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RESEARCH ARTICLE

Gaze strategies during visually-guided versus memory-guided grasping

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Abstract Vision plays a crucial role in guiding motor actions. But sometimes we cannot use vision and must rely on our memory to guide action—e.g. remembering where we placed our eyeglasses on the bedside table when reaching for them with the lights off. Recent studies show subjects look towards the index finger grasp position during visually-guided precision grasping. But, where do people look during memory-guided grasping? Here, we explored the gaze behaviour of subjects as they grasped a centrally placed symmetrical block under open- and closed-loop conditions. In Experiment 1, subjects performed grasps in either a visually-guided task or memory-guided task. The results show that during visually-guided grasping, gaze was first directed towards the index finger's grasp point on the block, suggesting gaze targets future grasp points during the planning of the grasp. Gaze during memory-guided grasping was aimed closer to the blocks' centre of mass from block presentation to the completion of the grasp. In Experiment 2, subjects performed an 'immediate grasping' task in which vision of the block was removed immediately at the onset of the reach. Similar to the visually-guided results from Experiment 1, gaze was primarily directed towards the index finger location. These results support the 2-stream theory of vision in that motor planning with visual feedback at the onset of the movement is driven primarily by real-time visuomotor computations of the dorsal stream, whereas grasping remembered objects without visual feedback is driven primarily by the perceptual memory representations mediated by the ventral stream.

Keywords Visuomotor control · Delayed reaching · Memory · Sensorimotor · Gaze

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Introduction

When we want to pick up an object, we typically use vision to both guide our hand to the object and to shape our hand for grasping. More precisely, the brain uses immediate and 'real-time' visual feedback of the object's location, shape and orientation during the motor planning and control of the hand's movements to maximize success in grasping the object (Land et al. 1999; Saunders and Knill 2004). However, in many daily tasks, we often reach to previously seen objects that are no longer visible, for example, reaching for your eyeglasses or to turn on your alarm on your bedside table shortly after turning off the lights. During these so-called memory-guided actions, the motor planning and control must rely on a stored visual representation of the object's details previously acquired when it was last viewed. But it remains unclear if people still tend to look to the remembered locations of these objects in the dark as they would if they were able to see them.

A growing body of research comparing memory-guided reaching to visually-guided reaching has provided much insight into the kinematic changes of the hand's movements when vision of the target is unavailable in tasks that require subjects to either point to a target (Elliott and Madalena 1987; Heath and Binsted 2007; Thomson 1983; Westwood et al. 2003) or grasp an object (Berthler et al. 1996; Chieffi and Gentilucci 1993; Heath et al. 2006; Hesse and Franz 2010; Hu and Goodale 2000; Jakobson and

Goodale 1991; Jeannerod 1984; Santello et al. 2002; Schettino et al. 2003; Wing et al. 1986). Overall, the majority of these studies show that memory-guided actions are typically less accurate, slower and with wider grip apertures (the distance between the index finger and thumb during a precision grasp) when compared to visually-guided actions (c.f., Hesse and Franz 2010; Schettino et al. 2003). These studies underscore the importance of vision for action by focusing on limb motor behaviour. What remains less clear is how gaze behaviour differs for on-line visually-guided acts versus delayed memory-guided acts.

Studies that have investigated gaze behaviour in eye-coordination tasks where subjects had to interact or manipulate an object using vision have found a tight coupling between eye movements and hand movements such that the eyes typically are directed at the object before the hand (Binsted et al. 2001; Johansson et al. 2001; Land et al. 1999; Neggers and Bekkering 2000). When observers move their eyes to simply look at an object, they typically direct their gaze at the object's centre of mass (COM) (Brouwer et al. 2009; Kowler and Blaser 1995). But when observers plan to grab an object, gaze is directed to key contact positions on the object that mark where to grasp it (Brouwer et al. 2009; De Grave et al. 2008; Desanghere and Marotta 2011; Flanagan and Johansson 2003; Johansson et al. 2001). More specifically, Brouwer et al. (2009) showed that as subjects reach out to grasp an object with their index finger and thumb (i.e. a precision grip), their gaze was first directed to the object's COM and then directed towards the region of the object that was the grasp site for the index finger. More recently, however, Desanghere and Marotta (2011) showed the opposite gaze pattern using symmetrical objects; they found that gaze was first directed towards the grasp site for the index finger, and then gaze was directed lower towards the object's COM. This preference to look in the direction of the index finger still occurs (albeit less so) when the grasp site for the index finger on the object is occluded (De Grave et al. 2008). Altogether, these studies suggest that gaze behaviour plays a key role in real-time grasping movements. Moreover, gaze is strategically directed to the contact points on an object for the fingers to grasp it, and the placement of the index finger is preferentially selected during precision grasps.

Is gaze behaviour different during delayed reaching to remembered objects? One study that investigated gaze behaviour as subjects reached with a pen to mark the location of remembered targets showed evidence that eye movements become somewhat erratic and largely decoupled from hand movements compared to the stereotypical coordinated action of the eyes and hand when the targets remained visible (Flanagan et al. 2008). In the same study, the researchers showed similar results in an object manipulation task where subjects were required to grasp a bar and use it to contact a target either with or without visual feedback. When performing this task with visual feedback, gaze position and hand movements were strongly linked with gaze directed ahead of the hand to grasp sites and relevant landmarks to guide the bar to the target. In the condition where subjects were able to only briefly view the bar and task environment before performing the task in the dark, the data revealed that gaze was largely scattered and rarely directed to the key landmarks correlated with grip position or target location. However, what remains unclear and not presented in these results are the subjects' gaze patterns during the brief time they were able to view the task environment when critical visual information was available to plan the delayed reaching and grasping. It is possible that during this encoding phase, the subjects' gaze pattern still resembled the gaze patterns that are typically observed during real-time actions with on-line visual feedback for the purpose of constructing and storing a visuomotor representation for using in the future. On the other hand, with no need to make an immediate motor action, gaze behaviour might be consistent with gaze patterns that are typically observed during passive viewing (Brouwer et al. 2009; Kowler and Blaser 1995) and the future hand movements might be governed by memorized perceptual representations of the objects and environment whose prior construction was divorced from visuomotor calibration processes.

Where do we look at objects to collect visual information about them when the objects are a target for future memory-guided grasps? The present study was aimed at addressing this issue. We further explored the gaze behaviour as subjects reached out and grasped a centrally placed symmetrical block in either a visually-guided task or memory-guided task in Experiment 1 and an immediate grasping task in Experiment 2. In the visually-guided task, subjects performed a closed-loop grasp with visual feedback of the block and hand. In the memory-guided task, subjects were shown the block for 1 s, controlled by a special shutter glass window, and then prompted to make an open-loop grasp either immediately after the shutter glass closed (no delay) or after a 2-s delay. Two delay conditions were used and randomly interleaved in the memory-guided task so that subjects would not become accustomed to a single delay interval in case some interesting differences in hand kinematic data might emerge. The reason for selecting 2 s as the duration for the delay interval was theoretically driven from previous research on memory-guided actions. Evidence from previous studies suggest that visual representations for controlling motor movements are held briefly (>2 s) in the dorsal stream before decaying rapidly when visual feedback is removed (Elliott and Madalena 1987; Elliot and Calvert

1990), and it has been argued that after which motor movements are carried out by stored visual representations of the ventral stream (Goodale et al. 2005; Westwood and Goodale 2003). In the immediate grasping task in Experiment 2, visual feedback was available during the planning of the movement but was removed immediately at the onset of the reach. Our primary interest was in clarifying what gaze strategies are employed in these different tasks when vision is used to support either immediate action with real-time visual feedback or delayed action based on stored visual information.

Experiment 1

Methods

Subjects

Twenty-two subjects (8 males and 14 females; mean age 21.9 years) participated in this study for course credit as part of their introductory psychology course. Since this study includes a between-group design, subjects were evenly divided into two groups ($n = 11$ each group) with one group performing the memory-guided task and the other group performing the visually-guided task. All subjects had normal or corrected-to-normal visual acuity and were right handed according to self-report. All procedures were approved by the University of Manitoba's Fort Garry Campus Research Ethics Boards, and informed consent was obtained from each subject.

Apparatus

Kinematic data of the subjects' right hand and limb movements were recorded using an Optotrak Certus 3-D tracking system (Northern Digital, Waterloo, ON, Canada) at a sampling rate of 150 Hz and a spatial accuracy within 0.01 mm. Six infrared emitting diodes (IREDs) were used to collect hand kinematic data, two were fastened onto the subjects' index finger (positioned on the left side of the cuticle), two on their thumb (positioned on the right side of the cuticle), and two on the wrist (positioned on the radial portion of the wrist) of their right hand. Eye position was recorded using the EyeLink II eye tracking system (SR Research Ltd., Mississauga, ON, Canada) at a sample rate of 250 Hz with a spatial resolution of <0.5°. Data from the Opotrak and the EyeLink II recordings were integrated into a common frame of reference via MotionMonitor software package (Innovative Sports Technology, Chicago, IL, USA). The MotionMonitor system compensated for head movements via co-registering the position data of IREDS fixed to the EyeLink II's headband with respect to the subject's head. Eye position was calibrated using the EyeLink II's native nine-point calibration/validation procedure on the computer monitor, after which participants were positioned in front of the display board. To ensure accurate calibrations of <1° error and reliability of binocular eye data, accuracy checks both immediately following calibration and after the completion of the experiment were taken by having participants fixate a marker on the display while positional eye data were obtained, which yielded mean measurement errors of fixations across all subjects in the horizontal and vertical dimensions as 0.34° and 0.52°, respectively. Stimulus presentation was controlled using a 30.5 cm × 30.5 cm "switchable glass" window (Polytronix, Inc, Dallas, Texas, USA). Switchable glass consists of a polymer-dispersed liquid crystal film embedded within the glass that has the capability to change between opaque and transparent states by applying an electrical current through the film. Figure 1 shows how the switchable glass controls the subjects' view of the blocks.

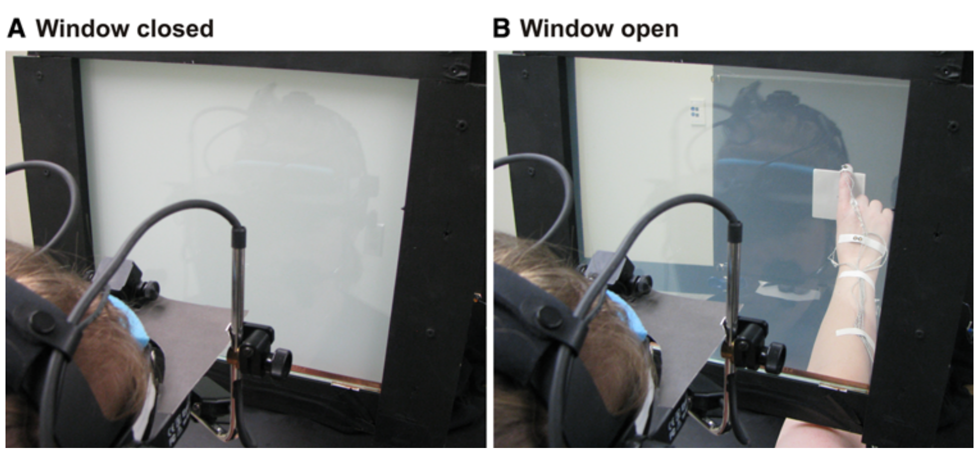


Fig. 1 Switchable glass window. **a** The window is completely opaque when it is closed so that the subject cannot see the display board and block. **b** The window is transparent when opened so that the subject can see the display board and block

The glass window was hung ∼10 cm directly in front of the subjects' face, completely obstructing view of the table, block and their hand. The window was suspended from above so that it would not in any way interfere with the natural hand and arm movements during the reach. Subjects' head was stabilized using a chin rest, and they sat on a height-adjustable chair that was adjusted according to the height of the subject so that all subjects used the same chin-rest height (30.5 cm above table); keeping the subjects head and upper body at the same height allowed us to ensure that all subjects had the same clearance under the window for making unimpeded arm movements. The glass window and auditory tone were controlled by custom-made software running on an Inspiron 545 Dell computer (Duo Core 3.16 GHz). The entire experiment was conducted in a fully lit room by fluorescent lighting from the ceiling directly above the workspace and the subject, which resulted in no noticeable difference in the illumination between the window's opaque and transparent states. This was confirmed by comparing the average pupil diameter when the window was opaque ($M = 3.8$ mm SD $= \pm 1.5$) to when it was transparent ($M = 3.6$ mm SD $= \pm 1.2$) in one randomly selected representative subject and finding no statistical difference ($t_{(34)} = 0.99$; $p > 0.05$).

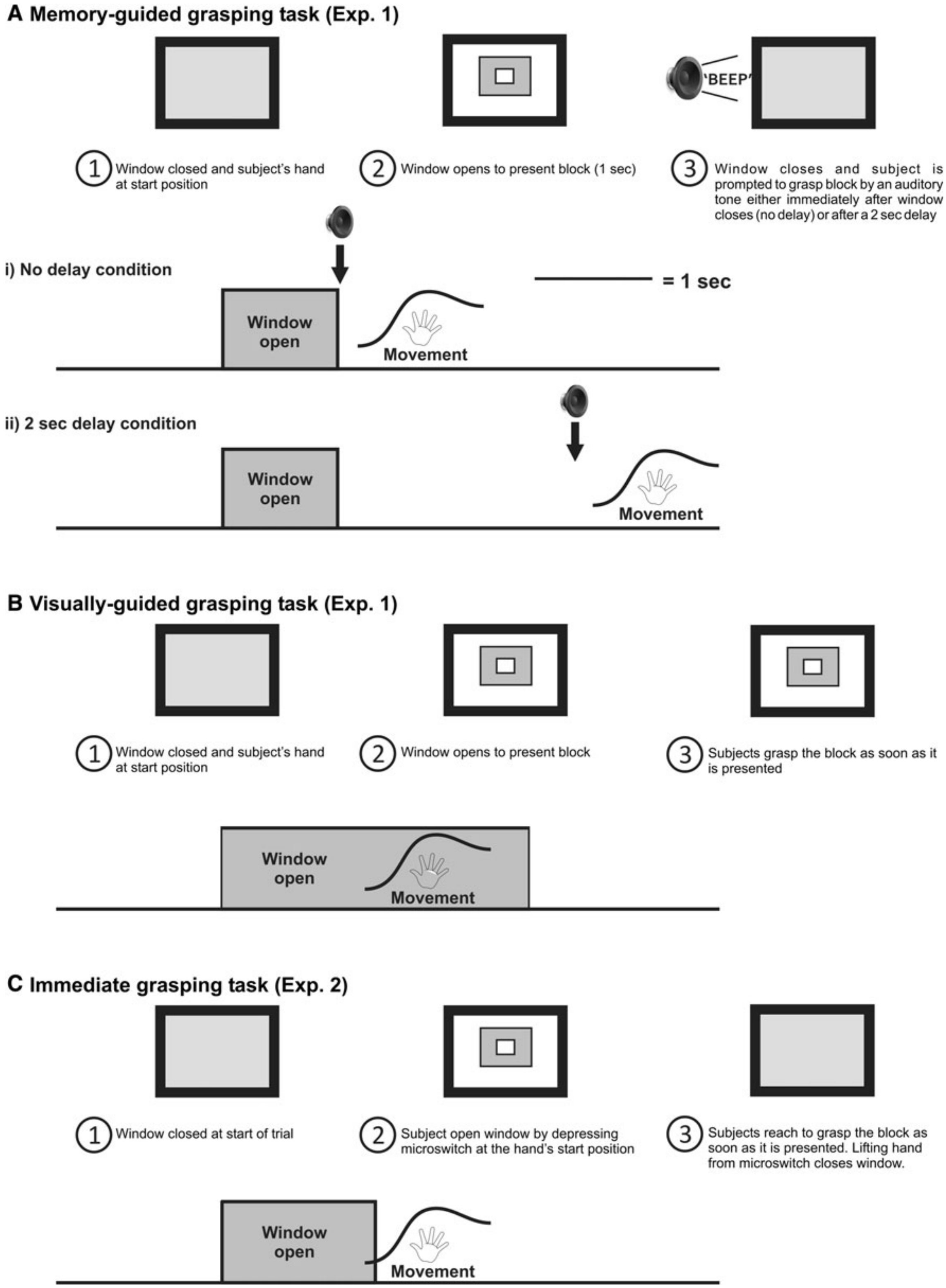
Stimuli

Subjects grasped centrally placed Efron blocks (Efron 1968). Efron blocks range in size, but have the same surface area. Five white coloured Efron blocks were used in this study: 15.2 cm × 4.2 cm (labelled as Block A), 12.2 cm × 5.2 cm (Block B), 10.2 cm × 6.2 cm (Block C), 9.0 cm × 7.1 cm (Block D) and 8.0 cm × 8.0 cm (Block E). The Efron blocks were presented on a black, 20 cm × 20 cm vertical presentation board that was positioned 50 cm in front of the subject from the chin rest. The distance between the subject and block is consistent with other previous reaching and grasping studies (Brouwer et al. 2009; de Grave et al. 2008; Desanghere and Marotta 2008, 2011; Hesse and Franz 2009; Radoeva et al. 2005) and achievable by all our subjects without making any movement unnatural. Two pegs protrude from the presentation board to allow for the blocks to be suspended in such a manner that every block's vertical and horizontal centre was aligned with the board's centre. The display board was positioned beside the computer monitor that was used to calibrate the eyes, such that the blocks were suspended vertically at an equal distance from the participant as the calibration monitor. Seven IREDs were positioned along the edge of the display board to create a rigid body with the origin corresponding to the centre of the board and, consequently, to the centre of each presented block.

Fig. 2 General experimental paradigm of the memory-guided task (**a**) and visually-guided task (**b**) in Experiment 1 and the immediate grasping task in Experiment 2 (**c**). In the memory-guided task, the window closed and subjects hold their hand at the start position on the tabletop. During the *viewing phase*, the window opens for 1 s to present the subjects with the block on the display board. Then, the window closes and the subject is prompted to reach for block by an auditory tone either immediately after window closes (no-delay condition) or after a 2 s has passed (2-s delay condition). The part of the trial where subjects reach when the window is closed is called the *vision-blocked phase*. In the visually-guided task, the trial begins the same way with the window closed and subjects hold their hand at the start position. Subjects are instructed to reach immediately for the block as soon as the window opens to present the block. In the immediate grasping tasks, subjects depress microswitch positioned at the start location with grasping hand to open the window. Upon seeing the block, subjects were instructed to grasp it. Window would close when subjects lifted their hand off the microswitch, so that subjects performed the movement without visual feedback

Procedure

Figure 2 shows the general experimental paradigm of the memory-guided (Fig. 2a) and the visually-guided (Fig. 2b) grasping tasks. In the memory-guided task, each trial began with subjects holding their right hand at the central starting position (10 cm away from subject and 40 cm from block) and the glass window closed (i.e. opaque) completely obstructing view. While the window was closed, the experimenter mounted one of the five blocks on the display board and initiated the start of the trial by pressing a mouse button. Upon pressing the mouse, the window opened (became transparent) to reveal the block on the display board for 1 s, and then closed automatically. This presentation of the block when the window was transparent was called the *viewing phase* of the trial. Subjects were instructed to reach and grasp the block when prompted to by a short auditory tone (∼200 ms). This auditory tone was delivered either immediately after the window closes (no-delay condition) or after a 2-s delay. The window remained closed as subjects reached to grasp the block. Subjects were instructed to make a natural reach to grasp the block like they would when reaching for a mug or peppershaker, that speed was not important and to grasp the block using only their index finger and thumb. The period of the trial after the window closed was called the *vision-blocked phase*. Subjects were not instructed about where on the block to grasp it. Subjects were instructed to grasp the block using only a vertically oriented pincer grip with the index finger up, but not to remove it from the display board, and hold their hand and finger positions on the block until the experimenter indicated it was okay to let go of the block (after about a second) and return their hand to the starting position. Blocks and delay conditions were pseudorandomly interleaved so that there were 7 trials for each block in both delay conditions.



The visually-guided task was similar to the memory-guided task, except the window opened to present the block and remained open during the subjects' reaching and grasping of the block. As before, each trial began with subjects holding their right hand at the central starting position and the glass window closed. While the window is closed, the experimenter mounted one of the five blocks on the display board and initiated the start of the trial by pressing a mouse button. Upon pressing the mouse, the window opened to reveal the block on the display board. Subjects were instructed to grasp the block using only their index finger and thumb after the window opened. Subjects were able to see their hand and the block during their reaching and grasping. Again, subjects grasped the block, but did not remove it from the display board, until the experimenter indicated it was okay to let go of the block. Blocks were pseudorandomly interleaved so that there were 7 trials for each block. Due to the length of time to complete a typical experimental session in either task ($\sim$1.5 h), subjects were evenly divided into the memory-guided task group and the visually-guided task group to avoid subject fatigue. Task assignment was interleaved.

Data analysis

The main goal of the present study was to clarify where subjects looked on an object in memory-guided task relative to a closed-loop, visually-guided task. To that end, we were mainly concerned with the subjects' eye position, but we did analyse hand kinematic data as well. Eye fixations were determined by a dispersion algorithm (see Salvucci and Goldberg 2000) with a minimum duration threshold of 150 ms and a maximum dispersion threshold of 1 cm. The dispersion algorithm identifies fixations from the raw eye position data points when consecutive data points are located within a specified spatial window (maximum dispersion threshold) for a minimum period of time (minimum duration threshold). Analyses of eye fixations were conducted on their position along the horizontal and vertical axes and their duration. Analyses of hand data were conducted on the index finger and thumb grasp positions along the horizontal axis of the block (horizontal grip axis), maximum grip aperture (MGA) between the index finger and thumb during the reach component of the movement, and the peak hand velocity. Horizontal and vertical coordinates of the gaze and the hand were relative to the exact centre of the block (i.e. the block's COM).

Results and discussion

The main goal of this study was to clarify how we obtain visual information about an object that will be the motor goal in a delayed memory-guided grasping task by measuring where subjects look at the object prior to reaching out for it compared to visually-guided grasping where subjects are able to see the object throughout the reach and grasp. First, we analysed the vertical and horizontal position of eye fixations on each block in the visually-guided task and in each delay condition in the memory-guided task. Then, we analysed the hand kinematics of the reach and grasp of each block with respect to maximum grip aperture (MGA) and peak hand velocity during the reach and the horizontal grip axis during the grasp. Even though the kinematic data were not the main focus of our study, our hand kinematic results are expected to add to the growing body of literature on how the hand is carried and shaped during delayed grasping as shown in previous studies (Hesse and Franz 2009; Hu et al. 1999; Hu and Goodale 2000; Rolheiser et al. 2006).

Preliminary gaze analysis

Before proceeding to our main results, we conducted a preliminary analysis of the eye data with regard to the number of fixations in each experimental condition. First, we excluded trials where the eye position signal was missing due to loss of the corneal reflection, which accounted for 3.3 % of all the trials in the visually-guided task and 4.1 % of all the trials in the memory-guided task. Of the remaining trials, subjects made an average of 2.08 fixations per trial in the visually-guided task (93 % of the trials had only two fixations) and 2.15 fixations per trial during the 1 s preview of the block (the viewing phase) in the memory-guided task (88 % of the trials had only two fixations). The mean number of fixations in the two tasks were not significantly different as determined by an independent groups *t*-test ($t_{(20)} = 0.93$; $p > 0.05$). Given that the majority of the trials in both tasks had only two fixations when vision of the block was available, we mainly focused our subsequent eye position analyses on the vertical and horizontal positions of the first and second fixations. We then examined gaze position during the vision-blocked phase of the trials in the memory-guided task, which was the period from removing vision of the block when the window turns opaque to the moment subjects grasped the block.

Gaze positions during visually-guided grasping

Figure 3a shows the mean vertical position of the first and second eye fixations for each block in the visually-guided task. We conducted a repeated measures ANOVA on these data with Fixation (first and second fixations) and Block (all 5 Efron blocks) as factors. The main effect for Fixation was significant, indicating that first fixations were higher than second fixations ($F_{(1,10)} = 25.95$; $p < 0.01$). The main effect for Block was significant ($F_{(4,40)} = 5.37$; $p < 0.01$); post hoc comparisons revealed significant differences between blocks A versus E, A versus C, and C versus E (all comparisons $p < 0.05$). The interaction was not significant ($F_{(4,40)} = 1.65$; $p > 0.05$). The mean horizontal position of the eye fixations for each block is shown in Fig. 4a. A repeated measures ANOVA (Fixation and Blocks as

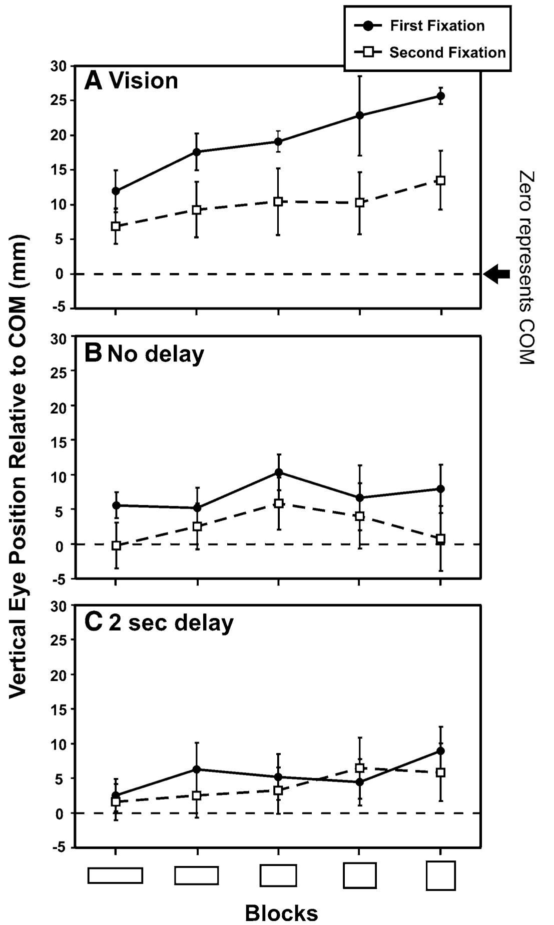


Fig. 3 Mean *vertical* eye position in visually-guided and memory-guided tasks. The main results of the visually-guided task (**a**) show first fixations (*closed circle*) were higher than second fixations (*open square*) and directed towards the contact point for the index finger. The main results of the memory-guided task for both the no-delay condition (**b**) and the 2-s delay condition (**c**) show the *vertical* position of first and second fixations were statistically the same and close to the blocks' COM. *Error bars* represent standard error

factors) on these horizontal eye position data yielded no significant effects either main effects or their interaction ($p > 0.05$).

Gaze positions during memory-guided grasping

The mean vertical position of the first and second fixations for each block during the 1 s viewing phase when the block was visible in the memory-guided task is shown separately for the no-delay condition (Fig. 3b) and the 2-s delay condition (Fig. 3c). We conducted a repeated measures ANOVA for the data in the memory-guided task with Delay (no delay vs. 2-s delay), Fixation (first and second fixations) and Block (all 5 Efron blocks) as factors. No significant differences were found among any of the main effects: Delay ($F_{(1,10)} = 0.014$; $p > 0.05$), Fixation ($F_{(1,10)} = 1.81$; $p > 0.05$) and Block ($F_{(4,40)} = 1.58$; $p > 0.05$). Nor did we find any significant effects among their interactions ($p > 0.05$).

Figure 4 shows the mean horizontal position of eye fixations in the memory-guided task with no-delay (Fig. 4b) and a 2-s delay (Fig. 4c) during the viewing phase. As before, we conducted a repeated measures ANOVA on these data in the memory-guided task with Delay, Fixation and Blocks as factors. Only the main effect for Block was found to be significant ($F_{(4,40)} = 4.06$; $p < 0.01$) with post hoc comparisons revealing a significant difference between block B and E ($p < 0.05$). All other main effects and interactions were not significant ($p > 0.05$).

We were also interested in examining if subjects changed their gaze position after vision of the block was removed from the moment the window turned opaque to the moment they grasped the block (the vision-blocked phase of the trial). Specifically, we conducted a series of

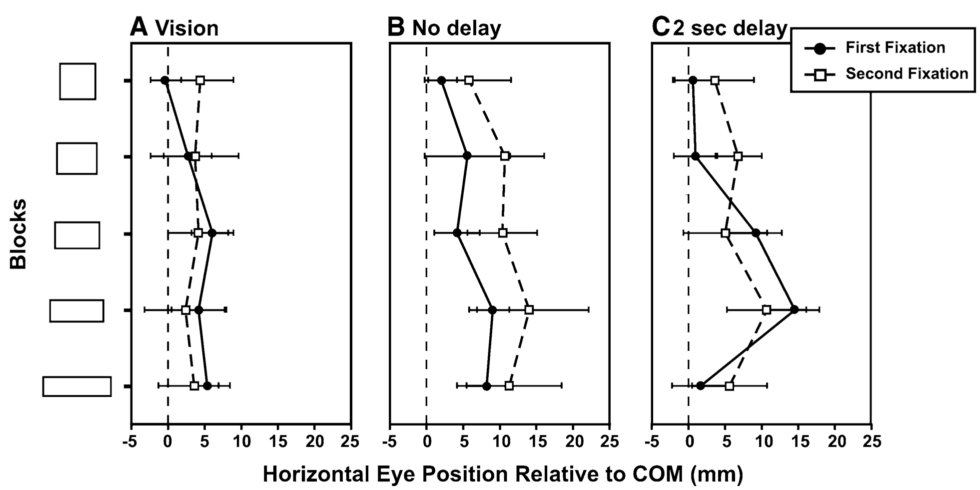


Fig. 4 Mean horizontal eye position in visually-guided and memory-guided tasks. *Horizontal* positions of both first and second fixations (*closed circle* and *open square*, respectively) were statistically the same in the visually-guided task (**a**) and both delay conditions in the memory-guided task (**b** for the no delay and **c** for 2-s delay). No statistical differences were found among tasks or conditions. *Error bars* represent standard error

repeated measures ANOVA's to compare the mean vertical and horizontal gaze positions between the first and second fixations when the window was transparent during the 1 s viewing phase (the fixations that were the focus in our prior analyses) and the fixations during the vision-blocked phase. During the vision-blocked phase, subjects made an average of 1.12 fixations per trial in the no-delay condition and 2.01 fixations per trial in the 2-s delay condition. Given that the no-delay trials tended to have a single fixation during the vision-blocked phase, we compared this one fixation to the first and second fixations during the prior 1 s viewing phase. In the 2-s delay condition, we compared the 2 fixations during the vision-blocked phase with the first and second fixations of the viewing phase. Table 1 shows the mean vertical and horizontal gaze positions during the vision-blocked phase.

Beginning with the no-delay condition, we conducted separate 2-way repeated measures ANOVA's with factors Fixation (3 fixations: first and second fixations during the viewing phase and one fixation during vision-blocked phase) and Block (5 blocks) for both the vertical and horizontal gaze positions. We found no significant differences between the subjects' fixation during the vision-blocked phase compared to the first and second fixations during the viewing phase in both analyses for vertical or horizontal positions ($F_{(2,20)} = 1.21$; $p > 0.05$ and $F_{(2,20)} = 0.45$; $p > 0.05$, respectively). Also, no effect was found for the main effect of Block ($F_{(4,40)} = 1.36$; $p > 0.05$ from the vertical position analysis and $F_{(4,40)} = 0.41$; $p > 0.05$ from the horizontal position analysis) and no significance was found for the Fixation × Block interaction ($F_{(8,80)} = 0.55$; $p > 0.05$ from the vertical position analysis and $F_{(8,80)} = 0.97$; $p > 0.05$ from the horizontal position analysis).

We conducted the same separate 2-way repeated measures ANOVA's to compare the vertical and horizontal positions of the 2 fixations in the vision-blocked phase to the first and second fixations during the viewing phase in the 2-s delay condition. Similarly, we found no significant differences between the subjects' 2 fixations during the vision-blocked phase compared to the first and second fixations during the viewing phase in both analyses for vertical or horizontal positions ($F_{(3,30)} = 0.46$; $p > 0.05$ and $F_{(3,30)} = 0.54$; $p > 0.05$, respectively). And as before, we found no effect for Block in the analysis for vertical position ($F_{(4,40)} = 1.74$; $p > 0.05$) and horizontal position ($F_{(4,40)} = 2.07$; $p > 0.05$). Finally, no significant Fixation × Block interaction was found in either analyses ($F_{(12,120)} = 0.55$; $p > 0.05$ from the vertical position analysis and $F_{(12,120)} = 0.63$; $p > 0.05$ from the horizontal position analysis). Altogether, these results show that overall subjects maintained their gaze fixations near the blocks' COM during the vision-blocked phase as they reached and grasped the block.

Comparing gaze positions between visually-guided and memory-guided grasping

We also compared the vertical and horizontal gaze positions between the visually-guided task and the viewing phase in the memory-guided task. The data across the delay conditions in the memory-guided task were collapsed because we did not find any statistical differences in eye position between the two delay conditions in our earlier analysis shown in the previous section. The analysis for vertical gaze position was conducted by a mixed-design ANOVA with Task as the between-group factor and Fixation and Block as within-group factors. Significant main effects were found for Task ($F_{(1,20)} = 6.97$; $p < 0.01$), indicating that fixations were overall higher in the visually-guided task than the memory-guided task; for Fixation ($F_{(1,20)} = 32.22$; $p < 0.01$) indicating that first fixations were overall higher than second fixations; and Block ($F_{(4,80)} = 6.59$; $p < 0.01$). Post hoc comparisons showed that first fixations were higher than second fixations ($p < 0.05$) and overall fixations for the shorter blocks A and B were significantly lower than blocks C, D and E (all comparisons $p < 0.05$). Significance was found for the Task × Fixation interaction ($F_{(1,20)} = 10.08$; $p < 0.01$).

Table 1 Mean horizontal (x) and vertical (y) fixation positions (mm) during vision-blocked phase for each block and delay condition in the memory-guided task

Block	No delay (for 1 fix)		2-s delay (1st fix)		2-s delay (2nd fix)	
	x	y	x	y	x	y
A	8.4 (20.1)	0.6 (8.2)	7.6 (16.6)	1.7 (8.8)	2.5 (11.9)	5.7 (12.3)
B	3.2 (11.5)	1.6 (15.1)	10.8 (14.5)	5.9 (7.7)	3.4 (16)	5.9 (16.6)
C	13.4 (20.3)	2.1 (12.8)	6.8 (12.5)	5.6 (12.8)	2.3 (10.7)	9.2 (9.8)
D	9.5 (9.7)	6.6 (6.3)	3.8 (10.9)	11.6 (15.7)	−1.3 (16.3)	11 (13.9)
E	10.2 (12.8)	4.2 (9.4)	5.7 (17.9)	6.5 (5.1)	3.7 (18)	8.4 (15.1)

Positive and negative horizontal positions indicate right and left of block's COM, respectively. Positive and negative vertical positions indicate above and below block's COM, respectively. Standard deviations are in parentheses

All other interactions were not significant ($p > 0.05$). Finally, we conducted a similar mixed-design ANOVA for horizontal gaze position with Task as the between-group factor (collapsing delay conditions in the memory-guided task) and Fixation and Block as within-group factors. No significant effects were found for any of the main effects or interactions ($p > 0.05$).

Reaching and grasping kinematics

We were also interested in examining how the reaching and grasping kinematics might differ between the visually-guided and memory-guided tasks (Fig. 5). We analysed the maximum grip aperture (MGA) of the index finger and thumb during the reach (Fig. 5a), the peak hand velocity of the hand during the reach (Fig. 5b) and the horizontal grip axis joining the opposing fingertips on the block relative to the block's COM (Fig. 5c). We analysed these data in the same way we analysed the eye data by first looking for within-group effects in both the visually-guided and memory-guided tasks and then testing for between-group differences between these two tasks.

For the MGA data, our ANOVA comparing MGA among the different blocks in the visually-guided task yielded a significant effect ($F_{(4,40)} = 29.0$; $p < 0.01$). Post hoc tests yielded significant results for all comparisons ($p < 0.05$) except for the comparisons of blocks A versus B and B versus C. For the memory-guided task, we conducted a 2-way repeated measures ANOVA with Delay and Block as factors, which yielded non-significant results for Delay and the interaction ($p > 0.05$), but did yield a significant result for Block ($F_{(4,40)} = 3.87$; $p < 0.01$). Post hoc tests revealed significant differences only for comparisons of blocks A versus D and A versus E ($p < 0.05$). We then conducted a mixed-design ANOVA between the visually-guided and memory-guided task collapsing across delay conditions with Task as the between-group factor and Block as the within-group factor. A significant effect was found for Task ($F_{(1,20)} = 12.12$; $p < 0.01$). Consistent with the separate within-group ANOVAs, we found a significant effect for Block ($F_{(4,80)} = 22.31$; $p < 0.01$) with all post hoc comparisons found to be significant ($p < 0.05$) except for comparisons of B versus C and D versus E. The Task × Block interaction was also significant ($F_{(4,80)} = 3.05$; $p = 0.02$).

We also analysed the mean time to MGA as the percentage of time during the reach movement when the MGA occurred. In the visually-guided task, the time to MGA was significantly different among the different blocks (Block A = 70 %; B = 68 %; C = 76 %; D = 75 %; E = 79 %) as determined by a one-way ANOVA ($F_{(4,40)} = 4.53$; $p < 0.01$). Post hoc tests revealed the only significant comparisons for Blocks A and B versus Block E ($p < 0.05$). A 2-way ANOVA for the time to MGA in the memory-guided

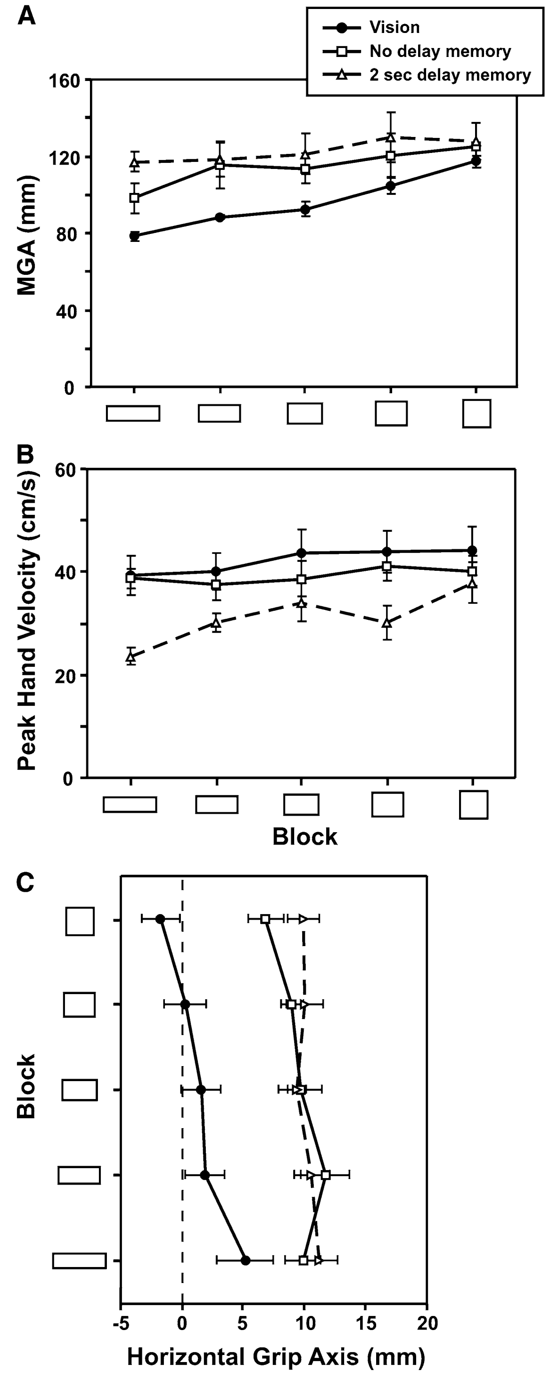


Fig. 5 Reaching and grasping kinematic data for the visually-guided task (*closed circles*) and the no-delay condition (*open square*) and 2-s delay condition (*open triangle*) of the memory-guided task. **a** In the visually-guided task, the maximum grip aperture (MGA) during the reach was clearly scaled with block size, whereas the MGA in the memory-guided task tended to be overall larger. **b** Peak hand velocity was generally fastest in the visually-guided task and slowest in the 2-s delay condition. **c** The horizontal grip axis, determined by connecting a line through the index finger and thumb grip locations on the block, was closest to the blocks' COM in the visually-guided task than in the memory-guided task, which was significantly more displaced right of the COM. *Error bars* represent standard error

task did not yield a significant effect for block ($F_{(4,40)} = 1.97$; $p > 0.05$) or the interaction between block and delay condition ($F_{(4, 40)} = 0.32$; $p > 0.05$). A significant main effect for delay condition was found ($F_{(1,10)} = 8.73$; $p < 0.01$) where the time to MGA in the no-delay condition was 74 % and in the 2-s delay condition was 67 %. Since we found a significant difference between the delay conditions, we conducted two independent between-group analyses between the visually-guided data and each delay condition. For the analysis between the visually-guided task and the no-delay condition, we found no significant effect for Task ($F_{(1,20)} = 0.01$; $p > 0.05$) or the interaction between Task and Block ($F_{(4,80)} = 0.53$; $p > 0.05$). A significant effect for Block (A = 71 %; B = 69 %; C = 75 %; D = 76 %; E = 76 %) was found ($F_{(4,80)} = 3.64$; $p < 0.01$). Post hoc tests revealed only significant comparisons for Block B versus both Block D and E ($p < 0.05$). A significant effect for Task was found for the analysis between the visually-guided task and the 2-s delay condition ($F_{(1,20)} = 17.24$; $p < 0.01$) where the mean time to MGA in the visually-guided task was 74 % and in the 2-s delay condition was 67 %. No significant effects were found for Block ($F_{(4,80)} = 1.06$; $p > 0.05$) or the interaction between Block and Task ($F_{(4,80)} = 1.83$; $p > 0.05$).

Analyses on peak hand velocity (Fig. 5b) showed no significant differences when reaching for different blocks in the visually-guided task ($F_{(4,40)} = 2.0$; $p > 0.05$). Similarly, the 2-way repeated measures ANOVA (Delay × Block) of the memory-guided task data revealed no significance for Block ($F_{(4,40)} = 1.83$; $p > 0.05$), but we did find a significant effect for Delay ($F_{(1,10)} = 53.03$; $p < 0.01$). The Block × Delay interaction was not significant ($p > 0.05$). The mixed-design ANOVA between the visually-guided task and the memory-guided task, collapsing delay conditions, yielded no significant effect for the Block × Task interaction ($p > 0.05$). Previous research has shown that closed-loop reaching movements are typically faster than open-loop reaching movements (e.g. Berthler et al. 1996; Chieffi and Gentilucci 1993; Schettino et al. 2003). However, we did not find a significant difference for Task ($F_{(1,20)} = 2.89$; $p = 0.1$), indicating that peak hand velocities in the visually-guided task were statistically the same as the velocities in the memory-guided task. It is unclear why reaches were not faster in the visually-guided task as found in the previously cited studies. One possibility could be that subjects deliberately made slower movements in response to the part of the pre-experiment instructions when subjects were told that speed was not important. Another possibility could be the different way the blocks were presented here relative to most other grasping studies. Other grasping studies usually require subjects to grasp objects placed on the surface of a table (Berthler et al. 1996; Heath et al. 2006; Hesse and Franz 2010; Hu et al. 1999; Jakobson and Goodale 1991; Melmoth and Grant 2006; Milner et al. 2001; Santello et al. 2002; Whitwell et al. 2008; Whitwell and Goodale 2009; Wing et al. 1986; Winges et al. 2003). Some studies mount grasping objects on a slightly tilted surface (Hesse and Franz 2009; Westwood and Goodale 2003), but the stimuli are still close to the tabletop. The blocks in the present study were mounted on a vertical board above the table at the subject's eye level. Reaching above the tabletop could have affected their reaching velocity profiles. To our knowledge, the only other grasping studies that also mounted the grasping stimuli vertically and above the table in a way most similar to ours here are Brouwer et al. (2009), de Grave et al. (2008) and Radoeva et al. (2005). Unfortunately, these studies did not report hand velocity data in which we could compare velocities, so it is unclear whether the hand velocity data we report are typical for reaching to objects when mounted vertically at eye level. The main effect for Block was significant ($F_{(4,80)} = 3.53$; $p < 0.01$), and follow-up post hoc comparisons revealed the only significant comparisons when comparing block A with blocks C and E ($p < 0.05$).

Analyses on the horizontal grip axis data (Fig. 5c) in the visually-guided task yielded a significant effect for blocks ($F_{(4,40)} = 13.11$; $p < 0.01$). Post hoc analyses revealed significant differences for comparisons between block A versus D, A versus E, and E versus C (all $p < 0.05$). The 2-way (Delay × Block) repeated measures ANOVA of the memory-guided data yielded no significant effects for either factor or their interaction ($p > 0.05$). Last, the mixed-design ANOVA between the visually-guided task and the memory-guided task, collapsing delay condition, yielded significant effects for Task ($F_{(1,20)} = 23.11$; $p < 0.01$), Block ($F_{(4,80)} = 11.27$; $p < 0.01$) and their interaction ($F_{(4,80)} = 2.98$; $p = 0.02$). Post hoc comparisons confirmed that grip axes were more rightward in the memory-guided task and overall grip axes were more leftward towards the COM for blocks C, D and E compared to block A and for block E compared to block B (all comparisons $p < 0.05$).

To summarize the main results of Experiment 1, subjects in the visually-guided task tended to first look to the top half of the block towards the grip site for the index finger followed by a fixation closer to the block's COM. In contrast, subjects in the memory-guided task tended to maintain their gaze closer to the COM. We also analysed the kinematic data and found that subjects grasped the blocks closer to their COM in the visually-guided task compared to grasping in the memory-guided task though the grip axes in the visually-guided task shifted leftward as block width decreased. Last, no statistical difference was found for MGA between delay conditions in the memory-guided task, but these MGAs were larger than in the visually-guided task, possibly to allow for a greater margin of error when visual feedback was not available. These

MGA results are similar to previous findings by Whitwell and colleagues (Whitwell et al. 2008; Whitwell and Goodale 2009) who found MGA is generally larger for open-loop movements and this difference is most evident when the open- and closed-loop trials are blocked (like in the present study) or when subjects are presented with successive trials of the same type.

Experiment 2

The results from Experiment 1 show different gaze behaviour between our visually-guided and memory-guided reaching and grasping tasks. These results raise an important question: why did the subjects in the memory-guided task not look towards the index finger location like the subjects in the visually-guided task when vision of the block was available during the viewing phase at the beginning of the trial?

To explain this difference, we suggest that gaze targeting of the index finger location was coupled to the immediate real-time computations of movement planning only at the time the movement was required and not before. This idea is consistent with the 'real-time hypothesis for motor control' by Westwood and Goodale (2003) in which they proposed that real-time motor planning utilizes dedicated visuomotor computations only when the movement is cued and only if vision is available at the time of the movement onset. Following up on a point raised by an anonymous reviewer, if it is the case that our results conform to the Westwood and Goodale's real-time hypothesis, we might observe the same gaze strategy of targeting the index finger location in a similar grasping condition that is an intermediary between the immediate and closed-loop reaching of the visually-guided task and the delayed and open-looped reaching of the memory-guided task.

In this second experiment, we investigated subjects' gaze behaviour while they performed the same reaching and grasping movements in an immediate grasping task. Here, subjects had vision of the block up to the moment they initiated their reach movement. This was accomplished by having the window close via the subjects lifting their grasping finger off a microswitch that controlled the window. That way, unlike the memory-guided task in Experiment 1, visual occlusion of the block was initiated by the movement onset and therefore after the movement was fully planned with visual feedback.

Methods

Subjects

Eleven subjects (5 males and 6 females; mean age 23.2 years) participated in this study for course credit as part of their introductory psychology course. All subjects had normal or corrected-to-normal visual acuity and were right handed according to self-report. All procedures were approved by the University of Manitoba's Fort Garry Campus Research Ethics Boards, and informed consent was obtained from each subject.

Apparatus, stimuli and procedure

The apparatus, blocks and procedure were the same as those in Experiment 1, with two exceptions: (1) the switchable window was controlled by a microswitch, which the subjects were required to press with their right index finger and thumb pressed together to open the window and view the block; and (2) subjects were instructed to make their reach immediately upon seeing the block. The switchable window closed as soon as the subjects released the microswitch, thereby occluding the block and the hand during the movement. The microswitch was positioned at the central start position (10 cm away from subject and 40 cm from block). Subjects performed seven trials for each block in pseudo-random order.

Results and discussion

Excluded trials due to a lost in eye position signal accounted for 2.9 % of all trials. Of the remaining trials, subjects made a single fixation in 73 % of the trials and two fixations in the other 27 % of the trials. Since we are mainly interested about gaze behaviour, we focused our analysis on the vertical and horizontal eye positions of the first and second fixations. Figure 6a shows the mean vertical gaze positions for the first and second eye fixations for each block. A repeated measures 2-way (Fixation × Block) ANOVA on the data for vertical gaze position yielded significant results for Fixation ($F_{(1,10)} = 12.76$; $p < 0.01$) and Block ($F_{(4,40)} = 14.56$; $p < 0.01$). Post hoc comparisons revealed significant differences when contrasting block E with blocks A, B and C (all comparisons $p < 0.05$). The interaction was not significant ($F_{(4,40)} = 1.9$; $p > 0.05$). We conducted the same repeated measures 2-way ANOVA for the horizontal gaze position (Fig. 6b). No effects were found for Fixation ($F_{(1,10)} = 0.001$; $p > 0.05$), Block ($F_{(4,40)} = 0.81$; $p > 0.05$) nor the interaction ($F_{(4,40)} = 0.83$; $p > 0.05$).

Similar to the memory-guided task in Experiment 1, in the immediate task, subjects made their reaching and grasping movements without visual feedback. However, the crucial difference between the immediate and memory-guided tasks was that in the immediate task, vision of the block was removed immediately after movement onset (as soon as the subjects lifted their finger off the microswitch). This means that in the immediate task, the movement was fully planned with vision opposed to the memory-guided

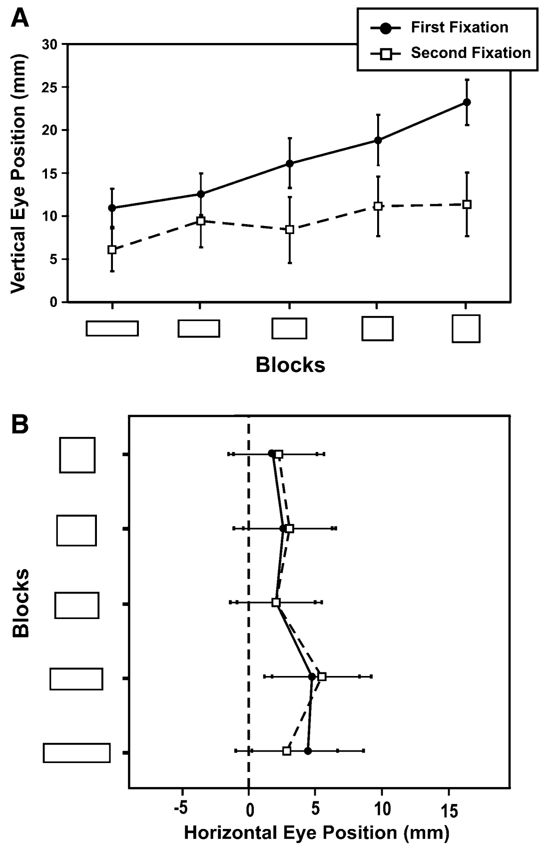


Fig. 6 Mean *vertical* and *horizontal* eye position in the immediate grasping task of Experiment 2. The main results of vertical eye position (**a**) show first fixations (*closed circle*) were higher than second fixations (*open square*) and directed towards the contact point for the index finger. No difference was found for the horizontal positions of both first and second fixations (**b**). *Error bars* represent standard error

task where delayed movements are presumed to be planned only when they are required at the presentation of a movement cue and without vision (Milner and Goodale 2006; Westwood and Goodale 2003). Our immediate task results show gaze behaviour similar to that in the visually-guided task in Experiment 1. Subjects tended to first look towards the top half of the block towards the grip site for the index finger. Taken together, the results from our study offer evidence that the gaze strategy of looking at the top part of the block towards the index finger was dependent upon the movement being planned and executed in real time when visual feedback was available.

Discussion

The aim of the present study was to explore subjects' gaze behaviour as they reached out and grasped a centrally placed symmetrical block either with or without visual feedback. In Experiment 1, reaching and grasping in the visually-guided task was performed with full vision of the block, whereas in the memory-guided task, subjects were briefly presented with block (for 1 s) and then made the reach for the block without visual feedback after the presentation of a movement cue. In Experiment 2, subjects performed a so-called 'Immediate grasping' task that was intended as an intermediary condition between the visually-guided and memory-guided tasks. In the immediate grasping task, subjects had vision of the block up to the moment they started their reach by lifting their finger off a switch that operated the window so that the movement was fully planned with, yet performed without, visual feedback. Our analysis focused on where subjects were looking on the different blocks in these different tasks. Altogether, our main results show that in the visually-guided and the immediate grasping tasks, subjects tended to first look towards the top edge of the blocks, corresponding to the index finger's grasp point, and then direct their gaze downward closer to the blocks' COM. In contrast, subjects performing the memory-guided task tended to look lower and closer to the blocks' COM throughout the trial, including the brief visual presentation of the block, when there was the 2-s delay interval, and during their reach for the block. We did not find any differences between tasks or delay conditions for the horizontal gaze positions. In general, subjects tended to look slightly to the right of the blocks' horizontal midline corresponding to the blocks' COM.

The results of the visually-guided and immediate grasping tasks are consistent with previous evidence that acting on visible objects activates task-specific gaze behaviour that strategically directs gaze to acquire critical visual information for visuomotor planning (Brouwer et al. 2009; De Grave et al. 2008; Desanghere and Marotta 2011; Flanagan and Johansson 2003; Johansson et al. 2001). Specifically, gaze is typically directed to the contact points for the digits when grasping an object. Indeed, the visually-guided results here are similar to a recent study that tested the gaze locations of subjects performing a similar visually-guided grasping task (Desanghere and Marotta 2011). Our results add to these previous findings by showing that gaze targeting for index finger placement is dependent upon visual feedback being available in real time when the movement is required and not before. This coupling between gaze and hand movements for real-time grasping we and the previously cited eye–hand coordination studies observed adhere to the 'just-in-time' strategy of visuomotor behaviour, where gaze is directed to acquire specific visual information just at the moment it is required for motor control (Ballard et al. 1995). One possible explanation why the index finger might have preferential visual coding for computing its grasp site rather than the thumb may be related to the lower visual field advantage in grasping (Brown et al. 2005); that is, grasping performance is less precise when objects are in the upper visual field than in lower visual field. Since the index finger grasp site is always on the top edge of the object in the upper visual field, relative to the subjects' eye level, correcting for less grasping accuracy can be easily accomplished by directing gaze closer to the block's top edge.

In contrast, the results of our memory-guided task suggest that acting on remembered objects engaged different visuomotor strategies. Specifically, the gaze behaviour in the memory-guided task did not show evidence that the brain needs to construct a sensorimotor representation contingent on where the index finger makes contact with the block as in the visually-guided and the immediate grasping tasks. While gaze behaviour in the visually-guided and the immediate grasping tasks showed evidence of the moment-to-moment coding of the visuomotor contingencies when the reach was computed and performed immediately upon viewing the block, in the memory-guided task without the immediate goal of on-line motor programming, there seems to be a switch to more general default perceptual analysis of the block's properties that might allow the brain to use the resulting memory representation for a variety of future tasks, including future programming of action movements towards the block. Furthermore, even during the reach when vision of the block was removed and subjects were looking directly into the uniformly grey and opaque glass of the switchable window, subjects did not attempt to look at the remembered locations of potential contact points. These results are consistent with previous findings by Flanagan et al. (2008) that show the linkage between gaze and hand movements is less robust during memory-guided actions. They found that while observers reached to remembered target locations in the periphery their gaze did not move with their hand, but instead they tend to keep their gaze close to the central cross they were looking at when the targets were visible. Similarly, in another grasping study, De Grave et al. (2008) found that observers were less likely to look at the area of an object that would be the index finger's preferred contact point if this contact point was occluded. Taken together, the results from the present study and these two cited memory-guided studies show converging evidence that gaze and hand movements become decoupled, or at least loosely coupled, in situations where action is directed towards an object without on-line and continuous vision of the motor target.

Our main findings conform to the two-streams theory of vision where visual processing for perception and action are broadly segregated into separate pathways in the brain, the ventral stream for perception, which terminates in the temporal cortex, and the dorsal stream for action, which terminates in the parietal cortex (Goodale and Milner 1992). Our visually-guided and immediate grasping results of gaze initially directed to the index finger's grasp site suggest that gaze behaviour during these actions is driven by the moment-to-moment requirements of the task for real-time visuomotor control of the hand's movements. Several human neuroimaging and patient studies have implicated parietal regions of the dorsal stream for performing such real-time operations for on-line visuomotor guidance (Connolly et al. 2003; Culham and Valyear 2006; Glover 2003; Grea et al. 2002).

On the other hand, so-called "off-line" visuomotor guidance of memory delayed actions appear to rely more on ventral stream processing as revealed by studies that show parietal-damaged patients with impaired visually-guided reaching behaviour actually show improved motor performance when reaching for remembered targets (Milner et al. 2001, 2003). Evidence of improved reaching performance in these otherwise visuomotor impaired patients with parietal lesions suggests that the mode of visuomotor control switches from the damaged on-line computational processes of the dorsal stream to the intact perceptual memory processes of the ventral stream (Himmelbach and Karnath 2005). As the results in the present study show, gaze in the memory-guided task was directed to the block's COM, resembling gaze behaviour during passive viewing of other solitary stimuli (Brouwer et al. 2009; Kowler and Blaser 1995; Melcher and Kowler 1999). Since the eyes were not directed to specific contact points on the block that would be motor goals for the digits either during the viewing or vision-blocked phases of the memory-guided trials, it is unlikely that the dorsal stream operations were engaged in the same way as during visually-guided grasping. We do not rule out the possibility that parietal visuomotor areas were still activated in neurologically healthy observers during memory-guided reaching; but if real-time movement planning does require visual inputs to these parietal areas to be immediately available and depends on gaze being strategically directed to critical visual information for on-line motor control as suggested by the previously cited research, and shown in our visually-guided results, then this would suggest that the subjects in our memory-guided task also switched the primary mode of visuomotor control from dorsal on-line computations to perceptual memory processes of the ventral stream.

There is an obvious advantage to being able to manually interact with objects without looking at them. The eyes and hands can be decoupled and allowed to carry out two tasks simultaneously. Indeed, there are many natural situations where we reach and grasp objects outside our field of vision, for example, reaching to pick up a coffee mug on your desk without looking away from your computer screen. Manual actions to a no-longer-visible object utilize stored visual information that was acquired when the object was previously viewed. The results of the present study provide new insight into the question of how gaze is deployed during delayed memory-guided reaches.

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