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Planning movements well in advance

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It has been suggested that the metrics of grasping movements directed to visible objects are controlled in real time and are therefore unaffected by previous experience. We tested whether the properties of a visually presented distractor object influence the kinematics of a subsequent grasping movement performed under full vision. After viewing an elliptical distractor object in one of two different orientations participants grasped a target object, which was either the same object with the same orientation or a circular object without obvious orientation. When grasping the circular target, grip orientation was influenced by the orientation of the distractor. Moreover, as in classical visuomotor priming, grasping movements were initiated faster when distractor and target were identical. Results provide evidence that planning of visually guided grasping movements is influenced by prior perceptual experience, challenging the notion that metric aspects of grasping are controlled exclusively on the basis of real-time information.

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

The anatomical and functional distinction between the dorsal and ventral streams of visual processing has been studied extensively (e.g., Goodale & Milner, 1992; Milner & Goodale, 1995; Mishkin, Ungerleider, & Macko, 1983; Ungerleider & Mishkin, 1982). However, the precise nature of this separation is still under debate. Milner and Goodale (1995) proposed that the distinction between the ventral and the dorsal stream corresponds to the distinction between perceptual representation (perception) and visuomotor control (action). According to their view, also known as the "two visual systems" hypothesis, the ventral stream is mainly involved in object identification and recognition whereas the dorsal stream mainly processes visual

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information for the control of actions (e.g., grasping).

One of the critical assumptions is that the two streams are assumed to process information on different time scales (Goodale, Jakobson, & Keillor, 1994; Milner et al., 2001; Rossetti, 1998). To be able to recognize objects, viewpoint-independent information must be stored over a long time in the ventral stream. In contrast, spatial information in the dorsal stream that one relies on when interacting with the object only needs to be available for a few milliseconds since the relative positions of the observer and the goal object change all the time. Therefore, it is assumed that the information required for an action must be computed immediately before the beginning of the movement in real time (Westwood & Goodale, 2003; Westwood, Heath, & Roy, 2003). Consequently, whenever a movement is directed to a visible object (closed loop) the dorsal stream carries out fast, metrically accurate, visuomotor computations. The perceptual mechanisms of the ventral stream are only engaged in movement planning and control if the target is removed from view prior to response initiation (open loop). According to this "real-time view" of motor programming, metric aspects of previously seen targets should not influence visually guided movements.

The fact that motor representations in the brain are activated by the mere presence of an object (e.g., Chao & Martin, 2000; Grafton, Fadiga, Arbib, & Rizzolatti, 1997; Grèzes & Decety, 2002; Grèzes, Tucker, Armony, Ellis, & Passingham, 2003) and that previous movements influence goal-directed actions under some conditions (de Lussanet, Smeets, & Brenner, 2001; Jax & Rosenbaum, 2007) challenges such a clear functional distinction. Furthermore, it was shown by Haffenden and Goodale (2000, 2002) that learned perceptual information can affect the kinematics of goal-directed actions as well. Visuomotor priming studies also seem to be inconsistent with the real-time view of motor programming (Craighero, Fadiga, Rizzolatti, & Umiltà, 1998; Craighero, Fadiga, Umiltà, & Rizzolatti, 1996). In this paradigm, reaction times (RTs) of grasping movements are shorter when grasping a target object that has congruent properties with a previously seen priming object than when grasping one that is incongruent with the prime. Craighero et al. (1998; Craighero et al., 1996) concluded that prior visual information is used when performing a grasping movement. However, recent studies criticized this conclusion (Cant, Westwood, Valyear, & Goodale, 2005; Garofeanu, Kroliczak, Goodale, & Humphrey, 2004; Goodale, Cant, & Króliczak, 2006). They argued that in the studies of Craighero et al. (1998; Craighero et al., 1996) participants only received auditory information about the nature of the target object. Participants never saw the target stimulus they were supposed to grasp. Thus, the grasping movement was open loop and had to be planned in advance. According to the real-time view of motor programming, the visual properties of a previously seen object, stored in the ventral stream, had to be used to perform those grasping movements. This would explain the priming effect, which is expected to occur when the metrics of the movement are derived from memory and not from direct visual information.

To resolve this potential problem, Cant et al. (2005) and Garofeanu et al. (2004) performed studies in which participants were able to see the target object during the programming phase of the movement or during the entire grasping movement. This ensured that the grasping movements towards the target could be programmed in real time (dorsal stream) from direct visual input. No priming effect was found in these studies (Cant et al., 2005; Garofeanu et al., 2004). Cant et al. (2005) interpreted these results as further evidence for the real-time view of motor programming and concluded that object orientation and position are object features that are always computed de novo by the visuomotor system when an action is required. In other words, the programming of movement parameters concerning the precise metrics of a closed-loop movement is assumed always to be carried out in real time and not to be influenced by previous experience.

We think, however, that all studies discussed so far have a serious limitation. In all these studies, only RT was examined to determine whether the orientation of a previously shown object influences the movement towards a target object. However, RT might not be the best measure of information processing, because participants can start a movement before having analysed all information needed for that movement (van Sonderen & van der Gon, 1991). Therefore, in the study by Cant et al. (2005), participants could have started the grasping movement before specifying the exact orientation of the hand at the time of grasp and then adjusted the orientation of the hand online. Thus, measuring RT in a visuomotor priming paradigm might not reveal all use of prior information. The study of Jax and Rosenbaum (2007) is one example overcoming this "RT-limitation". They showed that the hand's path curvature of visually guided grasping movements was primed by the presence of an obstacle in previous trials, whereas no typical priming effects were found on RT.

In our study we tested directly whether visually guided grasping movements can use prior metric information. We examined the effect of a visually presented distractor object not only on the RT of a subsequent grasping movement, but also on kinematic variables, such as grip orientation. We presented distractor objects in a certain orientation before participants had to grasp either a similarly oriented target or a circular target with no obvious orientation. The target objects were fully visible during grasping such that, according to the real-time view of action, the dorsal stream should calculate the metric aspects of the object in real time. In consequence, kinematic variables such as the grip orientation should not show any influence of the distractor object if the real-time view of action is correct. If, however, perception and memory are involved in the execution of visually guided grasping movements as proposed by other studies (e.g., Haffenden & Goodale, 2000, 2002; Jax & Rosenbaum, 2007) then the orientation of the distractor object should influence the selected grip orientation when grasping the target.

Method

Participants

A total of 10 participants were recruited from within the Faculty of Human Movement Science of the Vrije Universiteit Amsterdam. All participants were right-handed by self report and had normal or corrected-to-normal visual acuity. The study was approved by the local ethics committee.

Apparatus and stimuli

Three cylindrical objects made of white plastic material served as distractor or target stimuli. One of the objects was a cylinder with a circular base with a diameter of 5 cm. The other two objects had an elliptical base (small: 5×2 cm, large: 7×5 cm; these were grasped along the 5-cm and 7-cm axes, respectively). All objects were 10 cm in height.

On each trial, a distractor and a target object were placed on a sliding carriage, each at one end in appropriately shaped cut-outs (Figure 1). One of the objects was visible whereas the other was hidden from view. There was a surface at each side of the apparatus to occlude the view of the target when the distractor was presented and vice versa. To quickly change the object that the participant could see the sliding carriage was moved to the opposite side of the apparatus. This brought the other object to the same visible position. Each elliptical object could be placed in one of two orientations: 0° or 30° with respect to the participants' midline. The starting position of the hand was at the nearest corner of the surface above the right occluder (see Figure 1).

Trajectories of the grasping movements were recorded using a two-camera Optotrak 3020 system at a sampling rate of 200 Hz. A small triangular plastic plate on which three infrared light-emitting diodes (IREDs) were mounted was attached to the nail of the thumb of the right hand, and a second one to the nail of the index finger. This enabled us to calculate the trajectories of the grasp positions from the trajectories of the three IREDs. To determine the grasping positions on the digits relative to the IREDs on the plastic plate, a calibration trial, in which participants held an extra IRED between index finger and thumb, was recorded before the experiment started. In order to determine the moment in time at which the target object was lifted, an additional IRED was affixed to the

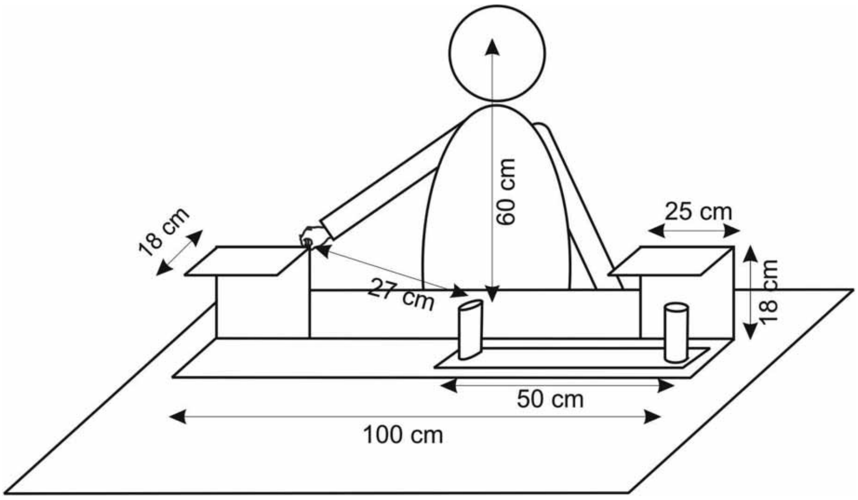

Figure 1. *Schematic drawing of the experimental set-up (front view) showing a participant with the hand at the starting position.*

target object. During the experiment participants wore liquid-crystal shutter glasses (Milgram, 1987), which could rapidly suppress vision by changing from a transparent to an opaque state.

Procedure

Participants stood in front of a table, which was adjusted to the height of their hips. They looked down at the objects with a viewing distance of about 60 cm. Before starting the experiment, 10 practice trials were executed for familiarization with the task. At the beginning of each trial participants placed their hand at the starting position, and the shutter glasses turned opaque. Subsequently, the experimenter placed a distractor and a target object on the sliding carriage. When the shutter glasses became transparent participants had to look at the distractor object, which was visible for 500 ms. Then the shutter glasses turned opaque again for an interstimulus interval (ISI) of 2 seconds. During the ISI the experimenter replaced the distractor by the target by moving the sliding carriage. Thus, the target object appeared at the same location as the previously shown distractor. After the ISI the shutter glasses became transparent again, and at the same time an auditory signal cued the participants that they should grasp the target object. Participants were instructed to pick up the target object as quickly as possible. They were to grasp the upper half of the objects from the side using thumb and index finger (precision grip). They were to put the target object in front of themselves on the table and move their hand back to the starting position on top of the right occluder. The shutter glasses remained transparent during the entire grasping movement, so that participants had full vision of their hand and the target object.

Each of the three cylindrical objects (circular, small elliptical, or big elliptical cylinder) of each orientation (0° or 30°) could serve as a distractor. The subsequent target was either the same elliptical object in the same orientation (control trials) or the circular cylinder (test trials; for an overview of all conditions see Figure 2). Each type of control trial was presented 25 times and each type of test trial 10 times. Control trials were presented more often than test trials in order to increase the probability that participants use the distractor object to plan the subsequent grasping movement. The condition in which the circular distractor was followed by the circular target was presented 10 times. This latter condition served as a baseline condition for grip orientation when normally grasping a circular cylinder. This results in a total of 150 trials, which were presented in random order.

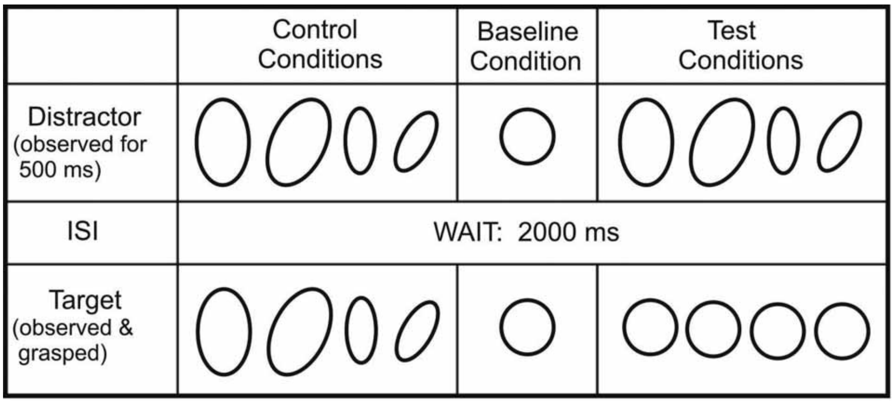

Figure 2. *Schematic representation of all nine combinations of distractor and target. The 0° stimuli were oriented sagittally, and the 30° stimuli are rotated clockwise. Each test condition and the baseline condition were presented 10 times. The four control conditions were each presented 25 times.*

Data analysis

As the task primarily involved horizontal movements, and only the horizontal orientation of the cylinders was manipulated, we only analysed the horizontal orientation of the hand. Grip orientation is defined as the angle of the horizontal projection of the line connecting the grasping positions of the index finger and the thumb (a sagittal line corresponds to a 0° orientation of the grip, and a clockwise rotation is defined as positive). This angle was determined at different moments before and during the grasping movement.

Movement onset was defined by a velocity criterion. The first frame in which a digit exceeded a velocity threshold of 0.2 m/s was taken as movement onset. Movements were analysed until the marker mounted on the target object exceeded a velocity threshold of 0.2 m/s, which was considered as the lift-off of the object. Reaction time (RT) is defined as the time between the auditory signal (and the target becoming visible) and movement onset. Movement time (MT) is defined as the time between movement onset and the lift-off of the target object. Maximum grip aperture (MGA) is defined as the maximum distance in 3D between the calculated grasp positions of the thumb and the index finger during the grasping movement.

Data of the test and control conditions were analysed using repeated measures analyses of variance (ANOVAs). Dependent variables were RT, MT, MGA, and the orientation of the hand at different moments in time (one second before movement onset, ISI; at movement onset; at MGA; and at lift-off of the target object). Values are presented as means $\pm$ standard errors of the means. A significance level of $\alpha = .05$ was used for all statistical analyses.

Results

Grip orientation in time

Our main interest was in the influence of the orientation of a distractor object on the grip orientation when subsequently grasping a target object. For this we analysed the test trials: trials in which the participants grasped the circular target object after having seen a small or large elliptical distractor object in a certain orientation (0° or 30°). A 2 (distractor orientation: 0°/30°) × 2 (distractor size: large/small) repeated measures ANOVA was performed at four different moments in time (ISI, movement onset, moment of MGA, and lift-off of the object). Each panel of Figure 3 shows the grip orientation when the circular target object was grasped at one of those moments in time. During the ISI and at movement onset grip orientation was not affected significantly by the orientation of the previously seen distractor object, $F(1, 9) = 0.54$, $p = .48$

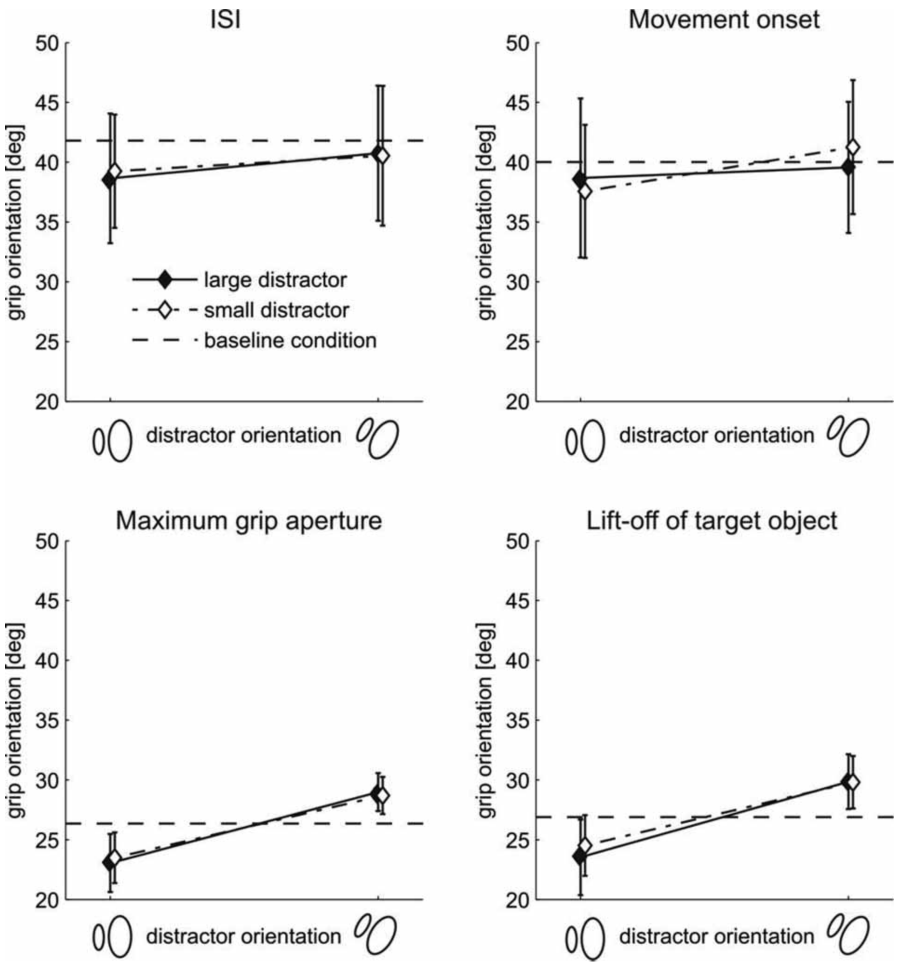

Figure 3. *Grip orientation (in degrees) when grasping the circular object (test trials) as a function of orientation and size of the distractor at four different moments in time: during the interstimulus interval (ISI), at movement onset, at maximum grip aperture (MGA), and at the moment of lift-off of the object. All error bars depict* ± 1 SEM *(between subjects).*

for ISI, and $F(1, 9) = 1.44$, $p = .26$ for movement onset. Grip orientation at MGA did depend on the orientation of the distractor object ($23.3^\circ \pm 2.2^\circ$ for distractor in 0° orientation and $28.9^\circ \pm 1.6^\circ$ for distractor in 30° orientation), $F(1, 9) = 14.07$, $p = .01$. This effect on grip orientation was just as large at the moment the target object was lifted ($24.0^\circ \pm 2.8^\circ$ for distractor in 0° orientation and $29.8^\circ \pm 2.2^\circ$ for distractor in 30° orientation), $F(1, 9) = 6.99$, $p = .03$. Thus, viewing a distractor object can influence the selected grip orientation when subsequently grasping a different object at the same position. None of the ANOVAs showed an effect of distractor size or an interaction between size and orientation (all $p > .43$).

In trials in which the circular target object was grasped after having seen the same circular object as distractor (baseline trials), mean grip orientation was $26.4^\circ \pm 2.3^\circ$ at maximum aperture and $26.9^\circ \pm 2.9^\circ$ at the lift-off of the object. These values can be regarded as the preferred grip orientation when grasping a circular object (baseline). The orientation of the 0° distractor object is rotated anticlockwise with respect to this baseline. Thus, the orientation of the 0° distractor is expected to affect the grip orientation of the target in a anticlockwise direction. The 30° distractor is oriented more clockwise relative to the baseline and therefore should affect the grip in a clockwise direction. This prediction for the test trials is confirmed by our results. As expected grip orientation in the control trials (same size and orientation of distractor and target object) at MGA and at lift-off of the object is biased to the presented orientation (13.3° ± 1.1° for 0° orientation and 31.1° ± 0.9° for 30° orientation at MGA; 8.6° ± 1.0° for 0° orientation and 32.8° ± 1.0° for 30° orientation at lift-off of object).

Reaction and movement times

Reaction times shorter than 100 ms were excluded from the analysis. This occurred in less than 1% of the trials. In the visuomotor priming literature, RTs of grasping movements are expected to be shorter if the target has congruent properties with the visually presented prime (e.g., Craighero et al., 1998; Craighero et al., 1996). To examine whether the RTs are shorter in our control trials, in which the distractor is congruent with the target, than in our test trials, in which it is not, a 2 (distractor size: large/small) × 2 (distractor orientation: 0°/30°) × 2 (congruency: control/test trials) repeated measures ANOVA was applied to the data. The baseline trials in which the circle served as both distractor and target object were not included in this analysis. As shown in Figure 4, participants had shorter RTs in the congruent control trials (300 ms ± 25 ms) than in the incongruent test trials (330 ms ± 23 ms), $F(1, 9) = 58.61$, $p < .001$. The mean difference between the test and the control trials was 30 ms ± 4 ms. This finding is consistent with the visuomotor priming literature and confirms that the execution of grasping movements is affected by prior visual experience. There was no main effect of distractor size, $F(1, 9) = 4.42$, $p = .07$ or distractor orientation, $F(1, 9) = 0.15$, $p = .71$. Furthermore, no significant interactions were found (all $p > .07$).

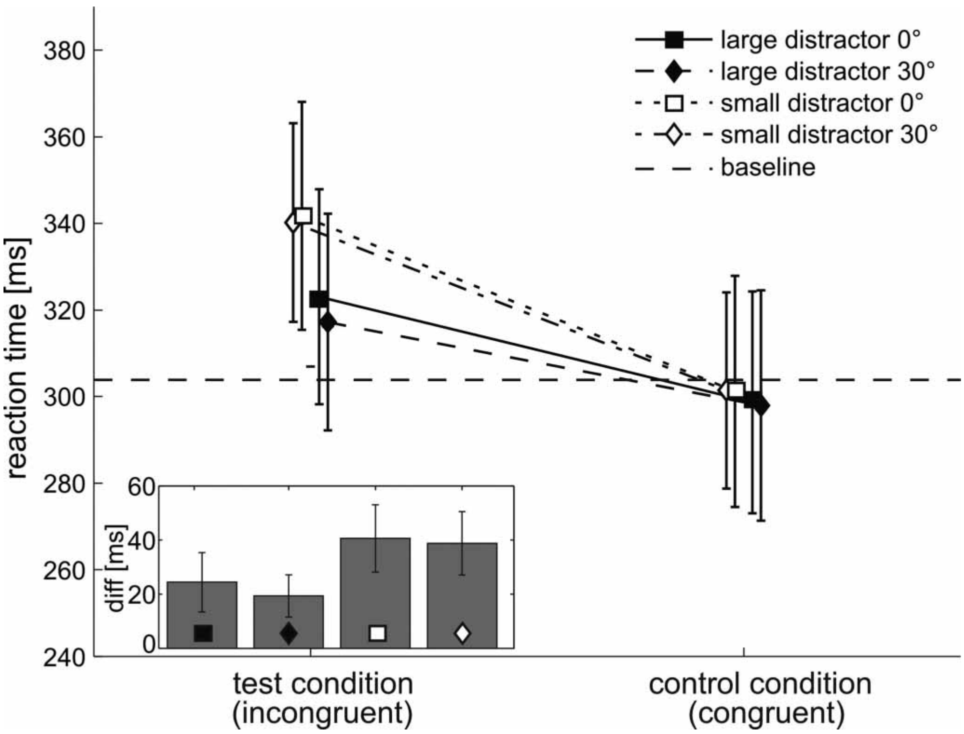

Figure 4. *Reaction times in test (incongruent) and control (congruent) trials. The inset shows the mean differences between the RTs for control and test trials for the different distractor objects. All error bars depict* ±*1* SEM *(between subjects).*

To analyse distractor effects on MT a similar 2 (distractor size: large/small) × 2 (distractor orientation: 0°/30°) × 2 (congruency: control/test trials) repeated measures ANOVA was conducted. This test revealed no significant main effects or interactions (all $p > .13$). Thus, MT was unaffected by all presented distractor–target variations.

Maximum grip aperture

In order to investigate whether there is an influence of distractor size and orientation on MGA when grasping the target object, a 2 (distractor orientation: 0°/30°) × 2 (distractor size: large/small) repeated measures ANOVA was carried out on the test trials. The ANOVA only revealed a main effect of distractor size, $F(1, 9) = 10.99$, $p = .01$. Participants opened their hand wider when grasping the circular target object after having seen the small distractor object (MGA: 86.3 mm ± 2.8 mm) than they did after having seen the large distractor object (84.0 mm ± 2.8 mm; Figure 5, left panel). The mean value of MGA for the baseline condition (distractor and target object are circular) was 84.5 mm ± 2.2 mm. Since the size of the target object was always the same in the test trials, this finding demonstrates that the MGA is also influenced by the properties of a previously presented distractor object, although the direction of the effect was contrary to what one might expect. No main effect of distractor orientation and no interaction were found ($p > .55$).

The right panel of Figure 5 shows the maximum grip aperture in the control trials (same size and orientation of distractor and target object). A 2 (distractor orientation: 0°/30°) × 2 (distractor size: large/small) repeated measures ANOVA carried out on the control trials showed that, as expected, the larger target

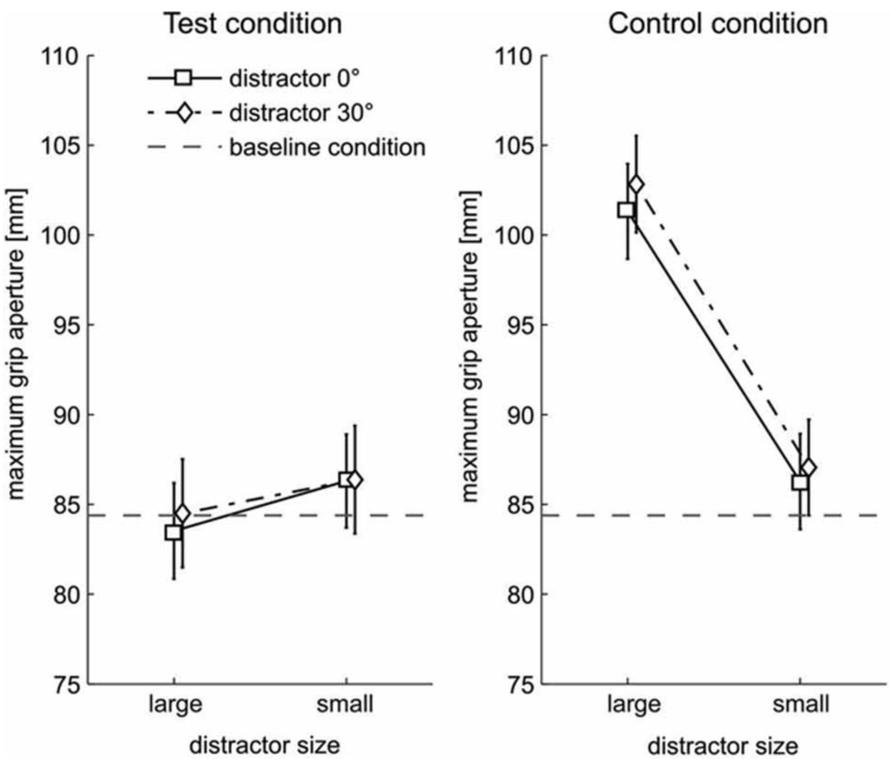

Figure 5. *Maximum grip aperture as a function of distractor size and orientation in test trials (left) in which the circular target object was grasped and in control trials (right) in which distractor and target object were identical. The dashed line represents the mean MGA when grasping the circular cylinder in the baseline condition. All error bars depict* ±*1* SEM *(between subjects).*

object was grasped with a larger MGA (small: 86.7 mm $\pm$ 2.6 mm; large: 102.1 mm $\pm$ 2.6 mm), $F(1, 9) = 488.06$, $p < .001$. This is in agreement with the grasping literature showing an increase in MGA for larger objects (e.g., Jeannerod, 1981, 1984; Smeets & Brenner, 1999). No effect of distractor orientation on MGA, $F(1, 9) = 4.20$, $p = .07$ and no interaction ($p = .50$) were found.

Discussion

We investigated whether the planning and execution of a closed-loop grasping movement can be influenced by a previously presented distractor object. Grip orientation was affected by the orientation of the distractor object at the time of the MGA and at the moment the object was lifted. It was unaffected during the ISI and at movement onset, showing that the effect evolves during movement execution towards the target rather than the participants orienting their hand in response to the distractor during the interval before the target is presented. The influence of distractor orientation on grip orientation suggests that visually guided grasping can be planned well in advance, and that during this planning previous visual experience is taken into account (Haffenden & Goodale, 2000, 2002). These results are inconsistent with the real-time view of motor programming (Westwood & Goodale, 2003; Westwood et al., 2003), whereby metric aspects of actions in response to visible targets are calculated in real time, not using any stored information.

Beside the effect on grip orientation we also found that the RT was influenced by the presentation of the distractor object. RT is the standard variable used in visuomotor priming studies (Cant et al., 2005; Craighero et al., 1998; Craighero et al., 1996; Garofeanu et al., 2004). When the target was the same object in the same orientation as the distractor, RTs were shorter than when this was not so. These results are similar to the findings of Craighero et al. (1998; Craighero et al., 1996), who also found a lower RT in congruent trials. According to the real-time view of motor programming, visually guided grasping should be unaffected by previous visual experience (Cant et al., 2005, Garofeanu et al., 2004), and information about the properties of the distractor should be "overwritten" by the visual presentation of the target object. Here we showed that visually guided grasping movements are affected even after an ISI of 2 s.

A difference between the present study and the priming studies of Cant et al. (2005) and Garofeanu et al. (2004) is that in our study the distractor provided information that was potentially useful for planning the movement, because in the control conditions (two thirds of the trials) the orientation of the distractor and the target were identical, while in the test conditions the target had no obvious orientation. Therefore, one could think of a strategy in which participants always prepared for the orientation of the distractor. In the control condition this would result in an optimal preparation while the costs of a slightly unnatural grip orientation in the test condition would probably be low. This is in line with the arguments of Jax and Rosenbaum (2007) who concluded that in movement planning and control a balance of biomechanical and computational costs is accomplished. The computational advantage of preprogramming a movement based on the prime disappears if the prime provides no helpful information for the execution of the movement, so it is not self-evident from our results that the priming effects persist in such situations.

We also found an effect of distractor size on MGA in the test trials. Participants opened their hand wider when grasping a circular target after they saw a small distractor than when the same target was grasped after viewing a large distractor. There are two possible explanations for this unexpected result. First, in the framework of the grasping model of Smeets and Brenner (1999), the increase in MGA is due to the increased accuracy requirements for grasping objects with smaller contact surfaces. In our control condition we found a larger MGA for grasping the small elliptical object than for grasping the circular cylinder, although the grasp axis was the same length (in accordance with Cuijpers, Smeets, & Brenner, 2004). A transfer of this effect to the test condition suggests that the estimated accuracy demands of the movement are influenced by prior information. The second possibility is that the effect is due to the size contrast between distractor and target object: The target object is perceived as being larger when it is presented after a smaller distractor. Further research should clarify which of these alternatives is true. However, independent of which interpretation is true, the effect on MGA also contradicts the real-time view of motor programming and the idea that the information used at that stage is not susceptible to previous experience.

In conclusion, our study shows that fully visually guided movements can be influenced by the properties of a previously presented object, which contains relevant information about the target. This planning in advance is reflected in a change of movement parameters, in particular grip orientation, by the properties of the previously perceived object. Thus, our study provides further evidence that perception (Haffenden & Goodale, 2000, 2002) and memory (de Lussanet et al., 2001; Jax & Rosenbaum, 2007) are involved in the execution of visually guided movements. This finding contradicts the real-time view of motor programming.

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