirror neuron system is selective for individual finger movements. In order to demonstrate that the body part dimension of an action affects both imitation and the mirror neuron system, it must be shown that, in parallel with Buccino et al.'s (2001) and Wheaton et al.'s (2004) findings, observation of a hand in motion selectively primes hand movement, rather than foot movement, and vice versa for observation of a foot in motion.

Several studies suggest the occurrence of effector priming for various combinations of hand, foot and mouth movements in human and nonhuman subjects (e.g. Akins and Zentall, 1996; Bach and Tipper, 2007; Berger and Hadley, 1975; Dawson and Foss, 1965; Voelkl and Huber, 2000), but, on closer examination, it becomes clear that none of these studies isolated the effects of effector observation from those of movement observation. For example, Bach and Tipper (2007) found that observation of a model kicking a ball facilitated foot responses relative to hand responses, whereas observation of a model typing on a computer keyboard facilitated hand responses relative to foot responses.

Although interesting in its own right, this result does not demonstrate effector priming because it could have been observation of hand use (effector priming), or observation of a movement - repetitive tapping - typically performed with the hand (movement priming) that facilitated hand responses.

To find out whether, like the mirror neuron system, imitation is sensitive to the effector dimension of action, Experiment 1 used an automatic imitation procedure in which we held constant the movement trajectory that was observed and executed, and varied only the effector that was selected for the performance of this movement type. In this choice-RT study, participants were required to lift their hand or their foot in response to a task-relevant letter (H or F), while a task-irrelevant image of a hand or foot lifting movement was simultaneously presented. If body parts are matched in automatic imitation, observed effectors should prime response effectors. That is, hand lifting responses should be initiated faster in the presence of a hand than a foot lifting action, while foot lifting responses should be faster when a foot rather than a hand action is observed.

1.2. Mapping observed to executed actions

In imitation, observed actions are related to the *same* executed actions. For example, when we imitate an observed foot action, we are more likely to perform this action with our foot than with our hand. Similarly, the observation of foot actions activates areas of premotor and parietal cortex involved in the execution of foot actions more than areas

involved in the execution of hand actions (e.g. Buccino et al., 2001). It may seem obvious that observed foot actions are more similar to executed foot than hand actions, but, on reflection, it is evident that this intriguing and distinctive feature of imitation, and of the mirror neuron system, needs to be explained (Brass and Heyes, 2005). Given that the actions of the self and those of others are not seen from a third party perspective, it is not clear how the processes underlying imitation ‘know’ that observed foot actions are equivalent to executed foot actions rather than to executed hand actions, or how the mirror neuron system acquires its ‘mirror’ properties.

One possibility is that the matching of observed to executed actions is innate and experience-independent (Meltzoff and Moore, 1997; Gallese and Goldman, 1998). However, this is an unlikely hypothesis for the mirror neuron system in the light of several recent studies demonstrating its responsiveness to ‘unnatural stimuli’, such as the observation of tool use (Ferrari et al., 2005; Järveläinen et al., 2004; Obayashi et al., 2001) and the sound of paper ripping (Kohler et al., 2002), and of studies showing that the responsivity of the mirror neuron system varies with expertise in the observed action domain (e.g. Calvo-Merino et al., 2005; Lahav et al., 2007). If the development of imitation, and the mirror neuron system, is instead experience-dependent, then it may draw on three kinds of experience: unimodal sensory (Ferrari et al., 2005), unimodal motor (Calvo-Merino et al., 2006) or sensorimotor experience (Heyes, 2001; Heyes et al., 2005; Keysers and Perrett, 2004; Lahav et al., 2007; Obayashi et al., 2001). Unimodal sensory experience is provided by passive observation of an action, whereas unimodal motor experience arises from repeated execution of an action. In contrast, sensorimotor

experience derives from correlated observation and execution of the same action. Thus, development of the capacity to, for example, match observed with executed foot movements, could result from observation of foot movements (unimodal sensory), execution of foot movements (unimodal motor), or from correlated experience of observing foot movements while performing foot movements (sensorimotor).

Building on the results of Experiment 1, Experiment 2 examined the role of sensorimotor experience in the development of imitation when unimodal sensory and unimodal motor experience were controlled. According to one sensorimotor account, the Associative Sequence Learning (ASL) model of imitation and the mirror neuron system (e.g. Heyes, 2001; Brass and Heyes, 2005), unimodal sensory and unimodal motor experience contribute to the establishment of sensory and motor representations, respectively, as a pre-requisite for sensorimotor learning, but they are not sufficient to establish the direct matching between an observed action and the same executed action that is necessary for imitation. ASL proposes that, instead, the formation of links between sensory and motor representations of the same action, and therefore of mirror neurons, depends on the correlated experience of observing and executing the same action. In the course of normal development, correlated experience of this kind is obtained through self-observation (e.g. watching one's own hand while it is moving), and through social interactions in which the individual is imitated by others, or engages in synchronous action with another agent. The model implies that when observation of one action is repeatedly paired with execution of another, nonmatching links will be formed between a sensory representation of one action (e.g. foot lifting) and a motor

representation of a different action (e.g. hand lifting). On the basis of this assumption, Experiment 2 used body part priming to measure the strength of automatic imitation before and after a period in which subjects received ‘counter-mirror’ sensorimotor training. ‘Counter-mirror’ sensorimotor training required a group of participants (the incompatible group) to executed hand movements while observing foot movements and vice versa over the course of several training sessions. Another group (the compatible group), which served as a control, executed hand movements while observing hand movements, and foot movements while observing foot movements. The actions were familiar – they had been observed and executed by the subjects repeatedly before the experiment – and the groups received equal amounts of unimodal sensory and unimodal motor experience of the hand and foot actions in the course of training. Therefore, if the development of imitation depends on unimodal visual and/or motor experience alone, training should not result in an appreciable difference between groups; the compatible and incompatible groups should show equivalent priming effects before and after training. However, if the sensorimotor hypothesis is correct, and the development of imitation depends on the contingency experienced between action observation and action execution, then the incompatible group, but not the compatible group, should show less effector priming after training than before training.

2. Experiment 1

Experiment 1 sought evidence of effector priming in an automatic imitation paradigm. In a choice-RT task, we measured the effect of task-irrelevant hand and foot

action images on the speed of hand and foot responses to task-relevant letters. In order to keep movement type constant across effectors, stimulus and response movements were hand and foot lifting actions, which exhibit maximal spatial and configural overlap and are easily and routinely performed with both effectors. Up-down spatial compatibility between the relative positions of stimulus and response effectors was controlled by presenting the observed hands and feet side by side on the screen, while hand and foot responses were made seated, with the arm positioned above the foot. Furthermore, hand and foot stimuli were shown from a canonical rather than first-person perspective (from the side), and their lateral positions varied randomly. Task-irrelevant apparent lifting motion was induced by showing an image of a hand and a foot at rest immediately followed by the action image of either a lifted hand or a lifted foot while the other effector remained at rest. Electromyographic (EMG) recordings from forearm and lower leg muscles involved in the performance of hand and foot lifting movements were used to measure response times (RTs).

It was predicted that responses would be facilitated when the irrelevant body part stimulus matched the body part used for responding (compatible trials), while responses would be slowed when the stimulus and response effectors were different (incompatible trials). As a baseline condition we included trials in which the imperative stimulus (H or F) was not accompanied by an action image. The comparison with baseline allowed us to investigate the relative contributions of facilitation and interference from body part stimuli in compatible and incompatible trials, respectively.

2.1. Results

Errors (trials in which the wrong effector or both effectors were moved) and RTs greater than 2.5 times above or below the standard deviation from the subject's mean RT were removed from the data set before RT analysis. The error data were subjected to error analysis. The RT and error data are shown in Fig. 1.

Fig. 1 about here

The RT data were subjected to a 2 x 3 ANOVA in which response effector (foot or hand) and irrelevant stimulus (foot, none or hand) were within-subject factors. This analysis provided clear evidence of effector priming: a significant interaction between response effector and irrelevant stimulus ($F(2, 48) = 7.0, p = .004$). Simple effects analyses based on estimated marginal means were performed separately for each of the two levels of response effector on the three levels of the irrelevant stimulus (with Bonferroni correction). Foot responses to imperative letters were faster during the observation of task-irrelevant foot movements (388.1ms) than during the observation of hand movements (401.8ms, $p = .011$, two-tailed) or of no movements (400.8ms, $p = .010$, two-tailed). Hand responses were also faster in the presence of task-irrelevant hand movements (394.8ms) than in the presence of foot movements (409.5ms, $p = .052$, two-tailed) or of no movements (408.0ms, $p = .026$, two-tailed). The effect of the irrelevant

stimulus on RTs thus appears to have been due to facilitation in effector-compatible trials rather than to interference in incompatible trials. Overall RTs were similar for foot and hand responses ($F(1, 24) = 1.5, p = .236$).

A 2 x 3 (response effector x compatibility) ANOVA of the error data showed that error rates were markedly higher for hand (1.76) than for foot responses (.45; response effector: $F(1, 24) = 46.1, p < .001$), but there was no evidence of effector priming (response effector x irrelevant stimulus: $F(2, 48) = 2.0, p = .160$). The pattern of facilitation without interference present in the RT data was thus not mirrored in the error rates, but it should be noted that error rates were very low (<1% of trials).

In summary, the results of Experiment 1 demonstrate effector priming. Hand and foot responses were facilitated by observation of actions performed by the same body part. Interestingly, no interference effects were found. The facilitation effect could not have been due to the type of movement made by the irrelevant action stimulus because the hand and foot stimuli performed the same lifting movement. Similarly, the priming effect could not have been due to spatial compatibility because the hand and foot stimuli were presented in a plane orthogonal to that of the hand and foot responses, and the left-right position of the hand and foot stimuli varied over trials.

The results of Experiment 1 are similar to the findings of a recent study by Bach et al. (2007) who showed that the observation of a typing action of the hand and a kicking action of the foot selectively primed button press responses made with the hand or the

foot. In our study, body part priming resulted in participants making responses that matched those of the task-irrelevant action stimulus on both the effector and the movement dimensions. Our findings therefore extend those of Bach et al. by showing that body part priming can give rise to automatic imitation.

Importantly, Bach et al. (2007) showed that selective priming of body parts can be purely attentional and independent of observed movement; they found that a color target appearing in the location of a passive hand on a seated model or in the location of a passive foot on a standing model was sufficient to induce selective priming. It was argued that responses made with a specific effector can be primed simply by drawing attention to it. It is possible that a similar attentional process could account for the effector priming shown in our Experiment 1, but it is unlikely for the following reasons. The hand and foot stimuli shown in our experiment were relatively large and always presented together, flanking a small task-relevant letter (see Fig. 5). It is difficult to see how observers could not pay attention to both of the effectors when they were fixating the centre of the screen. Also, unlike Bach et al.'s (2007) study, our experimental design contained no contextual cues that could have served to draw attention to the task-irrelevant body part dimension of an upcoming trial. For example, whenever the image showed a standing person in Bach et al.'s study, the color target could only appear on the foot or on the head (neutral condition), but never on the hand. That is, the images themselves were informative as to the specific body part(s) where the target was likely to appear, and may thus have drawn attention toward one effector but away from the other.

The mirror neuron system is somatotopically organized; observation of hand and foot movements selectively evokes activity in regions that are involved in the execution of hand and foot movements, respectively (Buccino et al., 2001; Wheaton et al., 2004). By demonstrating effector priming for hand and foot movements, the results of Experiment 1 show for the first time that, in parallel with similar effects in the mirror neuron system, imitative behavior is sensitive to the effector dimension of observed action. Therefore, these results may be taken as support for the hypothesis that imitation is mediated by the mirror neuron system.

3. Experiment 2

To examine the role of sensorimotor experience in the development of the capacity to match an observed action with the same executed action, Experiment 2 used effector priming to measure the strength of automatic imitation before and after a period in which participants received either incompatible or compatible sensorimotor training. Effector priming was assessed before and after training using a choice-RT procedure similar to that used in Experiment 1. Neutral trials (no observed movement) were not included. Training was conducted for one hour each day over three days, and assessed 24 hours after the third training session. A related procedure has previously been employed by Heyes et al. (2005) to investigate effects of correlated sensorimotor training on imitation of different movements performed with the same effector.

For the incompatible training group, action stimuli were paired with responses performed by an incompatible effector. That is, hand action stimuli required foot movement responses and vice versa. For the compatible training group, which served as a control, hand and foot action stimuli were paired with responses performed by the same effector. During training, the two groups observed and executed the hand and foot movements with equal frequency. Therefore, if either unimodal sensory experience, unimodal motor experience or both are sufficient for learning to match an observed action with the same executed action, then one would expect the two groups to show similar body part priming effects after training. However, in contrast with the compatible group, the incompatible group experienced a non-matching sensorimotor contingency during training, e.g. a correlation between observation of hand movements and execution of foot movements. Therefore, if the development of the capacity to imitate is driven by sensorimotor learning, then after training there should be less effector priming in the incompatible group than in the compatible group.

3.1. Results

3.1.1. Pre-training test

Analysis of the data from all 32 participants prior to training (see Fig. 2) indicated that the body part priming effect found in Experiment 1 was replicated in Experiment 2. A 2 x 2 ANOVA of RTs, in which response effector (foot or hand) and irrelevant stimulus (foot or hand) were within-subject factors, indicated a significant effect of body part priming (response effector x irrelevant stimulus: $F(1, 31) = 26.8, p < .001$). Simple

effects analyses showed that foot responses were faster during observation of task-irrelevant movements made by a foot (404.2ms) than by a hand (411.0ms, $p = .023$, two-tailed), and hand responses were faster during observation of a hand movement (399.1ms) than a foot movement (412.2ms, $p < .001$, two-tailed). Overall RTs for hand and foot responses did not differ ($F(1, 31) < 1$, $p = .603$).

Fig. 2 about here

In contrast to Experiment 1, effector priming was also evident in the error rates. A 2 x 2 (response effector x irrelevant stimulus) ANOVA of errors showed a significant interaction between response effector and irrelevant stimulus ($F(1, 31) = 9.5$, $p = .004$). When foot responses were required, fewer errors occurred during observation of a foot movement (0.78) than a hand movement (1.44, $p = .017$, two-tailed). When hand responses were required, fewer errors occurred when a hand movement (3.25) than a foot movement (4.13, $p = .061$, two-tailed) was observed. Overall more errors were made in trials where hand responses (3.69) than where foot responses (1.11) were required (response effector: $F(1, 31) = 54.0$, $p < .001$).

3.1.2. Training

Analyses of the RT and error data from the 20 participants in the training set (see Fig. 3) indicated that incompatible training was effective in accelerating responses and

improving error rates. A 3 x 2 mixed model ANOVA of RTs, where training session (session 1, 2 or 3) was the within-subject variable and training group (compatible or incompatible training) was the between-subject variable, showed that RT decreased over the course of training (training session: $F(2, 38) = 38.2, p < .001$), especially for the incompatible training group (training session x training group: $F(2, 38) = 5.7, p = .012$). Simple effects analyses showed that the training groups differed in response speed for training session 1 ($p = .015$) and session 2 ($p = .046$), but not for session 3 ($p = .233$).

Fig. 3 about here

A 3 x 2 (training session x training group) ANOVA of errors showed that error rates reduced over the course of training (training session: $F(2, 38) = 6.6, p = .008$), marginally more for the incompatible than for the compatible training group (training session x training group: $F(2, 38) = 3.0, p = .080$). Simple effects analyses showed that error rates were higher in the incompatible than in the compatible training group for training session 1 ($p = .001$), 2 ($p = .003$) and 3 ($p = .004$).

3.1.3. Effects of training (*Pre- versus post-training test*)

The results of primary interest, the comparison between the effects of incompatible and compatible training on effector priming, are shown in Fig. 4. Effector priming is

shown in terms of effect sizes: RTs (a) and errors (b) in effector-incompatible trials minus RTs and errors in effector-compatible trials.

Fig. 4 about here

The effector priming effects in the RT data (Fig. 4a) were subjected to a 2 x 2 x 2 mixed-model ANOVA, where test (before or after training) and response effector (foot or hand) were within-subject factors, and training group (compatible or incompatible training group) was the between-subject factor. As predicted by the sensorimotor learning hypothesis, there was a significant interaction between test and training group ($F(1, 19) = 5.4, p = .033$). The magnitude of the body part priming effect declined as a function of training in the incompatible group but not in the compatible group (Fig. 4a). Simple effects analyses of the factor test were conducted for each group and confirmed that body part priming was significantly reduced following incompatible training ($p = .049$, two-tailed), but not following compatible training ($p = .259$, two-tailed). A 2 x 2 x 2 mixed-model ANOVA applied to the effector priming effects in the error data (Fig. 4b) did not reveal any significant main effects or interactions.

Experiment 2 showed that, in line with the predictions made by the ASL model of imitation and the mirror neuron system, body part priming in imitation was reduced following the repeated exposure to nonmatching sensorimotor pairings such as observing

a hand action while performing a movement with the foot. This suggests that the links between an observed and an executed action that mediate imitation are plastic rather than fixed, and that correlated sensorimotor learning plays a role in their development. It further suggests that the effects of an observed action on the motor system may not be restricted to priming the execution of the same action. In a similar vein, a recent study (Newman-Norlund et al., 2007) showed that the mirror neuron system also responds to actions that are complementary to those observed (grasping an object with a grip different from that used by the person who hands us the object). As activity was found to be greater for complementary actions (using a different grip) than for imitative actions (using the same grip), it was argued that the preparation of complementary actions recruits a class of neurons responsive to ‘broadly congruent’ actions, to which the majority of mirror neurons belong (e.g. Rizzolatti and Craighero, 2004), while imitative actions activate ‘strictly congruent’ mirror neurons. However, it is possible that, instead of recruiting a distinctive class of neurons, complementary actions resulted in greater mirror neuron system activation because, unlike imitative actions, they require the representation of different sensory and motor acts, the effects of which may have been additive. Nevertheless, this study shows that the motor system is primed not only by matching actions but also by nonmatching actions.

4. General Discussion

Single-cell studies in monkeys and human neuroimaging research have shown that the response of the mirror neuron system to the observation of actions is sensitive not only to the type of movement, but also to the body part with which an action is

performed. The present study tested whether automatic imitation, like the mirror neuron system, is sensitive to the body part dimension of action (Experiment 1). In a choice-RT procedure that assessed the effects of observing task-irrelevant actions on movement responses to letters, we found that hand and foot responses were facilitated in the presence of an observed action performed with a compatible body part, relative to an incompatible body part and when no action was observed. This is the first demonstration of effector or body part priming for hand and foot movements when this movement can be performed with both effectors, and it supports the assumption that imitation is mediated by the mirror neuron system. In addition, the present study used body part priming to test whether correlated sensorimotor experience is what enables us to relate observed actions to the *same* executed actions (Experiment 2). We conducted a training study in which some participants learned to respond to an observed action (e.g. hand movement) with the incompatible effector (foot movement), while others received the same exposure to action stimuli and motor responses, but the stimulus-response relationships were compatible. We found that body part priming was reduced following incompatible training, compared to compatible training, which supports the hypothesis that sensorimotor learning is necessary for the development of the capacity to match observed and executed actions; unimodal sensory and/or motor experience are not sufficient.

4.1. Body part priming and somatotopy in the mirror neuron system

The present study showed that the observation of a hand in motion selectively primes hand movement, rather than foot movement, while observation of a foot in motion selectively primes foot rather than hand movement. We used hand and foot actions that not only are routinely performed by both effectors, but that also share a high degree of spatial-configural overlap, in order to dissociate the effects of body part observation from those of movement observation. Our findings extend those of previous behavioral studies on body part priming (Bach and Tipper, 2007; Bach et al., 2007; Berger and Hadley, 1975) by showing that it occurs even when actions are matched on the movement dimension, and by demonstrating that body part priming gives rise to automatic imitation. While automatic imitation of index and middle finger lifting actions has recently been shown (Bertenthal et al., 2006), the present study is the first demonstration of body part priming of hand and foot movements that parallels the distinct somatotopy found in the mirror neuron system's response to the observation of hand and foot actions.

Experiment 1 showed that observed body parts are automatically matched with those used for responding in imitative behavior. These results, which were replicated in the pre-training test in Experiment 2, add substantial weight to the hypothesis that the mirror neuron system mediates overt behavioral imitation. Recent neuroimaging studies have shown that the neural response of the human mirror neuron system is sensitive to different body parts with which an observed action can be effected (Buccino et al., 2001; Sakreida et al., 2005; Wheaton et al., 2001; Wheaton et al., 2004). Buccino et al. (2001) and Wheaton et al. (2004) demonstrated that hand, foot and mouth actions selectively activate distinct regions of human ventral premotor and parietal cortex, which correspond

to the regions involved in action execution with these effectors. Action observation somatotopy in the human mirror neuron system is in line with similar findings from monkeys. Although single-cell studies in monkeys have identified mirror neurons in premotor cortex that respond independently of the effector (hand or mouth) used to perform an action (grasping a peanut), most monkey mirror neurons are effector-specific (see Ferrari et al., 2001). Consistent with non-overlapping motor circuits for different effectors (Alexander et al., 1990), there is minimal overlap between connections from somatotopic regions of ventral premotor cortex and SMA to primary motor areas (Tokuno et al., 1997).

Bach et al. (2007) argued that body part priming is the result of mapping an observed effector onto the observer's own body schema, in line with findings demonstrating common structural descriptions of the human body in healthy subjects and neuropsychological patients (Buxbaum and Coslett, 2001; Reed and Farah, 1995; Schwoebel et al., 2004). It has been indicated that such representations are engaged in imitation, which involves the selection of the appropriate body part to reproduce an action (Bach et al., 2007; Chaminade et al., 2005). Inferior parietal cortex, which is part of the mirror neuron system (e.g. Iacoboni et al., 1999), has been suggested to support a visuospatial description of one's own body, and thus may play a crucial role in body part coding for imitation (Chaminade et al., 2005). It is therefore possible that the body part priming effect on automatic imitation that was found in the present study arises in inferior parietal, rather than premotor, areas of the mirror neuron system.

By demonstrating that the mirror neuron system's sensitivity to effector variables, as indicated by neurological measures, is reflected in overt imitative performance, our study extends the growing body of research on the parallels between imitative performance and the activity of mirror neuron system. Research to date has indicated that movement variables have parallel effects on imitation and the mirror neuron system. Evidence that the mirror neuron system is sensitive to movement type has been provided by both single unit recording in monkeys, and electrophysiological and TMS studies in humans. Mirror neurons in F5 of monkey premotor cortex respond differentially to observation of different hand actions (e.g. holding versus tearing) and types of grip (e.g. power versus precision grip; di Pellegrino et al., 1992; Gallese et al., 1996; Rizzolatti et al., 1988). A similar sensitivity exists for different mouth actions (Ferrari et al., 2003). Human studies have indicated that observing different finger and different facial actions evokes differing activity in the mirror neuron system (Puce et al., 2000; Stefan et al., 2005; see also Strafella and Paus, 2000; Wheaton et al., 2001). A wealth of research on imitation has provided evidence that this neural sensitivity to movement type is reflected in overt behavior by showing that action observation primes the execution of actions of the same topography (e.g. Brass et al., 2001; Craighero et al., 2002; Dimberg et al., 2000; Kerzel and Bekkering, 2000; Press et al., 2005; Vogt et al., 2003).

Interestingly, our study found a facilitation effect from observing a compatible effector, but no interference when an incompatible effector was observed (Experiment 1). This raises the possibility that interference effects occur when the two response alternatives are mutually exclusive (e.g. the hand opening and closing), but are weaker or

absent when they are not exclusive (e.g. the foot and the hand lifting). As actions by different effectors can be performed simultaneously, the sight of an incompatible effector may not necessarily interfere with the ongoing movement. By contrast, interference from observation of an incompatible action may be inevitable for actions that are performed by the same effector. This possibility should be investigated in future research, also because the pattern of facilitation without interference seen in our RT data was not mirrored in the error rates. Among the studies that have used either two alternative actions of the same effector (Brass et al., 2001; Heyes et al., 2005; Kerzel and Bekkering, 2000; Press et al., 2005) or the same action of two alternative effectors (Bertenthal et al., 2006) to investigate motor priming when spatial compatibility was controlled, none has, to date, distinguished between the relative contributions of facilitation and interference to the automatic imitation effect.

Finally, our behavioral paradigm allows us to draw conclusions about the effector dimension of action at the representational level, which extend those drawn from neuroimaging. Buccino et al. (2001) and Wheaton et al. (2004) showed that observing hand actions and observing foot actions activates specific areas of premotor cortex known to be involved in executing hand actions and executing foot actions, respectively. However, from these data one cannot conclude that observation of hand actions activates the representation of a specific hand movement, and that observation of foot actions activates the representation of a specific foot movement. Our study shows that such effector-specific representations are indeed evoked; the sight of a hand action specifically

facilitated the execution of hand movements, and the sight of a foot action specifically facilitated the execution of foot movements.

4.2. Effects of learning and expertise on the mirror neuron system

The results of Experiment 2 provide strong support for the hypothesis that the development of the capacity to imitate depends on correlated sensorimotor experience. If overt imitative behavior is mediated by the mirror neuron system, our findings suggest that the matching of observed to executed action in the mirror neuron system may similarly develop on the basis of learned contingencies present in the environment. This suggestion echoes the findings of previous studies which have indicated that experience of some kind plays a role in development of the mirror neuron system. For example, neuroimaging research has shown that mirror neuron system activation by action observation varies with the observer's expertise. Greater activation in premotor and parietal cortices has been shown for ballet and capoeira dancers observing actions which they had been trained to perform (Calvo-Merino et al., 2005), dancers observing actions they rated they could perform well (Cross et al., 2006), and piano players observing piano playing (Haslinger et al., 2005). Järveläinen et al. (2004) found that the degree of primary motor cortex activation when observing actions involving chopsticks correlated with the amount of recent experience with using chopsticks. Furthermore, highly familiar actions activate human premotor cortex more than non-familiar actions (Grezes et al., 1998), and in musically naïve observers activation in mirror areas is elicited by the observation of guitar playing which they are required to imitate (Buccino et al., 2004;

Vogt et al., 2007), and by hearing sequences of tones which they had learned to play on the piano (Lahav et al., 2007).

These effects of learning and expertise could be the result of either unimodal sensory exposure (Ferrari et al., 2005), unimodal motor experience (Calvo-Merino et al., 2006), or correlated sensorimotor experience (Heyes, 2001; Heyes et al., 2005; Keysers and Perrett, 2004; Lahav et al., 2007; Obayashi et al., 2001). Experiment 2 explicitly examined the role of sensorimotor experience in such learning effects. Following incompatible training, in which action stimuli (e.g. hand movement) were paired with responses made with an incompatible body part (foot movement), participants demonstrated less body part priming than a control group (compatible training) who observed as well as performed both hand and foot movements equally often, but for whom the stimulus-response relationships were effector-compatible. Since the effects of training on effector priming differed for the two groups, the results of Experiment 2 provide specific support for the sensorimotor learning hypothesis. As we did not draw a direct contrast between sensorimotor training and pure visual learning or pure motor learning, we cannot rule out the possibility that either type of unimodal experience contributed to the training effect. However, since our findings show that specific types of sensorimotor training have specific effects on body part priming, they strongly suggest that sensorimotor correlations are necessary for learning that an observed action matches the same executed action; pure sensory and/or motor experience are not sufficient.

It is interesting to note that incompatible training reduced but did not completely eliminate the effector priming effect, suggesting that it is relatively strong. Such robustness would be expected from a sensorimotor learning account of imitation, as the visuomotor links subserving the body part priming effect shown in Experiment 1 and at pretest in Experiment 2 are the results of lifelong learning. Consistent with this interpretation, it was found in a study examining the experiential origins of spatial compatibility effects (Tagliabue et al., 2000) that a fixed amount of incompatible sensorimotor training reversed the Simon effect in children, but only eliminated it in adults.

Although previous studies have not dissociated the effects of unimodal and sensorimotor experience on the development of the mirror neuron system, close examination of some of their findings reveals that they are consistent with the sensorimotor hypothesis. Calvo-Merino et al. (2006) found that, even though mixed-gender training gives rise to similar visual exposure to male and female movements, the observation of ballet movements specific to one's own gender elicited greater mirror neuron system activation than the observation of other-gender movements. The findings of the present study suggest that dancers' sensorimotor learning, for example through self-observation in a mirror, rather than their unimodal motor experience, was responsible for these training-related modulations of mirror activity. Our findings also disambiguate reports that the observation of tool use activates mirror neurons in monkey premotor cortex in the absence of any motor experience with using tools (Ferrari et al., 2005; see also Arbib and Rizzolatti, 1999). Rather than the result of generalization of hand and

mouth actions to actions performed with tools on the basis of prolonged visual exposure to tool use alone, it is likely that this activation reflects the learning of new sensorimotor associations. For example, if tool use observation was reliably paired with the monkey's motor experience of reaching for food rewards, visual exposure to tool use would come to activate motor areas via sensorimotor links established in this manner.

4.3. An associative learning account of experience-related effects on imitation and the mirror neuron system

The Associative Sequence Learning (ASL) model (e.g. Heyes, 2001; Brass and Heyes, 2005) explains the effects of sensorimotor experience on the development of imitation and the mirror neuron system in terms of task-general principles of associative learning. ASL proposes that correlated experience of observing and executing the same action gives rise to bidirectional excitatory links, or 'vertical associations', between sensory and motor representations of the focal action, and that mirror neurons are a product of this learning process. Importantly, ASL stresses that the formation of vertical sensorimotor links, and therefore of mirror neurons, depends exclusively on the contiguity and contingency between action observation and execution; it does not involve a special-purpose learning mechanism that is intrinsically biased in favor of the formation of links between *matching* sensory and motor representations. Therefore, the model implies that nonmatching vertical associations, links between a sensory representation of one action (e.g. foot lifting) and a motor representation of a different action (e.g. hand lifting), will be formed when, as during incompatible training (Experiment 2),

observation of one action is paired with execution of another (see also Heyes et al., 2005). By showing that the repeated exposure to nonmatching sensorimotor pairings results in the weakening of body part priming normally found in imitation, we have shown that sensorimotor pairings are plastic rather than fixed or the result of experience-independent knowledge of which observed and which executed actions match. ASL proposes that specific experiences obtained in the course of development, such as during self-observation while moving and through being imitated by others or engaging in synchronous actions with others, provide us with the knowledge of what an action looks like when we do it, and thus enables us to imitate the actions of others. In the same manner, ASL proposes that correlated sensorimotor experiences endows mirror neurons with their distinctive property of responding to the same action regardless of whether it is performed or merely observed. This implies that if nonmatching sensorimotor pairings such as those provided in Experiment 2, were the norm during development, observation of an action would prime the execution of a nonmatching rather than a matching action, and lead to ‘counter-imitative’ behaviors as well as to ‘counter-mirror’ activation in the mirror neuron system.

4.4. Conclusion

In conclusion, this study demonstrates for the first time that automatic imitation, like the mirror neuron system, is sensitive to the body part with which an action is effected even when different body parts can be used to perform the same action. We have also shown that effector priming can be reduced by sensorimotor experience in which

observation of one body part in motion is paired with performance of the same action with a different part of the body. These findings support the assumption that the mirror neuron system mediates imitative behavior, and suggest that, whether or not it is mediated by the mirror system, our capacity to match observed with executed actions, originates in sensorimotor learning.

5. Experimental Procedure

5.1. Experiment 1

5.1.1. Subjects

Twenty-five right-handed volunteers (11 men, mean age: 25.4 ± 3.1 years) participated in the experiment. Ten of them were recruited through the Department of Psychology, University College London, and the remaining 15 were recruited via the Max-Planck-Institute for Cognitive and Brain Sciences in Leipzig. All had normal or corrected-to-normal vision. The experiment was carried out with local ethical approval and written consent of each participant.

5.1.2. Stimuli and apparatus

Each trial consisted of a warning stimulus and an imperative stimulus. Warning stimuli consisted of a compound image of a hand and a foot side by side in a resting position (see Fig. 5a for examples). Then, a letter was presented in the centre of the screen, situated between the hand and the foot images. The letter was the imperative stimulus, indicating a hand (H) or a foot (F) lifting response. At the same time, either the hand or the foot was shown in a lifted position, while the other effector remained unchanged (compatible and incompatible trials), or both effectors remained unchanged (neutral trials). Hand and foot lifting movement stimuli were task-irrelevant (see Fig. 5b for examples).

Fig. 5 about here

Hand and foot images showed a male and a female right hand and foot, taken from a side angle, and presented on a laptop computer screen (60Hz, 400mm diagonal, 96DPI) in color on a black background. The hand in the resting position occupied between 11.1° (female model) and 12.4° (male model) of the horizontal visual angle, and between 2.6° (female) and 3.6° (male) of the vertical visual angle. The foot in the resting position occupied between 12.2° (male) and 13.5° (female) of the horizontal, and between 9.5° (female) and 11.3° (male) of the vertical visual angle. In lifted positions, the hand was flexed at the wrist by an angle of 60° (male) to 65° (female) from the resting position. The foot was flexed at the ankle by an angle of 46° (male) to 51° (female) from the resting position. The replacement of a resting by a lifted posture during a trial created the appearance of lifting motion.

In pairs, hand and the foot images from the same model were always presented together. The location of the hand with the respect to the foot (e.g. the hand on the left and the foot on the right) was always the same for warning and imperative stimuli of each trial. Imperative stimuli consisted of a capital letter H or F printed in white ink, and occupied between .76° (F) and .86° (H) of the horizontal and .96° of the vertical visual angle.

Response onset of hand and foot movements was measured by recording the electromyogram (EMG) from the flexor carpi radialis (FCR) muscle of the right forearm

and the tibialis anterior (TA) muscle of the lower right leg. The response time (RT) interval began with the onset of the imperative stimulus, and ended with the onset of the EMG response (for further details see Heyes et al., 2005).

5.1.3. Design and procedure

Participants sat at a viewing distance of approximately 600mm in front of the stimulus presentation screen. The participant's right forearm lay prone in a horizontal position stretched out away from his/her body, supported by an armrest from the elbow down. The lower right leg was slightly stretched away from the body in the same direction as the arm, with the foot resting firmly on the floor. Participants made hand / foot movement responses by flexing the hand / foot at the wrist / ankle such that the front of the hand / foot moved upwards. After making each response, participants returned their hand or foot to the resting position.

Each trial began with the presentation of the warning stimulus, which was shown for a variable duration (800 to 1440ms) before it was replaced by the imperative stimulus (640ms). Participants were instructed to respond to the imperative stimulus as quickly as possible, without making errors, by lifting their hand or their foot as soon as they saw the letter "H" or "F", respectively. They were instructed to ignore the task-irrelevant movement of the hand or foot occurring at the same time. After the presentation of the imperative stimulus, the screen went black for 3000ms before the next trial.

Two blocks of 120 trials were presented, following a short practice block of 12 trials. Imperative letters and task-irrelevant movements were *compatible* (e.g. the letter H accompanied by an image of a lifted hand and a resting foot), *incompatible* (e.g. the letter

H accompanied by an image of a lifted foot and a resting hand) or *neutral* (e.g. the letter H accompanied by an image of a resting hand and a resting foot). The twenty-four trial types, defined by compatibility (compatible, neutral or incompatible), model (male or female), location (hand presented on the left of the screen, foot presented on the right, or vice versa) and relevant stimulus (H or F), were equiprobable and randomly intermixed within each block.

5.2. Experiment 2

5.2.1. Subjects

Thirty-two right-handed volunteers (16 men, mean age 25.6 +- 3.3 years), recruited through the Max-Planck-Institute for Cognitive and Brain Sciences in Leipzig, were screened for participation in the training study. Twenty-four of these volunteers, who showed an effector priming effect of more than 5ms prior to training, were randomly allocated to one of two training groups: compatible training and incompatible training. One participant did not complete the test subsequent to training as scheduled, and three were excluded because they failed to comply with task instructions during training. Therefore, data indicating the effects of training on effector priming were obtained for 20 participants (11 men, mean age 25.4 +- 3.4 years).

5.2.2. Stimuli and apparatus

Tests for effector priming before and after training were identical. The stimuli and the design of pre- and post-training tests were the same as in Experiment 1, with the

following exception. Neutral trials were not presented; they were replaced by an equal number of compatible and incompatible trials to keep the overall number of trials the same as in Experiment 1.

During the training phase, each trial consisted of a warning and an imperative stimulus. Warning stimuli consisted either of a compound image of a hand and a foot side by side in a resting position (compound effector), or of a single image of either a hand or a foot in a resting position presented in the centre of the screen (single effector). The warning stimulus was shown for a variable duration between 800 and 1280ms. The imperative stimulus consisted of either a hand or a foot in a lifted position. For compound effector stimuli, the other effector remained in the resting position. Imperative stimuli were shown for 640ms, and indicated different responses in the two training groups (see Design and procedure).

Hand and foot images were derived from four different models. In addition to the two models used in Experiment 1 and in pre- and post-training tests in Experiment 2, actions from two additional models were presented during training in order to encourage attention to the stimuli and to promote greater generalization of learning. These consisted of postures made by two female right hands and feet, taken from an angle that was from the side with an increased elevation (see Fig. 6). The hand in the resting position occupied between 11.1° and 11.4° of the horizontal visual angle, and between 5.3° and 6.1° of the vertical visual angle. The foot occupied between 11.5° and 12.9° of the horizontal, and between 11.2° and 12.2° of the vertical visual angle. In lifted positions, the hand was flexed at the wrist by an angle of 40° and 45° from rest, and the foot was flexed at the ankle by an angle of 16° to 22° from rest. To introduce further variation, a

second set of all the stimuli described above was constructed, which presented the same stimuli at 75% of their described sizes. All other aspects of stimulus presentation and response measurement were identical to Experiment 1.

Fig. 6 about here

5.2.3. Design and procedure (Training phase)

The Design and Procedure in the training phase were the same as during pre- and post-training tests, with the following exceptions. Participants in the incompatible training group were instructed to respond to the imperative stimulus by lifting their hand as soon as they saw a lifted foot, and by lifting their foot as soon as they saw a lifted hand. Participants in the compatible training group were instructed to respond to the imperative stimulus by lifting their hand as soon as they saw a lifted hand, and by lifting their foot as soon as they saw a lifted foot.

Training was conducted over the course of three consecutive days. On any given day, the training session consisted of 384 trials, divided into six blocks by short breaks, following a short practice block of 12 trials. There were 32 trial types, defined by imperative stimulus presentation (compound or single effector), model (four models: two showing hands and feet from a side angle, and two showing hands and feet from the side with an increased elevation), size (100% or 75%) and relevant stimulus (hand or foot

movement). These were equiprobable and randomly intermixed within each training session. Compound effector stimuli were equally often presented with the hand on the left and the foot on the right of the screen or vice versa.

Before the second and third training sessions, the participant was shown their mean RT and error rate for the previous training session(s) and given financial incentives to improve their performance in the next training session. The post-training test for effector priming was conducted approximately 24 hours after the third training session¹.

¹ This test was preceded by an fMRI scan, the results of which are reported elsewhere (Bird et al., in preparation). During the scan, hand and foot action execution consisted of actions other than lifting (e.g. rotation) and was not made in response to observed hand and foot actions.

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Figure captions:

Fig. 1 - Mean RTs (lines) and number of errors (bars) for foot responses (solid line and bars) and hand responses (dotted line and bars) to task-relevant letters as a function of irrelevant stimulus movement, Experiment 1. RT is a measure of the onset of the EMG response in FCR (forearm) and TA (lower leg) muscles. Vertical bars indicate standard error of the mean.

Fig. 2 - Mean RTs (lines) and number of errors (bars) for foot responses (solid line and bars) and hand responses (dotted line and bars) to task-relevant letters as a function of irrelevant stimulus movement for all 32 participants prior to training, Experiment 2. RT is a measure of the onset of the EMG response in FCR (forearm) and TA (lower leg) muscles. Vertical bars indicate standard error of the mean.

Fig. 3 - Mean RTs (lines) and number of errors (bars) for compatible (solid line and bars) and incompatible (dotted line and bars) training groups as a function of training session for the 20 participants in the training set, Experiment 2. RT is a measure of the onset of the EMG response in FCR (forearm) and TA (lower leg) muscles. Vertical bars indicate standard error of the mean.

Fig. 4 - Effector priming as a function of compatible and incompatible training for the 20 participants in the training set, Experiment 2. Figure 4a shows effector priming in RTs (numerical difference between RTs in incompatible and compatible trials) before

and after training for compatible (solid bars) and incompatible (dotted bars) training groups. Figure 4b shows effector priming in errors (numerical difference between the mean number of errors made in incompatible and compatible trials) for the two training groups in the same conditions. Vertical bars indicate standard error of the mean.

Fig. 5 - Examples of warning (a) and imperative (b) stimuli in compatible (top panel) and incompatible (bottom panel) trials. Note that in (b) the letter (“F”) is the imperative stimulus, indicating a foot response. This was accompanied by a task-irrelevant movement that was either compatible (top panel) or incompatible (bottom panel) with the required response. In neutral trial (not shown), both effectors remained at rest.

Fig. 6 – Examples of additional warning (a) and imperative (b) stimuli used during training sessions (Experiment 2). In (b) the effector movement is the imperative stimulus, indicating a foot response during compatible training or a hand response during incompatible training (top panel), and indicating a hand response during compatible training or a foot response during incompatible training (bottom panel).