RESEARCH ARTICLE

Visual information throughout a reach determines endpoint precision

Anna Ma-Wyatt · Suzanne P. McKee

Received: 6 April 2006 / Accepted: 16 October 2006 / Published online: 16 November 2006 © Springer-Verlag 2006

Abstract People make rapid, goal-directed movements to interact with their environment. Because these movements have consequences, it is important to be able to control them with a high level of precision and accuracy. Our hypothesis is that vision guides rapid hand movements, thereby enhancing their accuracy and precision. To test this idea, we asked observers to point to a briefly presented target (110 ms). We measured the impact of visual information on endpoint precision by using a shutter to close off view of the hand 50, 110 and 250 ms into the reach. We found that precision was degraded if the view of the hand was restricted at any time during the reach, despite the fact that the target disappeared long before the reach was completed. We therefore conclude that vision keeps the hand on the planned trajectory. We then investigated the effects of a perturbation of target position during the reach. For these experiments, the target remained visible until the reach was completed. The target position was shifted at 110, 180 or 250 ms into the reach. Early shifts in target position were easily compensated for, but late shifts led to a shift in the mean position of the endpoints; observers pointed to the center of the two locations, as a kind of best bet on the position of the target. Visual information is used to guide the hand throughout a reach and has a significant impact on endpoint precision.

A. Ma-Wyatt (⊠) School of Psycology, University of Adelaide, Adelaide, SA 5005, Australia e-mail: anna.mawyatt@adelaide.edu.au

S. P. McKee The Smith-Kettlewell Eye Research Institute, 2318 Fillmore St, San Francisco, CA 94115, USA **Keywords** Reaching · Visual feedback · Perturbation · Motor control · Psychophysics

Introduction

As we move around our environment, we constantly make hand movements that are rapid and goal-oriented. We reach to swat a fly, to pick up an object or to hit a button on the radio while driving. These are actions with consequences and it is therefore important for people to be able to make movements that are both precise and accurate. If we miss, or are too variable when we make these movements repeatedly, there will be a negative outcome—we miss the object, knock over the cup of coffee, or hit the wrong button. For a goal-directed movement, how do we ensure that we can maintain a high degree of endpoint precision and accuracy, even when a target shifts?

To make a rapid goal-oriented reach to an object, observers localize the target in space, formulate a plan to move the hand, and then execute the movement. In a previous study, we compared precision on comparable localization tasks for both rapid pointing and visual judgments (Ma-Wyatt and McKee 2006). For targets presented beyond 4° eccentricity, pointing error, as measured by the standard deviation of endpoint distribution, rose with eccentricity and was identical to visual thresholds (d' = 1), indicating that the precision of pointing was limited by visual precision. These results showed that the initial visual information available during the planning stage of the movement can significantly influence endpoint precision, even over as small a range as 24° in the central visual field (a lateral extent of ~ 18 cm at a reaching distance of 40 cm).

Several models of motor control contain an internal model of the movement that is generated before execution of the motor plan (e.g., Wolpert et al. 1995; van Beers et al. 2002). This internal model includes predicted states for visual and proprioceptive information that can be compared to feedback during the movement. Online guidance of hand or arm movements is achieved by comparing the current feedback with the model's prediction. Past work has suggested that different types of visual information can be used as effective feedback at different times in the reach (Paillard 1996). Visual information available in the periphery during the initiation of the movement can be used to alter the visual direction of the movement (e.g., Bedard and Proteau 2004). Later in the movement, as the hand reaches the target, the observer is able to use the higher resolution information provided by the fovea to make a corrective movement towards the target (e.g., McIntyre et al. 1998). It has also been suggested that the initial position of the hand can be used to improve motor performance (e.g., Rossetti et al. 1994). People can use both position and motion information about the target, as well as eye and hand position, for online control of movements (e.g., Whitney et al. 2003; Saunders and Knill 2004). They can also use altered visual information about target position to correct a trajectory online on at least 50% of trials (Saunders and Knill 2003), regardless of the time at which the perturbation occurs during the reach. In the absence of visual feedback during the reach, there are significant changes in reach characteristics like movement time and time of peak acceleration, suggesting that visual feedback is used during the movement to alter the movement plan (e.g., Connolly and Goodale 1999; Sheth and Shimojo 2002).

These studies have demonstrated that it is possible to use feedback during the reach to alter the characteristics of the reach. However, it is not known how visual information is used to update and refine rapid goaldirected movements online to improve endpoint precision. The movements in the studies described above were typically slow reaches (generally speaking, \sim 800 ms for a reach usually 30–50 cm in extent) with continuous visual feedback about the position of the target. Estimates of the time needed for visual feedback to affect movements vary from 250 ms (Keele and Posner 1968) to 160 ms (Saunders and Knill 2003). The results are generally consistent with a model in which sensory feedback is compared to the motor plan (e.g., van Beers et al. 2002; Sober and Sabes 2003, 2005). For a slow reach, there may be enough time to collect a lot of visual information, and for many samples to be compared to the internal model to update the movement.

For a rapid reach, these feedback models may be less relevant because the time available for altering the trajectory is so short.

Consider what happens if a briefly presented target (110 ms) has disappeared long before a rapid pointing movement can be completed. Now the observer is pointing to a remembered location within the coarse framework provided by the surroundings. Does vision help keep the hand on track, guiding the fingertip on the planned trajectory to the previously visible target? Accuracy (systematic error) is a measure of bias and it is well known that people are able to correct a bias with feedback, as demonstrated in prism adaptation studies (e.g., Kitazawa et al. 1995). Precision, however, is a measure of random error, and is undoubtedly limited by internal sources of noise that cannot be eliminated (McIntyre et al. 1998). It is therefore appropriate to examine how the variability of the endpoint, i.e., its precision, is affected by the availability of visual information during the reach. To examine the benefits of visual feedback on motor guidance, we used photographic shutters to close off the view of the hand at different times during rapid pointing. We measured how the loss of visual feedback during the trajectory affected endpoint precision.

Our previous study (Ma-Wyatt and McKee 2006) demonstrated that observers could improve endpoint precision if the target remained visible until finger touched it. Nevertheless, the visual eccentricity of the target at the time the movement was initiated still affected endpoint precision for targets presented at one of eight randomly-selected isoeccentric locations. McIntyre et al. (1998) have suggested that as the hand nears the target, observers are able to correct the position of the hand to improve their performance. We interpreted these findings as showing that our observers were able to correct the trajectory on some trials, but on others, were relying on the initial visual information about location to guide pointing. Clearly, whether a correction is possible depends on the speed of the movement, and the time at which the observer recognizes that the fingertip will miss the target. In the current study, we examined whether the ability to correct a trajectory in response to a shift in target location was related to the amplitude of the shift and the time it occurred during the reach, and therefore the time to process the visual information. Observers had to point to a target in the periphery. At a given time during the reach, the dot had a 50% chance of changing to another, more peripheral location. To explore the timing of these presumed corrections, we tested the effect of a perturbation presented early in the reach (110 ms), at an intermediate time in the reach (180 ms) and late in the reach (250 ms).

Methods

Four experienced observers participated in all three experiments. Two were naïve to the purposes of the experiment (LM and KM); the other two were authors (AMW and SPM). All observers had normal or corrected to normal visual acuity.

Stimuli and apparatus

Stimuli were presented on a 15" touchscreen (ELO Touch Systems, Elo Entuitive Systems). This was a standard CRT, overlaid with a touchsensitive layer. Pressure from the fingertip triggered a program that calculated the x, y position of the finger. The sensitivity of this information was tested by measuring the variability of the response to a regular artificial surface (an unused pencil eraser) touched with care to the same position. The error associated with this response was less than 0.1° in the x and y direction, and well within the error associated with a finger press. The experiment was conducted using custom written software from Matlab (Mathworks), using the Psychophysics Toolbox extensions (Brainard 1997; Pelli 1997). All experiments were conducted in a semi dark room. The touchscreen was placed on a table draped in black, non-reflective cloth. This same cloth was also used for curtains that allowed the testing area to be separated from the rest of the room. Two individual photographic shutters (Vincent Associates, Model CS45S3T1) were mounted on the chin rest. The shutters each had an aperture 25 mm in diameter. They were mounted on the chin and head rest, allowing them to sit close to the observer's eyes without significantly restricting their field of view. Tests showed that observers had a binocular view of approximately 90%

of the width of the monitor—an area that completely overlapped the screen where the stimuli were presented.

The contrast of the dot was 60% and the dot subtended 0.5° of visual angle at a viewing distance of 40 cm. This was a comfortable reaching distance for all observers. Before participating in the experiment, observers were trained on rapid pointing, to ensure that they were comfortable with the task and the associated time constraints. All observers were trained psychophysical observers and had also participated in earlier pointing experiments in our laboratory.

The target could appear at one of nine locations (see Fig. 2b). These nine locations consisted of eight equidistant locations on a circle whose radius determined target eccentricity, and one at the same location as the central fixation point. We tested targets at an eccentricity of 8°. For each trial, one location was selected and a small positional jitter added.

General procedure

Observers were seated 40 cm away from the touchscreen. On each trial, the observer fixated a central fixation point and made a key press on the keyboard in front of them to initiate the presentation of test stimulus. They were then presented with a target for 110 ms. Due to the short duration, the target had disappeared before a foveating saccade could occur and before the finger reached the screen. Observers were instructed to make a rapid point to the target as soon as they saw it (see Fig. 1 for a schematic representation of one trial, and of the experimental setup). Endpoints were registered by the touchscreen.



Fig. 1 a Diagram (from above) of an observer sitting in front of the monitor, with hand resting on the keyboard (*left*). Observer reached from the keyboard to touch the monitor on each trial (*right*). b Timeline of a trial in which a photographic shutter was

used to close off the visual field 110 ms into the observer's pointing movement. In this example, the shutter closed 110 ms into the trial, as soon as the target disappeared

Procedure for Experiment 1: shutters

The time of the point was taken to be the time from when the observer pressed the key to initiate the trial until the observer touched the screen. The shutter closed 50, 110 or 250 ms after the key was pressed. Total pointing times were usually of the order of 400 ms. Since there was little variability in movement times across shutter conditions or across observers (see Fig. 5), the shutter obscured a comparable and appropriate part of the trajectory for all observers.

We also conducted a control in which the shutter remained open throughout the point to ensure that the shutters did not significantly interfere with the field of view for a point. Observers completed approximately 150 trials for each condition.

For each trial, the touchscreen registered an x and y coordinate for the endpoint. Data were collected over several sessions conducted on separate days. Raw data, forming an incomplete data set, from one session for one observer are shown for illustrative purposes only in Fig. 2a. We took the difference between the endpoint and the target location for each trial. We measured this error along a single dimension for each target location (see Fig. 2b). Precision was calculated as the standard deviation of the population of error responses. Because we had collected more than a hundred trials for each condition, it was appropriate to assume that the population was normal and that the standard deviation was a sound estimate of population variability.

Procedure for Experiment 2: perturbation of a single target position during the point

We made small perturbations of target location and measured endpoint accuracy and precision. The



Fig. 2 a A subset of raw data from one testing session for Experiment 1, for one observer. Each *open circle* represents a touchpoint, each *closed circle* represents the target location. Stimuli were presented at an eccentricity of 8° . **b** We calculated the error between

perturbation could occur at different times during the reach. The initial target location was always to the right of fixation. The target, a high contrast white dot subtending 0.5° , appeared at an eccentricity of 8° for 110 ms and then disappeared for 67 ms. On half the trials, the target reappeared at the same location and for the other half, it was shifted laterally by an amount (~0.5°) that was easily visible on every trial, because of apparent motion produced by the rapid shift in position. On its second exposure, the target duration was 110 ms. Figure 3 shows a schematic diagram of a perturbation trial. For each trial, the target had a 50% chance of shifting or reappearing at the same location. We tested three different amplitudes in blocks: 0.5, 2 and 8°.

The time of perturbation was measured from the observer's initiation of a pointing trial by a key press. The perturbation could occur early in the reach (110 ms after trial onset), at an intermediate time



Fig. 3 Timeline for a trial in which the target position is perturbed. The time interval between the initial presentation and the perturbation will vary and the amplitude and the direction of the perturbation will also be varied across blocks



b)

the endpoint and the target location along the axis indicated, at each target location. We calculated precision by collapsing these measures into a single population and taking its standard deviation. *Circle* is shown for purposes of illustration only

(180 ms) or late in the reach (250 ms) in separate blocks of trials. Observers made a rapid point to the target and were given negative feedback if their response was too slow (>500 ms) and these trials were excluded from analysis. We excluded these trials because time pressure was important to the aims of the experiments. If we did not limit the time of the movement, the proportion of time in the trial in which the target was obscured or the target was shifted would change significantly. The average movement time across observers was 440 ms. Observers completed at least 150 trials for each condition.

For each endpoint, we calculated the difference between the final target location and the endpoint. We then used this error measure to calculate precision as described in the previous section. We calculated accuracy by taking the mean of the endpoints for each trial.

Results

Experiment 1: shutter closure

We calculated the ratio between thresholds, i.e., the standard deviation of the pointing distribution, for trials in which the observer viewed the target with the shutter open, compared to conditions in which the shutter closed at a set time into the reach. The ratio scores are plotted in Fig. 4. We have also plotted the mean pointing time across conditions for each observer, presented as a colored arrow for each observer (Fig. 4).



Fig. 4 Ratio scores for four observers, plotted as a function of the time of shutter closure. Data based on pointing to one of eight locations at an eccentricity of 8° (± 5 cm from center of screen)

Since the shutters were closed at a given time into the movement, it was important for observers to point under time pressure to ensure that the proportion of the movement that was conducted without vision was comparable across observers and across conditions. Figure 5 shows the mean movement times with standard errors for four observers. Movement times are comparable across shutter conditions for observers. However, times are generally longer for the condition in which the shutter remained open throughout the point, suggesting that observers were moving more quickly to minimize the reliance on visual memory when the shutters were closed.

Since the closure of the shutter also reduced the duration of the target, one could argue that the decrease in precision could be attributed to memory loss associated with a delay between the target presentation and the touch being made. Previous work has shown that for both visual localization and saccades to remembered targets, there is an increase in variability with an increase in delay (e.g., White et al. 1994). The shutters closed 50 ms into the reach in one condition, thereby reducing the duration of the target dot to 50 ms, so we also ran a control condition to test whether precision and accuracy were significantly influenced by target duration. Observers viewed the target dot through open shutters, and were instructed to make a rapid point to the target as soon as they saw it. Accuracy and precision were comparable for target durations of 50 and 110 ms (see Fig. 5). We therefore believe that our results cannot be attributed to the short target duration associated with the shutter closure.

Movement time was measured from the key press to initiate a target presentation until touching down on the screen. The time of shutter closure was measured from the initiating key press. Movement times were generally around 400 ms for the shutter conditions, comparable to other times for rapid pointing over 40 cm (e.g., Trommershauser et al. 2003). As can be seen from Fig. 5, movement times are comparable across all conditions. The visual target was never present when the observer's finger reached the screen. Our results demonstrate that for memory guided rapid pointing, visual information about the location of the hand in space and its position relative to the remembered location are used throughout the reach to guide the hand along the planned trajectory.

Precision generally decreased if the shutter was closed for part of the trial, compared to trials in which the shutter remained open throughout the trial. Precision was worst if the shutter was closed 50 ms into the trial. We conducted a one-way ANOVA on the ratios





for all observers across shutter latencies. There was a significant effect of shutter latency (P < 0.001, $F_{3,12} = 21.2$), demonstrating that pointing precision is significantly affected by shutter latency.

Our results show that observers are able to use visual information throughout a reach in order to improve precision. In fact, the longer the amount of time that the hand is viewed before the observer touches the monitor, the more precise the observer's performance becomes.

Experiment 2: single perturbation of target location at different times during the reach

Figures 6, 7, 8 show the mean locations of the endpoints with standard error bars for four observers, for three different perturbation times. For an early perturbation of target location, observers are able to correct for the new target (Fig. 6). For intermediate perturbations during the movement, observers were also able to adjust their pointing trajectory so again, there was a substan-



Fig. 6 Accuracy for a perturbed and unperturbed target location (mean data for four observers). The size of the perturbation was 0.5° . *Error bars* represent one standard error of the mean (symbols sometimes larger than error bars)



Fig. 7 Accuracy for a perturbed and unperturbed target location (mean data for four observers). The size of the perturbation was 4°. *Error bars* represent one standard error of the mean (symbols sometimes larger than error bars)



Fig. 8 Accuracy for a perturbed and unperturbed target location (mean data for four observers). The size of the perturbation was 8° . *Error bars* represent one standard error of the mean (symbols sometimes larger than error bars)

tial difference between the mean of their points to the perturbed and static targets (Fig. 7). For a late perturbation, observers were unable to change their motor plan, because there was no difference between means for the perturbed and static targets (Fig. 8). Observers adopted an interesting strategy to cope with late perturbations. They pointed to the centroid of the two possible locations, thereby 'hedging their bets' about the likely location of the target. These results suggest that observers might be able to keep a tally of target locations. In all cases, observers overshot the target. To make a meaningful comparison between conditions in which observers pointed to different amplitudes, all data were normalized relative to the true target location. We used these ratios for statistical analysis.

We conducted a two-way repeated measures ANOVA on the data for all observers for each shift amplitude, with perturbation amplitude and time of perturbation as the two factors. In the 0.5° condition, there was no significant main effect of time of perturbation (P = 0.7; $F_{1,18} = 0.15$) or of target position (P = 0.4; $F_{2,18} = 0.98$). For a perturbation amplitude of 4°, there was a significant main effect of time of perturbation (P < 0.05, $F_{2,17} = 4.3$), and no significant main effect of target position (P = 0.08, $F_{2,17} = 3.5$). There was a significant interaction between these effects (P < 0.001; $F_{2.17} = 15.6$).

For a perturbation amplitude of 8°, there was significant main effect of time of perturbation (P < 0.01, $F_{1,12} = 7.9$), but not target position (P = 0.36, $F_{2,12} = 0.88$). There was also a significant effect of interaction (P = 0.29, $F_{2,12} = 1.4$). These results indicate that the time of the perturbation, but not the amplitude of the shift, significantly affects the observer's ability to point accurately to the final target location.

Precision for each observer for different perturbation times is shown in Fig. 9. We conducted a two-way repeated measures ANOVA to test whether there was a significant effect of size of perturbation on precision, and whether there was a significant difference between precision at each target location. ANOVAs were run separately for the early (110 ms), mid (180 ms) and late (250 ms) perturbation conditions. In each case, there was a significant effect of size of perturbation on precision (P < 0.001), but no significant difference between precision at each target location (P > 0.05).

Generally, the precision decreased as a function of the size of the target perturbation, but there was no significant effect of time of perturbation on precision. Precision was significantly different for each position when



Fig. 9 Precision group data for perturbation amplitudes of 0.5, 4 and 8°. *Error bars* represent one standard error of the mean (symbols sometimes larger than error bars)

the perturbation size was >4. The precision appears to be related to the shifted, second position, as opposed to the true target location. This is probably because on several trials the observer pointed at the wrong location. For example, if the perturbation meant that the final target location was 16° and the observer pointed to the initial target location instead, then the error would be 8° and trials like this would significantly increase the observer's variability at the final target location.

The pattern observed for the late condition suggests that the observer has adopted a strategy that minimizes the loss of accuracy for either position. These data suggest that the observer can code the change in locations, and also take into account the probability that the target will appear in a certain location. Apparently, the visual system is able to code the position of targets across trials, consistent with findings in the saccadic literature (e.g., Maljkovic and Nakayama 1996; McPeek et al. 1999).

Experiment 3

In the late condition, observers seemed to point to the average position of the two locations. In these conditions, there was an equally likely probability that the target would appear at either 8°, or the perturbed location. Since observers were pointing to the midpoint of these two locations, the data suggest that observers are keeping track of the two target positions and hedging their bets. In this experiment, we explicitly tested this prediction by altering the proportion of times that the target appears at one location. If it is the case that observers are able to take into account the proportion of times that a location appears in one position, then they will adjust their "best bet" accordingly and the position pointed to should now shift towards the more probable location.

The conditions were identical to those described in the previous section for the late condition, with a perturbation size of 8° , except that now the target appeared at the perturbed location on 75% of trials. Observers were informed that this was the case before they started.

When the targets are now presented at the two positions in the proportions 75:25, observers now respond at the more likely location on all trials in the late (250 ms) condition (Fig. 10). If observers were able to compensate perfectly for the perturbation of position, then all points should lie on y = x.

These results confirm that people can keep an ongoing register of locations (e.g., Maloney et al. 2005), suggesting that they use prior information about target



Fig. 10 Group data for the 75 and 50% conditions for a late (250 ms) perturbation of target location. Data are mean pointing positions for each target, *error bars* represent 1 standard error of the mean

locations as well as current visual information to update their movements. These strategies are designed to minimize endpoint errors. Our results are also consistent with experiments on saccades, which suggest that observers are able to build up a map of locations over successive trials.

Discussion

In the first experiment, the shutters obscured both the hand and the target for a proportion of the hand movement. We demonstrated that precision decreases if a shutter is closed part of the way into the reach. Precision is worst if the shutter closes 50 ms into the reach, but it is also compromised if the shutter is closed at later times in the reach. It has been argued that a comparison is made between the target position and the hand position during the terminal phase of the movement (e.g., Jeannerod 1988; McIntyre et al. 1998), but this argument is based on conditions where the target was visible until the finger reached the screen, unlike our own. Interestingly, in our conditions, we found that removing visual feedback about the hand trajectory was most marked if the shutter closed 50 ms into the trial. Trials on which the shutters closed 250 ms into the trial resulted in only a 20% reduction in precision. Visual information is used to monitor position throughout the movement, and its absence can significantly affect precision.

Our results clearly show that the observer is using visual feedback about the position of the hand during

the movement to improve endpoint precision. Since the target was only visible for 110 ms, in all but one condition, the shutter closure meant that observers only lost sight of their hand reaching towards a blank screen. It seems that visual feedback about the position of the hand during the trajectory is used to update the position throughout the movement. An estimate of the hand's position is derived from both proprioceptive and visual information about the position of the hand in space. It is known that visual information is more precise than proprioceptive information, and that people are able to weight information from proprioceptive and visual sources depending on the noise associated with each source of information (e.g., Ernst and Banks 2002; Sober and Sabes 2003). Under conditions in which the observer loses sight of their hand during the movement, there would be increased reliance on the proprioceptive information about the hand position in order to make a correction to the planned trajectory. Since proprioceptive information is inherently noisier than visual information, it makes intuitive sense that endpoint precision should therefore suffer. We see this result clearly in Experiment 1. We do not have an exact estimate of the precision of proprioception but given little visual information (shutters close at 50 ms), it looks like proprioceptive guidance of the trajectory is four times as noisy as visual guidance of the trajectory (since the thresholds have doubled).

Our results showed that visual guidance occurs even when the hand disappears-visual feedback is used to guide the hand along the planned trajectory. The results of Experiments 2 and 3 showed that people can respond to a change in target location during a rapid reach. Observers were able to correct their movement if the perturbation occurred early in the reach, but not late in the reach. The amplitude of the perturbation also significantly affected the observer's ability to correct. For the smallest amplitude, 0.5° , the same pattern of results observed with larger amplitudes is evident in the data but failed to reach statistical significance, which makes intuitive sense. If you pause to look at the size of your finger it is evident that a finger pad is about 1° in diameter, indicating that there is perhaps little incentive for the observer to correct their movement and shift to the other location. For a large perturbation, however, there is more incentive for the observer to attempt to correct since the observer would now clearly miss the target.

A response to a perturbation of target location can be constrained by the amount of time it takes to process visual feedback and to initiate a change in hand position in response to that visual feedback. The results of our experiments suggest that this time is probably \sim 150 ms, a value that is compatible with previous estimates of the time needed for visual feedback to update an arm trajectory during a reach (e.g., Saunders and Knill 2003). The results of the late perturbation condition and the third experiment illustrate that the observer also makes decisions about where to shift their hand. Harris and Wolpert (1998) have argued that the brain executes motor commands to minimize the effect of signal dependent noise on motor variance. Noise increases with the size of the control signal, so people move more slowly for larger movements to minimize endpoint variation. It is possible that for a larger amplitude shift, later in the movement, observers are conservative and strategically decide to go for the middle point in order to minimize their endpoint inaccuracy. If the target perturbation occurs late in the reach, too late for observers to use the visual feedback, observers develop a strategy based on the probability of target position as the results of Experiment 3 clearly demonstrate. This last result is evidence that people use prior history about target locations when taking into account the execution of a hand movement, an idea consistent with the priming of pop out effects observed in saccades (Maljkovic and Nakayama 1996; McPeek et al. 1999).

Since our results are consistent with these findings, it also allows the further suggestion that a common visual representation is used for both saccadic eye movements and pointing.

Previous work in the literature has also demonstrated that people are able to make probabilistic estimates of sensory feedback and use information that has been gathered in the past to alter behaviour on the present trial (e.g., Komilis et al. 1993; Kording and Wolpert 2004). Much of this earlier work has focused on the accuracy of the movement and the characteristics of the movement trajectory (e.g., Komilis et al. 1993), and others have provided brief feedback about the finger location but none about the endpoint location or the rest of the environment (e.g., Kording and Wolpert 2004). In our daily lives, we constantly make goal-directed movements, for which the outcome of the movement is important, so important in fact that we might use different strategies depending on how quickly we have to move. There is a well-known tradeoff between speed and accuracy (Fitts law). Our results show that if people have enough time, they use the current visual information to redirect their finger to the target. If they are under time pressure, however, they use a strategy that is based on what they have seen over previous trials. Our results demonstrate that we can actively use visual information throughout the movement to improve our pointing performance.

Our results are also consistent with work indicating that movements are planned in eye-centered co-ordinates (e.g., Batista et al. 1999). Henriques et al. (1998) demonstrated that observers point to targets whose location is coded in an eye-centered framework. In our data for Experiments 2 and 3, it is clear that observers consistently overshoot in the direction of the perturbation. Due to the timing of the perturbation, observers' eyes were not at the final target location when the perturbation occurred but would have landed there by the time the hand movement was completed. If the target location were coded in eye-centered coordinates, one would predict an overshoot in the direction of the perturbation and this is in fact what we observed.

We conclude that observers use visual information throughout a reach to control a movement and improve endpoint precision and accuracy, and not only to provide feedback for the correction of a trajectory in response to a perturbation. Generally speaking, the longer the observers are able to see their hand during the reach, the more precise and accurate the endpoints.

Acknowledgments This work was supported by a Rachel C. Atkinson Fellowship to A.M.W. and NEI EY06644 to S.P.M. The authors thank Preeti Verghese and Laura Renninger for valuable discussions, and Doug Taylor for valuable assistance with shutter wrangling.

References

- Batista AP, Buneo CA, Snyder LH, Andersen RA (1999) Reach plans in eye-centered coordinates. Science 285(5425):257– 260
- Bedard P, Proteau L (2004) On-line vs. off-line utilization of peripheral visual afferent information to ensure spatial accuracy of goal-directed movements. Exp Brain Res 158(1):75– 85
- Brainard DH (1997) The psychophysics toolbox. Spat Vis 10:433– 436
- Connolly JD Goodale MA (1999) The role of visual feedback of hand position in the control of manual prehension. Exp Brain Res 125(3):281–286
- Ernst MO, Banks MS (2002) Humans integrate visual and haptic information in a statistically optimal fashion. Nature 415(6870):429–433
- Harris CM, Wolpert DM (1998) Signal-dependent noise determines motor planning. Nature 394(6695):780-784
- Henriques DY, Klier EM, Smith MA, Lowy D, Crawford JD (1998) Gaze-centered remapping of remembered visual space in an open-loop pointing task. J Neurosci 18(4):1583– 1594
- Jeannerod M (1988) The neural and behavioural organization of goal-directed hand movements. Clarendon Press, Oxford
- Keele SW, Posner MI (1968) Processing of visual feedback in rapid movements. J Exp Psychol 77(1):155–158

- Kitazawa S, Kohno T, Uka T (1995) Effects of delayed visual information on the rate and amount of prism adaptation in the human. J Neurosci 15(11):7644–7652
- Komilis E, Pelisson D, Prablanc C (1993) Error processing in pointing at randomly feedback-induced double-step stimuli. J Motor Behav 25(4):299–308
- Kording KP, Wolpert D (2004) Bayesian integration in sensorimotor learning. Nature 427:244–247
- Maljkovic V, Nakayama K (1996) Priming of pop-out: II. The role of position. Percept Psychophys 58(7):977–991
- Maloney L, Dal Martello MF, Sahm C, Spillmann L (2005) Past trials influence perception of ambiguous motion quartets through pattern completion. Proc Natl Acad Sci USA 102(8):3164–3169
- Ma-Wyatt A, McKee SP (2006) Initial visual information determines endpoint precision for rapid pointing. Vision Res (in press)
- McIntyre J, Stratta F, Lacquaniti F (1998) Short-term memory for reaching to visual targets: psychophysical evidence for bodycentered reference frames. J Neurosci 18(20):8423–8435
- McPeek RM, Maljkovic V, Nakayama K (1999) Saccades require focal attention and are facilitated by a short-term memory system. Vis Res 39(8):1555–1566
- Paillard J (1996) Fast and slow feedback loops for the visual correction of spatial errors in a pointing task: a reappraisal. Can J Physiol Pharmacol 74:401–417
- Pelli DG (1997) The VideoToolbox software for visual psychophysics: transforming numbers into movies. Spat Vis 10:437– 442
- Rossetti Y, Stelmach G, Desmurget M, Prablanc C, Jeannerod M (1994) The effect of viewing the static hand prior to movement onset on pointing kinematics and variability. Exp Brain Res 101(2):323–330
- Saunders JA, Knill DC (2003) Humans use continuous visual feedback from the hand to control fast reaching movements. Exp Brain Res 152(3):341–352
- Saunders JA, Knill DC (2004) Visual feedback control of hand movements. J Neurosci 24(13):3223–3234
- Sheth BR, Shimojo S (2002) How the lack of visuomotor feedback affects even the earl stages of goal-directed pointing movements. Exp Brain Res 143:181–190
- Sober SJ, Sabes PN (2003) Multisensory integration during motor planning. J Neurosci 23(18):6982–6992
- Sober SJ, Sabes PN (2005) Flexible strategies for sensory integration during motor planning. Nat Neurosci 8(4):490–497
- Trommershauser J, Maloney LT, Landy MS (2003) Statistical decision theory and the selection of rapid, goal-directed movements. J Opt Soc Am Image Sci Vis 20(7):1419–1433
- van Beers RJ, Baraduc P, Wolpert DM (2002) Role of uncertainty in sensorimotor control. Philos Trans R Soc Lond B Biol Sci 357(1424):1137–1145
- White JM, Levi DM, Aitsebaomo AP (1992) Spatial localization without visual references. Vision Res 32(3):513–526
- White JM, Sparks DL, Stanford TR (1994) Saccades to remembered target locations: an analysis of systematic and variable errors. Vision Res 34(1):79–92
- Whitney D, Westwood DA, Goodale MA (2003) The influence of visual motion on fast reaching movements to a stationary object. Nature 423:869–873
- Wolpert DM, Ghahramani Z, Jordan MI (1995) An internal model for sensorimotor integration. Science 269(5232):1880– 1882