

No evidence for visuomotor priming in a visually guided action task

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Abstract

Craighero et al. [Craighero, L., Fadiga, U., Umiltà, C.A., & Rizzolatti, G. (1996). Evidence for visuomotor priming effect. *Neuroreport*, 8, 347–349] showed that grasping movements were initiated more quickly when the goal object shared the same orientation as a previously seen ‘prime’ object. Because the goal object was never visible in these experiments, however, it is unclear whether the data should be construed as evidence for a general visuomotor priming effect (as the authors contend), or only as evidence for a more specific priming effect on memory-guided actions. In Experiment 1, we demonstrated that memory-guided but not visually guided grasping can be primed by passive viewing of a prime object. In Experiment 2, we compared the effects of a prime object on the grasping and naming of a visible target object. Participants were faster to name the target when its shape was the same as the prime, consistent with well-established perceptual priming effects. Under the identical set of testing parameters, however, reaction time for grasping was unaffected by the orientation or the shape of the prime. In Experiment 3, participants grasped the goal object after either viewing or grasping a prime object. Reaction time for grasping was unaffected by the visual features of the prime in both tasks. Taken together, these results are consistent with the view that perceptual memory – which presumably underlies visual priming effects – is largely irrelevant for programming the metrics of actions to visible objects. Visually guided actions are programmed in real-time by dedicated visuomotor modules that appear to be insensitive to the priming effects that are a hallmark of visual perception.

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Keywords: Priming; Grasping; Visuomotor; Naming; Perception; Action

1. Introduction

Human beings are able to reach out and grasp objects with remarkable skill – and vision plays a central role in the control of this adaptive behaviour. Pioneering behavioural and neuropsychological work by Marc Jeannerod demonstrated that the posture of the grasping hand is exquisitely tuned to the intrinsic features of a goal object, such as its size and shape, reflecting the joint contribution of feedforward and feedback visuomotor processes (Jeannerod & Biguer, 1982). The visuomotor transformations that underlie the control of skilled actions such as grasping have more recently been shown to be mediated largely by the dorsal stream of visual projections, which arise in primary visual cortex and project to the posterior parietal cortex (Goodale & Milner, 1992; Jeannerod, Arbib, Rizzolatti, & Sakata, 1995). In contrast, the visual

processing mediating the conscious perception of object features has been shown to depend on the ventral stream of visual projections, which also arise in primary visual cortex but project instead to the temporal lobe (Goodale & Milner, 1992). The evolution of two separate visual pathways for action and perception presumably reflects the fact that the visual control of an object-directed action requires quite different transformations of visual input from the transformations required to generate a conscious percept of that same object (Goodale & Humphrey, 1998).

Because observers and goal objects often do not stay in a static relationship with one another, the required coordinates for action are most effectively computed immediately before the movements are initiated; i.e., in real-time. A corollary of real-time visuomotor transformation is that neither the coordinates for a particular action nor the resulting motor program need to be stored in memory. Indeed such storage could create interference between competing action plans for multiple objects in the visual array, or between action plans to the same

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object following a change in the spatial relationship between target and actor.

There is considerable empirical evidence that grasping movements made after the goal object has been removed from view are qualitatively different from the actions programmed while the object remains visible (Goodale, Jakobson, & Keillor, 1994; Hu & Goodale, 2000; Milner, Paulignan, Dijkerman, Michel, & Jeannerod, 1999; Westwood & Goodale, 2003). Much of this evidence suggests that the control of actions to remembered objects depends critically on visual processing that is carried out in the perceptual stream of ventral cortex – processing that does not typically intrude on the control of visually guided actions. Visual perception operates over a much longer time scale than that used in the visual control of action. Indeed, object recognition would not be possible unless perceptual information about previously encountered objects were stored in memory.

Thus, vision-for-action and vision-for-perception use fundamentally different temporal scales. But if the visual control of action works in real-time, then one might expect that previous exposure to a goal object would have little effect on the programming of the precise metrics of the reach and the grasp in manual prehension. Data from a study conducted by Craighero et al. (1996) however, appear inconsistent with this argument, at least at first blush.

In Craighero et al.'s (1996) study, participants reached out to grasp an unseen target bar with a precision grip 100 ms after viewing a prime with congruent, incongruent or neutral orientation with respect to the target. A verbal cue before the trial conveyed to participants the orientation of the target. Reaction time was faster for congruent relative to neutral and incongruent primes, suggesting the visuomotor system could be primed by passive viewing. Presumably, some aspect of grasp programming was carried out prior to the action based on the visual information from the prime stimulus.

A critical aspect of the Craighero et al. (1996) study was the fact that the target object was never actually visible to the participants. In other words, participants had to plan their action from memory for target orientation, rather than from direct visual input – a situation that is quite contrary to what is normally encountered in our routine interactions with objects. Given the dependence of memory-guided actions on visual processing carried out in the perceptual system (Goodale et al., 1994; Hu & Goodale, 2000; Milner et al., 1999; Westwood & Goodale, 2003), this could explain why priming was seen in Craighero et al.'s experiment. In the present series of experiments, we sought to determine whether or not visually guided grasping movements could also be primed. This question has direct relevance for the real-time view of motor programming (Goodale, Westwood, & Milner, 2004), which suggests that dorsal-stream visuomotor networks transform visual target information into motor commands at the moment the action is required, and not before.

In Experiment 1, we show that memory-guided but not visually guided grasping can be primed by passively viewing

an object 1250–1750 ms prior to the response. In Experiment 2, we demonstrate priming in a naming task but not a grasping task, verifying that the null priming effects seen for visually guided actions in Experiment 1 are not due to peculiarities of stimuli or timing parameters.

In Experiment 3 we show that visually guided grasping is influenced neither by passively viewing nor actively grasping a prime object, ruling out the possibility that the null priming effects for Experiments 1 and 2 were due to insufficient engagement of the visuomotor system by the prime stimulus.

2. Experiment 1

Experiment 1 used a paradigm similar to that of Craighero et al. (1996) to examine whether or not visually guided actions can be primed. Goal-directed movements were made to a target object in both visually guided and memory-guided conditions. Because the metrics of visually guided grasping movements are programmed largely on the basis of visual information gleaned just before the action is initiated (Westwood & Goodale, 2003), we did not expect to find evidence of priming in the visually guided task. Memory-guided movements, however, can be planned at any time using visual information delivered by the perceptual system (Hu & Goodale, 2000; Westwood & Goodale, 2003). Since the perceptual system is known to be sensitive to previously viewed stimuli, we expected to find reliable priming effects in the memory-guided grasping task, similar to the findings of Craighero and colleagues. We used a priming interval that was much longer than the one used by Craighero et al. (1996), who used an interval of only 100 ms between the priming stimulus and the response. In fact, the effective interval in their study may have been even shorter since the priming stimulus in their experiment was not masked, allowing visual persistence of the stimulus. As a consequence, they may not have been measuring the effects of priming, but rather the effects of having a stimulus present during the initiation of the response that was either congruent or incongruent with the orientation of the goal object. We reasoned that true priming (the re-activation of representations of objects or actions laid down earlier) would be evident at much longer intervals (1250–1750 ms) – but again only in the memory-guided grasping task.

2.1. Method

2.1.1. Participants

Eleven right-handed, undergraduate psychology students (four female, seven male) from the University of Western Ontario participated in this experiment. Participants had normal or corrected-to-normal vision, and no history of neurological impairment. They received \$10 for their participation. All participants gave informed consent and the study was approved by the local ethics committee.

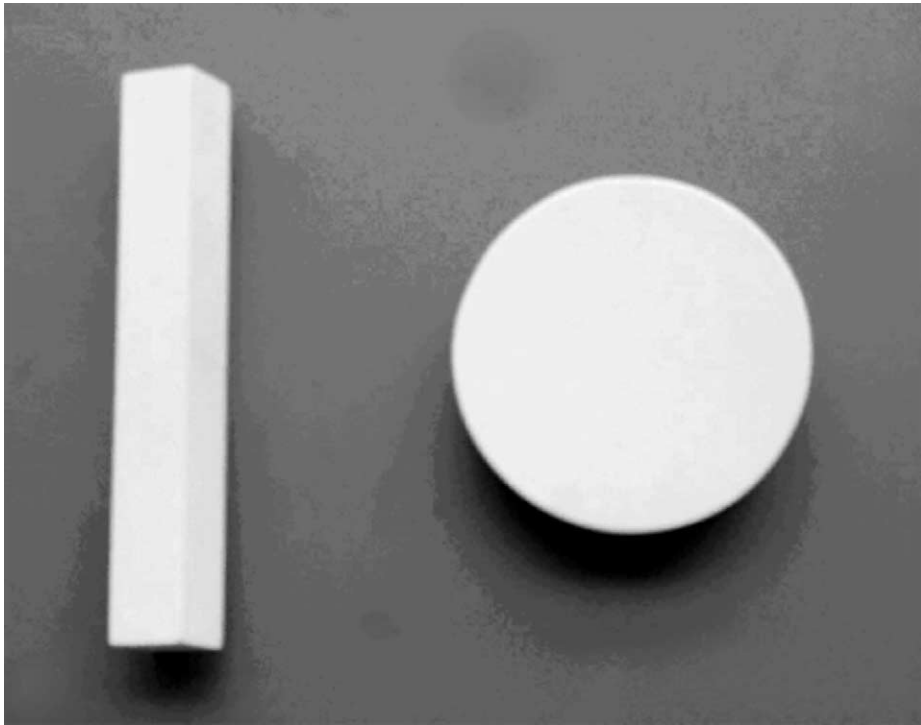


Fig. 1. Stimuli used in Experiment 1. The rectangular wooden block was used as both the prime and target object in all experimental conditions, and the circular wooden block was used as the prime in one of the control conditions.

2.1.2. Apparatus

Rectangular gray wooden blocks (24.9 cm long, by 3.4 cm wide, by 3.4 cm high) served as prime and target stimuli. A circular gray wooden block (15.2 cm radius) was used as the

prime stimulus in one of the control conditions (Fig. 1). A turntable device was used to present the objects to participants (Fig. 2). The prime and the target objects could be placed in two different orientations: 45° , or -45° from a sagit-



Fig. 2. Turntable apparatus used to present prime and target objects to participants in all three experiments.

tal plane extending out from the participants' midline. During the experiment, participants wore liquid-crystal goggles (Plato Translucent Technologies, Toronto, Ont.) (Milgram, 1987), which could rapidly be made transparent or opaque.

2.1.3. Procedure

In both the visually guided and the memory-guided grasping tasks, participants were instructed to grasp the target object as quickly as possible upon hearing an auditory cue. The order of the two tasks was blocked and counterbalanced across participants. In each task, participants depressed a start switch located in front of the turntable with their thumb and forefinger. Following Craighero et al. (1996), each trial began with a verbal pre-cue indicating the orientation of the target object (i.e., 'left', indicating 45° left from midline, or 'right', indicating 45° right). Following a 1500 ms interval, the goggles became transparent and revealed the prime object for a duration of 500 ms. The goggles then were occluded for a randomly varied inter-stimulus interval (ISI) of 1250, 1500, or 1750 ms. During the ISI, the turntable was rotated in order to position the target object in the workspace. After the ISI, an auditory signal cued participants to respond. In the visually guided task, the goggles were made transparent coincidentally with the auditory cue and then vision was occluded when the response was initiated or after 500 ms, whichever came first. Thus, participants received direct visual information about the target object during the movement programming phase but not the on-line control phase. In the memory-guided task, the goggles remained occluded after the auditory cue, so participants received no direct vision of the target object at any time. Reaction time was measured as the interval between the auditory cue and the release of the start switch.

Each task consisted of 24 trials in each of four different priming conditions (congruent, incongruent, no-prime, and neutral), which were randomly interleaved for a total of 96 trials. In the congruent and incongruent conditions the rectangular prime object was presented in either the same or different orientation with respect to the target object. In the no-prime condition no object was presented during the prime-viewing period; this condition was included to determine a baseline reaction time for visually guided and memory-guided grasping. In the neutral condition a circular object was presented during the prime-viewing period; this condition was included to determine whether or not viewing any object at all – even one that bears no visual similarity to the upcoming target object – can influence the speed to initiate a grasping movement.

2.2. Results

Reaction time data were analyzed using 2×4 repeated-measures analysis of variance, $\alpha = 0.05$. Main effects of interest included task (memory-guided and visually guided grasping) and condition (congruent, incongruent, no-prime and neutral). [A separate analysis of variance had revealed no significant main effects or interactions associated with

the different ISIs.] Pairwise post-hoc comparisons were performed on significant main effects using the Bonferroni procedure, $\alpha = 0.05$. An outlier analysis was performed for each participant, and reaction times that were three standard deviations above or below the mean reaction time for each task were excluded from analysis.

A significant main effect of condition was obtained, $F(3, 30) = 3.46$, $P < 0.05$, M.S.E. = 151.62. The interaction between task and condition approached significance, $F(3, 30) = 2.34$, $P = 0.09$, M.S.E. = 94.43. Because of the inherent differences between the two tasks, post-hoc Bonferroni pairwise comparisons were performed separately for the visually guided and memory-guided grasping tasks (Fig. 3). No significant differences were found between any conditions in the visually guided task (all P 's > 0.05 ; congruent: $M = 251.50$ ms, S.E.M. = 14.47; incongruent: $M = 254.86$ ms, S.E.M. = 14.12; no-prime: $M = 260.56$ ms, S.E.M. = 14.22; neutral: $M = 254.77$ ms, S.E.M. = 14.69). In the memory-guided grasping task, however, participants initiated their grasp to a congruent target object ($M = 255.66$ ms, S.E.M. = 14.99) significantly faster than they did to an incongruent target ($M = 273.38$ ms, S.E.M. = 15.79), $t(10) = 4.07$, $P < 0.05$. All other comparisons in the memory-guided task were non-significant (all P 's > 0.05 ; no-prime: $M = 266.87$ ms, S.E.M. = 16.23; neutral: $M = 264.97$ ms, S.E.M. = 15.11).

We also devised a composite measure to compare the overall sensitivity to priming in the memory-guided and visually guided tasks (Fig. 4). For each subject in each task, we subtracted the mean RT on congruent trials from the mean RT on incongruent trials and then divided this difference by 2 [$D_{\text{comp}} = (RT_{\text{IC}} - RT_{\text{C}})/2$]. This composite measure, which represents the average effects of congruent and incongruent

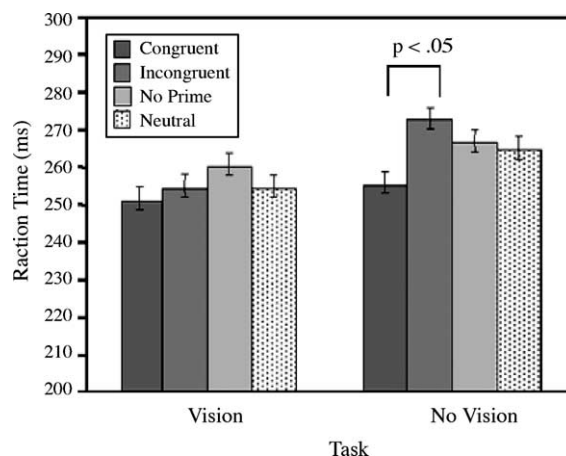


Fig. 3. Reaction times for each experimental condition in the visually guided and memory-guided tasks used in Experiment 1. Reaction times for visually guided grasping were not significantly different for the four conditions. For memory-guided grasping, however, reaction times for the congruent prime/target relationship were significantly faster than the incongruent condition. In all cases, Bonferroni pairwise comparisons were used. The term 'neutral' represents a condition where a circular wooden block was used as the prime object.

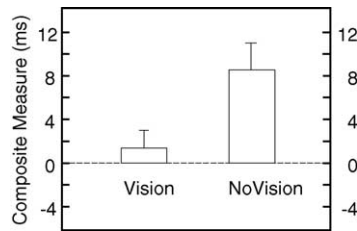


Fig. 4. Composite measures calculated to compare overall sensitivity to priming in the memory-guided and visually guided grasping tasks in Experiment 1. For each subject in each task, mean RTs for congruent conditions were subtracted from mean RTs for incongruent conditions and then this difference was divided by two. This composite measure represents the average difference in the effect of congruent and incongruent priming on reaction time.

priming on reaction time, reflects the specific effects of orientation priming rather than the general effects of preparatory set. We found that D_{comp} ($M = 8.86$ ms, $S.E.M. = 2.18$) for the memory-guided task was significantly higher than D_{comp} ($M = 1.68$ ms, $S.E.M. = 1.62$) for the visually guided task ($t(10) = 4.51$, $P < 0.001$), which did not differ significantly from zero ($t(10) = 1.04$, $P > 0.3$).

2.3. Discussion

The results of Experiment 1 were clear: memory-guided but not visually guided movements showed evidence of priming. In agreement with Goodale et al. (1994), this suggests that the dedicated visuomotor networks mediating object-directed movements operate in ‘real-time’, and the necessary computations are based on information about the object’s features and disposition that is derived from the retina rather than from stored cognitive information. When the object is not visible, the grasping movement must then be based on cognitive information – and this is presumably the reason that response latency was affected by congruent or incongruent stimuli presented just before the memory-driven movement was initiated.

As discussed earlier, memory-guided grasping could engage different brain mechanisms than visually guided grasping (Goodale et al., 2004). In other words, Craighero et al.’s (1996) claim that the visuomotor system can be primed needs to be qualified. Such priming, it appears, occurs only when visual information about the goal object is unavailable at the moment the cue to respond is presented.

One possible problem is that the paradigm we borrowed from Craighero et al. (1996) is somewhat unconventional. That is, in most perceptual priming studies no advance information is given about the features of the target stimulus (i.e., in Experiment 1 participants were given verbal information about the target’s orientation before the trial began). It is possible that if we had used a priming paradigm of the sort known to produce robust priming in a naming task with visible objects (Wiggs & Martin, 1998), for example, we might have obtained priming even in visually guided grasping. We explored this possibility in Experiments 2 and 3.

3. Experiment 2

In this experiment, we directly compared the effects of a prime stimulus on the grasping and naming of visible objects. Four objects with different shapes were used. Each object was given a one-syllable nonsense name, which participants learned ahead of time. Although each object had a distinctive shape, they all afforded the same kind of grasping movement. Each object could be presented in one of four possible orientations, each of which required an adjustment in the grasping response. We used a conventional priming paradigm in which we simply presented the prime object followed a short time later by the target object (i.e., unlike Experiment 1, participants were given no advance verbal information about the true orientation of the upcoming target object).

We expected that naming responses would be affected by the congruence between prime and target identity (i.e., shape and name) but not by the congruence between their orientations (Tarr & Pinker, 1989). Based on the results obtained in Experiment 1, we expected that grasping would show no priming effects whatsoever.

3.1. Method

3.1.1. Participants

Twelve right-handed, first year psychology students from the University of Western Ontario participated in this experiment. Participants ranged in age from 18 to 20 years and had normal, or corrected-to-normal vision, and no history of neurological impairment. Participants were selected using the Psychology Research Participation pool, and received one research credit towards their final grade upon completion of the study. All 12 (nine female, three male) students took part in both the naming and grasping tasks. All participants gave informed consent and the study was approved by the local ethics committee.

3.1.2. Apparatus

Four visually distinct, gray wooden blocks (24.9 cm long by 3.4 cm wide) were used in this experiment (Fig. 5). The blocks varied on two dimensions: cross-section (circle versus square) and tapering (tapered versus non-tapered); this was done to ensure that the naming task was sufficiently difficult. A turntable device was used to present prime and target objects to participants (Fig. 2); these objects could be placed in four different orientations: 45° , 22.5° , -22.5° , or -45° from the participant’s midline; four orientations were used to match the four possible identities in the naming task. The availability and timing of visual information was controlled using the goggles described in Experiment 1.

3.1.3. Procedure

Prior to the two experimental tasks, participants underwent a learning phase to ensure rapid and accurate naming of the four stimuli. Each of the four wooden blocks was handed to the participants in sequence, with the nonsense name be-

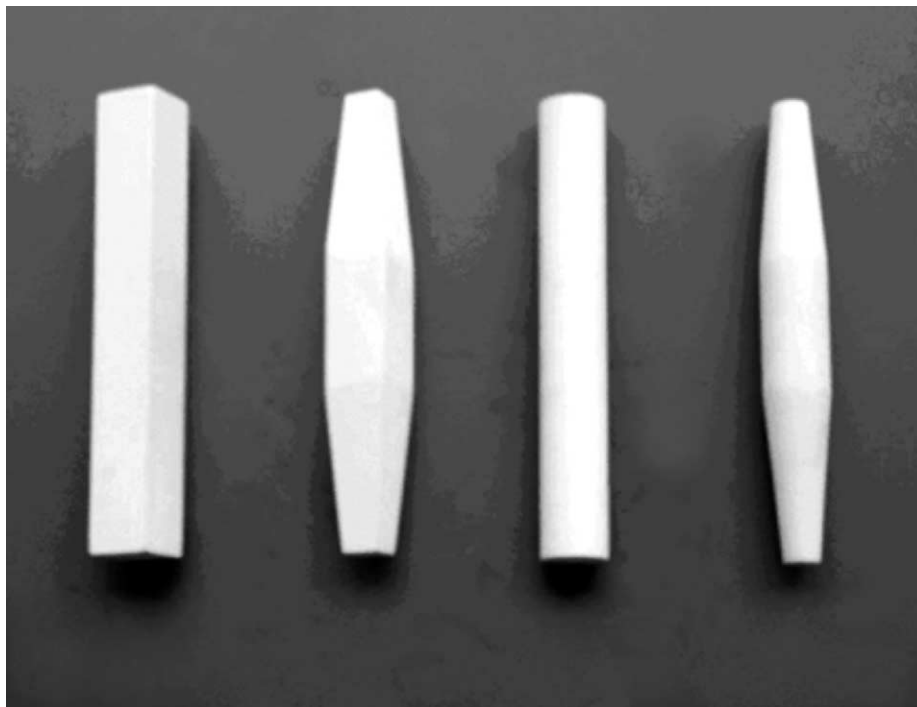


Fig. 5. Stimuli used in Experiments 2 and 3. In Experiment 2, each block was given a nonsense name (i.e., ‘kiff’, ‘fid’, ‘tam’, and ‘sup’) to ensure that participants did not confuse them with familiar objects. The shape of the blocks varied on two dimensions: cross-section (circle vs. square) and tapering (tapered vs. non-tapered).

ing given upon presentation. Monosyllabic nonsense names (‘kiff’, ‘fid’, ‘tam’, and ‘sup’) were used in order to reduce confusion with familiar objects. Participants were allowed to explore each object manually for a few seconds. Each object was handled twice in this manner. Participants then viewed and named each object one at a time. If the response was incorrect, the correct name was provided by the examiner. This training phase consisted of 56 trials, with object shape (4) and orientation (45° , 22.5° , -22.5° , or -45°) randomized across trials.

After the training phase, participants completed the naming and grasping tasks. Tasks were blocked with order counterbalanced across participants. For both tasks, participants viewed the prime object for 500 ms. The goggles were then closed for a randomly varied inter-stimulus interval (ISI) of 1250, 1500, or 1750 ms and then re-opened.

In the naming task, participants were instructed to say the name of the target object as quickly and accurately as possible. The goggles were closed by the participant’s vocal response or after 500 ms. No feedback was given as to the accuracy of responses during the experiment. Reaction time to name the target object was measured as the delay between the opening of the goggles and the onset of speech (as measured by a voice-activated microphone system); naming accuracy was evaluated after the experiment and incorrect trials were excluded from the analysis.

In the grasping task participants were required to reach out and grasp the target object rather than name it. Here, participants depressed a start switch with their thumb and

forefinger at the beginning of each trial. When the goggles opened after the prime-target ISI, participants reached out and grasped the target object as quickly as possible. Reaction time was recorded as the delay between the opening of the goggles and the release of the start switch.

For both tasks, there were five conditions each presented 16 times in random order, for a total of 80 trials per task. In one condition, the prime and target were identical in shape (S) and orientation (O), S+O+. In a second condition, prime and target objects had the same shape, but different orientation (S+O–). In the two remaining conditions, the prime and target objects had either a different shape and the same orientation (S–O+), or neither the same shape nor the same orientation (S–O–). There was also a control condition in which the prime stimulus was not presented; this was used to establish a ‘baseline’ reaction time for naming and grasping the target objects.

3.2. Results

Reaction time data were analyzed using $2 \times 3 \times 5$ repeated-measures analysis of variance, $\alpha = 0.05$. Main effects of interest included task (naming and grasping), ISI (1250, 1500, and 1750 ms), and condition (S+O+, S+O–, S–O+, S–O–, and control). Significant interactions were investigated using simple effects analysis, $\alpha = 0.05$. An outlier analysis was performed for each participant, and reaction times that were more than three standard deviations above or below the mean reaction time for each task were

excluded from analysis. Incorrect responses in the naming task were not analyzed. There were no ‘incorrect’ grasps.

A significant main effect of task was obtained, $F(1, 11) = 205.3$, $P < 0.01$, M.S.E. = 106 596.0, with reaction times for grasping being faster overall (Grasping: $M = 281.9$ ms, S.E.M. = 15.8 ms) than the reaction times for naming ($M = 775.0$ ms, S.E.M. = 35.2 ms). A significant main effect of condition was also found, $F(4, 44) = 10.0$, $P < 0.01$, M.S.E. = 12 685.8. This effect, however, was qualified by a significant task by condition interaction, $F(4, 44) = 9.9$, $P < 0.01$, M.S.E. = 13 326.9 (Fig. 6). Simple main effects analysis indicated that the effect of condition in the grasping task was not significant, $F(4, 44) = 0.5$, ns. As Fig. 6 shows, the reaction times for grasping were virtually identical for all the priming conditions. Reaction times in the naming task, however, were affected by condition, $F(4, 44) = 10.2$, $P < 0.01$, M.S.E. = 25 401.9. Multiple pairwise comparisons were performed between the different conditions. As Fig. 6 shows, when the prime and the target shared the same identity (S+O+ and S+O–), reaction times were faster than when their identity differed (S–O+ and S–O–) (all P 's < 0.05). The conditions in which the prime and the target shared the same identity also yielded significantly faster reaction times than the control condition in which no-prime was presented ($P < 0.05$). There was no difference, however, between the control condition and the conditions in which the identity of the prime and target were not the same (all P 's > 0.05). The orientation of the prime had no effect on naming latencies. In other words, the reaction times of conditions S+O+ and S+O– did not differ significantly from one another; nor did the reaction times of conditions S–O+ and S–O– (all P 's > 0.05).

3.3. Discussion

The results of Experiment 2 provide no evidence for visuomotor priming in a conventional priming paradigm that yields robust priming of naming responses. The complete absence of visuomotor priming lends additional support to the argument that grasping involves a direct conversion of visual input into action with little if any intrusion from earlier memories of the target object. The absence of priming on grasping in this experiment is even more compelling when one considers the fact that the same repetition-priming paradigm resulted in a difference of more than 150 ms between the various priming conditions in the naming task. [The fact that grasping was always faster than naming probably reflects the fact that converting vision into action co-ordinates can proceed much more quickly than converting vision into an object representation which is then used to access stored semantic memory.]

In the naming task, the presentation of the prime stimulus could have elicited an unspoken naming response from the participants, which then could have facilitated (or interfered with) the later naming of the target object. It is less likely that such passive viewing of the prime stimulus would have invoked an implicit grasping response. This difference in covert responding to the prime could account for the observed difference in priming between naming and grasping. Thus, to optimize the possibility of observing any priming in a visually guided task, we carried out an additional experiment in which participants were required to produce an overt grasping action when the prime was presented (an action that we assumed would engage the visuomotor system).

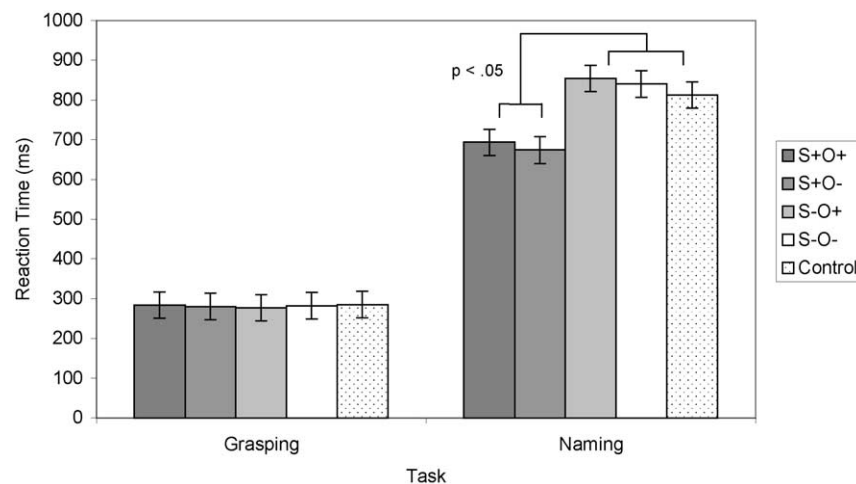


Fig. 6. Reaction times for each experimental condition in the grasping and naming tasks used Experiment 2. Reaction times for grasping were not different for the five experimental conditions. For naming, reaction times were reduced for conditions in which prime and target objects were the same shape. S+, same shape; S–, different shape; O+, same orientation; O–, different orientation.

4. Experiment 3

In this experiment, priming of grasping was studied in two different tasks. The first task (view–grasp) was similar to the visually guided grasping task used in Experiment 2. In the other task (grasp–grasp), participants were required to grasp the prime stimulus and then subsequently grasp the target object. If priming depends on the production of the same response during the presentation of the prime and target, then participants should show priming in the grasp–grasp task. We predicted, however, that priming would not be evident in either task, based on our assumption that the control of actions to visible objects engages real-time sensorimotor transformations that do not make use of stored cognitive information.

4.1. Method

4.1.1. Participants

Eleven right-handed, first year psychology students (six female, five male, aged 18–20 years) from the University of Western Ontario participated in this experiment. None of the students had participated in Experiments 1 or 2. Criteria for selecting and giving credit to participants were identical to Experiment 2. All participants took part in both experimental tasks.

4.1.2. Apparatus

The experimental apparatus was identical to Experiment 2 (see Figs. 2 and 5).

4.1.3. Procedure

Initially, participants underwent a learning phase identical to the one used in Experiment 2. This was to ensure that participants formed a cognitive representation of each target object and an association to a nonsense name, as in Experiment 2. Participants then completed the view–grasp and grasp–grasp tasks. The two tasks were blocked with order counterbalanced across participants. In the view–grasp task participants passively viewed the prime object, and then grasped the target object. In the grasp–grasp task participants grasped the prime object and then the target object. For both tasks, there were 16 trials for each of five conditions (S+O+, S+O–, S–O+, S–O–, control; as in Experiment 2), giving a total of 80 trials. Conditions were randomly intermixed. In Experiment 3 the prime–target ISI was randomly varied between 2500, 2750, and 3000 ms. These longer ISIs were necessary because participants required enough time to complete the initial grasping response in the grasp–grasp task and return to the start button. [A separate study run on 10 participants, each tested on 20 trials from the grasp–grasp task, showed that they were able to complete the sequence of movements in the priming phase with an average time of 1385 ms (S.E.M. = 24).]

4.2. Results

Reaction-time data were analyzed using a $2 \times 3 \times 5$ repeated-measures analysis of variance, $\alpha = 0.05$. Main effects of interest included task (view–grasp and grasp–grasp), ISI (2500, 2750, and 3000 ms), and condition (S+O+, S+O–, S–O+, S–O–, and control). Significant interactions were investigated using simple effects analysis, $\alpha = 0.05$. Reaction times that were found to be more than three standard deviations above or below the mean reaction time for each participant were excluded.

The view–grasp task had shorter reaction times ($M = 280.5$ ms, S.E.M. = 12.6 ms) than the grasp–grasp task ($M = 315.6$ ms, S.E.M. = 12.2 ms), $F(1, 10) = 5.9$, $P < 0.05$, M.S.E. = 17 365.9. Reaction time was not affected by condition, $F(4, 40) = 1.1$, ns (Fig. 7). Moreover, the task by condition interaction was not significant, $F(4, 40) = 1.1$, ns. In other words, there was no evidence that grasping the prime stimulus resulted in any more priming than passive viewing of the prime. A significant effect of ISI was detected, $F(2, 20) = 5.8$, $P < 0.05$, M.S.E. = 1062.7, but this effect was qualified by a significant interaction between task and ISI, $F(2, 20) = 4.5$, $P < 0.05$, M.S.E. = 490.9 (Fig. 8). A simple effects analysis indicated that there was no significant effect of ISI in the view–grasp task, $F(2, 20) = 1.3$, ns. However, ISI affected reaction times in the grasp–grasp task, $F(2, 20) = 7.7$, $P < 0.01$, M.S.E. = 992.5. Multiple pairwise comparisons between ISIs in the grasp–grasp task showed that reaction times for the 2500 ms ISI were significantly slower than both the 2750 and 3000 ms ISIs, all P 's < 0.05 . Reaction times for the 2750 and 3000 ms ISIs, however, did not differ significantly from each other, $t(10) = 0.6$, ns.

4.3. Discussion

Results from Experiments 1 and 2 indicated that passively viewing a prime stimulus did not affect the time to initiate a grasping response to a visible target. It is possible, however, that the absence of priming in these experiments was due to the fact that the visuomotor system mediating grasping was not adequately engaged by passive viewing of the prime stimulus. But this possibility is not supported by the results of Experiment 3, in which the RTs of movements in the grasp–grasp condition did not vary as a function of the similarity between the prime and the target object – despite the fact that the visuomotor system was clearly engaged by the prime object. This suggests that grasping movements directed at visible targets cannot be primed even when an identical, overt visuomotor transformation has taken place scant moments ago.

Reaction times were longer overall to grasp the target object in the grasp–grasp as compared to the view–grasp task. One possible explanation for this difference is the relatively great cognitive load demanded by the grasp–grasp task: the participants had to reach out and grasp the prime object, hand it over to the investigator, replace the thumb and forefinger

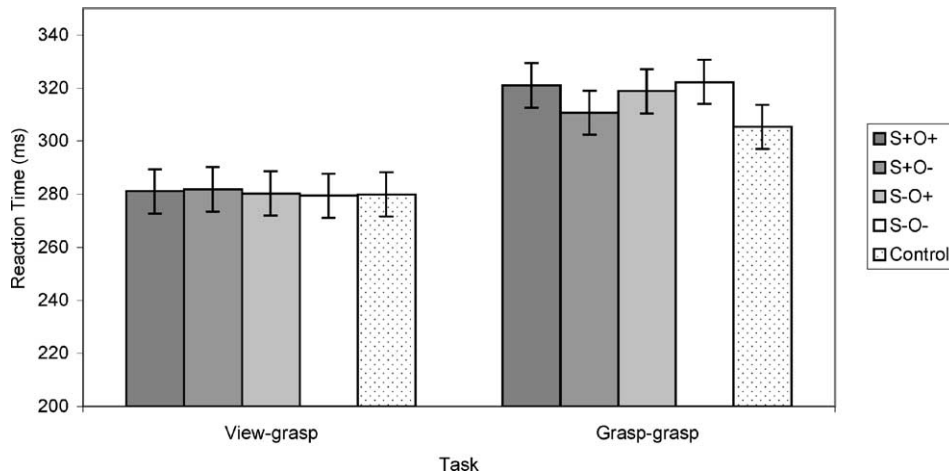


Fig. 7. Reaction times for each experimental condition in the view–grasp and grasp–grasp priming tasks used in Experiment 3. Reaction times for the view–grasp and grasp–grasp tasks were not significantly different for the five experimental conditions, although overall view–grasp showed faster reaction times than grasp–grasp. S+, same shape; S–, different shape; O+, same orientation; O–, different orientation.

back on the start switch, and then get ready to grasp the target object. In other words, the presentation of the prime could have interfered with the normal development of preparatory set for action. For this reason, participants could not prepare to respond to the target as well as they could in the view–grasp task, where the preparatory set was easier to maintain because only one grasping movement was required on any trial. This explanation is supported by the fact that, in the grasp–grasp task, reaction times for the shortest ISI (i.e., 2500 ms) were slower than any other responses. With this ISI, participants would have had the least amount of time to prepare for grasping the target object.

The fact that participants showed no priming in the grasp–grasp task shows that programming and executing a particular grasping movement has no effect on the program-

ming and execution of a later grasping movement, even if that movement is identical. This suggests that the earlier motor program (or any of the related computations) were not stored in a form that could be used by the real-time visuomotor system, since if they had been, we would have expected to see a reaction-time advantage when participants grasped the target object. The absence of such an advantage provides compelling evidence that grasping movements are largely programmed ‘bottom up’ on the basis of new retinal information each time a goal object is presented. Thus, the lack of a visuomotor priming effect in this experiment provides further support for the view that the visual control of action to visible targets operates in real-time and does not use stored information about the upcoming target or any earlier motor programming (Goodale et al., 1994).

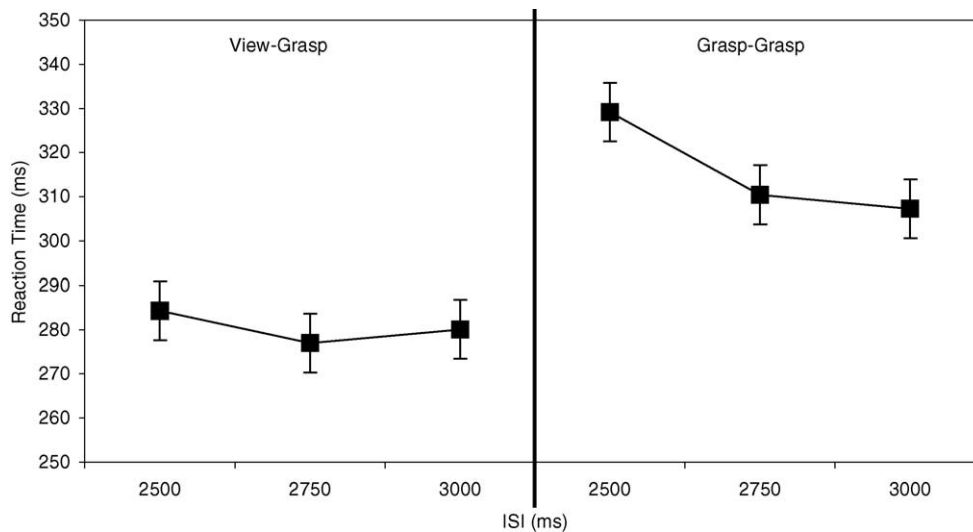


Fig. 8. Task by ISI interaction for Experiment 3. Reaction times for the view–grasp task were similar for all ISIs. For the grasp–grasp task, the mean reaction time for the 2500 ms ISI was significantly longer than the mean reaction times for the 2750 and 3000 ms ISIs, which did not differ from one another.

5. General discussion

Taken together, these experiments clearly demonstrate that visually guided grasping movements cannot be primed by previously viewing or even interacting with an object that is identical in all respects to the goal object. These findings contrast sharply with the vast wealth of behavioural evidence indicating that many aspects of visual cognition (e.g., object recognition) can be primed by previously viewed stimuli (Wiggs & Martin, 1998). Such a striking dissociation between action and perception is perhaps not surprising when one considers the fundamental differences between interacting with an object versus recognizing it (Goodale & Milner, 1992).

5.1. Object perception versus object-directed action

As discussed earlier, the metrics of a grasping action can be computed quickly and reliably from visual information that is present on the retina when the action is required. That is, there is no need to rely on stored information about the target object – at least insofar as the instantaneous spatial properties of the object (i.e., its size, shape, orientation and location) are concerned. Indeed, utilizing stored visual information could prove detrimental to motor performance, since the disposition of the object with respect to the actor can change quickly and unpredictably. In this regard, the visual control of action differs quite dramatically from object perception: the identity of an object in the visual scene remains stable over time, and it is therefore computationally efficient to retain in memory a representation of the object that can be used for a myriad of cognitive operations (e.g., recognition, comparison, association, behavioural inhibition).

5.2. Priming action systems

Our findings provide an important qualification to Craighero et al.'s (1996) notion that it is possible to prime the control of manual actions. As Experiment 1 clearly demonstrates, memory-guided but not visually guided actions can be primed by visual information from previously seen objects. The task utilized by Craighero and colleagues can be conceived of as a memory-guided task, since participants never saw the goal object; its metrics therefore must have been derived from memory on the basis of the verbal cue at the start of each trial. As such, in the present study we replicate Craighero et al.'s original finding (using a much longer interval between the prime and the response), but reach a rather different conclusion about the capacity of the visuomotor system to be primed.

Visually guided actions appear to be programmed primarily – if not exclusively – using visual information that is on the retina when the action is about to be executed. In other words, visually guided actions are programmed and executed in real-time. The present findings are entirely consistent with recent evidence indicating that separate mechanisms under-

lie the control of memory-guided and visually guided actions (Goodale et al., 2004). According to this line of evidence, memory-guided actions depend on visual processing that takes place in the perceptual system, since this system has the capacity to store in memory a representation of a target object. Visually guided actions, however, engage a quite separate set of visual mechanisms that are dedicated to the real-time transformation of retinal information into action. As outlined earlier, the perceptual system is exquisitely sensitive to priming effects; it is thus not surprising that memory-guided actions should also demonstrate priming.

5.3. Moving forward

There are several issues that still must be addressed in this research. One obvious limitation of the present study is that the key conclusions rest on a null effect; that is, the absence of statistically significant differences between priming conditions in the visually guided grasping tasks. Insufficient statistical power does not seem to be a legitimate concern however. There was no trend towards a difference in reaction time between priming conditions in the various visually guided grasping tasks, in *any* of the three experiments – even though there was a clear effect of the priming stimulus on reaction times in both the memory-guided grasping task as well as the naming task. We are quite confident, therefore, that there are no priming effects to be found in grasping, even with larger sample sizes.

Another factor to consider is the nature of the grasping posture required in the present study. The relatively large target objects that we used afforded a whole-hand grasp in which the thumb opposed the fingerpads of three or four of the remaining digits. Such a grasp arguably does not require as much spatial precision as a pincer grip, and thus might lead to faster reaction times. Nevertheless, it seems unlikely that a floor effect can explain the absence of priming in visually guided grasping. After all, priming *was* effective in the memory-guided grasping task even though the reaction times in this task were comparable to those seen in visually guided grasping. In fact, the reaction times we observed with the whole-hand grasp were little different from those we observed in an earlier study that required a pincer grip, where again perception-based information influenced memory-guided but not visually guided grasping (Westwood & Goodale, 2003).

The experiments in the present study focused specifically on the orientation of the prime and goal objects. In part, this decision was based on the previous work by Craighero et al. (1996). As discussed earlier, the orientation of an object with respect to the observer can change when either the actor or the goal object change position. As such, object orientation – and position – might fall in a special class of object features that the visuomotor system always computes *de novo* when actions are required. Perhaps visuomotor tasks that depend on intrinsic features of the object (e.g., shape, size, mass), which are stable over time, might be subject to priming. In-

sofar as the object's size and shape can be derived entirely from visual information on the retina, we would predict that these features would be computed on demand when actions are required, and would not be subject to priming by previously encountered objects. The computation of object mass, however, cannot be driven exclusively by retinal information and requires either episodic (e.g., prior experience) or semantic memory (e.g., knowledge of material density) (Goodale, 2000). For this reason, we predict that the control of motor output that depends on knowledge of object mass, such as the regulation of grip force and load forces (Gordon, Westling, Cole, & Johansson, 1993), should be sensitive to priming effects.

Acknowledgements

This research was supported by grants from the Canadian Institutes of Health Research and the Canada Research Chairs Program.

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