Hand action preparation influences the responses to hand pictures

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Abstract

The relations between stimuli triggering a hand grasping movement and the subsequent action were studied in normal human participants. Participants were instructed to prepare to grasp a bar, oriented either clockwise or counterclockwise, and to grasp it as fast as possible on presentation of a visual stimulus with their right hand. The visual stimuli were pictures of the right hand as seen in a mirror. In Experiment 1, they represented the mirror image of the hand final posture as achieved in grasping the bar oriented either clockwise or counterclockwise. In Experiment 2, in addition to the pictures of Experiment 1, another two pictures, obtained rotating the hands represented in the previous ones of 90°, were also used. Both experiments showed that the reaction times were faster when there was a similarity between hand position as depicted in the triggering visual stimulus and the grasping hand final position, the fastest responses being those where this similarity was the closest. In addition, Experiment 2 showed that reaction times to not rotated stimuli were faster than reaction times to the rotated stimuli, thus excluding a simple stimulus–response compatibility explanation of the findings. The data are interpreted as behavioral evidence that there is a close link between specific visual stimuli and specific motor actions. A neurophysiological model for this visuo-motor link is presented. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Actions are internally represented independently of whether or not they are subsequently executed. Anatomical evidence indicates that action representation results from the activity of the core part of the same cortical circuits that mediate action execution [25,26]. Action representation can lead either to an explicit image of the represented action (motor mental imagery) [11–14,19,38,48,49] (see for review Ref. [25]) or mediate implicit mechanisms, such as those involved in recognition of body parts shown in different orientations [18,33–35]. Recently, another form of implicit action representation has been demonstrated. When an individual observes objects or actions performed by another individual, there is an activation of the motor circuits involved in the execution of similar actions [6,19,20,22,30,44].

A series of experiments in monkeys provided cues on the possible mechanisms that subserve action representation in response to visual stimuli. In these experiments, it was shown that the premotor cortex of primates contains a 'vocabulary' of potential motor actions [43] that can be activated endogenously or following presentation of specific stimuli [16,32,42]. Endogenous activation occurs before action execution. Its duration depends on the behavioral requests. Passive activation occurs when the individual either observes an object (object-related activation) or a motor action made by another individual (action-related activation).

The 'object-related' activation is based on two main operations: extraction of the intrinsic visual properties of the object (size, shape and orientation) and matching the extracted visual description with the appropriate action. These operations are carried out by neurons located in area AIP of the parietal lobe and neurons located in premotor area F5 [41,45] (see for review Ref. [27]).

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Neurons of area F5 that respond to object presentation even in the absence of a subsequent movement and discharge in association with movements related to that object are called 'canonical neurons' [41].

The 'action-related' activation is based on the visual description of the observed action and its matching with a motor representation of a similar action. These operations appear to be performed in a circuit formed by the cortex of the superior temporal sulcus, the parietal area PF and area F5. Neurons of area F5 that discharge both when the monkey performs an action and when it observes another individual performing the same action are called 'mirror neurons' [16,42].

The organization of the anatomical connections between F5 and related parietal areas and the functional properties of these areas indicate a bi-directional influence of one area on another [29]. Thus, the activation of the parietal lobe areas connected with F5 determines the activation of this area, but, reciprocally, an activation of F5 determines an activation of those parietal areas. This arrangement has an important functional consequence. When F5 becomes active endogenously (as in motor preparation), there is not only a motor action representation, but also a concomitant pictorial representation of objects and/or actions.

Some recent experiments carried out in humans support the notion that motor preparation determines the activation of a sensory representation of the object that has to be grasped. These experiments showed that the time to initiate a grasping movement to a 3D object depends on the relation between the intrinsic properties of the object to be grasped and the visual properties of the imperative stimulus. Reaction time decreased when the intrinsic properties of the visual object used as imperative stimulus were congruent with those of the object to be grasped ('visuo-motor priming') [8,10]. It is important to note that the subject did not need to analyze voluntarily the imperative stimulus because the response to it was mandatory.

In a further series of experiments, the converse effect was shown. The preparation to grasp an object produced faster processing of stimuli congruent with that object. The facilitation was present also when, after preparation of hand grasping, subjects were required to refrain from executing the prepared grasping movement and to respond with a different effector [9].

The aim of the present work was to test whether motor preparation to grasp objects differently oriented would influence the response to visually presented hand pictures. For the neurophysiological considerations discussed above, we hypothesized that hand pictures congruent with the hand shape achieved at end of the grip would be responded to faster than hand pictures lacking such congruence.

The basic paradigm employed in the present experiment was similar to that used by Craighero et al. [9]. The subjects were required to prepare a grasping movement to one of two bars that differed in orientation. As visual stimuli hand postures representing the end point of grasping as performed by an individual located in front of the subject were used [28,46]. Some of them represented hand postures that were congruent with the prepared grasping response, others were incongruent. The subjects had to discriminate between various hand shapes and execute the response. The results showed that the response given to congruent visual stimuli was facilitated by motor preparation.

2. Experiment 1

This experiment was designed to study the relations between stimuli triggering a hand grasping movement and the subsequent action. Participants were instructed to prepare a hand grasping movement to one of two bars that differed in orientation (45° clockwise or counterclockwise). They had to execute the prepared grasping movement on presentation of a given hand shape (go signal) on the computer screen. The presented pictures were images of the right hand as seen in a mirror (see Fig. 1A,B). One represented the posture of the hand when it reached the bar clockwise oriented (Fig. 1A), the other represented the posture of the hand when it reached the bar counterclockwise oriented (Fig. 1B). At the presentation of the go signal, the subject had to respond either by grasping the clockwise or the counterclockwise oriented bar (see below). The hand shape represented in the picture was, in one condition, the mirror image of the final hand posture required as a response (congruent condition), while in the other this correspondence was lacking (incongruent condition). By comparing the grasping movement latencies in congruent and incongruent conditions, we were able to assess whether a motor preparation influences the discrimination of a static hand.

2.1. Method

2.1.1. Participants

Twelve students of the University of Parma between the ages of 20 and 25 years served as participants. All were right-handed, had normal or corrected-to-normal visual acuity, were naïve as to the purposes of the experiment and gave their informed consent.

2.1.2. Procedure

The experiment took place in a sound-attenuated room, dimly illuminated by a halogen lamp. A personal computer (Pentium, Intel) was used for stimulus generation and response recording. Particular care was taken in order to ensure the correct timing of stimuli presentation with respect to monitor vertical retrace and thus, to ensure a correct reaction time measurement. Stimu-

lus presentation and reaction time (RT) recording were controlled by using specifically designed software realized by the authors. The participants were seated in front of the computer screen with their head positioned on a chin-rest. The distance between the computer screen and participants' orbital plane was 57 cm.

The response consisted in grasping, as fast as possible, a plastic bar (6×2.5 cm) inserted inside a rectangular groove, hollowed in a plastic disk (diameter: 12 cm) placed on a horizontal plane (Fig. 1). The required grasping consisted in inserting the index finger in the hole in front of the bar and the thumb in the hole behind the bar and lifting the manipulandum. On 50% of trials, the bar orientation was 45° with respect to the participants' body (i.e. clockwise) and in the other 50%, the bar orientation was $-45°$ (i.e. counterclockwise).

The screen background was black. Stimuli to be discriminated consisted in pictures of the right hand as seen in a mirror (Fig. 1A,B). One represented the

posture of a hand when it had reached the bar clockwise oriented, the other represented the posture of the hand when it reached the bar counterclockwise oriented. Pictures were digitized from video recordings and showed in 16 gray levels.

Before the experiment, participants were briefly trained to grasp the bar, which was oriented clockwise or counterclockwise, without looking at it. Bar orientation was randomly changed trial by trial and the participants were informed, at the beginning of each trial, about the orientation of the bar by the word 'left' (counterclockwise) or 'right' (clockwise) on the computer screen. When ready, they initiated the trial by pressing a switch with their right hand palm. They had to maintain the switch pressed until the response onset. The switch was placed on the right side of the participant on a horizontal plane. The beginning of the trial was signaled by the appearance at the center of the computer screen of a gray background square ($7 \times 7°$) with a white fixation cross at its center. After a variable interval (3–5 s), the stimulus was presented at the center of the gray square around the fixation cross that remained visible. The task was a go/no-go experiment. Participants were submitted to one session subdivided into two blocks. Pictures A and B were presented in a randomized sequence. The same sequence was repeated during the two blocks. Each picture was presented 28 times. Participants were required to respond, as fast as possible, only to one of the two presented stimuli according to instructions given at the beginning of each block. RT was the time between the go stimulus and the releasing of the switch. The order of blocks was balanced among participants. Participants responded by grasping and lifting the bar with their right hand. The bar was located in front of the switch (distance: 12 cm) out of the participant's sight. The combination between pictures and bar orientation was set in order to obtain for each go-picture 14 grasping responses towards the clockwise bar and 14 grasping responses towards the counterclockwise bar.

Four types of error arose from inappropriate responding. They were Anticipations and Retardations in the initiation of the grasping movement, Wrong responses and Wrong movements. As anticipation errors were considered the RTs shorter than 120 ms. As retardation errors were considered the RTs longer than 1000 ms. Wrong responses were responses given to no-go stimuli. These three types of error were controlled on line by the computer and automatically discarded. As wrong movement errors were classified those trials in which participants executed the wrong grasping movement (e.g. participants performed the grasping movement to the clockwise bar when the orientation of the bar was instead counterclockwise). Movement accuracy was controlled visually by an experimenter located behind the participant. All trials
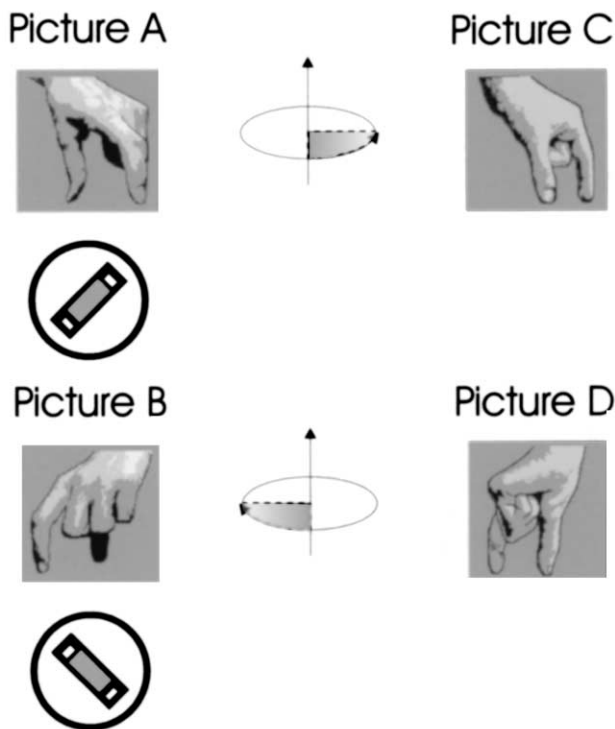

Fig. 1. Visual stimuli used in Experiment 1 (Pictures A and B) and in Experiment 2 (Pictures A–D). Pictures A and B represent a right hand executing the required grasping response, as seen in a mirror. Picture A represents the mirror image of a hand when it reaches the bar clockwise oriented. Picture B represents the mirror image of a hand when it reaches the bar counterclockwise oriented. Picture C results from a rotation of 90° of picture A towards right (clockwise); picture D results from a rotation of 90° of picture B towards left (counterclockwise). Note that in picture C, the index finger position is on the right of the thumb as in picture A, while in picture D the index finger position is on the left of the thumb, as in picture B. The drawings below pictures A and B represent the bar oriented clockwise and the bar oriented counterclockwise, that the participants were instructed to grasp in Experiment 1 and 2, respectively.
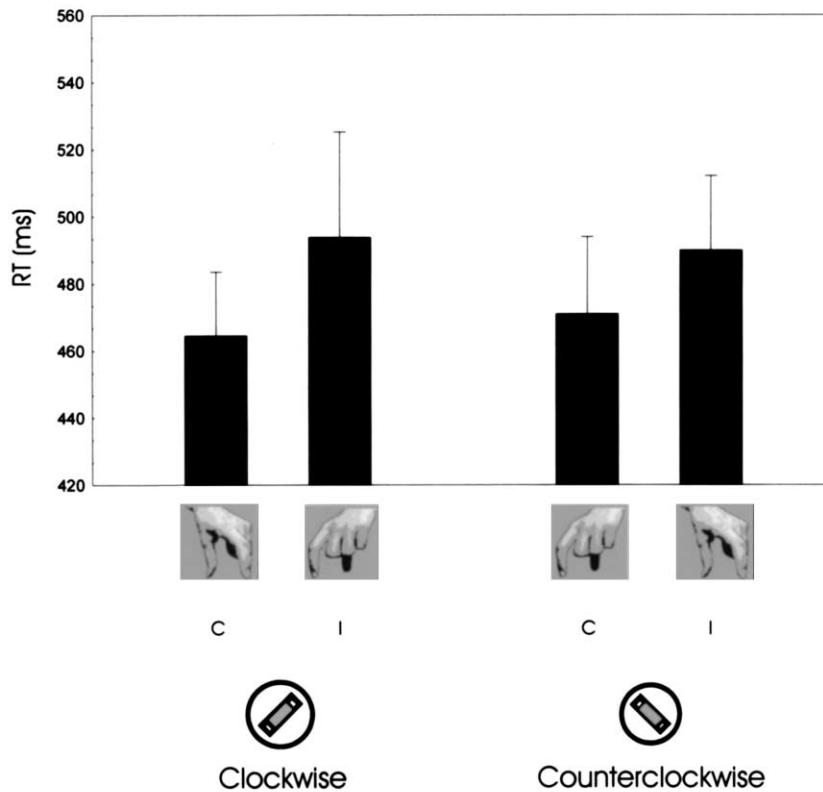
Fig. 2. Experiment 1: two-way interaction between Experimental condition and Bar orientation. Note that reaction time in the congruent condition was faster than in the incongruent condition when the prepared grasping was directed both to the clockwise and the counterclockwise oriented bar. Vertical lines represent S.E. C, congruent condition; I, incongruent condition.

with errors, apart the wrong response errors, were repeated. Every participant was tested in one experimental session that comprised two blocks of 56 randomized trials (total trials = 112) and was preceded by ≈ 30 practice trials.

2.2. Results

2.2.1. RT analysis

The results are summarized in Fig. 2. The response to both clockwise and counterclockwise oriented bar were faster when there was congruency between the go stimulus and the participant's hand end position.

The RTs (mean values) were submitted to an analysis of variance (ANOVA) with two within-subject variables: Bar Orientation (clockwise or counterclockwise) and Experimental Condition (congruent, i.e. the go stimulus in accordance to the participant's hand end position; incongruent, i.e. no specific relation between stimulus and the participant's hand end position). Experimental Condition was significant, $F(1,11) = 4.87$, $P < 0.05$. RTs were faster for the congruent condition (468 ms) than for the incongruent condition (492 ms). No other source of significance was present.

2.2.2. Error analysis

The number of errors was small. Retardation, wrong response and wrong movement error rates were 0.9, 1.34 and 0.7%, respectively. No anticipation errors were found.

3. Experiment 2

Experiment 1 showed that the RTs were faster when there was congruency between the hand depicted in the visual stimulus and the subsequent grip, than when this congruency was lacking. A possible explanation for this finding is that there is a specific visuo-motor link between triggering stimulus and subsequent action. There is, however, an alternative explanation. In the congruent conditions, the position of the index finger with respect to the thumb was the same in the stimulus and at the end of the grasping movement. Thus, the facilitation observed in the congruent condition could be due to compatibility between the position of the fingers in the picture (stimulus) and that in the subjects' hand at the end of the action (response). In particular, one can hypothesize that when the position of the index finger in the stimulus indicated right, grasping towards right

was favored and, conversely, when the position of the index finger in the stimulus indicated left, grasping towards left was favored.

Experiment 2 was designed to test this hypothesis. To this purpose, we presented as visual stimuli the same pictures presented in Experiment 1, plus two other hand pictures. The new hand pictures were obtained by rotating the hands represented in the previous ones of 90° (Fig. 1C,D). The two rotated pictures showed, as the previous ones, a hand with the index finger on the right of the thumb and a hand with the index finger on the left of the thumb, respectively. However, unlike in the previous pictures, the hand positions did not represent the final positions of the required responses. By comparing the grasping movement latencies of the four different pictures, we should be able to assess whether the congruency effect obtained in Experiment 1 depended on the fact that the pictures used in that experiment were the mirror images of hand final position, or this effect was due simply to the physical correspondence between finger positions in the stimuli and in the responses.

3.1. Method

3.1.1. Participants

Fifteen students of the University of Parma served as participants. They were selected as described in Experiment 1. All were naïve as to the purposes of the experiment and gave their informed consent.

3.1.2. Procedure

The apparatus and the response paradigm (go/no-go paradigm) were the same as in Experiment 1. Stimuli to be discriminated consisted of four pictures representing the left hand shaped in four different ways (Fig. 1). Two pictures were the same as in Experiment 1 (not rotated pictures: picture A and B). The other two showed the same hands as in Experiment 1 but rotated of 90° (rotated pictures): Picture C resulted from a rotation of picture A towards right (clockwise); picture D resulted from a rotation of picture B towards left (counterclockwise). Note that in picture C, the index finger is on the right of the thumb as in picture A, while in picture D the index finger is on the left of the thumb as in picture B. Participants were submitted to two sessions, each subdivided into two blocks. Pictures A and B were presented in one session, pictures C and D were presented in the other, using a randomized sequence. The same sequence was repeated in the two blocks of each session. Each picture was presented 28 times. Participants were required to respond only to one of the two pictures, according to which one was shown at the beginning of each block. The order of sessions and blocks was balanced among participants. The combination between pictures and bar orientation was set in such a way that for each go-picture, there were 14 grasping responses towards the clockwise bar and 14 grasping responses towards the counterclockwise bar. Each experimental session comprised two blocks of 56 randomized trials (total trials = 224) and was preceded by ≈ 30 practice trials.

3.2. Results

3.2.1. RT analysis

The results are summarized in Fig. 3. The left part of the figure shows that, as in Experiment 1, the RTs to the mirror image of the participant's hand final position were faster than when there was no relation between hand picture and the executed action. The right part of the figure shows that the RTs in response to the rotated pictures were slower than RTs in response to the original not rotated pictures. In addition, RTs were faster when the position of the fingers in the stimulus and that of the fingers at the end of the grasping was the same.

An analysis of variance (ANOVA) was performed on mean RTs. The within-subject variables were the orientation of the bar to be grasped as response—Bar Orientation (clockwise or counterclockwise), the type of pictures presented as go signal—Pictures (not rotated or rotated) and the index finger position with respect to the thumb of the hand shown in the picture—Index Direction (right or left). Pairwise comparisons with the Newman–Keuls method were conducted whenever appropriate. The significance level was always set at 0.05.

Bar Orientation, $F(1,14) = 6.67$, $P < 0.05$, Pictures, $F(1,14) = 17.47$, $P < 0.001$ and the two-way interaction Bar Orientation × Index Direction, $F(1,14) = 18.81$, $P < 0.001$, were significant. The significant Bar Orientation main effect indicates that RTs were faster when the bar was oriented counterclockwise than when it was oriented clockwise (482 vs. 493 ms). The significant Pictures main effect indicates that RTs were faster when the not rotated pictures were shown as a go signal (469 ms) than when the rotated pictures were used (506 ms).

The significant two-way interaction Bar Orientation × Index direction indicates that when the response was directed toward the *clockwise* oriented bar (required response = index finger position right with respect to the thumb), RTs in response to a picture representing a hand with the index finger positioned on the right of the thumb (475 ms) were faster than those in response to a picture with index finger positioned on the left of the thumb (510 ms). Conversely, when the response was directed toward the *counterclockwise* oriented bar (required response = index finger position left with respect to the thumb), RTs in response to a picture representing a hand with the index finger positioned on the right of the thumb (496 ms) were slower than those in response to a picture with the index finger positioned on the left of the thumb (468 ms).

The lack of significance of the three-way interaction indicates that the facilitation induced by the index finger position correspondence was present both for rotated and not rotated pictures. When the response was directed toward the clockwise oriented bar, the facilitation induced by this correspondence was of 35 ms for both not rotated and rotated pictures. When the response was directed toward the counterclockwise oriented bar, the facilitation was of 32 ms for the not rotated pictures and 24 ms for the rotated pictures.

3.2.2. Error analysis

Anticipation, Retardation, Wrong response and Wrong movement error rates were 0.1, 0.8, 1.43 and 0.5%, respectively.

4. Experiment 3

The results of Experiment 2 indicate that the facilitation in RTs is stronger when the visual stimulus is the mirror image of the hand end position (not rotated stimuli) than when there is only a similarity between stimulus and response (rotated stimuli). Before conclud-

ing, however, that this difference is due to a differential visuo-motor matching in the two conditions, one has to exclude visual factors and namely, that the discrimination of the rotated pictures is more difficult than that of the not rotated pictures.

In order to control for this, we carried out a third experiment in which we presented the same pictures as in Experiment 2, but we asked the participants to respond by releasing the switch in response to the go stimulus. No grasping responses were required. If a perceptual bias between the two set stimuli is responsible for the effect of Experiment 2, the difference between the rotated and the not rotated pictures should persist also in the new experimental condition.

4.1. Method

4.1.1. Participants

Fifteen students of the University of Parma between the ages of 20 and 25 years served as participants. All were right-handed, had normal or corrected-to-normal visual acuity, were naïve as to the purposes of the experiment and gave their informed consent. None participated in the previous experiments.
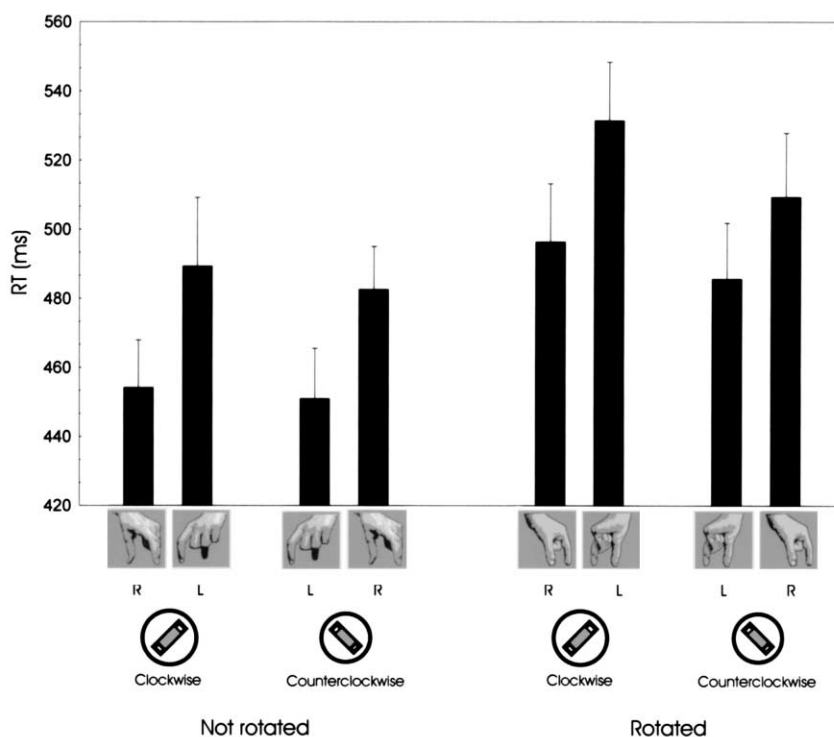

Fig. 3. Experiment 2: three-way interaction between Bar orientation, Pictures and Index direction. Note that for both not rotated and rotated pictures, when the response was directed toward the clockwise oriented bar, reaction times were fastest when a picture representing a hand with index finger position on the right of the thumb was presented. Conversely, when the response was directed toward the counterclockwise oriented bar, reaction times were fastest when a picture representing a hand with index finger position on the left of the thumb was presented. Finally, reaction times in response to the not rotated pictures were faster than reaction times to the rotated pictures. Vertical lines represent S.E. R, index direction right; L, index direction left.

4.1.2. Procedure

The apparatus, the stimuli and the experimental situation were the same as in Experiment 2, except that the response that participants had to make at the presentation of the go signal was the release of the switch pressed at the beginning of each trial. No grasping was required. Every participant was tested in two experimental sessions that comprised two blocks of 28 randomized trials (total trials = 112) and was preceded by ≈ 30 practice trials.

4.2. Results

4.2.1. RT analysis

An analysis of variance (ANOVA) was performed on mean RTs. The within-subject variables were the same as in Experiment 2 apart from the Bar Orientation factor that was not present. No sources of significance were found. (Picture main effect: $F(1,14) = 0.19$, $P = 0.67$. Mean RT in response to the not rotated stimulus was 468 ms and to the rotated stimulus was 474 ms). This result shows that the discrimination of rotated and not rotated hands used in the present experiment is equally difficult and that mere perceptive factors cannot account for the data of Experiment 2.

4.2.2. Error analysis

Retardation and Wrong response error rates were 2.6 and 1.6%, respectively. No Anticipation errors were found.

5. Discussion

Our aim in the present study was to examine whether the reaction time (RT) of grasping movements was affected by the similarity between the visual stimulus (hand pictures) that commanded the action and the hand position at the action end. The results showed that this was the case. The RTs were faster when the hand orientation in the visual stimulus (positions of the index finger and thumb) corresponded to that reached by the hand at the end of the action than when this correspondence was lacking. Most interestingly, fastest RTs were those when the hand shape in the stimulus was the mirror image of the hand shape at the end of the action.

How can these effects be explained? The present study was prompted by the idea, based on neurophysiological and anatomical data, that when individuals prepare a goal-directed grasping movement, they activate neurons located in area F5, which in turn, because of its backwards connections, activate neurons located in areas PF and STS. In both these areas and in particular in STS, there is a visual representation of biological effectors and biological motion [7,15,17,36,37]. This implies that grasping preparation evokes the prepared grip in motor terms (F5 and PF mirror neuron activity), but should evoke also a representation of the prepared action in visual terms (PF and STS visual neurons). These motor-evoked visual representations may facilitate the responses to all visual representations that are congruent with them and, to the highest degree, those corresponding to it more closely. The results confirmed these predictions.

There is, however, another possible interpretation of the results. It may be that the observed effects were not due to a motor-determined facilitation of the processing of visual stimuli, but rather to a facilitation of specific responses by the presentation of congruent visual stimuli. We have no elements to decide between these two alternatives, which, in fact, are not mutually exclusive.

It is important to note, when comparing the visual and motor interpretation of the results, that also the visual interpretation implies a close link between specific visual stimuli and specific responses. Thus, unless one maintains that this link is innate, also the hypothesis that does not imply a motor-determined activation of visual areas must admit that the motor activity plays an important role in creating the visuo-motor congruency.

The interpretations just offered of our results are based on neurophysiological findings. How do these interpretations relate to previous psychological findings and theories? From a theoretical point of view, it is interesting to note at the outset that the neurophysiological interpretation based on 'visual' facilitation due to action preparation is very close to the theory of voluntary movements, known as the theory of ideomotor action [21,24]. This theory goes back to William James [24], who discussing the ontogeny of voluntary movements stated, on merely logical basis, that, since in voluntary action the act must be foreseen, voluntary movements must be preceded by 'random, reflex or involuntary' movements (vol. 2, p. 487). These movements leave an 'image' of themselves in the memory which then is used when a movement is 'desired again, proposed as an end and deliberately willed' (vol. 2, p. 487).

What is this movement 'image' that movement execution leaves in memory? According to James, the movement 'image' is constituted by 'remote effects' defined as those effects that result when individuals observe themselves making a given movement and by proprioceptive information on the movement (kinesthesis). The consequence is that when we think of a movement, the 'movement idea' should be constituted by the images of peripheral sensations due to the 'remote effects' plus proprioception.

The theory of ideomotor action was proposed again in more recent times by Greenwald [21], in order to explain the way in which sensory feedback may be

involved in regulation of skilled performance. After discussing several possibilities, such as serial chaining, closed loop and fractional anticipatory goal response mechanisms, he concluded that the ideomotor mechanism is that most satisfactory and parsimonious for explaining response selection.

A theory close to that of the ideomotor theory of actions was proposed a few yeas ago by Prinz et al. [5,39]. According to this theory, stimuli and responses are represented in the cognitive system as events and therefore, coded in a commensurable format. The basic element of this system is the 'action concept'. The action concept is the association between movement- and effect-producing patterns. The action-concept model does not separate stimulus and response codes. Thus, perceiving and acting are not alternative functions, but, in a sense, one and the same thing. Whenever the stimulus code of action concept is activated, the related response code is formed automatically and, conversely, when the response code is activated, the related stimulus code is formed.

The theories of ideomotor action in their different versions differ from the neurophysiological theory we presented above essentially because they leave unspecified the anatomical substrate where the proposed processes take place as well as the neural mechanism underlying them. The neurophysiological findings, summarized in Section 1, allow an initial, albeit very preliminary, description of these mechanisms and, what is more important, suggest experiments to test them not only at psychological level but also with neurophysiological and brain imaging techniques. The 'neurophysiological ideomotor theory' has, therefore, a potentially richer explanatory capacity than its akin psychological theories, although in terms of their theoretical constructs both sets of theories are (at least at the moment) similar.

Given this theoretical framework, let us examine now in some detail the experimental findings where the relation between action and perception were studied and compare them with the present findings.

In a recent experiment inspired by the ideomotor theory of action, Brass et al. [4] instructed participants to execute finger movements in response to similar or opposite finger movements (lifting or tapping). The hypothesis tested was whether stimulus–response arrangements with a high ideomotor compatibility (similarity between the stimulus and the sensory feedback of the executed response) would determine stimulus–response compatibility effect, even in the case of simple reaction time experiment. Typically, the stimulus–response compatibility effects are present only when there is a choice between responses [1–3]. The results showed that when a subject prepares a finger movement, the responses are faster when the imperative stimulus consists in the presentation of a similar movement. The

authors concluded that in the case of high ideomotor compatibility, the compatibility effects occur also in the case of simple RT experiment.

The notion of ideomotor compatibility is important to interpret some of our results. In our experiments, grasping preparation gave advantage to those hand pictures in which the hand orientation matched that of the prepared response. This effect can be explained by the fact that the hand final position shared with the imperative visual stimulus the position of the index finger with respect to the thumb. The results of Experiment 2 indicate however that this factor is not sufficient alone to explain all the results. In Experiment 2, we had two sets of stimuli, one represented the veridical mirror image of the hand final position, the other set hands rotated of 90°. In both sets of stimuli, the index finger indicated the same direction. If the relative position of the index finger was the factor that determined the advantage of the congruent responses, both the rotated and not rotated stimuli should produce the same effect. In contrast, the results showed that the reaction times to rotated hand stimuli were longer than reaction times to the not rotated stimuli.

All these data are well accounted for by the ideomotor compatibility theory. The stimuli that share the relative position of the finger index and thumb with the position of the same fingers at the end of the response had ideomotor compatibility with the response, regardless of whether they represented rotated or not rotated stimuli. Among them, however, the veridical mirror images were those most highly compatible. As a consequence, the compatible stimuli were responded to faster than the incompatible ones and among the compatible stimuli those not rotated gave faster response than the rotated ones. In neurophysiological terms, F5 mirror neuron activation, due to action preparation, determined preferentially the activation of neurons that corresponded visually to the hand final position. However, given the stimulus generalization observed in many F5 and PF neurons [17–19,42], also other grip positions, similar to the preferred one, were favored.

In another series of experiments [5], the Munich group addressed the issue of whether the observation of an action facilitates the execution of that action with respect to conditions in which the same action is triggered by other imperative stimuli. The results showed that participants responded faster (lifting movement of index or middle finger) to the observation of a similar finger movement than to the presentation of a symbolic or spatial imperative stimulus. In addition, responses to the symbolic or spatial cues were facilitated when an irrelevant finger movement was congruent with them, while an interference effect was found when the irrelevant finger movement was incongruent. According to the neurophysiological formulation of ideomotor theory, there is a bi-directional link between the motor

actions represented in F5 and PF mirror neurons and the visual representation of the same actions located in PF and in STS. Thus, the mere observation of an action, although irrelevant for the task execution, activates automatically the parietal and frontal areas determining a motor facilitation of the finger response. This facilitation does not occur in the case of symbolic or spatial cues because no direct link exists between these stimuli and the action coded in the premotor areas.

The theory of ideomotor action explains well the data of the Munich group just reviewed [5], as well as our experiments where the participants acted in response to visual presentation of hand postures (present data) or in response to objects congruent to the prepared movement [9]. There is, however, another possible interpretation. One can postulate that the advantage of stimuli congruent with the prepared action is not due to a link between visual stimuli and motor action, but to visual priming not related to action preparation. For example, in our experiments, the participants may have formed a visual representation of the hand final position by observation of their hand (although this was prevented during the experiment). When this visual representation coincides with the presented stimulus, the response is faster than when this coincidence is lacking. This interpretation, although logically possible, becomes very weak when presented in more precise terms.

Let us suppose that in our experiments a visual image of the acting hand is indeed formed. This visual image should originate in the ventral visual stream and in the inferotemporal cortex. However, if this is so, this visual imagery should be of little help in producing the response advantage observed in the experiments. Firstly, the neural centers where this image originates are not linked (if not very indirectly) with the motor system. It is unlikely, therefore, that such a representation could be at the basis of the RTs facilitation that we have recorded. Secondly, and most importantly, the semantic representation typical of the inferotemporal cortex provides a general description of the stimuli such that it can be used for stimulus categorization, verbalization and memory. It does not provide a detailed description of the stimuli in such a format that it can be used for programming movements [25,31]. On the other hand, if a visual image of the stimuli originates in the dorsal stream and specifically in the STS/PF circuit, this 'pragmatic' [25] image arises in the same circuit that is active during motor preparation and it is not different conceptually from that postulated by ideomotor theory. Thus, when the visual imagery is specified in its function and neural substrate, the visual hypothesis and the ideomotor hypothesis tend to coincide. Note that when we speak of a visual image generated in the 'pragmatic' circuits, we do not maintain that it is perceived as a sort of visual illusion, we state only that there is an endoge-

nous activation of visual centers. The fact of whether this image is consciously perceived or not is outside the aim of the present discussion.

In conclusion, our data provide clear support for the notion that there is a strict link between motor activity and visual perception [9,23,40,47,51]. In addition, they suggest, consistently with neurophysiological data, that motor activity determine two separate visual effects. On one side, as previously shown by Craighero et al. [9], it gives an advantage to respond to objects whose intrinsic properties coincide with the prepared movement, on the other it facilitates the responses that are congruent with those of another individual executing the same action [4,5,8,10,50]. These two effects reflect the two types of visuomotor neurons present in the premotor cortex: the canonical neurons and the mirror neurons. The former code interaction with objects, the latter describe actions made by another individual. It is worth stressing that this latter mechanism may be of great importance in order to understand imitation. If one accepts that, any time when the premotor cortex becomes active, there is a visual representation of the prepared action in the pragmatic circuit, then learning by imitation may be achieved by comparing the action made by another individual with the visual representation evoked by motor preparation. Progressive matching of the two images will allow individuals to replicate the action that has to be imitated.

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