



Hand–foot motor priming in the presence of temporary inability to use hands

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To verify if the link between observed hand actions and executed foot actions found in apraxias is essentially induced by the constant use of foot substituting the hand, we investigated if the vision of a grasping hand is able to prime a foot response in normals. Participants were required to detect the time-to-contact of a hand grasping an object either with a suitable or a less suitable movement, an experimental paradigm known to induce a priming effect. Participants responded either with the hand or the foot, while having free or bound hands. Results showed that for hand responses motor priming effect was stronger when the hands were free, whereas for foot responses it was stronger when the hands were bound. These data are interpreted as a further evidence that a difficulty to move affects specific cognitive functions and that the vision of a grasping hand may prime a foot response.

Keywords: Action observation; Mirror neurons; Motor cognition; Object observation; Sensory motor representations.

In the last decade there has been a great amount of research investigating the role of mirror neurons in recognizing/understanding observed actions. Mirror neurons have been firstly described in Area F5, in the ventral premotor cortex of the monkey (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992) and subsequently a similar mechanism has been described also in humans (Buccino et al., 2001; Cochin, Barthelemy, Roux, & Martineau, 1999; Decety et al., 1997; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995). These neurons have the property to fire both during action execution and during the observation of the same action executed by another individual. Therefore, a common

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sensory motor representation is activated during both execution and observation of the same action. The congruence between the action motorically coded by the neuron and that triggering the same neuron visually may be very strict: In this case only the observation of an action which is identical to that coded motorically by the neuron (for example, grasping with a finger precision grip) can activate it (“strictly congruent mirror neurons”). More often, this congruence is only broad; if this is the case, the observed and the executed action coded by the neuron match relatively to the goal of the action itself (for example, grasping) but can be achieved in different ways (for example, grasping with the mouth or with the hand) (“broadly congruent mirror neurons”) (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rochat et al., 2010). These and other experimental evidences (Ferrari, Rozzi, & Fogassi, 2005; Kohler et al., 2002; Umiltà et al., 2001) clearly indicate that action sensory motor representations do not code movements but the goal of the action, that is defined as the efficacy of the motor acts (see Rizzolatti & Sinigaglia, 2008, 2010).

An impressive demonstration of this sensory motor representations property comes from an fMRI study (Gazzola et al., 2007) in which the authors scanned two aplasic subjects, born without arms or hands, while they watched hand actions and compared their brain activity with that of typically developed (TD) controls. All subjects additionally executed actions with different effectors (feet, mouth, and, for controls, hands). Results have shown that during the observation of hand actions aplasic individuals robustly activated regions generally attributed to the mirror neuron system and involved in the execution of foot or mouth actions. Even if in the study the same result was found also for TD controls, the authors proposed that a possible reason of the neuronal association between motor programmes of the foot or mouth and the vision of hand actions “is that aplasic individuals often interact with TDs, and during joint actions, the hand actions of the TDs would often occur in synchrony with the foot and, to a lesser extent, the mouth actions of the aplasic individuals. This synchrony could have lead to the enhancement of Hebbian associations between the sight of hand actions and motor programmes for corresponding mouth or foot actions” (p. 1238). This possibility appears supported by recent results indicating that if individuals are submitted to an incompatible sensorimotor training in which, for example, they performed index finger movements while observing little finger movements and vice versa (Catmur, Walsh, & Heyes, 2007) or raised their hand whenever they saw a raised foot and raised their foot whenever they saw a raised hand (Catmur et al., 2008), the mirror-system responses are effector-reversed, as indexed by motor evoked potentials enhancement (Catmur et al., 2007), and by fMRI results (Catmur et al., 2008). Given that Gazzola and colleagues did not discuss the result found for TDs, the degree of association between the observed effector and other effectors

remains unclear. In particular, if the association results only with alternative effectors commonly used to execute the observed action or with effectors that never or almost never executed it also, and if the absence from birth of the observed effector is a necessary prerequisite to determine the association or if a temporary inability in using it, it is sufficient as well. Gazzola et al.'s paper was not able to test such issue. In the comparison between the putative hand Mirror System (MNS) for TDs defined by the brain regions common to the vision of hand actions and execution of feet and mouth actions and the same putative hand MNS but defined by the brain regions common to the vision and execution of hand actions (see their Figure 2, p. 1237) a part from a clear difference in the posterior areas of the left hemisphere, no appreciable differences could be found in the rest of the brain.

Therefore, to investigate the proposed issue we decided to use a psychophysical paradigm recently used to demonstrate that the exact instant at which a grasping hand touches an object is faster detected when grasping action's kinematic parameters correspond to those predicted by the observer on the basis of contextual information (Craighero et al., 2008). In this work subjects were required to observe two grasping actions performed towards the same object differing in their suitability to grasp that object and to "tap the desk at the instant at which the experimenter will touch the to-be-grasped object".

The hypothesis at the origin of the work was that to perform the task subjects should predict time-to-contact. Prediction must be driven by an internal motor replica of the to-be-detected action (Umiltà et al., 2001), based on the related sensory motor representation cued by the to-be-grasped object. This possibility is found in the visuomotor priming literature (Craighero, Fadiga, Rizzolatti, & Umiltà, 1998; Craighero, Fadiga, Umiltà, & Rizzolatti, 1996; Tucker & Ellis, 1998) indicating that objects automatically activate the related sensory motor representation, potentiating the actions they afford. Consequently, at the beginning of each trial, subjects should activate the sensory motor representation relative to the most suitable action given the existing physical constraints, such as the orientation of the to-be-grasped object. When the to-be-detected action corresponds to the activated sensory motor representation, response should be faster than when it does not correspond to it, as suggested by motor priming, the classical effect showing that an observed action facilitates a compatible action (Brass, Bekkering, & Prinz, 2001; Brass, Bekkering, Wohlschläger, & Prinz, 2000; Brass, Zysset, & von Cramon, 2001), indicating that stimuli and responses are represented in a commensurable format (Brass et al., 2000; Craighero, Bello, Fadiga, & Rizzolatti, 2002; Wohlschläger & Bekkering, 2002; see Prinz, 2002). When observers see a motor event that shares features with a similar motor event present in their motor repertoire, they are primed to repeat it. The greater the similarity between the observed event and the motor event, the stronger the priming is (Prinz, 2002). In the present case the

observed action should facilitate the tapping response because compatibility strongly primes the hand to act (see Brass et al., 2000). The results of the experiment confirmed this prediction (Craighero et al., 2008).

However, according to the motor priming effect, facilitation should be present only when the response is given by the hand. The finding that an effector different from the hand is influenced by a motor priming induced by a grasping hand would necessarily indicate the presence of an association between the two effectors, based on the sharing of a sensory motor representation (see Gallese et al., 1996) or, in other words, on the possibility that the different effector may be effective in reaching a similar aim.

Therefore, to verify the association between different effectors, in the present work we submitted participants to two experiments based on the same paradigm used by Craighero et al. (2008), but whereas in the first experiment participants were asked to respond by using their hand, in the second experiment they were asked to respond by using their foot. In this second case, the presence of a difference in detection velocity between the most suitable and the less suitable action should indicate that the foot is influenced by a motor priming exerted by the vision of the grasping hand, suggesting that an effector that never or almost never executed the observed action shares a goal usually reached by the hand.

Furthermore, we wanted to verify if a temporary inability to use the hand modulates the effects of motor priming, suggesting a fast plasticity in the association between different effectors. For this purpose, we introduced a second experimental manipulation: Both experiments consisted of two sessions—in one session both hands were free, and in the other session both hands were bound. In the first experiment participants were required to give the response by pressing a switch with the index finger of their right free hand in one condition, and with the fist of their bound right hand in the other condition. In the second experiment, they were required to press the switch with their right foot while having free or bound hands.

EXPERIMENT 1

Method

Participants. Twenty-six undergraduate students (aged 19–30; 12 female) of the University of Ferrara participated in the experiment after giving their informed consent. All subjects were right-handed according to the Oldfield norms (Oldfield, 1971).

The study was carried out along the principles laid down in the Helsinki Declaration and procedures were approved by the local ethical committee of the University of Ferrara.

Stimuli and procedure. Participants were seated on a comfortable chair in front of a desk. The experimenter, seated in front of the participant at a 120 cm distance, grasped with her right hand, with a natural velocity precision grip, a plastic parallelepiped (a solid body of which each face is a parallelogram; Figure 1) ($9\text{ cm} \times 6\text{ cm} \times 2.5\text{ cm}$) located 60 cm from both participant's and experimenter's frontal plane, at the centre of the body-midline of both of them. The parallelepiped was placed with its longer axis facing the experimenter and the participant. The experimenter grasped the parallelepiped either with fingers' opposition space parallel (30 trials) or perpendicular (30 trials) to her frontal plane (Figure 1). Fingers' opposition space (defining the factor type of grasping) was randomly ordered and the relative instruction to the experimenter was written on the computer screen, and not visible to the participants. Perpendicular fingers' opposition space characterizes the grasping faster detected in the study by Craighero et al. (2008) and named "Most suitable grasping", and parallel fingers' opposition space characterizes the named "Less suitable grasping" (Figure 1).

Participants were submitted to two experimental sessions of 60 trials, which differed for the condition state of the hands (free vs. bound). The order of sessions was balanced among participants.

In the free hand condition participants' right hand was placed onto the desk and their left arm relaxed on the arm rest. They were instructed to "Tap the desk with your right index finger at the instant at which the experimenter will touch the to-be-grasped object".

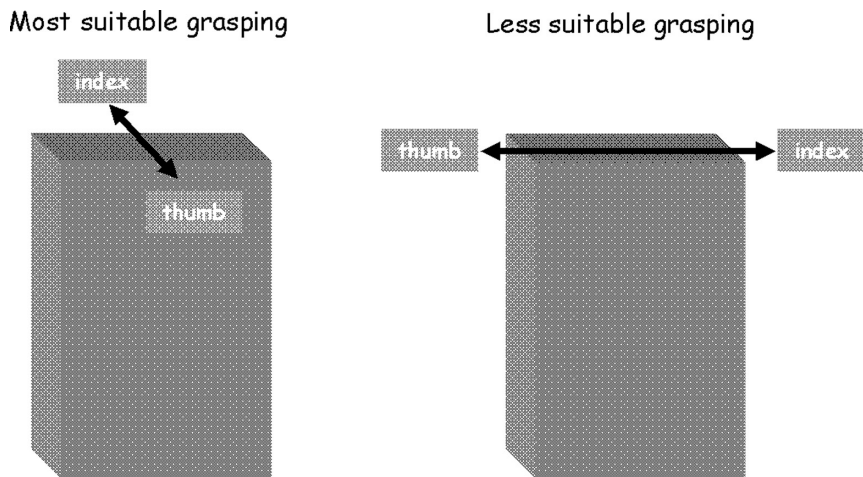


Figure 1. Schematic representation of the two grasping movements acted by the experimenter in the present experiments. The position of the index and thumb fingers is indicated with respect to the axis of the to-be-grasped object from the agent point of view.

In correspondence of the participant's right index finger a conducting pad was placed on the table, and the to-be-grasped object was covered by a conducting material. The pad and the object were linked to a low-current electric circuit. Both the experimenter and the participants were connected to ground, and time-to-contact of both the experimenter's hand and the object, and the participant's hand and the pad was indicated by the closing of the electric circuit at the instant of touch.

Response time was considered the time lag between the instant at which the demonstrator touched the object with either index finger or thumb and the instant at which the participant touched the pad. Errors were considered trials in which participants preceded or followed the agent's touch of at least 500 ms. All trials with errors were repeated (the number of error trials was irrelevant. Furthermore almost all the errors detected were attributable to temporary problems in the contact sensors).

In the bound hand condition, participants' both hands were in a fist posture, with the thumb inserted between the index and the middle finger, strapped up by a bandage. Both hands were placed onto the armrests with the wrist blocked by bandages. They were instructed to "Tap the armrest with your right fist at the instant at which the experimenter will touch the to-be-grasped object". The conducting pad was placed onto the right armrest and the bandages were such to allow a vertical movement of the fist. A second conducting pad was attached to participant's fist. Participants were required to maintain their right fist upraised until response, with a comfortable posture. By lowering the fist, the two conducting pads became in contact, closing the electric circuit and giving the response time. Except for this difference, the procedure was the same as in the free hand condition.

RESULTS

The mean response times (RTs) were submitted to an analysis of variance (ANOVA) considering as within-subjects factors state of the hands (free, bound) and type of grasping (most suitable, less suitable). Pairwise comparisons with the Newman-Keuls method were conducted whenever appropriate. The significance level was always set at .05.

Both main factors and the two-way interaction were significant. The significance of the factor state of the hands, $F(1, 25) = 6$, $MSE = 1175.9$, $p < .05$, indicated that the response given by the free hand (mean = 18 ms) was faster than the response given by the bound hand (34 ms).

The significance of the factor type of grasping, $F(1, 25) = 20.72$, $MSE = 133.3$, $p < .001$, indicated that the most suitable grasping (21 ms) was detected faster than the less suitable grasping (31 ms).

Very interestingly, the two-way interaction was significant, $F(1, 25) = 8.35$, $MSE = 114.2$, $p < .01$. Pairwise comparisons revealed that the most suitable grasping was detected significantly faster than the less suitable grasping but only in the free hand condition (free hand: most suitable = 10 ms, less suitable = 26 ms; bound hand: most suitable = 32 ms, less suitable = 37 ms) (Figure 2).

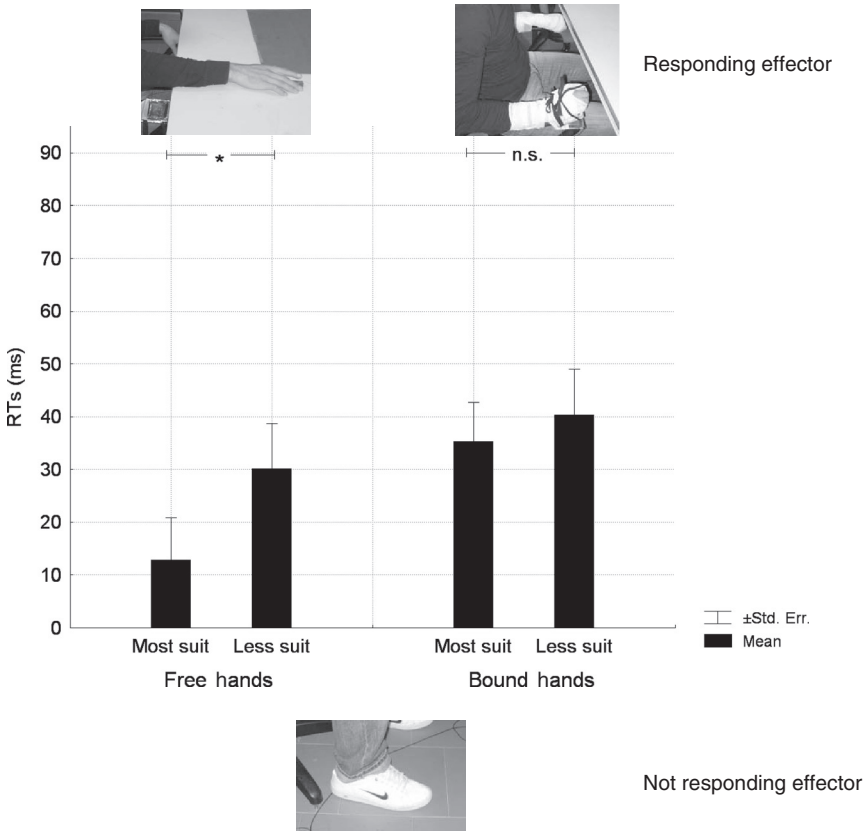


Figure 2. Experiment 1, hand responses. Mean response times (RTs; time lag between the instant at which the demonstrator touched the object with either index finger and thumb and the instant at which the participant touched the pad) for most suitable (Most suit) and less suitable (Less suit) grasping in the free hands and bound hands conditions. Thin lines above histograms indicate standard error of mean. Ordinates are in milliseconds. The asterisk indicates a statistical significance between the means, and n.s. indicates the absence of significance. The photos presented at the top of the figure show the responding effector (the hand) in the free hands condition (left) and in the bound hands condition (right). The photo presented at the bottom shows the not responding effector (the foot). To view this figure in colour, please see the online issue of the Journal.

Therefore, results of Experiment 1 indicated that the vision of a grasping hand modulated hand responses strongly when the hands were free to move. Experiment 2 was performed to investigate if the vision of a grasping hand was able to modulate foot responses as well, and if this modulation was influenced by the actual state of the hands (i.e., free or bound).

EXPERIMENT 2

Method

Participants. Twenty-six undergraduate students (aged 19–37; 15 female) of the University of Ferrara participated in the experiment after giving their informed consent. All subjects were right-handed according to the Oldfield norms (Oldfield, 1971). None of the subjects participated in the previous experiment.

Stimuli and procedure. The difference in the effector required to give the detection response was the only variation from the procedure used in Experiment 1.

In both free hand and bound hand sessions, participants were instructed to “Tap the floor with your right foot at the instant at which the experimenter will touch the to-be-grasped object”.

No vertical movement of the right fist was allowed. In correspondence of the participant’s right foot toe a conducting pad was placed onto the floor and a second one was attached to participant’s toe. Participants were required to maintain their right foot heel onto the ground and their toe upraised until response, with a comfortable posture. By lowering the toe, the two conducting pads became in contact, closing the electric circuit and giving the response time.

RESULTS

The mean response times (RTs) have been submitted to an ANOVA considering as within-subjects factors state of the hands (free, bound) and type of grasping (most suitable, less suitable). Pairwise comparisons with the Newman-Keuls method were conducted whenever appropriate. The significance level was always set at .05.

The factor type of grasping and the two-way interaction were significant.

The significance of the factor type of grasping, $F(1, 25) = 19.24$, $MSE = 329.20$, $p < .001$, indicated that the most suitable grasping (31 ms) was detected faster than the less suitable grasping (47 ms). However, the

significance of the two-way interaction, $F(1, 25) = 4.89$, $MSE = 206.22$, $p < .05$, and the relative pairwise comparisons revealed that the most suitable grasping was detected significantly faster than the less suitable grasping only in the bound hand condition (free hand: most suitable = 37 ms, less suitable = 47 ms; bound hand: most suitable = 25 ms, less suitable = 47 ms) (Figure 3).

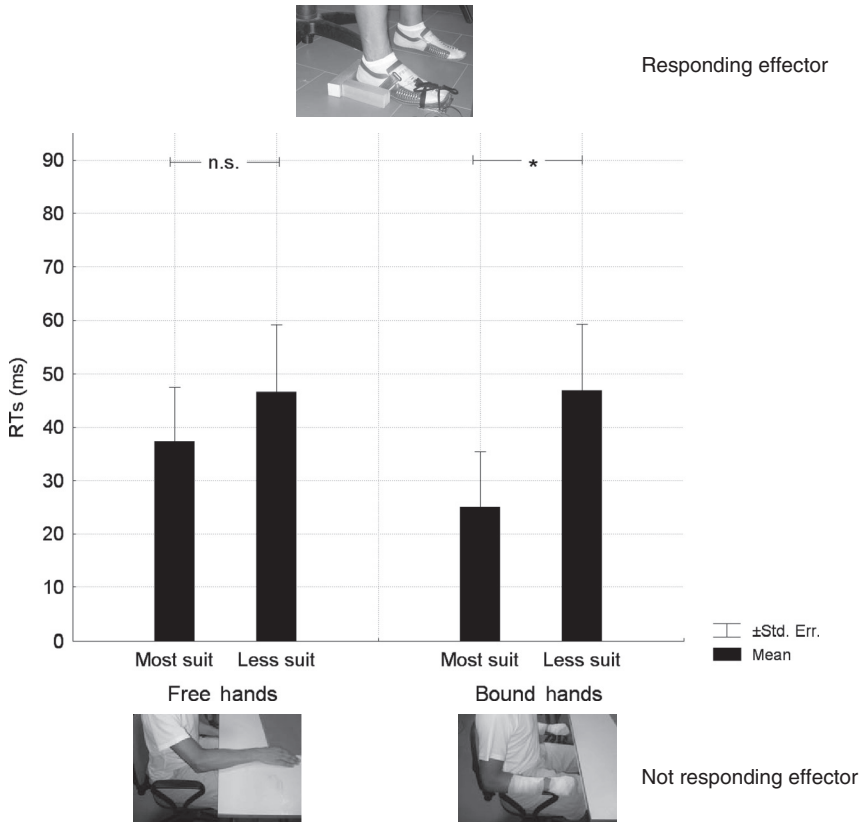


Figure 3. Experiment 2, foot responses. Mean response times (RTs; time lag between the instant at which the demonstrator touched the object with either index finger and thumb and the instant at which the participant touched the pad) for most suitable (Most suit) and less suitable (Less suit) grasping in the free hands and bound hands conditions. Thin lines above histograms indicate standard error of mean. Ordinates are in milliseconds. The asterisk indicates a statistical significance between the means, and n.s. indicates the absence of significance. The photo presented at the top of the figure show the responding effector (the foot). The photos presented at the bottom show the not responding effector (the hand) in the free hands condition (left) and in the bound hands condition (right). To view this figure in colour, please see the online issue of the Journal.

DISCUSSION

It has been claimed that perception–action coupling constitutes the fundamental mechanism of motor cognition (Sommerville & Decety, 2006). The term “motor cognition” refers to the hypothesis that much of how we think about others’ actions arises from the activation of our own motor representations (see Jeannerod, 2001). A variety of empirical evidence suggests that observed and executed actions are coded in a common cognitive (see Massen & Prinz, 2009) and neural (see Rizzolatti & Craighero, 2004) framework, enabling individuals to construct shared representations of self and other actions.

Neuronal evidence in the monkey reports that these shared representations may be built either on the sharing of both goal and effector or merely on the sharing of the goal and not of the effector (Gallese et al., 1996). However, in human research, evidence is present only for the former type of shared motor representations indicating that the sight of actions performed with different effectors specifically recruit cortex regions that are involved in the execution of actions with the same effector (Buccino et al., 2001; Gazzola, Aziz-Zadeh, & Keysers, 2006; Tai, Scherfler, Brooks, Sawamoto, & Castiello, 2004; Wheaton, Thompson, Syngeniotis, Abbott, & Puce, 2004).

In the present paper we wanted to verify if in normal individuals action observation may address shared representations even in the absence of a matching effector, as found by Gazzola and colleagues in aplasic patients (Gazzola et al., 2007). In particular, we wanted to investigate if in aphasics born without hands the link at a neuronal level between observed hand actions and executed foot or mouth actions (Gazzola et al., 2007) is determined by a direct matching between different effectors induced by the constant use of foot substituting the hand, which is absent in typically developed individuals, or if it might be always present also in normal individuals or only in normal individuals affected by a temporary limitation to perform hand actions.

To find a response we tested if the vision of a grasping hand determines motor priming effects on hand and foot responses both when the participants’ hands were free to move or bound.

In the first experiment participants were required to detect the exact instant at which a grasping hand touched the object by pressing a switch with the index finger of their right free hand in one condition, and with the fist of their bound right hand in the other condition. The required task was a motor task strongly involving subjects’ resources and hardly allowing a nonrequired concomitant motor task, such as the voluntary motor imagery of the expected action. The difference in detection times between the most suitable and the less suitable grasping action was bigger when the hands were free. There are two possible interpretations of the present results. The first

one deals with the possibility that when the hand was bound the visuomotor priming effect (i.e., objects automatically potentiate the actions they afford; Craighero et al., 1996, 1998; Tucker & Ellis, 1998) was not present. In other words, the vision of the object was not able to cue the most suitable action when the hand was unable to execute that action. Consequently, the motor priming effect (i.e., an observed action facilitates a compatible action; Brass, Bekkering, & Prinz, 2001; Brass et al., 2000; Brass, Zysset, & von Cramon, 2001) had no reason to be present since there was no compatible action to be primed. The second interpretation attributes the lack of motor priming effects to the impossibility for a bound hand to be primed by the vision of a grasping movement, even if the motor representation relative to the most suitable action was previously activated by the vision of the object. A possible third interpretation is that neither visuomotor nor motor priming effects were present when the considered effector was impaired to move.

The results of the second experiment seem to be in favour of the second interpretation. In fact, when the response was given by the foot, the difference in detection times between the most suitable and the less suitable grasping action was bigger when the hands were bound. The simplest explanation of these results is that the vision of the object was always able to activate the sensory motor representation of the most suitable action, even when the hand was bound. However, the motor priming effect influenced preferably the hand, and only when the hand was unable to move its effects on a different effector, such as the foot, could be revealed. Though, to confirm this possibility further experiments are required.

What is clear without additional investigations is the presence of a motor priming effect on the foot induced by the vision of a grasping hand, evidently indicating that these effectors may share a sensory motor representation.

The sharing of sensory motor representations between different effectors is not new. Raibert (1977) studied the phenomenon by attempting to write a sentence using different effectors: his right (dominant) hand, his right arm with the wrist immobilized, his left hand, his teeth, and his foot with the pen taped to it. The resulting sentences revealed an amazingly similar writing style even though they were written with different limbs and muscles, indicating that the same motor programme was driving their movements. The possibility that motor programmes consist of a representation of the goal of an action not dealing with the exact specification of which muscles should be implicated in its execution is clearly supported by the functional properties of motor neurons (devoid of any sensory function) present in the ventral premotor cortex of the monkey. Microstimulation (Hepp-Reymond, Hüsler, Maier, & Qi, 1994) and single neuron studies (Rizzolatti et al., 1988) showed that neurons in Area F5 of ventral premotor cortex selectively discharge during goal-directed hand/mouth actions. The specificity of the goal seems to be an essential prerequisite in activating these neurons. The

same neurons that discharge during grasping, holding, tearing, and manipulating are silent when the monkey performs actions that involve a similar muscular pattern but with a different goal (e.g., grasping to put away, scratching, grooming). Furthermore, the same neuron may discharge when the monkey grasps an object with its right or left hand or with its mouth, strongly indicating that these neurons code the goal of the action, independently from the acting effector.

The presence of hand-foot motor priming is an indirect evidence that in typically developed humans action representations may be built on the sharing of the goal and not of the effector, similarly to what happens for broadly congruent mirror neurons in monkeys (Gallese et al., 1996).

A further result, no less interesting than the former one, consists in the evidence that the actual physical state of the effector mainly involved in the to-be-performed cognitive task has an influence on performance. This evidence has been previously considered as an indicator of a causal relationship between motor system involvement and specific cognitive functions, in contrast with the interpretation believing the motor involvement as a mere epiphenomenon (see Craighero & Rizzolatti, 2005). This idea goes even further to what claimed by motor cognition hypothesis, implicating that not only the coding of others' actions but also other cognitive functions, such as orienting of attention and motor imagery, do not require a control system separated by sensory motor circuits but they derive from the activation of the same circuits that, in other conditions, determine perception and motor activity (Rizzolatti & Craighero, 1998).

Results of the first experiment indicated that when the hands were bound the detection response was less influenced by the type of observed grasping. From the previous discussion it emerges that the favoured interpretation of these results is that a bound hand is less primed by the vision of a grasping movement. In other words, the actual physical state of the responding effector cancelled the benefits deriving from the prediction of the to-be-detected action induced by the vision of the object. We interpret this result as an evidence of a causal relationship between the actual possibility to execute the observed action and the chance to use the related motor representation to perform the task.

The demonstration that a similar mechanism is present for orienting of attention comes from a series of experiments investigating the ability to orient spatial attention and the possibility to execute an eye movement towards the to-be-attended position. Evidence from brain imaging (Corbetta et al., 1998; Nobre, Gitelman, Dias, & Mesulam, 2000; Nobre et al., 1997), behavioural (Sheliga, Riggio, Craighero, & Rizzolatti, 1995; Sheliga, Riggio, & Rizzolatti, 1994, 1995), neurophysiological (Moore & Fallah, 2001), and neurological (Heide & Kömpf, 1998; Heilman, Watson, & Valenstein, 1993) studies suggests that orienting of spatial attention and planning eye

movements are strictly linked both at the functional and anatomical levels, even in tasks in which no eye movements are allowed. A psychophysical experiment investigating orienting of attention in monocular vision in patients affected by VI nerve palsy (Craighero, Carta, & Fadiga, 2001) showed that whereas during nonparetic eye vision stimulus detection in the attended location was faster than that in the unattended one, during paretic eye vision no difference in detection speed was present, indicating that the oculomotor palsy impairs orienting of attention. A similar result was also found for exogenous orienting of attention (Smith, Ball, Ellison, & Schenk, 2010; Smith, Rorden, & Jackson, 2004). The finding that eyes and attention share a common limit stop was further confirmed by a subsequent experiment on normal participants (Craighero, Nascimben, & Fadiga, 2004) demonstrating that in monocular vision visuospatial attention was significantly modulated by a forced posture of the eye simulating an oculomotor deficit. When the eye was kept at an extreme position in the orbit, limiting the execution of a saccade towards the temporal hemifield, no benefits for the cued position in the temporal hemifield were present, whereas they were still present when the cued position was shown in the nasal hemifield, towards which the eye was able to move.

Similarly, a series of experiments indicate that even motor imagery depends on the actual possibility to execute the related movement, impaired both by a pathology or by a constrained posture. Motor imagery consists of a dynamic process in which a subject feels him or herself executing a movement. It has been proposed that the mental simulation of an action relies on the same mechanisms as its actual execution, except for the absence of overt motor behaviour (Jeannerod, 1994). The presence of a parallelism between imagined and executed actions has been confirmed by several behavioural and neuroimaging data demonstrating that motor areas in the brain play an important role in motor imagery (see Olsson & Nyberg, 2010; see Munzert, Lorey, & Zentgraf, 2009). Upper limb amputees show difficulties in a left/right hand judgement task that implicitly requires motor imagery (Nico, Daprati, Rigal, Parsons, & Sirigu, 2004) and comparable results have been reported for patients with congenital hemiparesis (Steenbergen, van Nimwegen, & Crajé, 2007) and cerebral palsy (Mutsaerts, Steenbergen, & Bekkering, 2007). Starting from the evidence that motor imagery facilitates motor evoked potentials in muscles normally active during the movements to be imagined, Vargas and colleagues (Vargas et al., 2004) submitted participants to a transcranial magnetic stimulation experiment in which they had to perform a motor imagery task while asked to maintain different hand positions. Results have shown that when the hand position was compatible with the imagined movement, corticospinal excitability was higher than when the hand position was incompatible. The indication that the actual limb posture affects the process of motor imagery

(Parsons, 1994; Sirigu & Duhamel, 2001) comes also from an experiment in which subjects were asked to verbally judge the laterality of hands and feet pictures in two different postural conditions (Ionta, Fourkas, Fiorio, & Aglioti, 2007). In one condition, subjects kept hands on their knees in anatomical position; in the other, their hands were kept in an unusual posture with intertwined fingers, behind the back. Results showed that mental rotation of hands but not of feet was influenced by changes in hands posture.

All these data point out that the motor system greatly influences the way in which individuals perceive and elaborate the external world (Fadiga & Craighero, 2004; Rizzolatti & Craighero, 2004; Rizzolatti, Ferrari, Rozzi, & Fogassi, 2006; Rizzolatti & Sinigaglia, 2010) and that this influence may vary very quickly, according to the actual ability to move. Consequently, given that a temporary modification of the ability to move by no means may determine a modification in the hardware of neuronal connections, the influence of the motor system on cognitive functions seems to reflect more the functional role of the motor system than its anatomical organization.

In conclusion, the present results suggest that the link between observed hand actions and executed foot actions shown by Gazzola and colleagues in aphasics (Gazzola et al., 2007) is also present in typically developed individuals. However, this association between different effectors may be revealed only when the observed effector is impaired to move, maybe subserving the economy principle of distributing goal duties to the most appropriate effector.

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