Exp Brain Res (2000) 134:456–463
DOI 10.1007/s002210000489

RESEARCH ARTICLE

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The effect of a pictorial illusion on closed-loop and open-loop prehension

Received: 28 January 2000 / Accepted: 16 May 2000 / Published online: 8 July 2000

Abstract It has been proposed that movements to visible and remembered targets are sensitive to qualitatively different types of visual information. When the target is continuously visible, prehensile movements are thought to reflect veridical object size, whereas memory-dependent prehension is sensitive to the perceived size of the object. This hypothesis was explored by assessing the influence of illusory target width on prehension kinematics in three visual conditions: closed-loop (CL; full vision during the response), open-loop brief-delay (OL; visual occlusion coincident with the movement initiation cue) and open-loop 3-s delay (OL3; visual occlusion 3 s prior to movement initiation). To modulate illusory target width, objects were placed on backgrounds consisting of three forms of the Müller-Lyer (ML) figure. Peak grip aperture was sensitive to the ML figure in the OL and OL3, but not CL conditions, suggesting that perceptual information is used to modulate this grasping parameter when the movement is programmed and executed on the basis of visual memory. Peak-aperture velocity was affected by the ML illusion in all three visual conditions, suggesting that perceived object size might be important for modulating this aspect of prehension, independent of memory requirements. The different sensitivity of grip aperture and aperture velocity to illusory target width in the CL condition suggests that grasp preshaping might reflect multiple visuomotor processes. The results of this study are consistent with the tenets of the two-stream model of visual processing.

Key words Prehension · Motor control · Visual illusions · Visual memory

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Introduction

Knowledge about the location, size and orientation of a target object is thought to be necessary for the control of prehensile movements (Arbib 1981; Jeannerod et al. 1995). Such information is typically acquired through the visual modality, although targets can also be defined kinaesthetically (Adamovich et al. 1998). A large body of research suggests that important differences might exist between movements made to visible versus remembered targets, but there is no clear consensus about the nature of these differences (e.g. Becker and Fuchs 1969; Elliott and Lee 1996; Elliott and Madalena 1987; Gentilucci et al. 1996; Gnadt et al. 1991; Goodale et al. 1994; Hu et al. 1999; Westwood et al. 2000; White et al. 1994).

Elliott and Madalena (1987) reported that aiming movements to remembered targets were as accurate as those to visible targets, provided that the delay between target occlusion and the response was less than 2 s. Beyond this period, movement accuracy declined sharply, but was similar for delays of 2, 5 and 10 s. The authors proposed that target information is maintained in memory without appreciable decay for a brief period of time following visual occlusion. Target information is thought to decay quickly beyond this initial 2-s period, leaving a degraded but stable representation of the movement environment. A limitation of Elliott and Madalena's study is that response delays between 0 and 2 s were not investigated; indeed, evidence from the saccadic-eye-movement literature suggests that target memory might begin to decay within 350–800 ms of visual occlusion (Becker and Fuchs 1969; Gnadt et al. 1991; White et al. 1994).

Goodale and colleagues (Goodale et al. 1994; Hu et al. 1999; Milner and Goodale 1995) argue that movements to remembered targets depend on qualitatively different, not simply degraded visual information relative to movements made to visible targets. A key aspect of this proposal is that two parallel representations of the visual environment are thought to exist within the central nervous system; one visuomotor in nature, the other perceptual. The properties of these putative representations reflect the neurophysiological organisation of the visual system into dorsal and ventral streams, with the dorsal stream specialised for visuomotor control and the ventral stream for visual perception (Milner and Goodale 1995).

According to Milner and Goodale's (1995) model, the dorsal stream constructs and maintains a veridical representation of visual features that are relevant to movement control, such as object size, orientation and location. The dorsal stream is thought to process on-line visual information, updating the visuomotor representation to reflect the current status of the actor/environment interface. A corollary of this is that the dorsal/visuomotor representation decays rapidly following visual occlusion, within 2 s (Elliott and Madalena 1987) or much sooner (Becker and Fuchs 1969; Gnadt et al. 1991; White et al. 1994). Movements executed immediately following visual occlusion are thought to have access to the dorsal-stream representation and should, therefore, reflect veridical object properties; however, because of the rapid decay of visuomotor memory, a different source of information must be accessed for movement control following longer delays.

The ventral stream is thought to process object features such as form, colour and relative size, which are relevant for perceptual activities such as identification and recognition. Because the perceptual features of the environment are relatively stable, the ventral stream need not operate in the same on-line manner as the dorsal stream. Indeed, perceptual activities such as recognition depend on the retention of information for long periods of time; therefore, the ventral/perceptual representation persists for a longer period of time than that of the dorsal/visuomotor system. Movements executed beyond the memory capabilities of the dorsal stream are thought to depend on the ventral/perceptual representation, as this is the only available source of information.

Pictorial illusions can be used to determine whether a particular behaviour is sensitive to veridical or perceptual visual information, because such stimuli induce a mismatch between veridical and perceived object properties. To test Milner and Goodale's (1995) hypothesis that memory-dependent movements access perceptual rather than veridical information, Westwood et al. (2000) studied the effect of illusory object size on visuomotor and perceptual responses to visible and remembered targets. The memory-dependent condition was similar to the "pantomime" condition of Goodale et al. (1994), in which the target object was physically removed for 2 s prior to and during the response. In this condition ("pantomime"), participants were instructed to simulate a natural prehensile movement on the basis of remembered target features. In terms of peak grip aperture, prehension in the full-vision ("natural") condition was insensitive to illusory target size, whereas large effects emerged in the pantomime condition. Perceptual judgements of object size were sensitive to the illusion in both the natural and pantomime conditions and to the same extent as pantomimed prehension. These results support the hypothesis that memory-dependent movements access perceptual sources of information, whereas movements to visible targets are sensitive to veridical object properties.

A limitation of the pantomimed prehension paradigm is that this task might differ from natural prehension in important aspects other than memory-dependence. Indeed, Goodale et al. (1994) observed qualitatively different aperture-formation profiles for natural and pantomimed prehension, suggesting that different movement strategies might be employed in each task. Because the object cannot be grasped in the pantomime condition, participants might simply match grip aperture to the remembered width of the target object. Indeed, Westwood et al. (2000) observed qualitatively similar aperture-formation profiles for pantomimed prehension and a perceptual judgement task (aperture-scaling). Thus, pantomimed prehension might involve a response strategy that is similar to that of a perceptual judgement, which might account for the similar illusory effects observed for pantomimed prehension and perceptual judgements in Westwood et al.'s study.

Hu et al. (1999) studied memory-dependent prehension in open-loop visual conditions, thereby avoiding the limitations of the pantomimed prehension paradigm. In one open-loop condition (open-loop, OL), the onset of a 300-ms target-visibility phase cued the response, and, in the second (open-loop delay, OLD), response initiation was cued 5 s after the end of the 300-ms target-visibility phase. In the OL condition, the target was visible for most of the 450-ms premovement phase, whereas object memory was necessary for the premovement phase in the OLD condition. Vision of the target and limb was continuously available in the closed-loop (CL) control condition. Importantly, qualitatively similar aperture-formation profiles were observed for all three visual conditions, suggesting that a similar object-acquisition strategy was employed in each. A number of kinematic differences were observed for prehension movements in the CL and OLD conditions, whereas the CL and OL conditions did not differ significantly. Hu et al. argue that these data support Milner and Goodale's (1995) contention that memory-dependent visuomotor control accesses a perceptual representation of the target object; however, the kinematic differences observed in the OLD condition do not compel such an interpretation. Indeed, the observed kinematic differences might reflect a simple decay of information from the visuomotor system over the delay period, not a transition to a qualitatively different visual representation.

A stronger test of the perceptual-representation hypothesis would be to study the sensitivity of memory-dependent prehension to illusory target size, as done by Westwood et al. (2000). In the present study, the Müller-Lyer (ML) illusion was used to manipulate the perceived width of target objects, which were grasped in closed-loop (CL) and open-loop visual conditions [brief-delay (OL) and 3-s delay (OL3)]. If a veridical representation of the target object is available to the motor system in closed-loop conditions and following very brief response delays, then the ML illusion should not influence grasp preshaping in the CL and OL conditions. If the prehension of remembered target objects depends on perceptual sources of information following longer response delays, then illusory target width should affect various aspects of the grasp preshape in the OL3 condition. A similar paradigm has been used in the context of manual aiming, in which the ML figure is used to influence the perception of target location (Elliott and Lee 1996; Gentilucci et al. 1996); however, the results of such studies do not necessarily generalise to prehension tasks in which the illusion is used to influence the perceived size of the target (cf. Mack et al. 1985).

Materials and methods

Participants

Nine right-handed individuals (five males, four females) with a mean age of 21.2 years participated in this study. All had normal or corrected-to-normal vision, and none had experience with the prehension task or illusory contexts used in this study. All participants provided informed consent in accordance with guidelines established by the University of Waterloo Office of Human Research.

Apparatus and task

The form of the ML illusion used was the same as that employed by Westwood et al. (2000), illustrated in Fig. 1. Three background contexts were printed in black ink on white cards, reflecting the closed (Fig. 1A) and open (Fig. 1C) forms of the ML figure, and a control figure (Fig. 1B). Two sets of contexts were constructed, with centre lines of 50 mm or 70 mm. Small and large rectangular bars (50×7×7 mm and 70×7×7 mm) were placed over the centre line of the appropriately sized background context in a horizontal orientation, forming six possible target arrays (three contexts × two sizes).

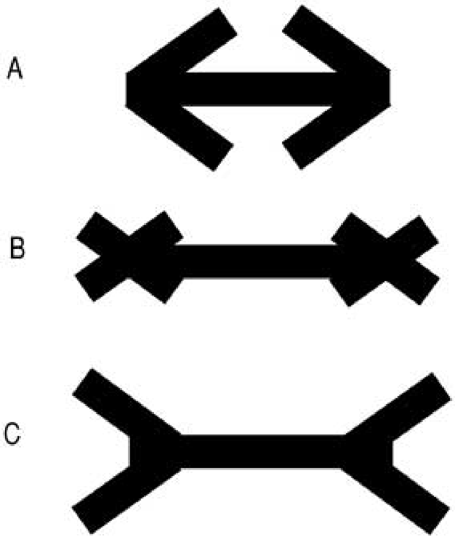

Fig. 1A–C Background contexts used in the study. **A** Closed form of the Müller-Lyer (ML) figure; internal line segment is typically perceived as shorter than the control figure. **B** Control background; perception of the length of internal line segment is not biased. **C** Open form of the ML figure; internal line segment is typically perceived as longer than the control figure

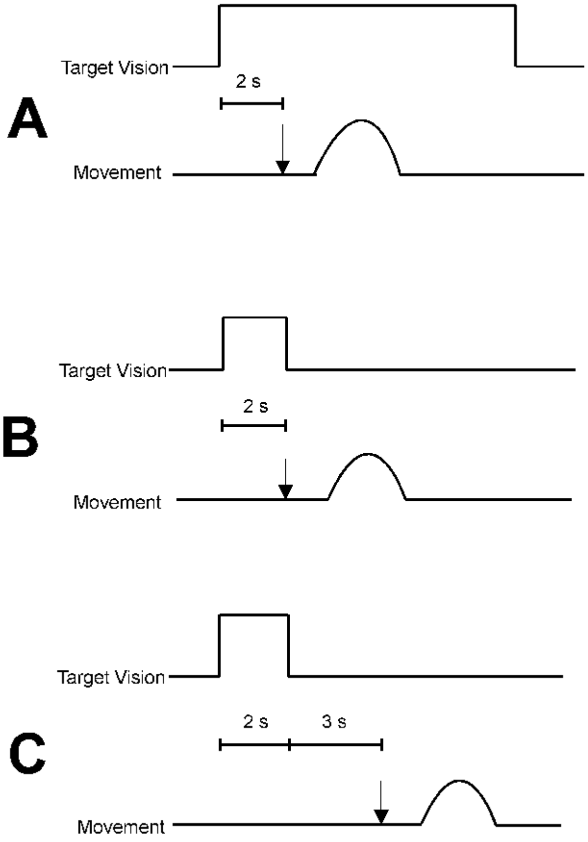

Fig. 2 Schematic representation of event sequences for (**A**) closed-loop (CL), (**B**) open-loop brief-delay (OL) and (**C**) open-loop 3-s delay (OL3) conditions. The *downwards arrow* indicates the auditory initiation cue. The premovement phase occurred between the auditory cue and overt movement, whereas the execution phase occurred following movement onset

The task was to reach towards, grasp, and pick up the rectangular bar from within the target array, in three visual conditions (see below). Participants always used their right hand and initiated the prehension movement from a designated starting position with the thumb and index finger pinched lightly together. Background contexts were placed 28 cm distal to the starting position, at the participant's midline. Five trials were performed for each of the six target arrays in each visual condition, for a total of 90 trials. Visual conditions were blocked and counterbalanced, and the target arrays were presented in random order.

Visual conditions

In all three conditions, the availability of visual information was controlled using a set of liquid-crystal goggles (Milgram 1987), the lenses of which could be triggered to adopt a transparent or opaque state. All conditions began with a 2-s phase, during which the goggles were made transparent and participants were instructed to view the target array. In the closed-loop condition (CL), an auditory tone immediately followed this phase, cueing the participant to initiate the movement (Fig. 2A). The goggles remained transparent for 4 s following the cue, which allowed sufficient time for all participants to complete the task with full vision. Participants were instructed to move at a comfortable pace, grasp the target bar and raise it a few centimetres above the table surface.

For the open-loop brief-delay condition (OL), the goggles were changed to the opaque state simultaneous with the auditory initiation cue (Fig. 2B). The goggles remained opaque for the duration of the response phase so the participant could see neither the target nor their hand. The target was, therefore, not visible during the premovement or execution phases of the response, requiring an object representation to be retained in memory for a duration ranging from 0 to 450 ms (i.e. the typical length of the premovement phase for cued prehension, Jakobson and Goodale 1991). Participants were instructed to move at a comfortable pace and make every effort to grasp the target object with their initial attempt; however, in the event that the target was missed, participants were instructed to search for the object until a stable grasp was effected. The purpose of this instruction set was to emphasise the importance of physically acquiring the target object without necessarily encouraging a primarily search-oriented strategy. The open-loop 3-s delay condition (OL3) was identical to the OL condition, except the auditory cue was given 3 s after the goggles turned opaque (Fig. 2C). Object properties must, therefore, be retained in memory for a duration of approximately 3 s in this condition.

Data collection and processing

Infra-red emitting diodes (IREDs) were placed on the lateral edge of the index finger, the medial edge of the thumb and on the styloid process of the wrist. Three-dimensional position data were collected using an OPTOTRAK 3020 system (Northern Digital; Waterloo, ON, Canada) sampling at 100 Hz for 4 s. IRED data were filtered off-line using a second-order dual-pass Butterworth filter employing a low-pass cut-off frequency of 6 Hz. Grip aperture was calculated as the resultant distance between the thumb and index IREDs, and wrist velocity was calculated by differentiating the resultant displacement time series for the wrist marker.

Several trials in the OL and OL3 conditions contained extensive searching for the target at the movement terminus, which consisted of opening and closing of the grasp. Because this searching process was not of direct interest in the present study, the primary movement was defined in the following manner: movement initiation was defined as the frame in which resultant wrist velocity exceeded 30 mm/s for 50 ms, and movement termination was the frame in which wrist velocity dropped below 30 mm/s for 50 ms. Prior research has indicated that resultant velocities below 30 mm/s are associated with corrective submovements (Elliott et al. 1999; Heath et al. 1998), supporting the use of this procedure to identify the primary movement. All dependent measures were averaged across the five trials for each target array in each condition.

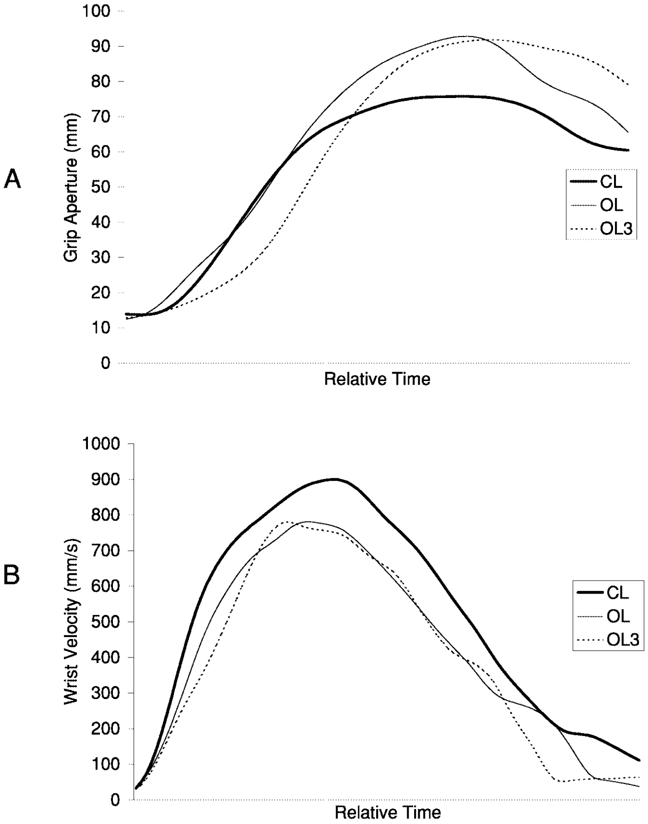

Fig. 3 **A** Representative aperture-formation profile for one participant in the closed-loop (*CL*), open-loop brief-delay (*OL*) and open-loop 3-s delay (*OL3*) conditions. Note that peak grip aperture exceeded the size of the final grip aperture in all three conditions, suggesting that a similar object-acquisition strategy was employed in each. **B** Representative wrist-velocity profile for one participant in each visual condition. Although peak wrist velocity was generally larger for the CL than the OL and OL3 conditions, the profiles are qualitatively similar

Results

Kinematic measures related to the spatial and temporal properties of the prehension response were analysed. These measures were subdivided into those related to the grasp-preshape component of prehension and those related to wrist transport, as defined by Jeannerod (1986). All dependent measures were analysed using fully-repeated measures ANOVA with factors condition (CL, OL, OL3), context (ML-Closed, Control, ML-Open) and target (50 mm, 70 mm). Only the significant effects (alpha=0.05) are described for each dependent measure. Significant main effects involving three means were explored using unprotected *t*-tests (alpha=0.01), and significant interactions were explored using simple-effects analysis (alpha=0.01).

Grasp preshape

Movement times were shorter for the CL than the OL and OL3 conditions, which did not differ, *F*(2,16)=9.3, *P*<0.01 (see Table 1). A main effect of visual condition indicated that peak grip aperture was significantly smaller for the CL than OL and OL3 conditions, which did not differ, *F*(2,16)=16.5, *P*<0.001. The 50-mm target was

Table 1 Kinematic measures related to the grasp preshape component of prehension in the closed-loop (*CL*), open-loop brief-delay (*OL*) and open-loop 3-s delay (*OL3*) conditions. *Values in parentheses* represent SEM

	CL	OL	OL3	*t*-test
Movement time (ms)	666 (46)	748 (58)	782 (67)	CL<OL=OL3
Peak grip aperture (PGA) (mm)	80 (2)	87 (2)	88 (2)	CL<OL=OL3
Relative time to PGA (%)	79.1 (2.6)	74.8 (2.6)	75.0 (2.0)	CL=OL=OL3
Peak aperture velocity (PAV) (mm/s)	372 (35)	354 (26)	358 (31)	CL=OL=OL3
Relative time to PAV (%)	25.9 (3.1)	28.5 (3.2)	27.0 (2.4)	CL=OL=OL3

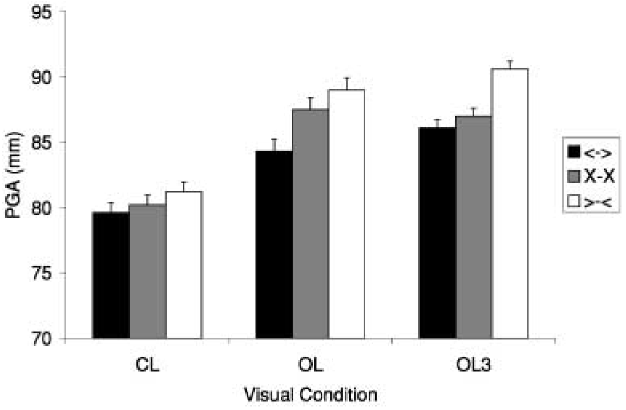

Fig. 4 Peak grip aperture (*PGA*) was affected by the context of the Müller-Lyer figure in the open-loop brief-delay (*OL*) and open-loop 3-s delay (*OL3*) conditions, but not in the closed-loop (*CL*) condition. *Bars* represent within-subject SEM values

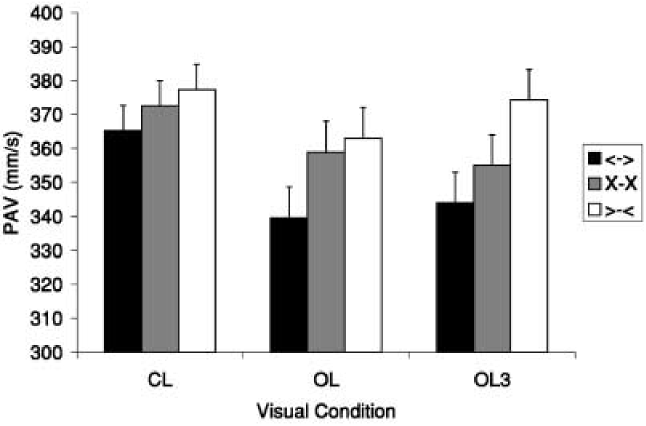

Fig. 5 Effect of the Müller-Lyer illusion on peak aperture velocity (*PAV*) was similar for prehension in the closed-loop (*CL*), open-loop brief-delay (*OL*) and open-loop 3-s delay (*OL3*) conditions. *Bars* represent within-subject SEM values

associated with smaller peak grip apertures than the 70-mm target in all conditions, $F(1,8)=207.8$, $P<0.001$, indicating that participants scaled grip aperture to reflect veridical changes in object width. Representative aperture formation curves are presented in Fig. 3A.

As illustrated in Fig. 4, the effect of the ML illusion on peak grip aperture depended on visual condition, $F(4,32)=5.4$, $P<0.01$. Simple effects analysis indicated that the effect of the ML illusion was not significant for the CL condition, $F(2,16)=2.1$, $P>0.05$, but was significant for both the OL, $F(2,16)=12.6$, $P<0.001$, and OL3 conditions, $F(2,16)=29.9$, $P<0.001$. Indeed, the effect of the illusion observed in the OL conditions was consistent with the perceptual effects of the ML figure observed by Westwood et al. (2000).

The timing of aperture formation was also of interest in the present study. Time to and time from peak grip aperture were expressed in relation to overall movement time because responses were generally slower in the two open-loop response conditions. When expressed in this relative manner, neither time to nor time after peak grip aperture was significantly associated with visual condition, $F(2,16)=0.9$, $P>0.05$, or target size, $F(1,8)=0.7$, $P>0.05$.

Peak aperture velocity was defined as the maximum rate of aperture increase. The 70-mm target was associated with larger peak aperture velocity than the 50-mm target, $F(1,8)=19.4$, $P<0.01$, indicating the sensitivity of this measure to veridical object width. Peak aperture velocity was not different for the three visual conditions, $F(2,16)=0.4$, $P>0.05$. As illustrated in Fig. 5, the ML figure influenced peak aperture velocity in all three visual conditions to a similar extent, $F(2,16)=14.3$, $P<0.001$.

The timing of peak aperture velocity was expressed in relation to overall movement time. Relative time to and after peak aperture velocity were not significantly related to visual condition, $F(2,16)=0.7$, $P>0.05$, but were sensitive to changes in true target width, $F(1,8)=7.84$, $P<0.05$. A relatively greater amount of time was spent prior to peak aperture velocity for the 50-mm (28.0% of MT) than the 70-mm target (26.3% of MT).

Wrist transport

Peak wrist velocity was defined as the maximum resultant velocity attained by the wrist IRED during the primary movement. The present analysis indicated that higher peak wrist velocity was attained in the CL condition than the OL and OL3 conditions, which did not differ, $F(2,16)=12.8$, $P<0.001$. Representative wrist-velocity curves are illustrated in Fig. 3B. The relative timing of peak wrist velocity was not different for the three visual conditions, $F(2,16)=0.92$, $P>0.05$ (see Table 2).

Wrist displacement in the primary movement axis was similar for all three visual conditions, $F(2,16)=2.0$, $P>0.05$. Goodale et al. (1994) observed target undershooting in their pantomimed prehension condition, suggesting that this might be a characteristic of memory-dependent responses. The absence of target undershooting in the open-loop conditions of the present study might relate to the physical presence of the target object

Table 2 Kinematic measures related to the transport component of prehension in the closed-loop (*CL*), open-loop brief-delay (*OL*) and open-loop 3-s delay (*OL3*) conditions. *Values in parentheses* represent SEM

	CL	OL	OL3	*t*-test
Peak wrist velocity (PWV) (mm/s)	818 (54)	738 (56)	718 (58)	CL>OL=OL3
Relative time to PWV (%)	36.2 (1.6)	37.0 (1.8)	35.9 (1.7)	CL=OL=OL3
Wrist displacement (mm)	251 (5)	248 (4)	244 (5)	CL=OL=OL3
Peak vertical trajectory (mm)	48 (3)	41 (3)	42 (4)	CL>OL=OL3

in all three conditions, which afforded knowledge of movement outcome on every trial. The vertical component of the wrist trajectory was largest for the CL relative to the OL and OL3 conditions, which did not differ, $F(2,16)=9.0$, $P<0.01$.

Discussion

The ML illusion was used to manipulate the perceived size of a target object that was grasped in closed-loop and open-loop visual conditions. Because peak grip aperture is known to vary with object width (Jeannerod 1986), the sensitivity of this movement parameter to illusory target width indicates the extent to which perceptual information is available to the visuomotor system. In the closed-loop condition, the object was visible during the premovement and execution phases of the response, whereas object vision was occluded for both phases in the two open-loop conditions. Memory for object size was thus necessary for response generation in the two open-loop conditions, with different retention intervals: between 0 and 450 ms for the OL condition (see below) and approximately 3 s for the OL3 condition.

Peak grip aperture was not significantly affected by the ML illusion in the closed-loop condition, suggesting that the visuomotor and perceptual systems operate largely independently when the target is continuously visible, consistent with previous literature (Aglioti et al. 1995; Haffenden and Goodale 1998; Westwood et al. 2000). The illusion significantly influenced peak grip aperture in both open-loop conditions, providing strong support for the notion that the perceptual system plays an important role in the grasping of remembered target objects (Goodale et al. 1994; Hu et al. 1999; Milner and Goodale 1995; Westwood et al. 2000). The effect of the illusion on peak grip aperture was similar for both open-loop conditions, suggesting that very brief retention intervals are sufficient to observe the influence of perceptual information on grasp formation. Cued prehension is associated with a premovement time of approximately 450 ms (Jakobson and Goodale 1991); thus, the length of the retention interval in our OL condition ranges between 0 and 450 ms, depending on the precise latency at which visuomotor transformation might occur. The present study, therefore, suggests that veridical target information might not be retained in memory for any appreciable period of time following visual occlusion.

The results of the present study are consistent with those of Westwood et al. (2000), who demonstrated that peak grip aperture in natural (i.e. closed-loop) prehension was unaffected by the ML figure, whereas large effects emerged in a pantomime (i.e. memory-dependent) condition. A limitation of Westwood et al.'s study is that pantomimed prehension might be associated with a different movement strategy than natural prehension. In the present study, an open-loop prehension task was substituted for the pantomimed prehension task to avoid this potential confound. Importantly, qualitatively similar aperture-formation profiles were observed for closed-loop and open-loop prehension (Fig. 3A), suggesting that similar movement strategies are employed in each task.

In contrast to the effect of illusory target width on peak grip aperture, the ML figure affected peak aperture velocity in open-loop and closed-loop visual conditions, suggesting that the control of aperture velocity is sensitive to perceptual sources of information independent of target visibility during the premovement and execution phases. This observation challenges Jeannerod's (1986) notion that the grasp preshape component of prehension reflects the operation of a single visuomotor channel. Instead, the present study suggests that grip aperture and aperture velocity are sensitive to qualitatively different aspects of the visual array and might, therefore, involve multiple visuomotor processes. It is interesting to note that the relative timing of peak aperture velocity, but not peak grip aperture was found to be sensitive to the veridical width of the target object, supporting the notion that these aspects of grasp preshaping might be sensitive to different object properties. Recently, Mason and Carnahan (1999) demonstrated a dissociation between the effect of target velocity on the spatial versus temporal aspects of grasp formation in a target interception task, further suggesting that grasp preshaping might reflect multiple visuomotor channels.

Hu et al. (1999) studied prehension in visual conditions somewhat similar to those of the present study, but did not incorporate a perceptual size illusion. Hu et al. included a closed-loop condition (CL), in which target vision was available during the premovement and execution phases, and two open-loop conditions, in which target visibility was occluded during the execution phase (OL) or in the premovement plus execution phases (OLD) following a 5-s delay (Fig. 6). Prehension kinematics did not differ significantly for Hu et al.'s CL and OL conditions, whereas OL and OLD conditions differed from each other in a number of measures. These data were interpreted as evidence that the perceptual system is involved in the control of prehensile movements made to remembered targets, a conclusion that is supported and extended by the results of the present experiment. The role of the perceptual system in memory-dependent prehension was directly demonstrated through the use of the ML size illusion. Moreover, illusory object-size effects on peak grip aperture emerged with extremely brief (i.e. 0–450 ms) retention intervals, suggesting that veridical object features might not be retained in memory for any appreciable length of time – certainly much less than the 2-s duration proposed by Elliott and Madalena (1987) and likely less than the 350-ms value suggested by Becker and Fuchs (1969).

Our data are largely consistent with the proposals put forth by Milner and Goodale (1995) in their two-stream model of visual processing. In closed-loop visual conditions, visuomotor control is thought to depend on the dorsal visual stream, which maintains a veridical representation of the environment. The ventral stream is thought to be responsible for perceptual processing and

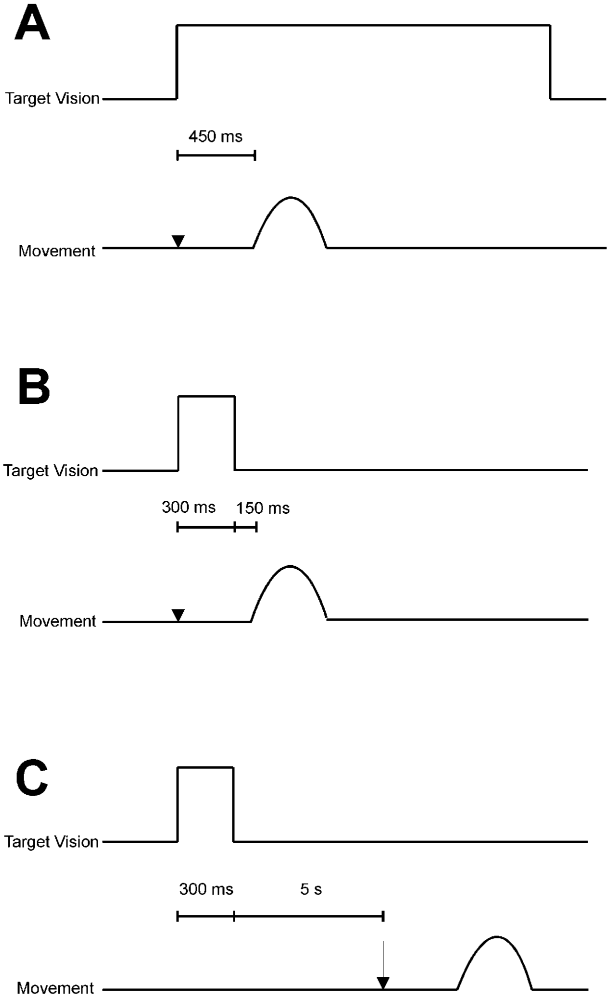

Fig. 6A–C Schematic illustration of Hu et al.'s (1999) visual conditions. **A** Closed-loop (CL), **B** Open-loop (OL), **C** Open-loop delay (OLD). Note that the target remained visible for all but the final 150 ms of the premovement phase in the OL condition

is highly sensitive to knowledge-based visual cues such as relative size, texture gradients, and so forth. The visuomotor system is proposed to operate largely independently from the perceptual system in closed-loop conditions, as evidenced by the relative sensitivities of visuomotor versus perceptual responses to pictorial size illusions in such conditions (e.g. Aglioti et al. 1995; Haffenden and Goodale 1998; Westwood et al. 2000). Mounting evidence suggests that the visuomotor and perceptual systems interact to a greater extent when movements are made to remembered targets, likely because the memory capabilities of the visuomotor system are temporally limited (Bridgeman et al. 1997; Gentilucci et al. 1996; Goodale et al. 1994; Haffenden and Goodale 1997; Hu et al. 1999; Milner et al. 1999; Westwood et al. 2000; Wong and Mack 1981).

In the closed-loop condition of the present study, two aspects of prehension were differently affected by a pictorial illusion: peak aperture velocity, but not peak grip aperture was sensitive to the ML figure. This finding suggests that certain aspects of visuomotor control access the perceptual system even in closed-loop visual conditions. A number of other studies have provided support for interactions between the visuomotor and perceptual systems in a variety of tasks and visual conditions (Binsted and Elliott 1999; van Donkelaar 1999; Gentilucci et al. 1996; Marotta et al. 1998; Pavani et al. 1999).

Of particular interest is the study of Marotta et al. (1998), who studied the effect of a size-contrast illusion (the Titchener Circles figure) on prehension in binocular and monocular viewing conditions. Peak grip aperture was not affected by the illusion in the binocular response condition; however, illusory effects were observed for monocular prehension, in a direction consistent with the perceptual effects of the figure. This finding suggests that illusory effects in visuomotor tasks might be related to the availability of retinal and extraretinal sources of information unique to binocular viewing (e.g. binocular disparity, vergence) at the time of response generation. Such cues can be used to compute the veridical size and location of the target object; however, if unavailable, as is true of monocular viewing, the visuomotor system is forced to rely upon contextual cues to estimate object size and location. Thus, the visuomotor system might operate independently from the perceptual system to the extent that normal binocular cues are available during the premovement phase; if not, then perceptual sources of information must be relied upon.

As a working hypothesis, it is proposed that prehensile grip aperture is scaled to veridical object size to the extent that normal retinal and extraretinal cues (e.g. target visibility, limb visibility, binocular vision) are available during the premovement phase. In the absence of one or more sources of information (e.g. monocular viewing, memory-dependence), the visuomotor system begins to access a temporally stable perceptual representation of the environment that is sensitive to knowledge-based cues relevant to target size and location.

Acknowledgements Portions of this research were supported by the Natural Sciences and Engineering Research Council (DW, MH, EAR) and the Heart and Stroke Foundation of Ontario (EAR). We wish to thank in particular anonymous reviewer B for helpful comments made on an earlier draft of this paper.

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