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## Focusing on body sites: the role of spatial attention in action perception

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**Abstract** Humans use the same representations to code self-produced and observed actions. Neurophysiological evidence for this view comes from the discovery of the so-called mirror neurons in premotor cortex of the macaque monkey. These neurons respond when the monkey performs a particular action but also when it observes the same behavior in another individual. In humans, such direct links between perception and action seem to mediate action priming, where a response is facilitated when a similar action is observed. An issue that has not been fully resolved concerns the role of selective attention in these processes. Action priming appears to be an automatic process in the sense that the observed action can be irrelevant to the observer's task and nevertheless prime similar responses. However, it is not known whether attention has to be oriented to the action for these processes to be engaged. It is demonstrated here that spatial attention indeed has to be oriented to the action related body site for action priming to take place. Furthermore, if attention is oriented to the appropriate body site, there need be no visual cues to action for action priming to emerge.

### Introduction

Humans have a tendency to non-consciously and non-strategically mimic the bodily states of other people (e.g. Chartrand and Bargh 1999; Van Baaren et al.

2004). Similarly, action observation facilitates the execution of similar actions and interferes with the execution of different actions (Bach and Tipper 2006; Stürmer et al. 2000; Brass et al. 2000; Kilner et al. 2003). Even when this mimicking behavior is not overtly exhibited, some sort of covert imitation takes place. Transcranial magnetic stimulation (TMS) to the motor cortex elicits stronger muscle activity when the participants simultaneously observe an action involving the same muscles than when they see an action involving different muscles (for reviews, see Fadiga et al. 2005; Maeda et al. 2002).

This tendency to imitate seems to arise because the human sensorimotor system directly links observed actions to actions the observer can produce. Neurophysiological evidence for this view comes from the discovery of the mirror neurons in the macaque premotor cortex. Mirror neurons fire not only when the monkey performs a particular action, but also when it observes a conspecific carry out the same action (DiPellegrino et al. 1992; Gallese et al. 1996). Imaging studies have confirmed that a similar system is also present in humans (e.g. Grèzes et al. 2003; Buccino et al. 2001; Iacoboni et al. 1999; Koski et al. 2002), and this system has been linked to the automatic imitation of actions by imaging and behavioral studies (e.g., Jackson et al. 2006; Leslie et al. 2004; Wohlschläger and Bekkering 2002).

However, mimicry effects are not restricted to the observation of action. Even bodily states that are not actions per se are mimicked, such as facial expressions (e.g., Dimberg 1982; Vaughan and Lanzetta 1980), body postures (e.g., Bernieri 1988; Chartrand and Bargh 1999) or regular arm movements that are not directed towards a goal (Kilner et al. 2003). Of particular

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importance is that even another person's passive body parts are represented with respect to the same body schema that also structures the representation of the observer's own body (e.g., Reed and Farah 1995; Thomas et al. 2006). For instance, simply viewing the hand or neck of somebody else increases perceptual sensitivity at the same body site in the viewer (e.g., Tipper et al. 1998, 2001). These findings indicate that perception–behavior links are an overarching property of the sensorimotor system and that all stimulus features that can also be features of an individual's own responses are mirrored (Wilson 2001; Hommel et al. 2001; Prinz 1990).

This new view of the human (and monkey) sensorimotor system had a major impact on various areas of research. In recent years it provided a unifying framework for such diverse fields as the study of language evolution (Rizzolatti and Arbib 1998; Arbib 2005), infant learning and imitation (e.g., Elsner and Aschersleben 2003), social cognition (Barsalou et al. 2003; Preston and de Waal 2002; Carr et al. 2003), and the causes of the autistic disorder (Williams et al. 2001; Théoret et al. 2005; Sebanz et al. 2005; Dapretto et al. 2006). Yet, not much is known about the processes that underlie this mirroring capacity, and models explaining the properties of the mirror neurons are scarce (see, however, Oztop and Arbib 2002).

One unresolved issue is, for instance, the role of attention in these processes. That is, is the imitation of bodily states a fully automatic process, or does it require that attention be directed towards the observed actions?

The prior literature suggests that action mirroring is indeed highly automatic. For example, mirror neuron activity is elicited during action observation even when the monkey has no intention of acting upon the target object (e.g. Gallese et al. 1996). Similarly, in humans, several studies have demonstrated that action mirroring takes place even when the observed actions are irrelevant to the participant's own task (e.g., Brass et al. 2000; Stürmer et al. 2000). For example, Bach and Tipper (2006) required participants to identify two individuals with either foot or finger responses. The individuals were shown in video clips either kicking a soccer ball or typing on a keyboard. Although these actions were irrelevant and spatially separated from the faces relevant to the identification task, they nevertheless facilitated the execution of similar responses (i.e., faster foot responses when viewing the kicking action; faster hand responses for the typing action).

Of course, such findings do not confirm that action mirroring takes place in the absence of attention. In the studies on monkeys as in those on humans, biological or

apparent motion was present in the stimuli. Motion is a powerful exogenous cue that draws attention to the moving part of the stimulus display (e.g., Posner and Cohen 1984), namely the actions in question. It therefore remains to be seen whether imitative tendencies are also evoked in the absence of such exogenous cues, or when these cues draw attention away from the actions.

The present study investigates this question. In the first experiment, participants made foot and hand responses to distinguish between targets of two colors that were superimposed on static image versions of the action movies used in the study of Bach and Tipper (2006). The photographs depicted the actions of kicking a soccer ball and typing on a keyboard (see Fig. 1, upper panel). We hypothesized that seeing these actions would facilitate responses with the same limbs even though they were irrelevant to the primary color decision task. However, if attention is necessary for actions to be mirrored, then it should make a difference where the color targets appear on the screen. More specifically, the actions should only be mirrored if the colored targets appear on the critical limbs—thus drawing attention to the actions. In contrast, the observed actions should not facilitate similar responses when the colored targets appeared near the head of the observed person, thus drawing attention away from the action.

The second experiment further explored the role of attention in imitation. We investigated whether drawing attention to body sites is by itself enough to evoke action with the same body site, even when these body sites are not involved in an action. We employed the same task but now the colored targets were superimposed over photographs from which all cues for action were removed. That is, images of the same individuals are shown in the same general environments, but they are passively standing or sitting, so that the depicted body sites are not involved in an action (see Fig. 1, lower panel). Furthermore, there were no objects present that would automatically evoke actions (see Tucker and Ellis 1998), such as the soccer ball or keyboard. The critical issue was whether orienting attention to the feet and hands suffices to elicit responses with the same body sites, even when these sites are irrelevant to the task at hand.

## Experiment 1: Action perception

In the first experiment, the participants saw photographs depicting the end states of the actions of typing on a computer keyboard and kicking a soccer ball (see Fig. 1, upper panel for examples). Colored targets were superimposed on these photographs, and appeared

**Fig. 1** Examples of the stimuli used in the experiments. The *upper panel* shows the images presented in Experiment 1 depicting the actions of kicking a soccer ball and typing on a keyboard, with the colored targets superimposed either over the limb involved in the action or on the person's head. The *lower panel* shows the stimuli presented in Experiment 2 with the same person in situations where he is not acting and where no target objects implying action were visible. Again, colored targets were superimposed either over the head or the limbs of the person

### Experiment 1: Action perception



### Experiment 2: Viewing body sites



either near the head of the person, or near the limb involved in the action (on the hand when typing on the keyboard, or on the foot when kicking a soccer ball). The participants were instructed to press a foot key if the target was of one color, and a finger key if the target was of the other color. Thus, the responses of the participants were either similar or dissimilar to the irrelevant action presented on the screen.

If imitative tendencies are evoked automatically irrespective of where attention is distributed on the stimulus display, there should be no effect of target position (head or limb involved in the action) on the compatibility effects. Foot responses should generally be faster and more accurate when the kicking action is presented and finger responses should be faster and more accurate when the typing action is presented. However, if these processes depend on the allocation of spatial attention towards the (irrelevant) actions, then the actions should only give rise to imitative behavior if the colored targets appear near the critical limbs. Action observation should not evoke compatibility effects when the colored targets appeared near the head of the observed person, because attention is drawn away from the action.

### Method

#### Participants

Twenty-four students (17 females) ranging in age from 18 to 25 years participated in the study. The assignment

of colors (red/blue) to response keys (foot/finger) was counterbalanced across participants. Participants satisfied all requirements in volunteer screening and gave informed consent approved by the School of Psychology at the University of Wales, Bangor and the North-West Wales Health Trust, and in accordance with the Declaration of Helsinki. All participants had normal or corrected-to-normal vision.

#### Material and apparatus

The experiment was controlled by Presentation run on a 3.0 GHz PC running Windows XP. Sixteen pictures made up the stimulus set (see Fig. 1, upper panel for examples). They subtended 6° visual angle vertically and 8° horizontally, given an average viewing distance of 60 cm. The photographs either showed a person hitting a key on a computer keyboard, or a person kicking a soccer ball. A colored target (either red or blue) was superimposed (alpha: 50%) on these actions. It was placed either near the head of the acting person, or near the limb involved in the action (near the hand for the typing action, near the foot for the kicking action). The visual angle between the critical body sites of head and foot was 5.5° in the kicking scene and between the head and hand in the typing scene it was 4.7°. In one half of the photographs, the action direction was always from left to right. To exclude possible confounds arising from compatibility of movement direction and response, for each of these eight images a

mirror-inverted version was created, in which the movement direction was from right to left.

#### Procedure and design

The participants were seated in a dimly lit room facing a color monitor at a distance of 60 cm. After the computer-driven instruction and a short training phase of 16 trials the experiment proper started. It lasted for about 15 min and consisted of 320 trials. The sixteen photographs were presented at equal rates in a randomized order. Thus, there were 160 trials in which a finger response was required. In these trials the observed person was equally often typing on a computer keyboard (compatible) or kicking a soccer ball (incompatible). The colored targets either appeared near the acting effector or near the head of the person. In the remaining 160 trials the colored target had to be identified with a foot response. In these trials, he was again either kicking a ball (compatible) or typing on the computer keyboard (incompatible). Again, the colored target appeared either on the acting effector or near the head of the person. Thus, participants saw exactly the same photographs in the limb and head trials. The head trials only differed to the limb trials with respect to where the colored targets were presented on the photographs.

The course of each trial was as follows: After the participants initiated the trial by pressing the space bar with their left hand, the photograph was presented after 500 ms. They identified the color of the target by either pressing the foot pedal with their right foot or the enter button on the computer keyboard with their right index finger. Participants were instructed to give their judgment in the interval in which the photograph was on the screen (1,100 ms). If their judgment was correct, the next trial started. If they committed an error or did not react in the given response interval of 1100 ms. an error-message was displayed.

#### Results

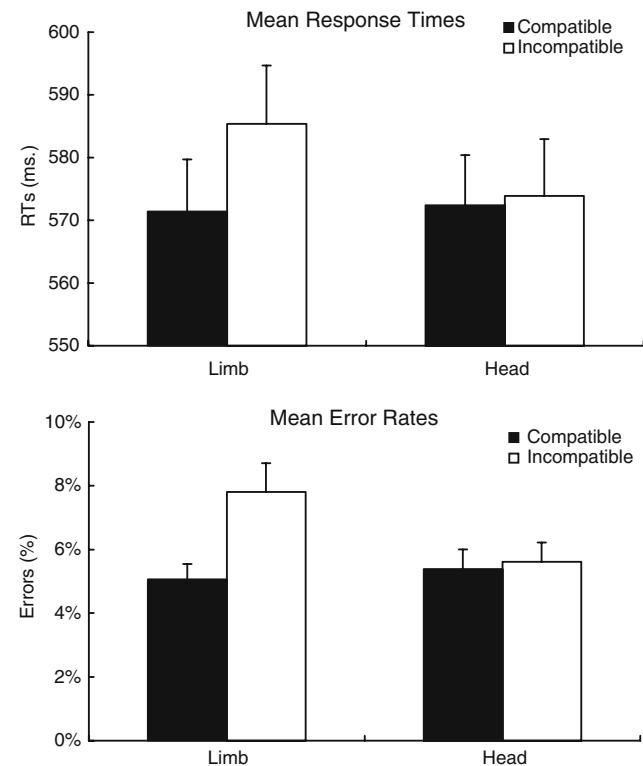
For the analysis of reaction times (RTs), trials where the participant made the wrong response or did not respond within the time limit were eliminated (6.4%). The remaining data were entered into repeated measures ANOVA with the factors compatibility (compatible/incompatible) and attention (to the limb involved in the action/to the head). There were main effects of compatibility ( $F[1,23] = 8.101, P = 0.008$ ) and attention ( $F[1,29] = 5.058, P = 0.032$ ), and a significant interaction of these factors ( $F[1,23] = 8.923,$

$P = 0.006$ ). Post hoc *t* tests showed that the advantage of compatible over incompatible responses was only present when attention was directed towards the limb involved in the action ( $P = 0.004$ ) but not when attention was directed towards the head ( $P = 0.25$ ).

The error rates were entered into the same ANOVA. Again, there were main effects of compatibility ( $F[1,29] = 11.093, P = 0.002$ ) and attention ( $F[1,29] = 4.671, P = 0.039$ ), plus an interaction of both factors ( $F[1,29] = 5.305, P = 0.029$ ). Post hoc *t* tests showed that the advantage of compatible over incompatible responses was present when attention was directed towards the limb involved in the action ( $P = 0.004$ ) but not when attention was directed towards the head ( $P = 0.66$ ) (Fig. 2).

#### Discussion

The present experiment demonstrated that action mirroring requires that spatial attention be directed towards the observed action. When the colored cues appeared near the limbs involved in the action, the results of the color decision task replicated prior reports of perceived actions facilitating compatible responses and/or interfering with incompatible



**Fig. 2** The vision-action-compatibility effects obtained in Experiment 1 (action perception) for RTs (upper panel) and error rates (lower panel)

responses (e.g., Brass et al. 2000; Kilner et al. 2003).<sup>1</sup> When, however, spatial attention was directed away from the action towards the head of the actor, the compatibility effects were completely eliminated in both RTs and Error Rates. Thus, only when observed actions are salient and at least some attention is directed towards them does the sensorimotor system directly link observed actions to one's own responses.

Experiment 2 investigates whether the mimicry effects in Experiment 1 are restricted to action observation, or whether drawing attention to resting body parts suffices to facilitate compatible responses that are performed with the same body part. This question is motivated by findings that suggest that—as is the case for action—the body parts of other persons are represented with respect to the observers own body, and might therefore also prime actions with these body parts.

## Experiment 2: Viewing body sites

Experiment 2 further explores the role of spatial attention for imitation. It addresses the question whether imitative tendencies can also be evoked in the absence of action perception, by simply drawing attention to the body sites that are also involved in the responses of the participants. As in Experiment 1, the participants had to discriminate between red and blue targets that were superimposed on photographs of a person. Now, however, all cues for action were eliminated from the stimuli. The persons were presented either standing on a field without a soccer ball visible and without performing a kicking action, or sitting next to a table from which the computer was removed and without performing a typing action (see Fig. 1, lower panel, for examples).

If the observation of action is a critical boundary condition for mimicry, all effects of mimicry should be abolished in the present experiment where no actions are presented, even when the colored targets appear on the body sites that were also involved in the

responses of the participants. If, however, viewing the body sites of another person can automatically prime actions with this body part of the viewer, then compatibility effects should still be observed.

### Method

#### *Participants*

Twenty-four students (23 females) ranging in age from 19 to 30 years participated in the study. One female participant was excluded from the analysis because she was not naïve to the purpose of the experiment. All other aspects of the participant selection were as in the previous experiment.

#### *Material and apparatus*

The apparatus was identical to that of the previous experiment. The materials again comprised 16 static images, from which all cues for action were eliminated (see Fig. 1, lower panel, for examples). In one half of the images, the actor was presented standing on the same field as in the soccer images of Experiment 1. However, the soccer ball was not present in the images and he was not performing a kicking action. Similarly, in the other half of the images, the person was sitting next to the same table as in the typing images of Experiment 1. However, no computer keyboard was present on this table, and the person was not performing a typing action. Colored targets were again superimposed on these photographs, either near the limbs (feet and hands) or the head of the actor, as in Experiment 1. Visual angles and exposure times were identical to Experiment 1. Again, the people could either be facing to the left or to the right.

#### *Procedure and design*

The experimental setup and the course of each trial were identical to the previous experiment.

### Results

The RTs were analyzed as before. Trials in which the participant made the wrong response or did not respond within the time limit were eliminated (6.9%). The ANOVA revealed a main effect of Attention ( $F[1,29] = 19.749, P = 0.0001$ ), and a marginally significant main effect of compatibility ( $F[1,29] = 4.019, P = 0.054$ ). The critical interaction between Attention and Compatibility was also replicated ( $F[1,29] = 9.483, P = 0.005$ ). Post hoc *t* tests showed that the advantage

<sup>1</sup> Please note that our paradigm does not allow us to differentiate between facilitation and interference accounts of the effect. The reason is that the 'head' condition is not an appropriate baseline condition. In the 'limb' condition, the colored targets could appear on either the feet or on the hands of the actor. In the 'head' condition, however, the colored targets always appeared on the actor's head. Thus, for any given trial, the probability for a target to appear on the head is 50%, whereas it is 25% for either of the limbs (feet or hand). This should speed up detection times of the targets in the 'head' condition, face, which might have speeded up detection times of the colored targets.

of compatible over incompatible responses was only present when attention was directed towards the limb, ( $P = 0.014$ ) but not when attention was directed towards the head ( $P = 0.864$ ). Comparing the size of the compatibility effects in Experiment 2 with Experiment 1 did not reveal any significant differences ( $F[1,58] < 1$ ).

The ANOVA analyzing the Error Rates showed no main effect of Compatibility, no main effect of attention, and no interaction between both factors (all,  $F[1,29] < 1$ ). However, numerically, the error rates show the same pattern as the RTs, with the advantage of compatible over incompatible responses being larger when attention was directed towards the limbs. Between-experiment comparisons tended to show that the compatibility effects were larger in Experiment 1 than in the present Experiment ( $F[1,58] = 3.937$ ,  $P = 0.054$ ) (Fig. 3).

## Discussion

Experiment 2 replicated the RT results of Experiment 1. Even though there were no cues to action in the stimuli, the responses of the participants were more

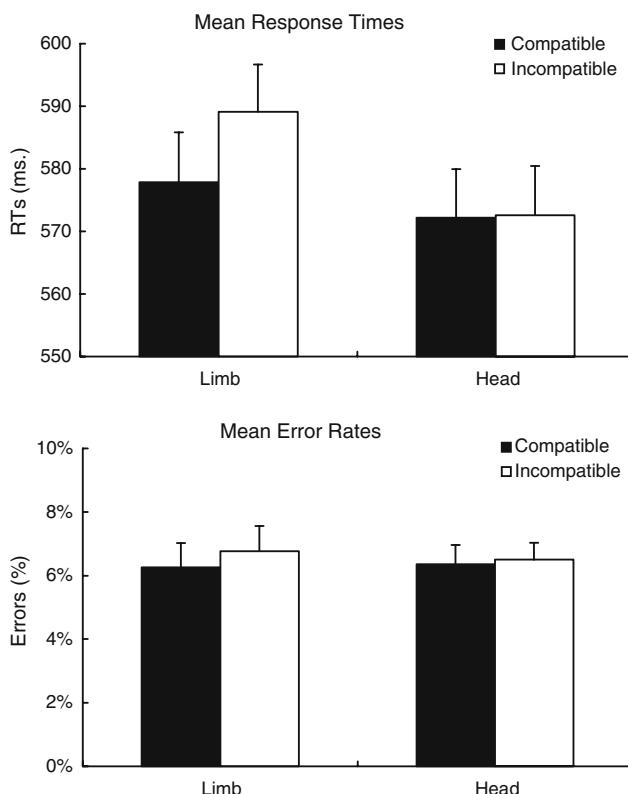
fluent when they involved the same limb that was also highlighted by the colored target. In contrast, all compatibility effects were eliminated when the colored targets appeared near the head of the individuals, thus drawing attention away from the limbs that were also involved in the responses of the participants. Therefore, Experiment 2 demonstrated that drawing attention to body sites suffices to facilitate responses involving the same body sites and/or to interfere with responses with different body parts, even when they are irrelevant and were not involved in an action.

## General discussion

Previous work has shown that actions are imitated automatically when the observed actions are irrelevant to the observer's own goals. Unresolved as of yet was the role of attention in these processes, as this was never controlled for or explicitly manipulated.

The current work resolves this issue. It replicated previous research demonstrating that the perception of task-irrelevant actions facilitates similar responses and/or interferes with dissimilar responses (e.g., Bach and Tipper 2006; Stürmer et al. 2000; Brass et al. 2000; Kilner et al. 2003). As in these prior studies, hand responses were faster and more accurate when observing a hand action than when observing a foot action, and vice versa for foot responses. However, the present work also demonstrated the critical role of spatial attention in these processes. In Experiment 1, compatibility effects were only observed when attention was drawn to the irrelevant actions by the colored targets relevant for the participant's primary task. When the colored targets drew attention away from the actions towards the head of the actor, the action system seemed to be effectively blind to the actions, and all compatibility effects were eliminated from RTs and error rates.

This suggests that one reason why observed actions were mimicked automatically in previous research, even when attention was oriented away from the action related body site, is because actions possess motion. Motion is a powerful exogenous cue that draws attention towards the moving stimulus properties, namely the actions in question. Hence in the previous studies of Bach and Tipper (2006), viewing video clips of action evoked compatibility effects, even though the participants' task required them to attend to the faces of the actors to enable identification of them. When, however, motion was removed from these stimuli, and static images were presented as in Experiment 1 here, visuomotor compatibility effects were no longer observed.



**Fig. 3** The vision-action-compatibility effects obtained in Experiment 2 (viewing resting body sites) for RTs (upper panel) and error rates (lower panel)

However, the role of attention in imitation seems to extend even further. Experiment 2 demonstrated that the allocation of attention to body sites is *by itself* enough to affect the action system. In this experiment, all cues to action were removed from the stimuli: the person was viewed passively standing or sitting and any potential target objects were also removed from the photographs. Nevertheless, similar (but smaller) compatibility effects as in Experiment 1 were observed when the colored targets simply drew attention to the body sites that were also involved in the responses of the participants. Thus, not action perception, but rather attention to a body site seems to be the critical boundary condition for imitative tendencies to emerge.

This finding is in line with the notion of a generalized body schema that represents locations on the observer's body and on the bodies of others in a common format (e.g., Reed and Farah 1995; Thomas et al. 2006). Perceiving the body parts of one's self or of somebody else rendered ones own discrimination of tactile stimuli on the same body sites more accurate (e.g., Tipper et al. 1998, 2001). Similarly, participants moving their legs were more efficient in detecting changes in a model's leg posture than in the model's arm posture, and vice versa for participants moving their arms (Reed and Farah 1995). As in the present study, this automatic coding of body parts seemed to be automatic; it was preserved even when the participants knew in advance where a possible change might occur (feet or hand).

Note, however, that these prior studies have only demonstrated effects on a purely sensory level. The present study is the first to demonstrate that drawing attention to the body site of another person suffices to prime actions with the same body site of the observer. Thus, generalized body schemas are not only involved in representing sensations on one's own and other's bodies, but are also involved in the production and perception of action (Goldenberg 1996). These data are also consistent with the view that the human sensorimotor system generally uses the same codes to plan one's own actions and to represent bodily stimuli in the environment (Wilson and Knoblich 2005; Wilson 2001; Prinz 1990; Hommel et al. 2001). Accordingly, all stimulus properties that can also be features of one's own actions can be used for action planning and will give rise to imitative tendencies when they are attended.

Future studies must address which neuronal structures mediate our effects. Current accounts of imitation stress the role of the so-called mirror neurons, as first described by DiPellegrino et al. (1992) for the macaque monkey. These neurons represent actions in the same way when they are observed or self-produced, and are

thus an ideal candidate for explaining the link between perception and action in imitation. Brain areas with mirror properties have also been discovered in the human parietal and premotor cortices (e.g., Grèzes et al. 2003; Iacoboni et al. 1999; Koski et al. 2002; Leslie et al. 2004). Consistent with the present findings of body part specific mirroring effects, these brain structures are somatotopically organized and represent foot and hand actions in anatomically distinct areas (Buccino et al. 2001).

Problematic for this account may be that the mirror neurons seem to be specifically involved in the representation of action. It has yet to be established if the known parietal and premotor mirror areas would also represent body parts in the absence of action perception, as suggested by Experiment 2 of the present study. Alternatively, there might be further areas with mirror properties that are specifically concerned with the coding of body part related information.<sup>2</sup> Lesion and imaging studies have associated the left inferior parietal lobe with disturbances of the body scheme, such that the patients could neither localize parts of their own body nor parts of the bodies of others (e.g. Goldenberg 1995). Consistent with the view that this area is also involved in imitation, a recent imaging study (Chaminade et al. 2005) found this area to be activated particularly for the selection of the appropriate body part (foot or hand) in imitation, but not for the selection of the appropriate action.

## Conclusion

Human imitative behavior is not as automatic as is typically assumed. For actions to be mirrored, spatial attention needs to be directed towards the acting body parts. In addition, our study showed that directing attention towards passive body parts of others is *by itself* enough to facilitate responses with these body parts. As such, our findings indicate some continuity between imitation in adults and the earliest forms of infant imitation, which, at first, only consist in the selection of the appropriate body part, but not yet in the performance of the appropriate action (Meltzoff and Moore 1997).

**Acknowledgments** The work was supported by a Wellcome Trust Programme grant awarded to SPT.

<sup>2</sup>The extrastriate body area (EBA) described by Downing et al. (2001) (Urgesi et al. 2004) also codes bodies and body parts, even in the absence of action perception. However, it does not seem to have a motor role (Peelen and Downing 2005), which makes its role in automatic imitation doubtful.

## References

- Arbib MA (2005) From monkey-like action recognition to human language: an evolutionary framework for neurolinguistics. *Behav Brain Sci* 28(2):105–124
- Bach P, Tipper SP (2006) Implicit action encoding influences personal-trait judgments. *Cognition* (in press)
- Barsalou LW, Niedenthal PM, Barbey A, Ruppert J (2003) Social embodiment. In: Ross B (ed) *The psychology of learning and motivation*, vol 43. Academic, San Diego, pp 43–92
- Bernieri FJ (1988) Coordinated movement and rapport in teacher-student interactions. *J Nonverbal Behav* 12:120–138
- Brass M, Bekkering H, Wohlschläger A, Prinz W (2000) Compatibility between observed and executed finger movements: comparing symbolic, spatial and imitative cues. *Brain Cogn* 44:124–143
- Buccino G, Binkofski F, Fink GR, Fadiga L, Fogassi L, Gallese V, Seitz RJ, Zilles K, Rizzolatti G, Freund H-J (2001) Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. *Eur J Neurosci* 13:400–404
- Carr L, Iacoboni M, Dubeau M-C, Mazziotta JC, Lenzi GL (2003) Neural mechanisms of empathy in humans: a relay from neural systems for action representation to limbic areas. *Proc Natl Acad Sci* 100:5497–5502
- Chaminade T, Meltzoff AN, Decety J (2005) An fMRI study of imitation: action representation and body schema. *Neuropsychologia* 45:115–127
- Chartrand TL, Bargh JA (1999) The chameleon effect: the perception-behaviour link and social interaction. *J Pers Soc Psychol* 76:893–891
- Dapretto M, Davies MS, Pfeifer JH, Scott AA, Sigman M, Bookheimer SY, Iacoboni M (2006) Understanding emotions in others: mirror neuron dysfunction in children with autism spectrum disorders. *Nat Neurosci* 9:28–30
- Dimberg U (1982) Facial reactions to facial expressions. *Psychophysiology* 19(6):643–647
- DiPellegrino G, Fadiga L, Fogassi L, Gallese V, Rizzolatti G (1992) Understanding motor events: a neurophysiological study. *Exp Brain Res* 91:176–189
- Downing PE, Jiang Y, Shuman M, Kanwisher N (2001) A cortical area selective for visual processing of the human body. *Science* 293:2470–2473
- Elsner B, Aschersleben G (2003) Do I get what you get? Learning about effects of self-performed and observed actions in infants. *Conscious Cogn* 12(4):732–751
- Fadiga L, Craighero L, Olivier E (2005) Human motor cortex excitability during the perception of others' action. *Curr Opin Neurobiol* 15(2):213–218
- Gallese V, Fadiga L, Fogassi L, Rizzolatti G (1996) Action recognition in the premotor cortex. *Brain* 119:593–609
- Goldenberg G (1995) Imitating gestures and manipulating a mannikin—the representation of the human body in ideomotor apraxia. *Neuropsychologia* 33:63–72
- Goldenberg G (1996) Defective imitation of gestures in patients with damage in the left or right hemisphere. *J Neurol Neurosurg Psychiatr* 61:176–180
- Grèzes J, Armony L, Rowe J, Passingham RE (2003) Activations related to "mirror" and "canonical" neurones in the human brain: an fMRI study. *NeuroImage* 18:928–937
- Hommel B, Müseler J, Aschersleben G, Prinz W (2001) The theory of event coding (TEC). A framework for perception and action planning. *Behav Brain Sci* 24:849–878
- Iacoboni M, Woods RP, Brass M, Bekkering H, Mazziotta JC, Rizzolatti G (1999) Cortical mechanisms of human imitation. *Science* 286:2526–2568
- Jackson PL, Meltzoff AN, Decety J (2006) Neural circuits involved in imitation and perspective-taking. *NeuroImage* 31:429–439
- Kilner JM, Paulignan Y, Blakemore SJ (2003) An interference effect of observed biological movement on action. *Curr Biol* 13:522–525
- Koski L, Wohlschläger A, Bekkering H, Woods RP, Dubeau M-C, Mazziotta JC, Iacoboni M (2002) Modulation of motor and premotor activity during imitation of target-directed actions. *Cereb Cortex* 12:847–55
- Leslie KR, Johnson-Frey SH, Grafton ST (2004) Functional imaging of face and hand imitation: towards a motor theory of empathy. *NeuroImage* 21:601–607
- Maeda F, Mazziotta J, Iacoboni M (2002) Transcranial magnetic stimulation studies of the human mirror neuron system. In: International Congress Series (1232). Recent Adv human brain mapping, pp 889–894
- Meltzoff AN, Moore MK (1997) Explaining facial imitation. A theoretical model. *Early Dev Parenting* 6:179–192
- Ozturk E, Arbib MA (2002) Schema design and implementation of the grasp-related mirror neuron system. *Biol Cybern* 87:116–140
- Peelen M, Downing P (2005) Is the extrastriate body area involved in motor actions. *Nat Neurosci* 8(2):125
- Posner MI, Cohen Y (1984) Components of visual orienting. In: Bouma H, Bouwhuis DG (eds) *Attention and performance X*. Erlbaum, Hillsdale, pp 531–556
- Preston SD, de Waal FBM (2002) Empathy: its ultimate and proximate bases. *Behav Brain Sci* 25:1–72
- Prinz W (1990) A common-coding approach to perception and action. In: Neumann O, Prinz W (eds) *Relationships between perception and action: current approaches*. Springer, Berlin Heidelberg New York, pp 167–201
- Reed CL, Farah MJ (1995) The psychological reality of the body schema: a test with normal participants. *J Exp Psychol Hum Percept Perform* 21:334–343
- Rizzolatti G, Arbib MA (1998) Language within our grasp. *Trends Neurosci* 21(5):188–194
- Sebanz N, Knoblich G, Stumpf L, Prinz W (2005) Far from action blind: representation of others' actions in individuals with autism. *Cogn Neuropsychol* 22(3–4):433–454
- Stürmer B, Aschersleben G, Prinz W (2000) Correspondence effects with manual gestures and postures: a study of imitation. *J Exp Psychol Hum Percept Perform* 26(6):1746–1759
- Théoret H, Halligan E, Kobayashi M, Fregnani F, Tager-Flusberg H, Pascual-Leone A (2005) Impaired motor facilitation during action observation in individuals with autism spectrum disorder. *Curr Biol* 15(3):84–85
- Thomas R, Press C, Haggard P (2006) Shared representations in body perception. *Acta Psychologica* 121:317–330
- Tipper SP, Lloyd D, Shorland B, Dancer C, Howard LA, McGlone F (1998) Vision influences tactile perception without proprioceptive orienting. *NeuroReport* 9:1741–1744
- Tipper SP, Phillips N, Dancer C, Lloyd D, Howard LA, McGlone F (2001) Vision influences tactile perception at body sites that cannot be directly viewed. *Exp Brain Res* 139:160–167
- Tucker M, Ellis R (1998) On the relations between seen objects and the components of potential actions. *J Exp Psychol Human Percept Perform* 24:830–846
- Urgesi C, Berlucchi G, Aglioti SM (2004) Magnetic Stimulation of Extrastriate Body Area Impairs Visual Processing of Non-facial Body Parts. *Curr Biol* 14:2130–2134
- Van Baaren RB, Holland RW, Kawakami K, van Knippenberg A (2004) Mimicry and prosocial behavior. *Psychol Sci* 15:71–74

- Vaughan KB, Lanzetta JT (1980) Vicarious instigation and conditioning of facial, expressive and autonomic responses to a model's expressive displays of pain. *J Pers Soc Psychol* 38:909–923
- Williams JHG, Whiten A, Suddendorf T, Perrett DJ (2001) Imitation, mirror neurons and autism. *Neurosci Biobehav Rev* 25:287–295
- Wilson M (2001) Perceiving imitatable stimuli: consequences of isomorphism between input and output. *Psychol Bull* 127:543–553
- Wilson M, Knoblich G (2005) The case for motor involvement in perceiving conspecifics. *Psychol Bull* 131:460–473
- Wohlschläger A, Bekkering H (2002) Is human imitation based on a mirror-neuron system? Some behavioural evidence. *Exp Brain Res* 143(3):335–341