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RESEARCH ARTICLE

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How the lack of visuomotor feedback affects even the early stages of goal-directed pointing movements

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Abstract Pointing movements made with a hidden cursor from the center of gaze to a stationary, visible target overshot the actual target location. The systematic error decreased when the final cursor location from the previous trial was shown, which likely led to the creation of an internal sensorimotor model of movement. However, the putative model had a short memory, and could not substitute for on-line visuomotor feedback on subsequent trials. Contrary to common belief, the effect of a lack of visuomotor feedback was seen even in the early acceleration stage of the movement trajectory. Unchecked in the absence of visual monitoring, the acceleration stage of the movement lasted longer, as was evidenced by the significantly larger value of the peak cursor speed. Moreover, the speed peaked much later in the course of the movement. Speed declined more rapidly thereafter. Consequently, the delayed deceleration stage lasted far less than the acceleration stage. In the absence of visual feedback, the shift rightward in time of the peak speed position (PSP) in relation to total movement duration and other changes in the trajectory imply that visual feedback must play a significant role in determining when acceleration ceases ($\mathrm{d}V/\mathrm{d}t=0$), and argue against the traditional notion that visuomotor feedback is unavailable until the later stages of movement. Moreover, our data suggest that non-visual modalities, e.g., proprioception, may be too slow to make up for the absence of vision.

Keywords Sensorimotor transformation · Localization · Dynamics · Proprioception · Forward model

We (Sheth and Shimojo 2001) and others (Musseler et al. 1999; Mateeff and Gourevich 1983) have shown that pointing movements to a briefly flashed target displayed prior to motor response are mislocalized closer to the center of gaze. Furthermore, we found that the magnitude of the effect was enhanced as the time interval between target presentation and motor response was increased (Sheth and Shimojo 2001). Even on perceptual judgment tasks that did not entail any pointing movements at all, the distance of the target from the center of gaze was consistently underestimated. These data led us to conclude that the distance of the target from the center of gaze (also distance from non-fixated but otherwise salient, rigid, temporally stable landmarks in the visual field) was being compressed while being stored in visuospatial memory. In this series of experiments, the target was hidden from view and the cursor was in view while the movement was being executed, which led us to ask the following question: Will the results be any different if the pointer is rendered invisible, but the target remains in view during the movement? As will be seen, we found that pointing judgments consistently overshot the target, unlike in Sheth and Shimojo (2001), in which localizations systematically undershot the actual target location. In exploring the cause of the discrepancy, we will address the following issues. First, can visual feedback shape movement – even in the initial, allegedly feedforward stage? Second, what role does a visible goal versus a visible pointer play in localization? Third, how effective and accurate are non-visual information (e.g., proprioceptive sources, motor outflow models) and offline visual information in the execution of accurate pointing movements when continuous, online visual feedback is not available?

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Materials and methods

Prior approval for the present work was obtained from the Committee for the Protection of Human Subjects at Caltech. All stimuli were presented on a Sony Trinitron monitor (75 Hz refresh rate; 37.5×28.5 cm) under control of a Mac Power PC running Matlab (Mathworks Inc.) and Psychophysics Toolbox (Brainard 1997; Pelli 1997). Six naive participants with normal or corrected-to-normal vision gave informed consent to participate. Participants sat in a dark room and the screen background was dark in all experiments. Targets were located at the horizontal meridian, nearly half a screen away from the upper and lower edges. The viewing distance was 57 cm with the head immobilized by a chin- and headrest (1 cm on the screen = 1° of visual angle). Viewing was binocular. The mouse pad was placed horizontally on the desk in front of the observer at a distance of about 25 cm from the screen about halfway between the observer and the screen. In our experiments, the mouse sampling rate was a constant 770 Hz, i.e., mouse coordinates were sampled once every 1.3 ms. The computer can reliably register a cursor movement as small as 1.8 arcmin (0.3 mm) on the screen.

No feedback task (NoFeed)

The observer centered his/her gaze on a 8-arcmin-diameter fixation point (FP) in the center of the screen at the outset of each trial and maintained gaze throughout the remainder of the trial. A circular, stationary target (40 arcmin diameter) was turned on at a random location along the horizontal meridian on the screen. The range of target locations was (0±12.5°) and could be specified with a resolution as low as 2 arcmin. The target was bright (53.3 cd/m^2) on a dark background (<0.01 cd/m^2). A 1-cm physical displacement of the mouse caused a corresponding cursor displacement on the screen of 3.0° (or 3 cm; gain = 3.0). Shortly after (30 ms) the appearance of the target, a mouse cursor appeared above the FP (‘+’ in Fig. 1A). Another 20 ms later (and before the observer could move the mouse), it disappeared. The observer then had to point and click the invisible mouse cursor on the location of the clearly visible target. At the beginning of the experiment, the observer was given 35 practise trials in which both target and cursor were visible throughout. In the experimental phase, the observer ran 100 trials in which the cursor was invisible both during the response and after the mousebutton press. There was an intertrial interval of 2 s which gave the observer enough time to place the mouse back to the “home” position on the mousepad.

Pre-experimental feedback task (Feed)

In this task, the test trials followed the same experimental design as in the previous task with one important difference: Just after the practise trials but prior to the test trials, there were 25 feedback trials, in which the cursor was displayed at its last position *only* (observer’s estimated target location) along with the target at the end of each feedback trial. Cursor and target were shown simultaneously for a period of 400 ms. The observer could compare estimated and true target positions, and thereby calibrate his/her pointing movements on subsequent test trials. Feedback (non-test) trials were excluded from analysis.

Test feedback task (AllFeed)

In this task, the terminal mouse cursor position was displayed at the end of each test trial, along with the target. Thus, offline feedback was provided throughout the session. Other experimental parameters were identical to the experiment above (Feed).

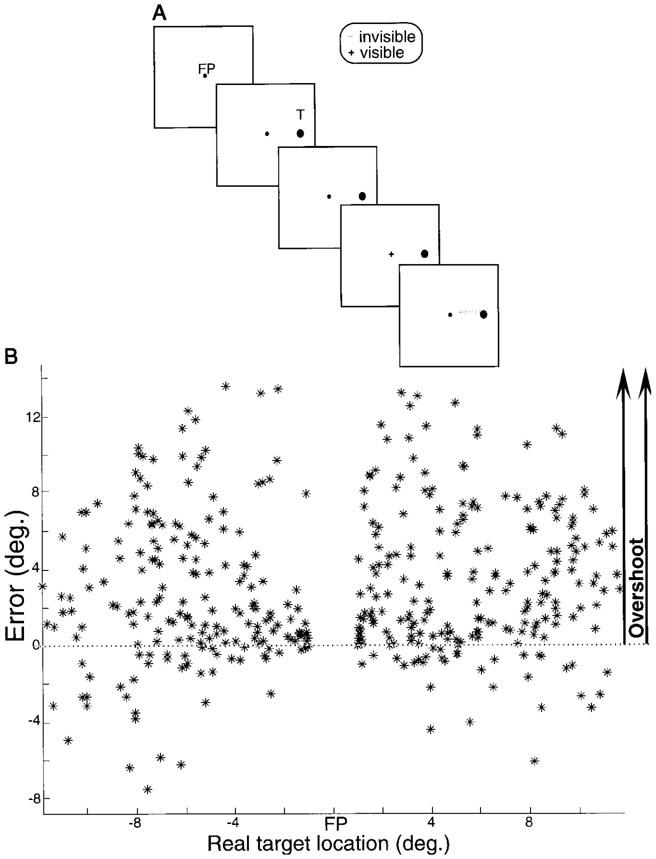

Fig. 1A, B Overshoot in pointing estimates. **A** The fixation dot (*FP*) appeared at screen center at the outset of each trial. A target (‘*T*’) was displayed at a location along the horizontal plane, its horizontal eccentricity randomly chosen from a uniform probability distribution about the FP. The target remained on until the end of response. Shortly after, a mouse cursor (*black* ‘+’) appeared in the location occupied by the fixation dot, and disappeared immediately after. The observer dragged the invisible cursor to the target position (*gray* ‘+’s) and clicked on the mouse button, indicating the termination of the trial. **B** Data from all (*n*=5) subjects are shown. *Each asterisk* represents a single trial. Trials (‘*’) are sorted according to the horizontal eccentricity of the target. Error is the difference of final mouse cursor eccentricity and target eccentricity. Positive values of error represent a centrifugal bias – a displacement away from the FP. Note the lack of a clear correlation between target eccentricity and error magnitude

Results

Overshoot in pointing movements

First, we studied the pattern of error in observers’ localization of target position when no visual information about cursor position was provided on test trials (Fig. 1A, see “Materials and methods”: NoFeed). As shown in Fig. 1B (five naive subjects), a predominant number of trials were above the no-error dotted line (group mean probability = 0.84), signifying an overshoot. Thus, endpoints of the pointing movements were displaced farther from the fovea than the actual target positions (termed a centrifugal bias, or hypermetria). We also measured the magnitude of overshoot by computing the error – the difference between the target location and the observer's terminal cursor position. Positive values of error indicate overshoot. The group mean error was +4.1° and it was significantly different from zero ($P<0.001$, *t*-test).[1] The group root mean square error (RMS error), which is a measure of accuracy regardless of direction, was 4.5°.

Transient usefulness of offline visual feedback (final cursor position only)

In all the paradigms described above, visual feedback was never furnished online. Only after the observer completed the movement and clicked the mousebutton on a given trial was the screen cursor at the moment of the buttonclick (the observer's estimate of target location) displayed. Thus, we could study the significance of visual information. Also, by assaying the limits of offline visual feedback, we could indirectly obtain an idea of the additional import, if any, of online visual feedback. Over the range of experiments (results described below), the frequency of offline visual feedback was progressively enhanced to gain a more nuanced understanding of both its capacity and its limitations.

Unlike the previous experiment in which the final cursor position was never shown after any trial – practise or test – in a new experiment (Feed, see "Materials and methods"), the final cursor position along with the target was displayed after every training trial (but not on test trials). Overshoot magnitude (group mean error = +3.8°, $P<0.001$, *t*-test), overshoot frequency (group mean probability = 0.81, same five subjects as in the previous task), and localization accuracy (mean RMS error = 4.3°) did not seem to be affected significantly ($P>0.15$, two-tailed unpaired *t*-tests comparing error and RMS errors individually; Fig. 2A) compared to the previous task (NoFeed) in which no feedback was provided at all.

Nonetheless, the presentation of the screen cursor at its final position was not useless. The effects of providing this sparse piece of visual information at the end of each training trial led to a noticeable improvement in localization in the test phase, but the improvement was transient. As Fig. 2B shows, the error was close to zero in the initial test trials, but grew linearly with test trial number [$F_{1,98}=99.67$, $P<0.001$, linear regression coefficient of determination (r^2)=0.50]. Since the final cursor position was not shown on any of the test trials, it seems that the internal model developed during the training stage associating hand movement with screen cursor movement must have gradually faded. Presumably, the internal memory or model that likely combined proprioceptive information with the single bit of visual knowledge regarding final cursor position was not consolidated.

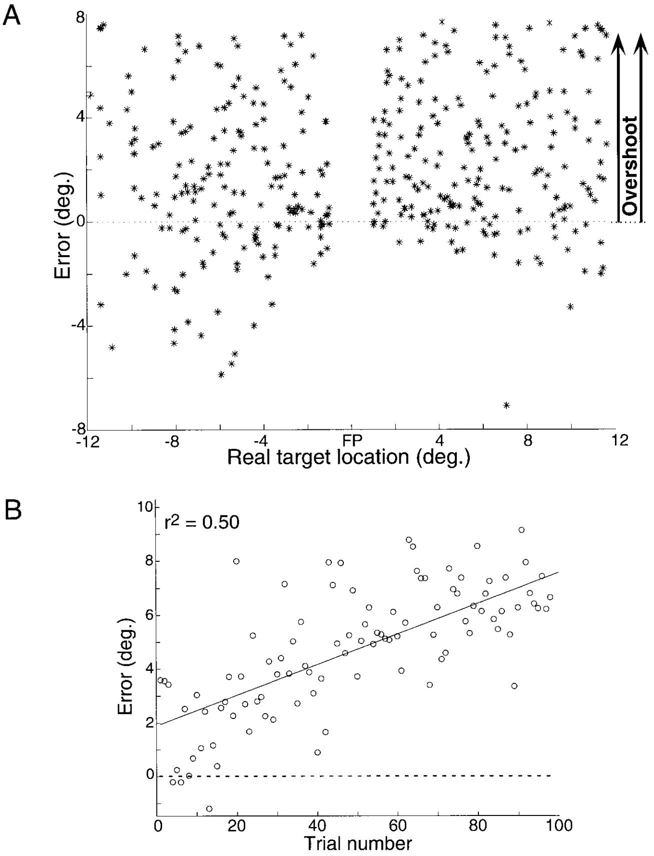

Fig. 2A, B Errors when terminal cursor position on the screen was shown on practise trials only, and the transient effects of offline visual information. Final cursor location was shown at the end of all practise trials but was not shown after completing a test trial. **A** Error on test trials in feedback task (Feed). All data (five naive subjects) are shown. Positive errors indicate hypermetria. **B** Error plotted as a function of trial number following the conclusion of practise trials with feedback. Each point ('*o*') is the mean of five subjects. *The line* represents the optimal linear fit in the least squares sense

To further reduce the error, in a new experiment (AllFeed, see "Materials and methods"), we increased the availability of offline feedback to a maximum – the cursor was displayed at its terminal position after every test trial (see "Materials and methods"). Based on our interpretation of the data shown in Fig. 2B, we expect that the visual presentation of the cursor at the end of the trial should improve localization on trials immediately succeeding it. Despite its transitory nature, memory of past final cursor position should still be effective, and the error should remain small since the cursor is displayed after every trial. This experiment tested our prediction. As evidenced by the comparably smaller fraction of trials (0.59) in which the movement overshot the target and the overall lower magnitude (group mean error = +0.2°) of the overshoot, the size of the overshoot was reduced con-

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[1] On a few trials when the target displacement was 2°, the errors were unusually large (>6°); these large overshoots mostly occurred in the beginning of the task when participants were not fully familiarized with the mouse and the gain. In subsequent tasks (see below), we displayed the final cursor position at the end of the trial for recalibration, and this procedure reduced considerably these large overshoots.

siderably ($0.1>P>0.05$, *t*-test) than before. Localization accuracy improved (mean RMS error = 2.4°) as well. Thus, the data were consistent with our prediction.

Power and weakness of internal models

Certainly, displaying the cursor at the end of a trial cannot improve localization on the trial per se but may on subsequent trials. The only way this information can be used is in providing information about limb and cursor dynamics to the programming of future movements (Ghez et al. 1995). The data above (Fig. 2B) show that such internal models are transient and must be refreshed from time to time.

Previously, Ghez et al. (1995) showed the entire cursor path following each trial. Here, only the final cursor location was displayed. Yet, we found significant improvements in localization, demonstrating that the final position is sufficient to recover the gain factor. Thus, our data also demonstrate the power of internal models in being able to utilize even the scarcest of information.

To sum up, observers were able to make use of offline visual information to improve accuracy and reduce overshoot magnitude to some extent. On the other hand, the incomplete level of success obtained with offline visual feedback bespeaks of the significance of continuous, online visual feedback in accurate localization.

Lack of online visuomotor feedback

The overshooting bias was opposite that found in Sheth and Shimojo (2001); hence, the mechanism must likely be different too. For this reason, accounts based on visual memory or visual perception, as proposed in Sheth and Shimojo (2001), are less likely. The high gain may have contributed to the overshooting bias in the first place, but having the cursor in view throughout the movement should have eliminated it. Therefore, how does a lack of dynamic visuomotor feedback control affect pointing movements? In order to study more carefully how the movement was affected by a lack of visual feedback, paths (position profiles) and trajectories (speed profiles) in the following conditions were compared: (a) invisible cursor and visible target – the conditions of the present study, (b) visible cursor, invisible target – the conditions of the previous study and (c) visible cursor and visible target – the baseline. All positions intermediate between the starting and terminal positions of the path were stored. Instantaneous speed was calculated by comparing the current pointer location with pointer locations at past time points (see “Materials and methods” for details).

Forward models

It is claimed that the initial part of a reaching movement is based on the generation of motor commands based a priori on the desired action and on an internal, feedforward model of the motor response (Shadmehr and Mussa-Ivaldi 1994). Feedback control comes into play later in the course of the movement to facilitate ‘mid-flight’ corrections of these commands based on errors detected during their execution (Bhushan and Shadmehr 1999). Although the motor plan, i.e., amplitude and direction of movement required in the present experiments, may vary, a few of its properties remain invariant under baseline conditions in which both the goal and effector remain in sight throughout. For instance, regardless of amplitude, direction or speed, the speed profile of reaching arm movements generally has a single peak, usually close to the midway point of the path (Atkeson and Hollerbach 1985). It is generally believed that, prior to the speed maximum, the acceleration stage of the movement is undertaken on the basis of an internal model (Jordan and Rumelhart 1992), with feedback control playing a role in the deceleration stage only.

Predictions about trajectories in the absence of visuomotor feedback

Indeed, the trajectories should be markedly different depending on when visuomotor feedback is required and when it is available. The shape of a trajectory is selected to minimize the variance of the final arm or cursor position (Harris and Wolpert 1998) in a fixed amount of time in the presence of signal-dependent noise. Thus, there is a time accuracy trade-off in arm movement. The classic speed profile that provides an optimal solution (in the least squares sense) in the case where goal and effector remain in sight throughout, is highly symmetrical about the midpoint of the movement (Fig. 3, dashed black bell-curve). An intuitive way proposed by one of us (Sheth, in preparation) of understanding this solution is to imagine that the cost function is dynamic with a greater emphasis on minimizing time in the early phase of the movement, and an increasingly greater weight placed on accuracy towards the later stages as the relative distance between effector and goal becomes increasingly important. With this in mind, the optimal solution is to gradually accelerate till the midway point of the movement, and then gently decelerate in order to carefully land at the end-point.

When the effector is hidden from view right from the inception of movement, the remaining distance between the moving effector and the stationary goal cannot be seen. We predict that visual feedback is important even in the early acceleration stage in determining the transition point from acceleration to deceleration, and making the gradual switch from minimizing time to maximizing accuracy. As a result, the acceleration phase should last longer and the maximum speed magnitude should be larger (Fig. 3, tall black curve). Once it is sensed that the arm has been diplaced a much larger distance than normal, or that the movement has lasted for too long, delayed non-visual, kinesthetic sensors will signal the mo-

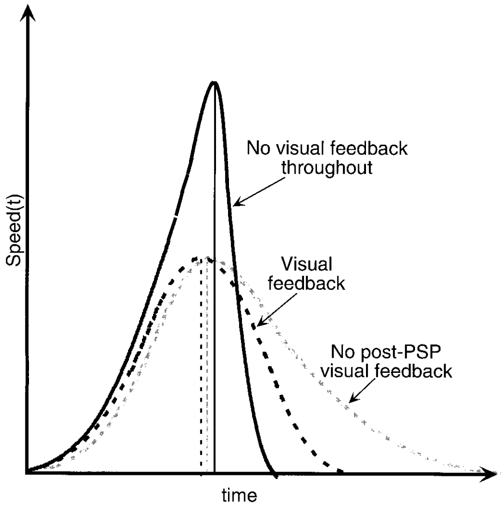

Fig. 3 Predicted characteristics of trajectories with and without continuous visuomotor feedback. If visuomotor feedback (*short dashed black curve*) is continually available, the speed should peak midway in the course of the movement (*dashed vertical line*). If visuomotor feedback is not provided at all during the movement (*tall black curve*), the PSP (*black vertical line*) should occur later in the movement, and the peak speed should be of larger magnitude. If visuomotor feedback is not provided during the deceleration phase only (but is present during the acceleration stage; *gray curve*), the deceleration should slow down, and the PSP (*gray vertical line*) should occur earlier relative to the total duration of the movement

tor controller to reduce stimulation to the arm muscles. Consequently, the arm speed should dip rapidly soon after it reaches maximum magnitude. Therefore, the curve should be skewed to the left in time, with the peak speed position (PSP) accordingly occurring later relative to the duration of movement. One may also conceive of a *Gedanken* experiment in which the availability of vision relative to movement duration is flipped: If the arm were to abruptly disappear from view at the start of the deceleration stage, the curve should be skewed rightward in time (Fig. 3; gray curve); the acceleration stage should be identical to baseline, but the decline in speed should be slower owing to the delayed shift in emphasis from time to accuracy.

Experimental data confirming predictions

To test our predictions, we compared trajectories under different conditions – one with (condition c) and two without visuomotor feedback (conditions a and b). The set of target positions was the same in all three conditions, but the order was randomized. Figure 4A shows four typical paths per condition for a naive observer (C.S.).[2] As expected, pointing judgments were hypermetric when the cursor was not visible (a), but hypometric when the target was not (b). Again as expected, the PSP (arrows) in the invisible cursor case (a) was, on average, further out in the movement than in the remaining two conditions. Figure 4B is a frequency histogram of maximum cursor speed under each of the three conditions [black (a), gray (b), and white (c)] for observer CS. As predicted on the basis of our hypothesis, peak speeds were generally larger when the cursor was concealed from sight. As assessed by a chi-square test, the peak speed frequency distributions in the invisible cursor condition (a) and baseline (c) were significantly different (a vs c: $\chi_9^2=172.0$, $P<0.001$), whereas the distribution in the invisible target condition (b) was not significantly different from baseline (b vs c: $\chi_9^2=12.6$, $P>0.05$). The larger peak speed values in (a) were not entirely the result of larger movement amplitudes. We compared the peak speed values for the subset of trials that were within the same range of movement amplitude for conditions (a) and (c) (Fig. 4C, left), and conditions (b) and (c) (Fig. 4C, right) separately. Movement amplitudes were not significantly different between either of the two condition pairs ($P>0.4$ for both, unpaired *t*-test). However, as Fig. 4C shows, the trajectories in (a) reached greater peak speed values (mean = 5.5 m/s) than in (c) (mean = 3.1 m/s; $P<0.001$), whereas the distributions of speed maxima on (b) (mean = 2.3 m/s) versus (c) (mean = 3.1 m/s) for movements of similar amplitude were not significantly different ($P>0.05$).

Representative trajectories in each condition are shown in Fig. 5A. The peak in cursor speed in the primary movement occurred later in the movement in (a) as compared with either (b) or (c). Frequency distributions of peak speed positions in the three conditions are given in Fig. 5B.[3] As anticipated, the peak speed position occurred later in the movement, closer to the end of the movement in (a). The distribution was significantly different from baseline (a vs c: $\chi_6^2=331.3$, $P<0.001$[4]) as well as from the invisible target condition distribution (a vs b: $\chi_6^2=330.9$, $P<0.001$). Data from another naive observer (U.Z.; not shown) also showed a similar and significant distinction between the three conditions: speed peaked later in the movement in (a) than in either (b) or (c) (a vs c: $\chi_4^2=311.5$, $P<0.001$; a vs b: $\chi_4^2=285.3$, $P<0.001$).

Finally, the data regarding the delayed PSP in (a) were not dependent on the gain. Another observer (R.K.), also naive as to the purposes of the task, ran on the same three conditions but with the mouse gain fixed at 1.0 (much lower than is common in daily experience; technical limitations did not permit gains below 1.0).[5] The mean PSP, as a fraction of the total movement dura-

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[2] We obtained qualitatively similar results in two other subjects.

[3] The occurrence of the peak speed in time (PSP) was normalized so as to lie within [0,1]: PSP = Timing of peak speed occurrence relative to movement initiation/Total movement duration.

[4] Since the seventh and ninth bins were empty, we merged the data in bins 7–9 for chi-square statistics (see Zar 1999, p. 470). We employed the same strategy in the comparison between (b) and (c) below.

[5] The centrifugal bias (four observers) was grossly reduced (+0.3°) and was marginally significant ($P=0.03$, *t*-test). In any case, the skewed left trajectory profile remained intact even at the low gain.

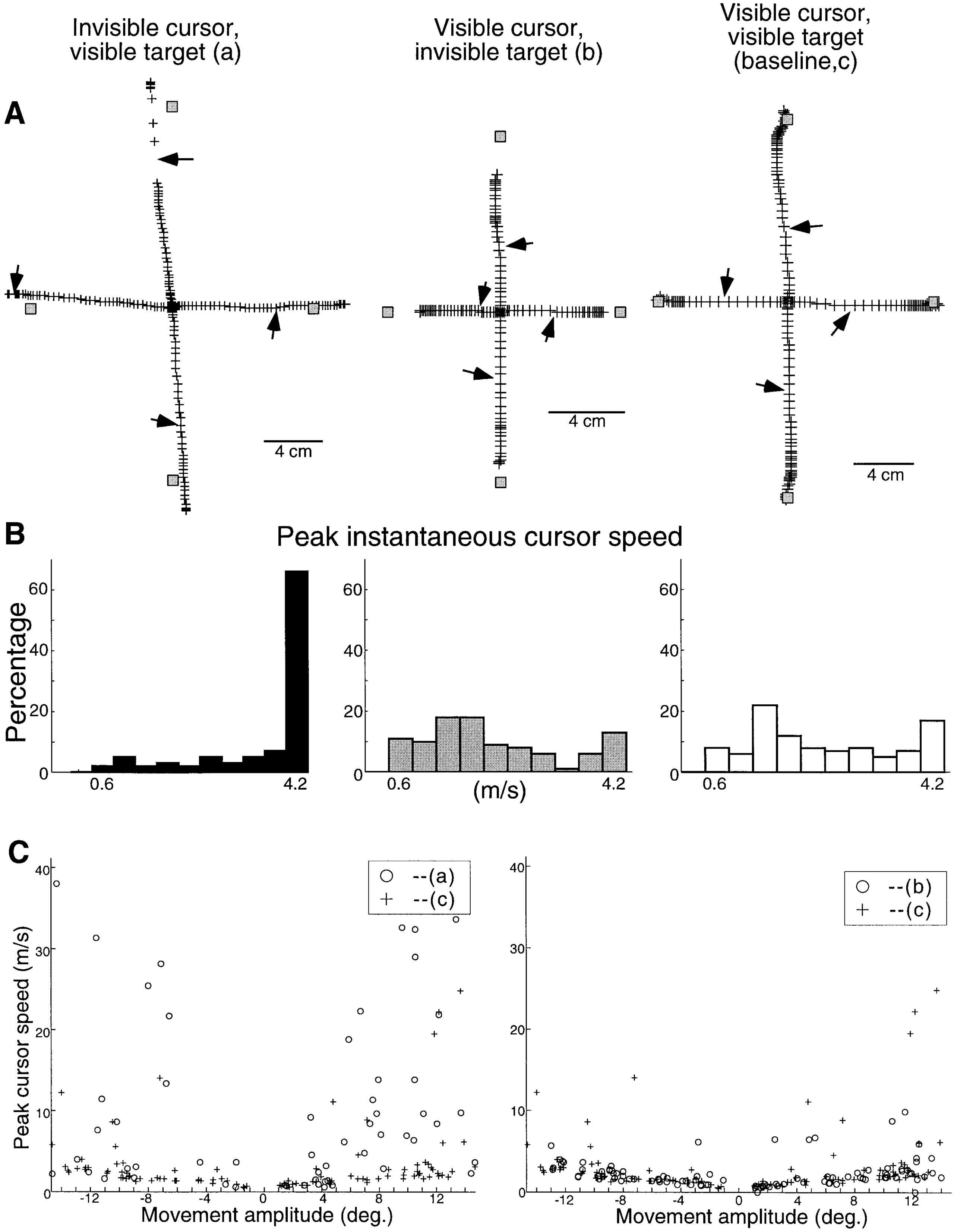

Fig. 4A–C Representative cursor paths and characteristics of peak speed values under three different experimental conditions for observer CS. **A** Four sample paths for each condition are shown. *Gray squares* represent the target location. *Arrows* mark the location of the speed maxima. For illustrative purposes, two of the four paths have been rotated by 90° and appear vertical. Cursor position was sampled every 1.3 ms (770 Hz). **B** Frequency histograms of peak speed values. Bin width is 0.4 m/s. *The leftmost bin* is the percentage of trials in which peak speed was within the range 0.4–0.79 m/s. **C** Comparison of peak cursor speed values (*ordinate*) for movements of similar amplitude (*abscissa*) in conditions (a) and (c) *on the left* and conditions (b) and (c) *on the right*

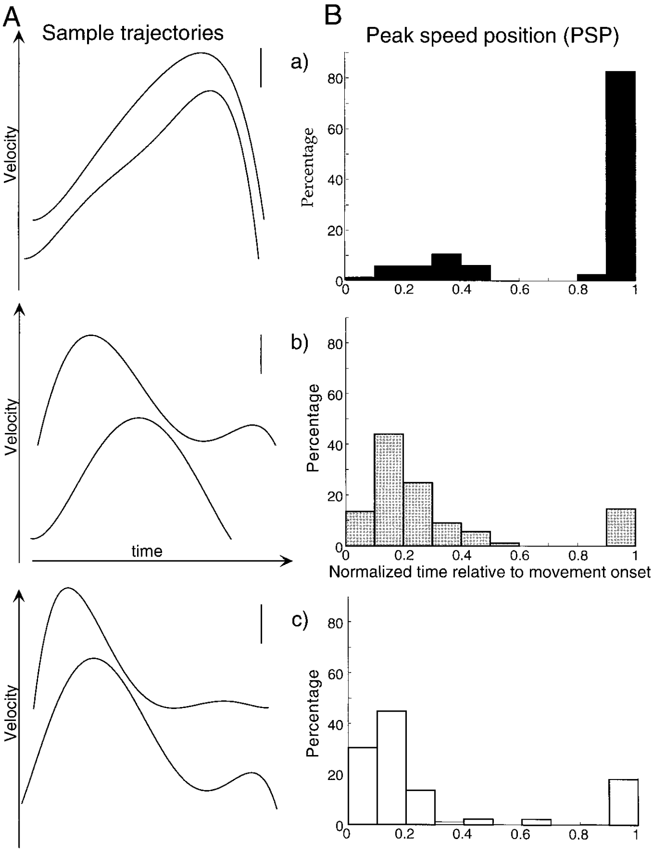

Fig. 5A, B Representative trajectories (all data fitted by a least squares best-fit fifth-order polynomial for illustrative purposes) and occurrence of peak speed (PSP) during the movement (CS). Data from conditions (a), (b) and (c) are shown *in the top, middle and bottom panels* respectively. **A** Two sample trajectories in each condition are shown. The duration of each trajectory (*abscissa*) is normalized. *From the top, the ordinate scale bar* represents 1.17 m/s, 1.18 m/s, 1.18 m/s, 0.59 m/s, 1.76 m/s and 0.64 m/s respectively. Note the PSPs in each condition. **B** Frequency histogram of the occurrence of the speed peak (PSP) with respect to movement duration [range (0,1); *0* movement onset, *1* total movement duration]. Bin width is 0.1. *The leftmost bin* is a count of trials for which the speed peaked in the initial 10% of the movement's duration

tion, was 0.88 in (a), 0.56 in (b), and 0.51 in (c). Thus, the PSP occurred much later in the movement when the cursor was hidden from sight. As before, the distributions were significantly different (a vs c: $\chi_6^2=134.7$, $P<0.001$; a vs b: $\chi_6^2=82.3$, $P<0.001$).

To summarize, the lack of dynamic, online visuomotor feedback had a powerful effect on fundamental properties of the movement, such as the location of the speed maximum and the overall shape of the trajectory.

Discussion

In the present study, it was shown that when the pointer was rendered invisible for the duration of the motor response, fundamental properties of movements were affected. Movement accelerated for longer times resulting in larger peak speeds, delayed PSPs, and shorter and more rapid decelerations than when the cursor was in sight and visual feedback was available. The displacement of the PSP in the trajectory to a later time in the movement and the skewed-left shape of the speed profile in the absence of visual feedback provide support for the view that even in the early stages of movement, visual feedback, when available, is used and plays a role in determining the transition point from acceleration to deceleration.

We showed that forward models based on some combination of offline visual information and non-visual information could substitute for vision with some accuracy, but were transient and had to be refreshed and re-updated on a regular basis. Furthermore, the rightward skew in trajectory profiles in the absence of vision seemed to suggest that proprioception acts late to curtail the movement, supporting earlier claims about the slowness of proprioception (Dassonville 1995).

Finally, we showed that turning off the pointer versus turning off the target had starkly different results. Here, the conditions were mirror-symmetrical to those of Sheth and Shimojo (2001), and movements overshot the target; in the previous study, responses undershot. As discussed earlier, the contrast occurs because systematic biases occur in visuospatial memory, leading to an undershoot in the former condition, whereas the absence of on-line visual feedback is responsible for the overshoot in the present study.

Dependence of the present findings on the usage of a computer mouse

The task has an important difference from "normal" movements in that a computer mouse is used. Normally, the target location seen by the eye and that "seen" by the hand are the same. Here, the eye looks directly at the screen while the hand rests on a mousepad. However, it is generally believed that it is easy to adapt to this particular visuomotor transformation (Goodbody and Wolpert 1999). Others have successfully designed experiments in the past in which visual feedback was provided on a vertical monitor remote from a horizontal workspace to guide reaching (Gordon et al. 1995; Ghez et al. 1995). Tentatively therefore, our results might be generalizable to arm movements in general.

It is notable that in the absence of visual feedback, the sequence of transformations required between the visual coordinates of the target and the motor coordinates to move the mouse is quite complex. The observer must learn to map the displacement of the hand to the displacement of the mouse on the mousepad, and also must learn the gain factor *G* between the mouse on the pad and the cursor on the screen. If visual feedback is continuously available (both target and effector are visible), the subject can simply update the motor plan based solely on the visual percept of the actual cursor displacement on the screen, and not have to learn any intermediate mappings. Hence, the reliance on visual feedback in the mouse task is normally quite substantial.

As for "natural" arm movements (which do not use a mouse), years of practise have taught adults to judge the distance the hand has been displaced from non-visual information only. No intermediate mappings or gains need to be learnt. In turn, this reduces the role of visual feedback in natural arm movements. Therefore, the present findings showing overshoot in cursor displacement in the absence of visual feedback may be unique to the use of a mouse. Additional experiments with more natural movement tasks, such as those involving a finger and touch screen, will determine the generalizability of our findings. It is comforting to note that Bock (1986, 1993) too has observed an overshoot in pointing movements using an invisible finger as pointer. In van Beers et al. (1996) also, hand movements overshot the target position (see Fig. 1 of their paper)[6] Therefore, our data are at least qualitatively congruent with studies based on natural arm movements. At the very least, the present results – displaced PSPs, asymmetric trajectory profiles – should generalize to other conditions in which visual feedback is necessary for accurate performance, but not available (or if available, is unreliable). Examples include unrehearsed movements demanding moderately high accuracy, the early learning stages of prism adaptation, arm movements in the dark in the presence of a force field, and so on.

Is visual feedback too slow?

Forward models of limb dynamics (Jordan and Rumelhart 1992; Wolpert et al. 1995; Flanagan and Wing 1997) were proposed because the visual system was considered to be too slow to provide feedback regarding effector location (Lee and Tatton 1975; Johansson and Westling 1984; Cordo et al. 1994; Blakemore et al. 1998). A forward model presumably gets around the problem of delays in the transmission of afferent information by building a prior prediction of the sensory consequences of a motor command. On a related note, forward models are useful in order to maintain stability in the presence of large feedback delays in sensorimotor loops (Wolpert 1997) – a theoretical concern raised on the basis of control systems theory.

Is visual feedback about current effector location really so slow as to be useless? A substantial amount of time elapses between the presentation of a target and the initiation of a movement (about 100 ms or so) – longer than the synaptic delays in conveying visual information from the periphery to the cortex. Therefore, we believe that the target and the effector are accessible to vision even before the movement is initiated under normal conditions. Moreover, the delay in perceiving the object at the new location is not constant. It is diminished, which alleviates concern for stability. More recent studies on visual motion perception have demonstrated that a moving object is perceived spatially ahead of a similar but stationary object physically aligned with it (Nijhawan 1994; Sheth et al. 2000). Via lateral connections in the retina (Berry et al. 1999) and cortex, neural activity caused by a moving object, such as a continuously moving arm or cursor, can spread to sites that map onto later positions of the trajectory. This facilitates a quicker detection of subsequent positions in the path as compared with "from scratch." Thus, online visuomotor feedback may be available from early on in the movement. In fact, studies claiming internal models are required have been based largely on experiments in which the limb or cursor was not visible during the movement (e.g., Wolpert et al. 1995). Indeed, the findings on visual perception beg the question: What good are forward models of motor control?

Importance of forward models

Forward models do exist and are necessary. It is highly plausible that, having made countless movements, adults have formed, at the very least, an associative memory of motor commands and actual movements[7], a memory resource than can be tapped for several purposes. Originally, forward models were conceived of on theoretical grounds and, in addition to the putative uses above, have been claimed to be useful in motor learning (Jordan and Rumelhart 1992), and in anticipating and canceling the sensory effects of a given movement (Wolpert 1997). In the present study itself, the results from the experiments on offline visual information – in which online visual feedback was not available, and a cursor with a high displacement gain was used – can be explained easily by the existence of an internal estimator of cursor position and speed given a particular motor command. Indeed, forward models are an ideal fallback for situations in which vision is not available.[8]

Does proprioceptive information underestimate movement amplitudes?

In the absence of online visual feedback, the current location of the pointer must be estimated on the basis of

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[6] In Wolpert et al. (1995), subjects had to keep moving a hand in the dark until they heard a tone. Unlike the other studies cited here in which the effector position was underestimated, their study found an overestimation of the distance moved. However, no target was present. Therefore, the movements were not goal directed in their study, and the results are not comparable with data on goal-directed movements from other studies (including ours).

[7] Forward and inverse models are subsumed under this notion.

[8] We wish to draw attention to the distinction between our point that visual feedback is available even in the early stages of the movement, and whether or not it is used. In typical laboratory situations, in which observers must repeatedly make movements to the same set of target locations within certain time constraints and moderate limits on accuracy, forward models come in handy, and are likely to be relied upon more than visual feedback.

proprioception. Proprioception could be inadequate either because it is too slow, or because it is just not as accurate as vision. According to the former (delay hypothesis), proprioception is accurate about past effector position, but too slow to provide current effector position (Dassonville 1995). This delay, in turn, could cause underestimates in effector position to accumulate. The data above (see Fig. 5) fit in nicely with the idea that proprioception is slow in tracking position and monitoring speed: Only when speeds go beyond some threshold (hence higher peak speeds in a), or the hand moves beyond some comfort zone (hence larger movement amplitudes in a), does proprioception "kick in" to stop the movement from running away leading to the delayed and rapid deceleration stage shown in Fig. 5A, B. According to the latter (low accuracy hypothesis), the proprioceptive modality simply cannot estimate physical effector position and/or speed as accurately as vision, regardless of time.[9] Compared to vision, proprioception may be both slower and less accurate. Future experiments will determine this debate.

Other implications of early online visual feedback

Based on our data, we conclude that visual feedback can play a significant role even in a movement's early stage. This hypothesis makes several experimentally testable predictions. We predict that if vision is transiently perturbed during the initial stages of a movement, movement parameters (amplitude, speed) should be noticeably affected from the start. We also predict that there should be significant differences between trained, highly practised movements to known locations in space and unrehearsed movements to novel locations. When accuracy is emphasized in reaching movements to novel targets, as is sometimes the case in real-world situations, a larger premium is placed on visual feedback, as compared to practised movements. Therefore, by our hypothesis, clear differences should be seen between untrained and trained movements even in the initial prepeak stage (PSP, speed magnitudes, etc.). Our preliminary informal observations (Sheth, in preparation; also see Taylor and Birmingham 1948) of asymmetrical trajectories with longer decelerations and *earlier* occurrences of the peak speed in non-rehearsed movements compared with practised ones support this claim. A greater reliance on visual feedback (due perhaps to a high demand on accuracy, and novelty of target position) likely causes the PSP to be time-shifted *ahead* in the course of the movement just as a lack of visual feedback – and therefore no reliance on it – caused the PSP to be pushed *behind* in the present study. The two results logically complement one another.

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[9] The conversion of information from proprioceptive to visual coordinates may be inaccurate too (Helms Tillery et al. 1991).

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