Visuomotor Priming

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Two experiments were performed to explore a possible visuomotor priming effect. The participants were instructed to fixate a cross on a computer screen and to respond, when the cross changed colour (“go” signal), by grasping one of two objects with their right hand. The participants knew in advance the nature of the to-be-grasped object and the appropriate motor response. Before (100 msec), simultaneously with or after (100 msec) the “go” signal, a two-dimensional picture of an object (the prime), centred around the fixation cross, was presented. The prime was not predictive of the nature of the to-be-grasped object. There was a congruent condition, in which the prime depicted the to-be-grasped object, an incongruent condition, in which the prime depicted the other object, and a neutral condition, in which either no prime was shown or the prime depicted an object that did not belong to the set of to-be-grasped objects. It was found that, in the congruent condition, reaction time for initiating a grasping movement was reduced. These results provide evidence of visuomotor priming.

INTRODUCTION

Object grasping is a highly complex motor behaviour that requires the capacity to configure the hand according to the shape of a potentially limitless number of known and unknown objects (see, e.g. Jeannerod, Arbib, Rizzolatti, & Sakata, 1995). The physical characteristics of the objects, such as size, shape and orientation, must be visually perceived and used to select the most appropriate hand shaping. One possible way that the brain can compute this

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visuomotor transformation is to link automatically the object representation (i.e. its visual properties) to a specific, predetermined grasping movement. Such a linkage would allow for rapid selection of specific object-related motor programs. In other words, and as also suggested by Goldberg and Seagraves (1987) for eye movements, to speed up response selection, it would be beneficial to select the appropriate motor program from an already existing repertoire of motor programs, rather than generate it anew (see Tucker & Ellis, in press).

Milner and Goodale (1992; Goodale & Milner, 1995) have recently proposed that the primate cortical visual areas are formed by two functional pathways. One, the “dorsal stream”, has direct links to motor control systems. The other, the “ventral stream”, is connected to systems that subserve perception and memory. The computations carried out in the ventral stream produce perceptual and cognitive representations of the visual characteristics of objects and their significance.

In the posterior parietal cortex, which belongs to the dorsal stream, these are neurons that are sensitive to the visual characteristics of the objects that are to be grasped. Each region within the posterior parietal cortex projects to separate regions within the premotor areas of the frontal lobes, where movements are programmed. Thus, the dorsal stream performs the sensorimotor transformations required for visually guided actions, such as grasping a specific object (for reviews, see Jeannerod et al., 1995; Milner & Goodale, 1995; Rizzolatti, Riggio, & Sheligia, 1994).

If size and orientation of a to-be-grasped object are processed by the dorsal stream, it is conceivable that such visual primes invoke stored information about the nature of the object, which in turn might determine the action programs initiated with respect to the object.

The notion that the representations of objects include, in addition to those visual characteristics which are computed in the dorsal stream, information about the actions that can be performed on those same objects, is not new (see, e.g. Eimer, Hommel, & Prinz, 1995). In this context, the term “affordances” has been used to refer to the fact that the actions appropriate for an object may be intrinsic to its representation (see Jeannerod, 1994; Tucker & Ellis, in press). This possibility is supported by neurophysiological and neuropsychological evidence.

In the monkey, neurons in the anterior intraparietal area (AIP) and in the ventral part of frontal premotor area 6 (F5) respond to visual objects in the absence of hand movements and are selectively sensitive to different types of grasping (for reviews, see Jeannerod et al., 1995; Milner & Goodale, 1995; Rizzolatti et al., 1994). It appears that the representation they compute is not concerned with object recognition, but rather with the appropriate object-related hand movement. Thus, areas AIP and F5 form a circuit that transforms visual information about the intrinsic properties of objects into hand movements aimed at interacting with those same objects.
In area F5, there are neurons that respond both when the monkey performs an action on an object and when it observes a similar action made by another monkey or by the experimenter. Rizzolatti and his colleagues (Di Pellegrino et al., 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996a) called these neurons “mirror neurons” and proposed that they compute an abstract representation of a specific action.

Fadiga, Fogassi, Pavesi and Rizzolatti (1995) stimulated the motor cortex of normal human participants (transcranial magnetic stimulation) and simultaneously recorded motor-evoked potentials. They reasoned that, if the observation of a movement activates the premotor cortex, this activation should induce an enhancement of motor-evoked potentials elicited by the magnetic stimulation of the motor cortex. Fadiga et al. found that motor-evoked potentials were selectively enhanced when the participants observed the experimenter grasping objects. Based on this result, they suggested that there is a brain system which is sensitive to both action observation and execution in humans. This issue was also addressed by the use of positron emission tomography (Rizzolatti et al. 1996b). The main finding was the presence of a selective activation in the posterior part of the left inferior frontal gyrus when participants observed the experimenter in the act of grasping objects.

A well-known single case study (Goodale, Milner, Jacobson, & Carey, 1991) reported results that are congruent with the neurophysiological findings we have summarized above. It showed that a brain-damaged patient retained the ability to execute appropriate automatic reaching and grasping responses to objects whose orientation, size and shape she could not explicitly report. The patient failed in a task requiring her to match the orientation of a hand-held card with the orientation of a slot. In contrast, when she was asked to reach out and “post” the card through the slot, her performance was excellent. When presented with pairs of plastic plaques, the patient could not tell whether they were same or different. Similarly, she could not estimate, with her index finger and thumb, the size of the plaques when they were shown one at a time. In contrast, when the patient was asked to grasp the plaques, her performance was indistinguishable from that of normal controls. This patient’s behaviour clearly suggests the existence of a direct link between object qualities, such as orientation, size and shape, and reaching and grasping responses that are guided by the same qualities.

In spite of the increasing neurophysiological and neuropsychological evidence, the behavioural evidence to date that the sight of an object also activates the representation of the actions that can be performed on it is somewhat sparse and indirect.

The most relevant study is that by Tucker and Ellis (in press). They addressed the issue of whether visual objects potentiate actions that may be performed on them, even in the absence of explicit intentions to act. They used a stimulus–response compatibility paradigm with photographs of common graspable objects.
as stimuli. The participants had to decide as fast as possible, by performing a keypress response with either the left or the right hand, whether each object was upright or inverted. Tucker and Ellis reasoned that if a visual object activates the hand most suited to perform a reach-and-grasp movement, facilitation should occur when the simple keypress response is executed with the congruent hand. Conversely, interference should occur when the response is executed with the incongruent hand. The results showed that the pictures automatically activated the hand that was more compatible with grasping the depicted object in a given orientation.

Of some relevance is a study by Tipper, Lortie and Baylis (1992). In a task that required selective reaching for a target with nearby distractors, they found interference on response latency if the distractor was on or near the hand’s trajectory to the target. They suggested that the distractors were automatically processed and motor programs were specified for them, thus producing the interference effect.

In conclusion, neurophysiological and neuropsychological evidence points to the existence of a direct visual route from objects to action. What is still lacking is clear evidence of the behavioural effects caused by this route. On the basis of the studies we have reviewed so far, it can be predicted that the motor program that is most appropriate for grasping an object is automatically activated by the visual presentation of that same object. To test this idea, we used an experimental paradigm similar to that used in classical studies of repetition and semantic priming, which showed that recognition of a stimulus is facilitated by having previously processed the same or a related stimulus (i.e. the prime; Bruce, 1983; Kutas & Hillyard, 1984; Meyer & Schvaneveldt, 1971; Warren & Morton, 1982). However, instead of exploring the effects of the prime on stimulus recognition, we tested its effects on object-determined motor responses.

It is worth noting that patients with frontal lobe lesions show a compulsive response that is known as “utilization behaviour” (e.g. Lhermitte, 1983). Utilization behaviour is characterized by the fact that visual stimuli may automatically—that is, in the absence of an intention to act—elicit motor responses, such as reaching and grasping. This compulsive response is perhaps an exaggeration of the type of normal visuomotor priming that is demonstrated in the present study. Pathologically enhanced visuomotor priming would manifest itself when control is lost due to frontal damage, and thus existing visuomotor connections cannot be suppressed.

### EXPERIMENT 1

In this experiment, the two to-be-grasped objects required precision grips of comparable difficulty. The two objects differed in their orientation in relation to the participants’ body midline. Note that orientation is among the object
features to which neurons in areas AIP and F5 are known to respond selectively (e.g. Jeannerod et al., 1995; Milner & Goodale, 1995).

Method

Participants. Ten students attending the University of Parma volunteered to take part in the experiment in exchange for a small fee. All of the students were right-handed, had normal or corrected-to-normal visual acuity, and were unaware of the purpose of the experiment.

Apparatus and Materials. The experiment took place in a sound-attenuated cubicle and ambient light was provided from the ceiling by a halogen lamp. Each participant was seated in a chair with the head positioned on a chin rest. A computer screen was located 57 cm from the participant’s orbital plane. The stimuli on the screen were a white or red fixation cross, each arm of which subtended 1° of visual angle, and the white outline drawing of a rectangle (width 2°, height 5°), which could be rotated 45° either clockwise or counterclockwise. On the right side of the participant’s body midline there was a switch, on which the participant placed the hand to start the trial. The to-be-grasped object was a rectangular bar (width 2.5 cm, height 6.0 cm), which could be rotated 45° either clockwise or counterclockwise in relation to the sagittal plane of the participant’s body. The bar was positioned in a rectangular hole hollowed out of a plastic disk. The hole was larger than the bar, so that the participant could insert his or her thumb and index finger into it to grasp the bar.

Procedure. Each participant was instructed to fixate the white fixation cross and to respond, when it turned red (‘go’ signal), by grasping and lifting the object with the right hand. Reaction time (RT) was measured between onset of the “go” signal and release of the switch at the start position. The instructions stressed both speed and accuracy. An electronic device monitored whether the object was lifted from its support. If the participant failed to do so, then that trial was discarded and replaced.

On each trial, the sequence of events was as follows (see Figure 1, in which the experimental events are represented as schematic computer displays). Before the beginning of a trial, the experimenter positioned one of the two objects (50% each, according to a random sequence) on the support in front of the participant. Then the participant pressed the switch with the hand shaped in a pinch position. This caused the appearance of the word “destra” (“right”, signalling a clockwise rotation) or “sinistra” (“left”, signalling a counterclockwise rotation) on the screen. Because the word always indicated the object that was to be grasped, the participant was fully informed about the nature of the to-be-grasped object before the beginning of each trial. It must be stressed that
the participant was not able to see either the object or the hand, and thus the grasping response did not occur under visual feedback.

The beginning of the trial was marked by the appearance of the white cross on the screen. After a variable interval (250–750 msec), the cross turned red, that is the signal to execute the response. On the experimental trials, before (stimulus onset asynchrony = −100 msec), simultaneously with (SOA = 0 msec), or after (SOA = 100 msec) the “go” signal, one of the two pictures (i.e. the prime) was presented. The three SOAs were randomly intermixed and occurred with equal probability (about 33% each).

The relations between the prime and the to-be-grasped object yielded a congruent condition (the two objects were the same, 35% of the trials) and an incongruent condition (the two objects were different, 35% of the trials). On 18% of the trials, no prime was presented, which yielded a neutral, control
condition. Finally, on about 12% of the trials, the prime was presented but the “go” signal was not delivered. These were catch trials, in which the participant had to refrain from responding.

Every participant produced 204 trials: 144 experimental trials (that is, 12 trials for each combination of to-be-grasped object, congruence condition and SOA), 36 neutral trials and 24 catch trials.

Results and Discussion

Reaction times for neutral trials were analysed separately (see below), because on neutral trials the SOA factor was absent (no prime was presented).

Reaction times for experimental trials were submitted to an analysis of variance (ANOVA), in which the three within-subjects factors were orientation of the to-be-grasped object (clockwise vs counterclockwise), type of trial (congruent vs incongruent) and SOA (–100, 0 or 100 msec). The three main effects were significant [orientation: $F(1,9) = 9.37, p < .05$; SOA: $F(2,18) = 6.59, p < .01$; type of trial: $F(1,9) = 6.23, p < .05$]. Reaction time was faster for the clockwise than for the counterclockwise orientation (342 vs 348 msec), and was faster for the –100 msec SOA and 0 msec SOA (339 and 340 msec) than for the 100 msec SOA (356 msec). Pairwise comparisons (Newman-Keuls test) showed that the RTs in the –100 msec SOA and the 0 msec SOA did not differ, whereas they both differed significantly from RT with the 100 msec SOA condition ($p < .05$ and $p < .01$, respectively). More interestingly, RT was faster on congruent than incongruent trials (342 vs 348 msec).

Also, the interaction between the type of trial and SOA was significant, $F(2,18) = 7.95, p < .005$. As shown in Figure 2, this indicated that the advantage of congruent over incongruent trials was present and significant ($p < .01$) with the –100 msec SOA (330 vs 348 msec). A similar, but non-significant trend was noted with the 0 msec SOA (336 vs 345 msec). In contrast, with the 100 msec SOA, incongruent trials were non-significantly faster than congruent trials (352 vs 361 msec).

In the ANOVA for neutral trials, the only within-subjects factor was orientation. It was not significant, although RTs were somewhat faster for the clockwise than the counterclockwise orientation (358 vs 362 msec).

The results clearly showed a priming effect. The task-irrelevant bi-dimensional drawing acted as a prime and decreased the latency for performing a grasping response towards a congruent real object.\(^1\)

Two response components can be distinguished in a RT task—selection of which response is needed and programming of the selected response (e.g.

\(^1\)No doubt, under the present experimental conditions, the participants were prepared to grasp objects. This was probably instrumental in producing the priming effect. It remains to be seen whether a comparable priming effect can be found in the absence of a readiness to grasp objects.
Klapp, 1995). Both components must be completed before the response is initiated, so that both can contribute to RT. In the present experiment response uncertainty and stimulus–response compatibility— that is, the factors that are known to influence response selection—were held constant. Therefore, the experimental manipulations affected programming rather than selection. It appears that the prime facilitated the programming of the appropriate response for grasping the target object.

It is important to point out that the priming effect was very clear only if the prime preceded the “go” signal. This must not be interpreted as an indication that the priming effect is weak and difficult to obtain. Rather, it indicates that, as is to be expected, the priming effect manifests itself only if the prime is shown while the response has yet to be programmed. When the prime appears simultaneously with or after the “go” signal—that is, when the programming of the response is already completed or nearly completed—the priming effect is much diminished or altogether absent.

The neutral condition, in which no visual prime was presented, was meant to provide a baseline to measure priming benefits and priming costs. The idea was that congruent trials might have produced faster RTs than neutral trials (i.e. benefits), whereas incongruent trials might have produced slower RTs than neutral trials (i.e. costs). Contrary to expectations, RT on neutral trials was somewhat slower than on incongruent trials.

There are two possible explanations for this. One is that the prime, which was present on congruent and incongruent trials and absent on neutral trials, had a non-specific arousing effect, thus speeding up response execution. The
other possibility is that the prime produced benefits in the absence of costs. That is, the prime facilitated the corresponding response, if congruent. However, it did not cause inhibition of the alternative response. This issue was addressed in Experiment 2.

The orientation and SOA main effects are only moderately interesting. Apparently, programming a clockwise grasping response was slightly easier than programming a counterclockwise grasping response. When presented after the “go” signal, the prime could not act as a warning. Because of that, RT was slower than with the other two SOAs.

EXPERIMENT 2

The aims of this experiment were to replicate the results of Experiment 1 and explore whether costs could be obtained on incongruent trials. The main experimental manipulation concerned neutral trials, in which a visual object was presented that was not included in the set of to-be-grasped objects.

Method

Participants. Seventeen students attending the University of Parma participated in the experiment. They were selected on the basis of the same general characteristics as the participants in Experiment 1. None of them had taken part in the previous experiment.

Apparatus, Materials and Procedure. These were the same as for Experiment 1, except for neutral trials. On neutral trials, the prime was the white outline of a circle (3° in diameter). Remember that, in the previous experiment, no prime was presented on neutral trials. Apart from that, congruent, incongruent, neutral and catch trials, SOAs and the event sequence were as in Experiment 1 (see Figure 1). Because of the additional 12 catch trials with the circle, overall there were 216 trials.

Results and Discussion

Reaction times were submitted to an ANOVA in which the three within-subject factors were orientation of the to-be-grasped object (clockwise vs counterclockwise), type of trial (congruent, incongruent or neutral) and SOA (–100, 0 or 100 msec).

The trial and SOA main effects were significant, $F(2,32) = 8.25, p < .01$ and $F(2,32) = 17.78, p < .001$, respectively. Reaction time was significantly faster for congruent trials (349 msec) than for incongruent (358 msec) or neutral (355 msec) trials ($p < .01$ and $p < .05$, respectively; Newman-Keuls test), whereas neutral and incongruent trials did not differ. Reaction time was significantly
faster with the $-100$ msec SOA (348 msec) and the 0 msec SOA (346 msec) than with the 100 msec SOA (367 msec; both $p < .001$), whereas the $-100$ and 0 msec SOAs did not differ.

The interaction between type of trial and SOA was also significant, $F(4, 64) = 3.05, p < .05$ (see Figure 3). It showed an advantage of congruent trials that was significant with the $-100$ msec SOA (congruent trials, 337 msec; incongruent trials, 355 msec; neutral trials, 353 msec; $p < .001$ and $p < .01$, respectively). In contrast, it disappeared at the 0 msec SOA (congruent trials, 346 msec; incongruent trials, 348 msec; neutral trials, 345 msec) and the 100 msec SOA (congruent trials, 364 msec; incongruent trials, 371 msec; neutral trials, 367 msec).

The results of the significant interaction between orientation, trial and SOA, $F(4, 64) = 2.52, p < .05$, are reported in Figure 4. In summary, this interaction showed that, with the $-100$ msec SOA, congruent trials were faster than incongruent ($p < .001$) and neutral ($p < .01$) trials for the counterclockwise orientation. With the 0 and 100 msec SOAs, RTs for the three types of trial were not significantly different regardless of orientation and SOA.

As in Experiment 1, congruent trials were faster than incongruent trials only when the prime preceded the “go” signal. This confirmed that the priming effect manifests itself only if the prime is shown while the response has yet to be programmed.

FIG. 3. The two-way interaction (type of trial × SOA) obtained in Experiment 2.
In Experiment 2, however, the three-way interaction was also significant. This indicated that the priming effect, though present for both orientations, reached statistical significance with the post-hoc test for the counterclockwise orientation only. Although the lack of a significant priming effect for the clockwise orientation may be attributable to a Type II error, we cannot explain why the priming effect was greater for the counterclockwise orientation.

As in the previous experiment, RT for neutral trials was not faster than RT for incongruent trials. Because in the present experiment a visual prime was shown on neutral trials, an explanation in terms of a non-specific effect of the prime can be ruled out. However, it would be premature to conclude that priming benefits occur in the absence of priming costs. The neutral prime in fact represented an object different from the to-be-grasped one. From this point of view, neutral and incongruent trials were equivalent. The issue of costs is in need of further exploration.

**GENERAL DISCUSSION**

The visual cortical system of primates is formed by a large number of interconnected areas in which two broad “streams” can be recognized: A ventral stream largely projecting to the inferior temporal lobe and a dorsal stream that
terminates in the inferior parietal lobe (Ungerleider & Mishkin, 1982). The ventral stream is responsible for the analysis of the qualities of objects. The dorsal stream is responsible for space computation (Ungerleider & Mishkin, 1982) and for object analysis for action (Goodale & Milner, 1992; Milner & Goodale, 1985). The posterior parietal cortex, in which the dorsal stream terminates, sends rich projections to the premotor areas of the frontal lobes, in which neural circuits are in charge of programming movements. Thus, the posterior parietal cortex and the premotor areas form a complex parieto-frontal visuomotor system.

In the monkey, an area crucially involved in the organization of hand movement is the parietal area, AIP. This area contains visual neurons that respond when the monkey fixates a specific object without moving, motor neurons that discharge when the animal performs a specific type of hand grip, and visuomotor neurons that discharge both during object observation and object-directed movements (Taira et al., 1991; see Jeannerod et al., 1995, for a review).

Area AIP projects to area F5, which belongs to the frontal premotor areas. Most neurons of area F5 discharge during goal-related hand movements, such as grasping, holding and manipulating (Rizzolatti et al., 1988; see Jeannerod et al., 1995, for a review). Many of these neurons are specific for particular types of hand prehension, such as precision grip, finger prehension and whole-hand prehension. The neurons of area F5 also discharge upon visual presentation of three-dimensional objects. Even more interestingly, the discharge often occurs only if the object’s size or orientation matches the type of grip to which the neuron is selectively sensitive. Finally, some neurons of area F5 respond both when the monkey manipulates a given object or when it observes the experimenter manipulating that same object (the so-called “mirror” neurons; Di Pellegrino et al., 1992; Gallese et al., 1996; Rizzolatti et al., 1996).

There is compelling evidence that AIP and F5 form a cortical network that transforms visual information into hand movements, which allow the monkey to interact appropriately with objects (Jeannerod et al., 1995). Motor information is then transferred to area F1 (precentral motor cortex), to which F5 is directly connected, as well as to several subcortical centres, for movement execution (Jeannerod et al., 1995). If a similar network exists in man, as some recent evidence suggests (Grafton, Arbib, Fadiga, & Rizzolatti, 1996), then it should be possible to prime a grasping response by presenting a prime depicting the object that “affords” that particular type of grasping.

In the present study, normal participants were primed, while ready to execute a grasping movement, by the visual presentation of task-irrelevant bi-dimensional drawings of objects. The results showed that drawings that were visually congruent with the to-be-grasped object reduced RT for the grasping response. This is evidence of visuomotor priming: seeing an object facilitates an action
congruent with the visual properties of that same object. This is clearly in accordance with the available neurophysiological evidence (e.g. Di Pellegrino et al., 1992; Gallese et al., 1996; Rizzolatti et al., 1996a).

It would also appear that the type of compulsive behaviour known as “utilization behaviour” (e.g. Lhermitte, 1983) is a pathological release of the normal, automatic object-to-action transformation process. Our findings indicate that the mere presentation of visual objects automatically evokes object-related motor responses. In patients in whom frontal control is severely impaired because of a lesion (e.g. Shallice, 1988), this mechanism may capture the motor system and determine the utilization behaviour. In normals, it represents a useful way for fast programming object-related actions.

It should be noted at this point that some studies with patients and normal subjects have addressed a related, but different, issue. They investigated whether there is a direct visual route that subserves the selection of learned actions to be performed on seen objects.

Riddoch and Humphreys (1987) described a patient who demonstrated impaired semantic information about seen objects and was poor at naming them. However, he could make specific learned gestures to the same objects. For example, when presented with a knife or a fork, the patient made correct cutting and prodding gestures, but failed when his semantic knowledge about the knife and the fork was tested. Riddoch and Humphreys argued that the patient’s relatively preserved ability to make gestures to visually presented objects was attributable to the operation of a direct route to action, which bypasses the semantic system (see also Riddoch, Humphreys, Coltheart, & Funnell, 1988).

Patients who, despite moderate to severe loss of semantic (functional and associative) object knowledge, were nevertheless able to perform almost normally on single-object use, have been described by Buxbaum, Schwartz and Carew (1997), Hillis and Caramazza (1995) and Sirigu, Duhamel and Poncet (1991). The opposite dissociation was found in other patients, who showed good visual object recognition and naming, but were impaired at making gestures to seen objects (Buxbaum et al., 1997; Motomura & Yamadori, 1994; Pilgrim & Humphreys, 1991; Riddoch, Humphreys, & Price, 1989).

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2 It should be noted that there is an alternative explanation of the results of the present study. Because the participants did not see the to-be-grasped object, they may have formed a visual image of it before the “go” signal was presented. If the image was congruent with the task-irrelevant prime, facilitation may have resulted. It is clear, however, that an incongruent prime should have disrupted the image of the to-be-grasped object, thus causing interference. Therefore, this alternative explanation also has difficulties explaining why interference was not found on incongruent trials.
These neuropsychological findings have led to the notion that there are two independent routes from seen objects to action (e.g. Riddoch et al., 1988; Rumiati & Humphreys, in press): One route that is mediated by the visual activation of semantic/functional knowledge about objects; a second route that is mediated solely by visual information derived from the objects. The direct visual route is thought to operate through associations between stored visual representations of objects and learned actions. The stored visual representations would belong to a structural description system, separate from semantic memory.

Klatzky, Pellegrino, McCloskey and Lederman (1993; see also Klatzky, Pellegrino, McCloskey, & Doherty, 1989) showed that normal people possess strong associations between objects and the actions commonly carried out with them. In their study, they explored people’s knowledge about the movements underlying functional interactions with objects. On the basis of clustering and multidimensional scaling analyses, they demonstrated that movement features were incorporated into the cognitive representation of objects. Subsequently, Klatzky, Fikes and Pellgrino (1995) showed that knowledge about objects and their functions could trigger an appropriate hand shape and the required configuration could be primed, before the onset of reaching, by the object’s colour.

In a study by Rumiati and Humphreys (in press), participants were asked to name or to make gestures to drawings of objects (e.g. writing to a pen, pounding to a hammer). Because the instructions were to respond as rapidly as possible without being too concerned about accuracy, errors were elicited. The errors could be visual (e.g. “hammer” for “razor”), semantic (e.g. “saw” for “hammer”) or mixed (e.g. “match” for “cigarette”). It was found that, in gesturing, participants made more visual errors and fewer semantic or mixed errors in comparison to naming. According to Rumiati and Humphreys, the fact that gesturing responses produced more visual errors is evidence of a direct visual route from objects to action.

At first sight, it would appear that these studies with patients and normal observers addressed a problem that is similar, if not identical, to the one explored in the present study—that is, whether there is a direct link between seen objects and actions that can be performed on them. There is, however, a profound difference that should not be overlooked. Here we dealt with a very simple action, grasping, that is guided by elementary object qualities, such as orientation, shape and size. In contrast, the other studies were concerned with the way objects are used. That these issues are different is attested by the fact that it makes sense to ask whether there is a direct route from an object to its use (and the studies reported above suggest there is), or rather the correct use of an object requires recognizing the object and accessing semantic information about it. In contrast, it makes little sense to ask whether the act of grasping an
object is mediated by semantic information. In fact, no doubt we can grasp objects we do not recognize.

The results of the present study could also be relevant to the premotor theory of spatial attention (Rizzolatti et al., 1994; Rizzolatti, Riggio, Dascola, & Umiltà, 1987; Umiltà, Riggio, Dascola, & Rizzolatti, 1991). According to this hypothesis, space is represented in several pragmatic maps. Some of them control oculomotion, whereas others control movements of the arm and other body parts. Spatial attention is thought to depend on the fact that, when the observer prepares to perform a goal-directed movement, neurons in the corresponding pragmatic map become active and facilitate sensory maps located upstream.

To date, evidence in favour of the premotor hypothesis has originated mainly from the role of the oculomotor system in spatial attention (see, e.g. Kustov & Robinson, 1996; for a review, see Rizzolatti et al., 1994). When the observer attends to a given location in space, a program for a shift of gaze to that location is prepared. For example, when attention is primed to the right side, the eyes, though still directed at fixation, are “implicitly” shifted to the right. This facilitates the sensory centres located on that side, which, in turn, facilitates detection of stimuli located in that region of space.

Considering that the basic neurophysiological organization of the non-oculomotor spatial maps is similar to the organization of the map that controls eye movements, the premotor hypothesis should also apply to other effector systems. Thus, directing attention to an object of a certain size, shape and orientation should result from the preparation of a specific motor program for grasping that object, in the same way as directing attention to a location in space results from the preparation of an eye movement to that location.

In the experiments described here, the participants were asked to maintain fixation when the “go” signal appeared in non-catch trials. Because the irrelevant visual object encircled the fixation cross, this object primed a motor response program for grasping a similar three-dimensional object. According to the premotor theory of attention, the reverse should also be true. When a subject is ready to grasp an object, RT to a picture of that object should decrease, because the motor program for grasping automatically activates the neural system that codes the representation of the object’s intrinsic properties. Thus,

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3 Cortical pragmatic maps are maps that transform spatial information into movements (e.g. Rizzolatti et al., 1994). The premotor hypothesis maintains that spatial attention can be subserved by any pragmatic map. In humans and primates, however, as a consequence of the strong development of foveal vision and the neural mechanisms related to foveation, a central role in spatial and selective attention would be played by those maps that code space for oculomotion.
the experimental paradigm presented in the present paper (or a variation of it) might also be used for studying object-related attentional phenomena.

REFERENCES


