

The hand's automatic pilot can update visual information while the eye is in motion

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Received: 29 July 2008 / Accepted: 8 April 2009 / Published online: 29 April 2009
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Abstract When participants reach for a target, their hand can adjust to a change in target position that occurs while their eyes are in motion (the hand's automatic pilot) even though they are not aware of the target's displacement (saccadic suppression of perceptual experience). However, previous studies of this effect have displayed the target without interruption, such that the new target position remains visible during the fixation that follows the saccade. Here we test whether a change in target position that begins and ends during the saccade can be used to update aiming movements. We also ask whether such information can be acquired from two targets at a time. The results showed that participants responded to single and double target jumps even when these targets were extinguished prior to saccade termination. The results imply that the hand's automatic pilot is updated with new visual information even when the eye is in motion.

Keywords Saccade · Manual aiming · Online control · Sequential aiming

Introduction

When we reach for an object, the object is usually the target of our visual fixation before our hand contacts the object. Studies of rapid aiming suggest that a rough command to

move the limb is generated ahead of an orienting saccade. The action command is then refined online, once the eyes acquire the target (Desmurget and Grafton 2000; Gribble et al. 2002). Double-step studies (so called because the target is displaced twice: once ahead of the orienting saccade and once during the saccade) have demonstrated that the motor command to the hand is modified in response to the displaced target, even though the participant is unaware of the jump (e.g., Bridgeman et al. 1979; Goodale et al. 1986; Prablanc and Martin 1992). These rapid corrections to target jumps are thought to be under the control of an 'automatic pilot' (Pisella et al. 2000), which guides the hand independently of conscious intention or awareness.¹

The lack of awareness experienced during the eye movement is referred to as saccadic suppression (Bridgeman et al. 1975), with some researchers speculating that the loss of awareness is associated with a failure to acquire any new information about target position until the saccade is completed (e.g., Prablanc and Martin 1992; Desmurget et al. 2004). Yet, no one has directly examined whether new target position information that is available only during the saccade can be incorporated into the motor commands to the hand. This is an important question because it distinguishes the theoretical possibility of continuous guidance of action during the saccade from a coarse-to-fine model of control in which information available only following saccade termination governs online modifications of the hand (Desmurget et al. 2005).

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¹ Even when jumps are perceptually accessible and participants are instructed to stop their movement (Pisella et al. 2000; Cressman et al. 2006) or to point in the opposite direction (Day and Lyon 2000) if the target moves, people fail to inhibit a deviation toward the displaced target. Recent evidence from our laboratory does suggest, however, that automaticity can be reduced by instructions that downplay the relevance of the target jump to the task, such as when people are told to ignore the jump (Cameron et al. 2009).

The present study investigates the online response to target jumps in an aiming task when the jumps are strictly intra-saccadic, meaning that targets are displaced only once the eyes are in motion and then are extinguished before the eye has completed its movement. We investigate the resolution of intra-saccadic information by measuring movement accuracy to targets that are presented peripherally during a fixation and then displaced during the first saccade made in response to their onset. Any corrections in hand movement made in response to these jumps are thus based on information that was acquired while the eyes are in transit. The goal is to understand the resolution and extent of target position information that can be acquired during an orienting saccade.

A second goal of the study is to probe the capacity of position processing in the hand's automatic pilot by comparing performance on single-target trials, where there is only a single target position to update, with performance on double-target trials, where either or both targets may be displaced prior to disappearing before the saccade is complete. Baldauf et al. (2006) have shown that people simultaneously allocate perceptual attention to the multiple targets of a sequential aiming movement (a reaching movement in which the participant contacts two or more targets in rapid sequence). In their study, participants successfully identified a symbol that was randomly and briefly displayed at one of multiple target locations during the reaction time period of the reach. Because the display time of the symbol was too short to allow sequential allocation of attention to each of the target positions, the authors concluded that attention was distributed among the positions. While this evidence suggests that identity information can be simultaneously gleaned from the multiple targets of an aiming response, it is not clear (1) whether spatial information for online action guidance can be acquired simultaneously from multiple targets or whether it is gathered in a serial fashion as the movement unfolds, and (2) in the case that spatial information can be acquired simultaneously from multiple targets, whether there is a performance decrement as a result (i.e., a capacity limit to attention-for-action). Indirect evidence from a study of eye–hand coupling (Neggers and Bekkering 2000; 2001), in which the eyes refused to leave a target until the hand had acquired it, despite instructions to saccade to a new target while the hand was in flight, suggests that the motor system may prefer serial processing of target information. However, because the hand movement was prepared to a single target in that study, the results may not allow us to predict the system's behavior in a multiple target setting.

The design of the present study, in which either or both targets of a sequential movement are displaced and then extinguished prior to saccade completion, allows us to probe the system's ability to acquire information about both

targets. Does it respond to perturbations in the first target only, or can it selectively respond to perturbations in either target?

Experiment 1

This experiment examines the online control of finger pointing to one or two targets that are displaced during the orienting saccade and disappear prior to saccade completion. Three main questions were addressed. First, if the finger's automatic pilot is capable of incorporating an intra-saccadic change in position into the movement, then the endpoint of the movement should be influenced by the change in target position. Second, if the visuomotor system is able to simultaneously process multiple target locations as the reach unfolds, then it should respond selectively to jumps in the first and second targets. Third, if there are capacity limits on the acquisition of position information then this influence should be weaker when there are two versus only one target.

Methods

Participants

Eleven volunteers (6 female, 5 male) from the University of British Columbia participated in the experiment. The average age was 22 (range: 18–34). All participants were right-handed and had normal or corrected-to-normal vision. All participants gave informed consent prior to participating in the study. Participants received \$20 compensation for approximately 2 h of participation. The experiment was conducted in accordance with the ethical guidelines of the University of British Columbia and in accordance with the ethical guidelines of the Declaration of Helsinki.

Apparatus

The targets to which participants made aiming movements were red dots of light (5 mm diameter) produced by light emitting diodes (LEDs). The LEDs were set beneath an inclined Plexiglas surface (Fig. 1). The home position LED was located to the left of the participant's midline. The LEDs used for target presentation were horizontally aligned at five distances to the right of the home position: 150, 175, 200, 225, and 250 mm (which will also be referred to as positions 2, 3, 4, 5, and 6, respectively). Participants sat with their head in a chinrest, their eyes positioned approximately 60 cm from the display surface. The participant held a stylus in his/her right hand. An infrared emitting diode was fixed to the front surface of the stylus, and this allowed us to track the movement with Optotrak (Northern Digital).



Fig. 1 Schematic layout of the visual display. Only the *filled circles* were visible to participants. The example illustrated is a first target (T1)-jump trial. The trials began with the hand-held stylus placed immediately below the fixation LED (on which the eye is gazing). The

The position of the stylus was sampled at a frequency of 500 Hz. The stylus's microswitch tip allowed precise recording of movement lift-off and touchdown.

Electrooculography (EOG) was used to monitor horizontal saccades. Disposable Ag–AgCl surface electrodes were placed at the outer canthi of the eyes with a ground electrode placed on the forehead. EOG signals were amplified (5–10 K) and band-pass filtered (0.1–30 Hz) using an AC preamplifier (Grass Instruments P511), and sampled at a rate of 500 Hz. The EOG signal was passed through an analog circuit that enabled online triggering of stimulus events around the midpoint of the saccade.

Procedure

Participants began each trial with the stylus placed just below the home position LED and their eyes fixated on the home position LED. On a given trial, one or two targets could appear to the right of fixation. Participants were told that if a single target appeared they should look and point to the target as soon as it appeared. Participants were told that if two targets appeared they should look and point to both targets as soon as the targets appeared, tapping the nearer target first and the farther target second. (Single and double target trials were randomly interspersed.) Participants were told to always execute their pointing movements as fast and as accurately as possible. Participants completed a total of 360 trials (preceded by 20 practice trials), divided into three blocks of 120 trials. Half of the trials were jump trials (trials in which one or both of the targets moved to a new location), and half were stationary trials.² Jump and stationary trials were

² We note that this is a higher percentage of jump trials (50%) than was employed by Pisella et al. (2000) (20%) and closer to the percentage employed by Prablanc and Martin (1992) (66%). Unlike Pisella et al.'s experiment, the target perturbation in our experiment was paired with the saccade, which removes awareness of the jump. In this way, our study is more similar to Prablanc and Martin's (1992). We would expect this lack of awareness to prevent any influence of the proportion of jump trials on a participant's explicit strategy (though there is always the possibility that the nature and frequency of target perturbations might have an implicit effect on a participant's performance).

two targets to the left (*filled circles*) then illuminate in the periphery, coincident with the offset of the fixation LED. During the first orienting saccade of the eye to the targets, T1 jumps one position to the right (shown by the *arrow*), and then both targets extinguish 20 ms later

randomly interspersed. On jump trials, the target jump was triggered by the saccade: using the EOG signal, we triggered the target jump at approximately the midpoint of the saccade. On single-target trials, only one type of jump was possible: a rightward jump of 25 mm. There were three possible locations for the target's initial position: 150, 175, and 200 mm to the right of the home position (i.e., positions 2, 3, and 4). Analysis of single-target trials is restricted to positions 2 and 3, however, so that comparisons to the first movement component on two-target trials are based on equivalent target distances. On two-target trials, three types of target jump were possible: (1) the nearer target (T1) jumped right while the farther target (T2) remained stationary, (2) T2 jumped right while T1 remained stationary, (3) both targets jumped right. Each of these trial types could occur at two locations. For T1-jump trials and for both-jump trials, starting target positions were 2 and 4 or 3 and 5; for T2-jump trials, starting target positions were 2 and 3 or 3 and 4.

On every trial the targets disappeared 20 ms after the saccade midpoint was reached (i.e., on displaced trials, the targets disappeared 20 ms after the target moved; on stationary trials, the targets disappeared 20 ms after the target jump would have occurred had the trial been a displaced trial). Consequently, the targets were gone by the time the saccade was completed.³

Statistical analysis

In the repeated measures ANOVAs outlined below, data were tested for violations of the sphericity assumption with Mauchley's test of sphericity. If the test was significant at $P < 0.10$, the Hyunh-Feldt adjustment to degrees of freedom was applied.

All other statistical hypothesis testing used $P < 0.05$.

³ In Experiment 1, average saccade MT was 72.9 ms (SD: 8.16 ms). Average time of the jump was 35.4 ms (SD: 7.25 ms) after the start of the saccade. Therefore, on average, the target disappeared 55.4 ms into the saccade, or 17.5 ms prior to the completion of the saccade.

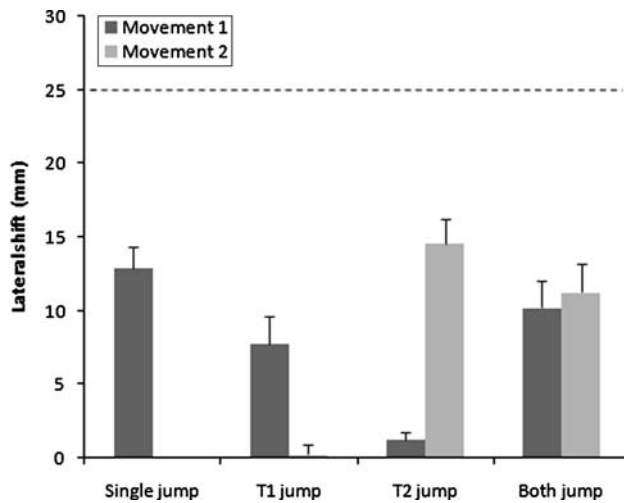


Fig. 2 Jump-induced shift in hand (jump trial endpoint minus stationary trial endpoint) for Experiment 1. Note that a complete response to a jumped target would produce a lateral shift of +25 mm (dashed line). Error bars represent one standard error of the mean

Results

Intra-saccadic target jump influences the automatic pilot

Motor sensitivity to target jumps was indexed by comparing the lateral stylus endpoint on jump trials with the lateral endpoint on stationary trials. Specifically, we computed a mean shift score by subtracting the mean stationary trial endpoint from the mean jump trial endpoint. If aiming was insensitive to target jumps, then these scores should hover around zero. Conversely, if pointing was as accurate for a jumped target position as to a stationary target then these scores should average 25 mm. Figure 2 shows mean lateral shift scores for each type of jump trial. These data demonstrate very conclusively that the finger was influenced by target jumps in all conditions. When the mean for each movement to a jumped target was compared to 0, using Bonferroni-corrected one-sample *t*-tests (Table 1), each of the five comparisons was significant.

Table 1 *T*-tests of lateral shift scores

Displaced target	Mean shift	SEM	<i>t</i> -value	df	<i>P</i>
Single	12.88	1.48	8.73	10	0.00001*
T1-M1	7.69	1.89	4.09	10	0.00217*
T2-M2	14.50	1.68	8.61	10	0.00001*
Both-M1	10.21	1.81	5.64	10	0.00021*
Both-M2	11.26	1.94	5.81	10	0.00017*

T1 Target 1, *T2* target 2, *M1* first movement, *M2* second movement, *SEM* standard error of the mean. Mean shift values are in millimeters

* Indicates significance at Bonferroni adjusted *P*-value of 0.01

Furthermore, Fig. 2 illustrates that the hand responded selectively to target jumps in two-target trials. When T1 jumped, only movement 1 (M1) adjusted; when T2 jumped, only movement 2 (M2) adjusted; and when both targets jumped, both M1 and M2 adjusted.

Capacity limits when pointing to two vs one target

If the automatic pilot is capacity-limited, we should see impaired adjustment to a T1 jump when a second target is present. Accordingly, we compared performance on single-target trials to M1 performance on two-target trials. (Distance from home position to T1 was equivalent in both cases.) Figure 2 suggests that M1 adjustment to a target jump was reduced relative to the single-target condition, and a one-way repeated measures ANOVA (4 levels: single, T1-jump, T2-jump, and both jump) of the M1 lateral shift data confirms that adjustment to the jump was related to trial type, $F(2.06, 20.56) = 21.18$, $P < 0.001$. Post hoc testing (Tukey's HSD, $P < 0.05$) revealed that single-target trial performance was significantly better than M1 performance on T1-jump trials. Single-target trial performance did not differ significantly from M1 performance on both-jump trials, however.

Amplitude of the orienting saccade on stationary and jump trials

To determine the influence of a target jump on the orienting saccade, we examined the EOG voltage change across each trial type (Fig. 3). The stationary target trials at single target positions 2, 3, and 4 demonstrate that the amplitude of the voltage change varies proportionally with the distance of the target, suggesting that the EOG signal accurately reflects orienting saccade amplitude. Consequently, we can compare jump and stationary trials in Fig. 3 and infer that the intra-saccadic target jumps did not systematically affect the amplitude of the orienting saccade.

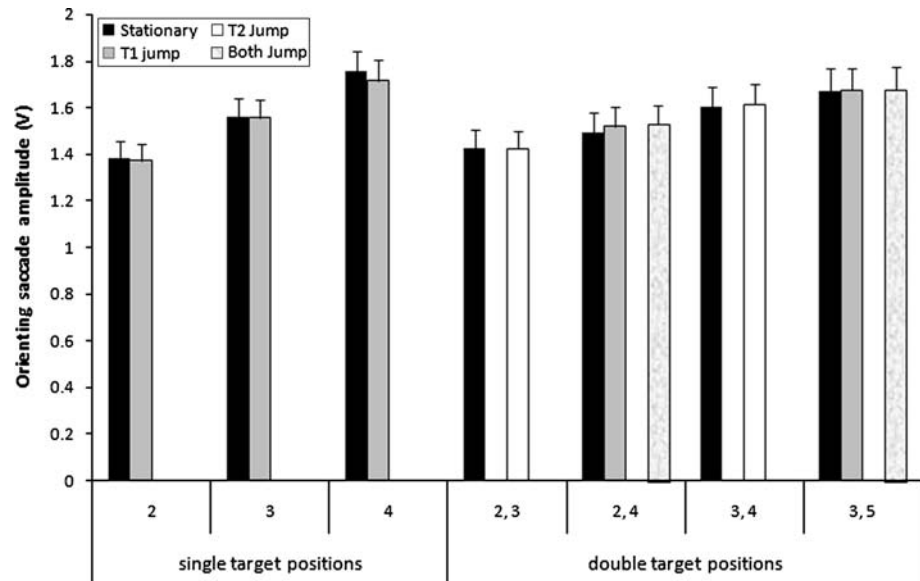
Discussion

Strictly intra-saccadic target jumps influence the reaching hand

Experiment 1 showed that target jumps that occur during a saccade influence the real-time control of finger pointing movements, both when only pointing to a single target and when pointing to two targets in quick succession. These results imply that intra-saccadic information about target position is accessible to the finger's automatic pilot.

There are two ways, however, that intra-saccadic target information might have influenced the hand's online

Fig. 3 Saccade amplitude for each type of trial, as measured by EOG voltage change. Error bars represent one standard error of the mean. Comparison of the *solid black bars* (stationary target trials) to the other bars (various types of jump trials) demonstrates the absence of evidence for an influence of a target jump on the magnitude of the saccade



response: a direct route (via retinal input acquired during the saccade) and an indirect route (via proprioceptive input from a modified eye position caused by an online response to the target jump). Although the saccade has traditionally been viewed as ballistic, recent evidence suggests that it is capable of some online modification (Gaveau et al. 2003; Chen-Harris et al. 2008; Prablanc and Martin 1992). We cannot, therefore, rule out a priori the indirect route as an explanation of our results.

Three lines of evidence, however, lead us to favor the direct route explanation. First, the EOG data from our experiment show no effect of the intra-saccadic target jumps on the amplitude of the orienting saccade. We acknowledge that EOG has a lower spatial resolution than other forms of eye-tracking and may have, therefore, failed to detect the online response. However, we did observe reliable scaling of the EOG signal to stationary target positions, with no sign of an amplitude increase on jump trials. If the online response of the eyes was present, it was presumably quite small. Second, the online modifications to saccades that have been found in the studies cited above involved either large target jumps (7.5° in Gaveau et al. 2003; 10° in Prablanc and Martin 1992) or repeated exposure to a systematic target jump (Chen-Harris et al. 2008). In fact, this last study found no online response of the saccade when jump direction was randomized. The target jumps in our study (2.5°) were a third or less the size of those used by Gaveau et al. (2003) and by Prablanc and Martin (1992), who observed an online response of the eyes that amounted to 7–19% of the target jump magnitude. It may be that a smaller target jump does not elicit an online modification of the eyes, or it may be that the size of the online adjustment in our study was simply too small for

EOG to detect.⁴ If we were to assume that the eyes adjusted to the jump by the same proportion observed by Gaveau et al. (2003) and Prablanc and Martin (1992), this amount would still be insufficient to account for the online response of the hand, which shifted by 51% of the jump magnitude on single-target trials. Of course, this argument assumes a 1:1 relationship between the shift in visual fixation and the shift in the hand. It is always possible that a small modification of the saccade amplitude can have a disproportionate impact on the behavior of the hand, leaving the possibility that a small online shift in eye position (undetected by EOG) led to the large shift in final hand position that we observed here.

The third line of evidence, and perhaps the most convincing, is that the two-target trials from our experiment show selective responding of the hand to jumps of either target. If the eyes were updating their position online, it could only ever be to one of the two targets and therefore would not account for the hand's behavior. Furthermore, the EOG data in Fig. 3 suggest that the orienting saccade was slightly larger on two-target T1-jump trials than on single-target jump trials (a result of the eyes landing partway between the targets on two-target trials). The hand, however, responded more to the jump on single-target trials, suggesting dissociation between the endpoint of the eyes and the endpoint of the hand. While these lines of evidence lead us to believe that the automatic pilot is

⁴ We note that EOG was sufficient for Prablanc and Martin (1992) to detect an influence of their larger target jump on saccade amplitude, suggesting that this methodology does not preclude detection of an online response when such a response is present, though it may only detect the effect when the jump is large.

accessing retinal information during the saccade, they are not conclusive. Future studies using more refined eye tracking may help resolve the issue.

The reaching hand responds to intra-saccadic jumps in either target

The results of Experiment 1 also imply that the visuomotor system is able to acquire information about more than one aiming target during the saccade and incorporate it into the movement. This implies that during a sequential reach, the visuomotor system samples from both targets in parallel, extracting spatial information for action in addition to symbolic information for perceptual report (Baldauf et al. 2006). At the same time, we hasten to add that we observed a reduction in pointing accuracy on one kind of two-target trial: accuracy to the first target on T1-jump trials was lower than accuracy to an equivalent single target. This contrasts with the results obtained by Baldauf et al. (2006), in which symbol identification at the location of the first reach target did not decline with the addition of more reach targets. The presence of a dual-target cost in our results, however, is likely the result of interference during motor output, rather than interference during information uptake. We suggest a motor locus for the interference because we did not observe a significant decrease in accuracy to T1 when both targets jumped, a condition that requires only the adjustment of the first component of the reach. (The distance between the first and second targets is unchanged when both targets jump). A T1-jump trial, on the other hand, requires the online adjustment of both the first and second reach components, and the online updating of the second component probably impairs performance of the first (Chamberlin and Magill 1989; Cameron et al. 2007). Alternatively, the reduced response to the jump in the T1-jump trials may result from a strategic undershoot to T1 that minimizes error to the stationary T2. This explanation would still place the interference at an output level, though the performance cost for the first movement component would result not from the assembly of the second component during the execution of the first, but rather from an anticipated failure to sufficiently reduce the amplitude of the second component and the consequent necessity to decrease the amplitude of the first.

Experiment 2

In Experiment 1 we observed partial adjustment of the hand to a strictly intra-saccadic target jump. While this effect suggests that the automatic pilot can update visual information while the eye is in flight, it does not tell us about the quality of this information relative to

post-saccadic information. In Experiment 2 we examine the relative contributions of intra-saccadic and post-saccadic target information to the online response of the hand. Specifically, we examine the mean lateral shift of the hand and the variability of the hand's endpoint when the target jumps and then disappears during the saccade (20 ms after saccade midpoint) and when the target jumps then disappears after the saccade is done (80 ms after saccade midpoint).

Methods

Participants

Five volunteers who did not participate in the first experiment participated in Experiment 2 (5 male, aged 25–42, two of which were the first and last authors). All participants were right-handed and had normal or corrected-to-normal vision. All participants gave informed consent, and the experiment was run in accordance with the ethical guidelines of the University of British Columbia and in accordance with the ethical guidelines of the Declaration of Helsinki.

Apparatus and procedure

A few small modifications were made to the apparatus and procedure of Experiment 1, with the most important being the addition of trials in which the target remained illuminated for 80 ms after the saccade midpoint (i.e., until after saccade completion). These trials made up half of all trials, and were randomly interleaved with trials in which the target was extinguished 20 ms after the saccade midpoint. We also restricted trial type to single-target trials and included both forward and backward target jumps. Stationary targets (50% of trials) were presented at positions 3, 4, or 5 (Fig. 1). Jump trials (50%) were 4–3 (backward, 33% of jump trials), 3–4 (forward, 33% of jump trials), or 4–5 (forward, 33% of jump trials)⁵ All trial types were randomly assorted. For analysis, values were collapsed across distance.

Results

Greater lateral shift when the target was present until after the saccade

The influence of the target jump on the reaching hand is shown by the lateral shift values in Fig. 4, which clearly

⁵Two kinds of forward jump were included in an attempt to match the backward jump in both the initial target position (position 4) and the region traversed by the jump (between positions 3 and 4).

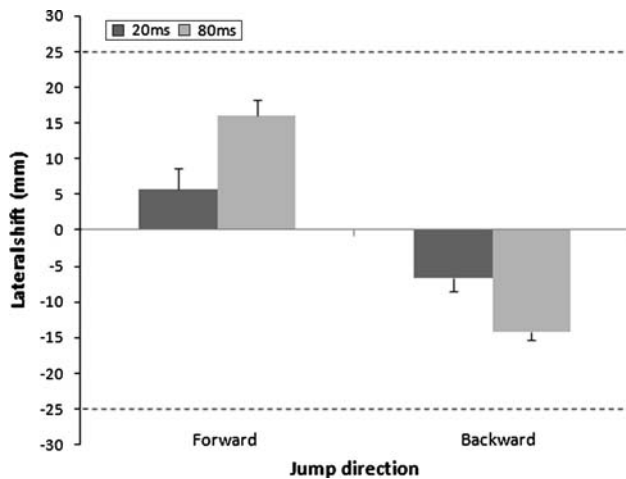


Fig. 4 Jump-induced shift in hand (jump trial endpoint minus stationary trial endpoint) for Experiment 2. Note that a complete response to a jumped target would produce a lateral shift of ± 25 mm (dashed lines). Error bars represent one standard error of the mean

show that the hand adjusted more to a target jump when target information was available until after completion of the saccade. To compute these values, the lateral stylus endpoint on the appropriate stationary trials was subtracted from the endpoint on jump trials, as in Experiment 1. A 2 direction (forward, backward) \times 2 time (20, 80 ms) repeated measures ANOVA revealed a significant interaction, $F(1,4) = 47.28$, $P = 0.002$, reflecting the greater adjustment of the hand in the 80 ms condition. A main effect for direction, $F(1,4) = 33.54$, $P = 0.004$, indicates that hand responded differently to forward and backward jumps, and the absence of a main effect for time, $F(1,4) = 1.5$, $P = 0.28$, merely reflects the cancellation of the means when values are collapsed across direction (indicating that lateral shift was roughly equivalent, but opposite in sign, across direction).

Reduced endpoint variability when the target was present until after the saccade

We also examined the variable error (VE) of the reach, which reflects the resolution of the information acquired by the orienting saccade. To compute VE, we calculated the standard deviation of the lateral endpoint of the stylus. As shown in Fig. 5, variability was less when the target stayed on until after saccade termination. A 3 direction (stationary, forward, backward) \times 2 time (20, 80 ms) repeated measures ANOVA revealed a significant main effect for time, $F(1,4) = 19.12$, $P = 0.012$, reflecting the reduced variability in the 80 ms condition. No significant effects for direction, $F(2,8) = 1.55$, $P = 0.27$, or direction \times time, $F < 1$, were found.

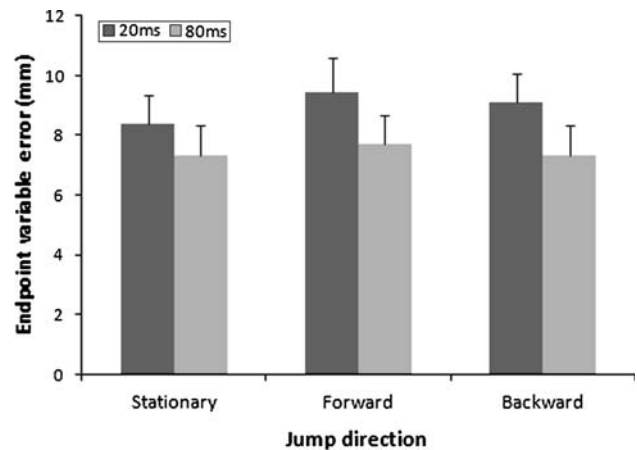


Fig. 5 Mean variable error in the primary movement dimension for Experiment 2. Error bars represent one standard error of the mean

No lateral shift in the orienting saccade as a result of target jumps

As in Experiment 1, we observed no influence of the target jump on the amplitude of the orienting saccade (Fig. 6). Moreover, the presence of forward and backward jumps in Experiment 2 (which increases the potential effect size) provides a stronger test of an online saccadic response. If the jump had influenced saccade amplitude, we would expect a positive shift for forward jumps and a negative shift for backward jumps, but Fig. 6 shows no such pattern.

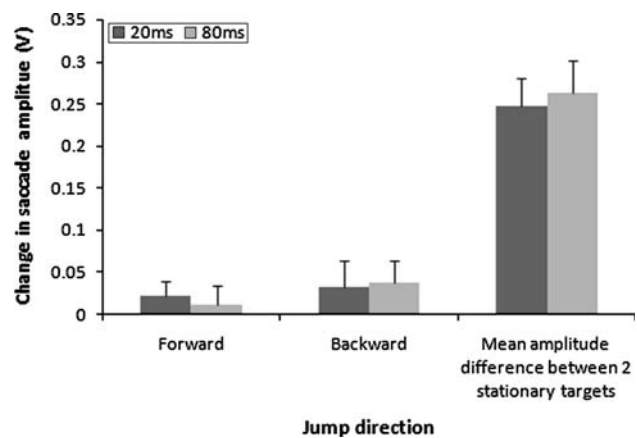


Fig. 6 Change in saccade amplitude as a result of a target jump in Experiment 2. (Change in amplitude = saccade amplitude on jump trial minus saccade amplitude on a corresponding stationary trial). Note that if saccades are being modified online, we would expect a negative change in the backward jump condition. The amplitude difference between two stationary targets (i.e., the mean of the difference between stationary targets 3 & 4 and 4 & 5) is provided for reference. Error bars represent one standard error of the mean

Discussion

Analyses of both the hand's lateral shift and endpoint variability indicate that participants were more accurate in the 80 ms condition. So, although the automatic pilot may begin to update visual information while the eye is in flight, updating evidently continues until after the saccade has ended.

Because our post-saccadic manipulation required extending the visibility of the jumped target from 20 ms to 80 ms, we cannot rule out the possibility that our results arise from extended exposure to the target, rather than a quality difference between intra- and post-saccadic information.⁶ In fact, the results may well reflect a combination of the effects of exposure time and post-saccadic processing. We can infer, however, that the 20 ms snapshot of the target acquired during the saccade provides an incomplete picture of the jumped target's location and that the automatic pilot continuously refines visual information as the saccade unfolds.

Although Experiment 2 replicates the finding from Experiment 1 that the hand adjusts to a strictly intra-saccadic target jump, we did observe a reduced adjustment to a single rightward target jump in Experiment 2 relative to Experiment 1: 5.7 mm vs. 10.0 mm (for single targets at equivalent distances in the two experiments). If this difference is real, the reason for it is not clear. Experiment 2 differed from Experiment 1 in several small ways: Experiment 2 contained both 20 ms and 80 ms exposure trials (interleaved), while Experiment 1 only contained 20 ms exposure trials; Experiment 1 contained both one and two-target trials (interleaved), while Experiment 2 contained only single-target trials; and Experiment 2 contained both forward and backward target jumps, while Experiment 1 contained only forward target jumps. There is no obvious reason why the first two differences would impact the degree of hand adjustment. The presence of bi-directional target jumps, on the other hand, might conceivably introduce greater uncertainty to the system, reducing the amount of online adjustment. Given that awareness of the target jumps was suppressed by the saccade, however, this uncertainty would probably have to arise implicitly.

Although the lateral shift comparison between 20 ms and 80 ms trials is more dramatic when confined to Experiment 2, if we compare the 80 ms trials of Experiment 2 to equivalent single-target 20 ms trials in Experiment 1, the lateral shift is still greater in Experiment 2's 80 ms trials (15.4 mm rightward hand shift in Experiment 2's 80 ms trials relative to a 10 mm rightward hand shift in Experiment 1's 20 ms trials). When we also consider the decreased

endpoint variability when the target remains lit until saccade completion, the central finding of Experiment 2 remains: accuracy improves when the target is present until saccade completion. This finding is consistent with research by Prablanc et al. (1986) that showed that extending the presence of a target until 120 ms after the primary saccade improved reaching accuracy relative to a condition in which the target disappeared at hand movement onset.

General discussion

Intra-saccadic target jumps influence manual aiming

Experiments 1 and 2 demonstrate that position information that is available only within the saccade can influence motor output. These results have at least three implications for our understanding of intra-saccadic processing and movement control. First, the real-time corrections to the target jumps imply that the automatic pilot guiding the hand is able to acquire updated target information prior to eye fixation on the target, i.e., the motor command assembled prior to the saccade can be modified with intra-saccadic information. Second, intra-saccadic information about more than one target can be acquired and incorporated into the ongoing movement. Third, the target information acquired during the saccade is incomplete and the automatic pilot continues to update visual information until after the orienting saccade has ended.

The ability to acquire intra-saccadic information about a target suggests that online control of the reaching hand may be subject to continuous refinement during an orienting saccade. Some researchers (e.g., Prablanc and Martin 1992; Desmurget et al. 2004; 2005) have suggested that motor refinement occurs only after the eyes have fixated the target. Such post-fixation models have, we suspect, been driven by the belief that all positional information about the target is suppressed during the saccade. However, there are at least three kinds of saccadic suppression,⁷ and one of them (*suppression of a flashed stimulus*) is relatively weak (MacAskill et al. 2003). Post-fixation models of online updating may have been influenced too strongly by the more dramatic *suppression of displacement* and the unnecessary corollary belief that this phenomenon prevents intra-saccadic access to a target's position. The failure to compare the pre- and post-saccadic target positions that underlies saccadic suppression of displacement (MacAskill et al. 2003) has, in our view, little to do with the question of whether the automatic pilot is able to acquire target position

⁶ Given the high velocity of the eyes during a saccade, however, one would certainly expect post-saccadic information to be more reliable.

⁷ These are (1) suppression of a flashed stimulus, (2) suppression of continuous motion, and (3) suppression of a discrete displacement (i.e., a jump) (MacAskill et al. 2003).

information during the saccade. In light of this, we recommend that care be used when discussing saccadic suppression in the context of manual online control. Saccadic suppression of a flash is relevant to this control. Saccadic suppression of displacement, however, is perhaps more pertinent to the perception of space constancy than it is to goal-directed action.

The position of more than one target can be acquired during a saccade

Our study included trials in which one, or both, of two aiming targets could relocate during the saccade. Participants' movements responded to these jumps, indicating that the visuomotor system's capacity for intra-saccadic position acquisition was sufficient to accommodate more than one target. These results also suggest that, during a multi-targeted reaching movement, spatial information is simultaneously acquired from each target in the sequence. However, we did observe a decrement in participants' adjustment to a target jump when a second target was also present (though only when the second target was stationary). We suspect that this effect is primarily due to a bottleneck in motor processing during sequential aiming (Chamberlin and Magill 1989; Cameron et al. 2007) or, possibly, to strategic undershooting, rather than to impairment in visual acquisition of multiple target information.

An alternative explanation for our results, however, considers the possible motion signals produced by the jumping targets and their impact on the reaching hand. Whitney et al. (2003) have shown that a moving visual display will influence one's reach to an adjacent stationary target. The online progress of the hand is biased in the same direction as the visual motion, which may have implications for reaches to double-step targets. If an intra-saccadic double-step is processed as a motion signal, this signal may cause the adjustment of the hand that we observed in the present study. Thus, reduced adjustment to a T1-jump in a two-target trial relative to a single-target trial could be the result of a diminished overall motion signal (since one target remains stationary in the first case). This same reasoning, however, should lead to a prediction of increased adjustment in a both-jump trial relative to a single-target trial, an effect that we did not observe. If motion signals are responsible for our effects, the signals appear to be specific to each target (i.e., they do not summate to produce an overall bias in the reach), given the selective responding that we observed in Experiment 1. We also note that, given the suppression of visual motion processing that occurs during a saccade (Burr et al. 1994), the possible effect of motion signals in our study should be less than that observed by Whitney et al. (2003), who measured a 3–4 mm bias with a design that did not involve eye movements.

Conclusion

Our results demonstrate that intra-saccadic target information can be used for real-time movement control. This contrasts with models of online control that suggest motor updating can only occur after the eyes have fixated the target. Our results also demonstrate that spatial information can be acquired from more than one target during the orienting saccade that leads a sequential aiming movement.

Acknowledgments This research was supported by a scholarship from the Natural Sciences and Engineering Research Council of Canada (NSERC) awarded to B.C. and by a NSERC Discovery Grant awarded to R.C. We thank Dr. James Danckert and an anonymous reviewer for helpful comments on the manuscript.

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