Seeing the last part of a hitting movement is enough to adapt to a temporal delay

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Being able to see the object that you are aiming for is evidently useful for guiding the hand to a moving object. We examined to what extent seeing the moving hand also influences performance. Subjects tried to intercept moving targets while either instantaneous or delayed feedback about the moving hand was provided at certain times. After each attempt, subjects had to indicate whether they thought they had hit the target, had passed ahead of it, or had passed behind it. Providing visual feedback early in the movement enabled subjects to use visual information about the moving hand to correct their movements. Providing visual feedback when the moving hand passed the target helped them judge how they had performed. Performance was almost as good when visual feedback about the moving hand was provided only when the hand was passing the target as when it was provided throughout the movement. We conclude that seeing the temporal relationship between the hand and the target as the hand crosses the target's path is instrumental for adapting to a temporal delay.

Keywords: interception, visuo-motor control, temporal delays, visual feedback

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Introduction

How vision contributes to our interactions with objects in common tasks has been studied both by analyzing eye movements (e.g., Brenner & Smeets, 2007, 2011a; Johansson, Westling, Bäckström, & Flanagan, 2001; Land & Hayhoe, 2001; Mrotek & Soechting, 2007) and by removing vision at specific times (e.g., Brenner & Smeets, 2011a; Dessing, Oostwoud-Wijdenes, Peper, & Beek, 2009; López-Moliner, Brenner, Louw, & Smeets, 2010; Marinovic, Plooy, & Tresilian, 2009; Spijkers & Spellerberg, 1995; van Soest et al., 2010). Not surprisingly, seeing the target object increases the accuracy with which the hand approaches it (e.g., Brenner & Smeets, 2011a; Carlton, 1981; Desmurget & Grafton, 2000; Elliott & Allard, 1985; Elliott, Binsted, & Heath, 1999; Elliott, Carson, Goodman, & Chua, 1991; Prablanc, Péllison, & Goodale, 1986; Spijkers and Spellerberg, 1995). Seeing the target also allows one to respond if the target is displaced while the hand is moving toward it (Brenner & Smeets, 1997; Desmurget et al., 1999; Desmurget, Péllison, Rossetti, & Prablanc, 1998; Gréa et al., 2002; Kertzman, Schwarz, Zeffiro, & Hallett, 1996; Oostwoud-Wijdenes, Brenner, & Smeets, 2011; Pisella et al., 2000; Prablanc & Martin, 1992). People generally look at the target, rather than the hand. Seeing the hand is presumably less important because people can feel where it is. Nevertheless, people do respond to changes in visual feedback about the position of the hand (Saunders & Knill, 2003, 2004, 2005) or of a cursor representing the hand (Brenner & Smeets, 2003a).

Besides being used for online corrections, seeing the hand is also important for aligning vision with proprioception. The felt and visually perceived positions of the hand drift apart when visual feedback about the position of the hand is removed (Brown,

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Rosenbaum, & Sainburg, 2003; Smeets, van den Dobbelsteen, de Grave, van Beers, & Brenner, 2006; Wann & Ibrahim, 1992). Vision of the hand before the movement is enough to prevent this from happening (e.g., Desmurget, Rossetti, Jordan, Meckler, & Prablanc, 1997; Desmurget, Rossetti, Prablanc, Stelmach, & Jeannerod, 1995; Elliot et al., 1991; Ghez, Gordon, Ghilardi, Christakos, & Cooper, 1990; Prablanc, Echallier, Jeannerod, & Komilis, 1979; Rossetti, Stelmach, Desmurget, Prablanc, & Jeannerod, 1994). The ease with which vision and proprioception are spatially aligned is evident from the quick adaptation to experimentally imposed spatial offsets (e.g., Cressman & Henriques, 2009, 2010; Morton & Bastian, 2004; Sarlegna, Blouin, Breschiani, et al., 2003; Sarlegna, Blouin, Vercher, et al., 2004; Scott-Alexander, Flodin, & Marigold, 2011).

The temporal alignment between vision and proprioception is different from the spatial alignment in that seeing the static hand will not make any difference. Temporal asynchrony becomes apparent only when the hand is moving. It is particularly evident when the hand is moving fast and temporal precision is crucial, such as when hitting or missing a moving target. In terms of timing, there are two ways in which seeing the hand move toward the target can be expected to improve performance in an interception task. The first and most obvious is that seeing the hand move toward the target will result in a higher accuracy during the trial in question because it allows one to correct for any initial errors. This mechanism for improving performance is likely to initially become more effective as the movement proceeds and the hand approaches the target but to lose its influence later in the movement when there is no longer enough time to make adjustments. The second potential way to use vision of the hand to improve performance is by using information from seeing oneself hit or miss the target to achieve a higher accuracy on subsequent trials. In that case, the improvement is achieved through better synchronization of movements of the hand with the visually perceived target. This could involve mechanisms that prevent vision and proprioception from drifting apart temporally (as described above for preventing them from drifting apart spatially), but it could also simply arise from adjusting the motor commands in response to visual feedback so that subjects gradually learn to hit the target with the cursor (as suggested for other aiming tasks; e.g., Brenner & Smeets, 2011b; van Beers 2009). Such mechanisms would benefit most from seeing the last part of the movement, when the cursor passes the target.

In this study, we first ascertain that visual feedback about the hand is used in fast interception and that providing such feedback in the form of a simple cursor movement is effective (Experiment 1). Then, we examine at what stage of the movement visual feedback about the hand is still useful for correcting the ongoing action (Experiment 2). Next, we examine whether providing feedback at the critical time for judging one's performance, but too late to adjust the ongoing movement, substantially improves performance (Experiment 3). Finally, we evaluate the influence of providing feedback as the hand moves back to the starting position (Experiment 4). Besides determining the temporal precision in each condition, we also measured the extent to which people accounted for a delay in the visual feedback.

Methods

Apparatus

Figure 1A illustrates the general experimental setup used for all the experiments. Subjects sat in front of a drawing tablet (WACOM A2) that recorded the movements of a handheld stylus. Stimuli were projected from above onto a horizontal back-projection screen positioned above the tablet. New images were projected at a frame rate of 85 Hz and a resolution of $1{,}024 \times 768$ pixels. A half-silvered mirror between the back-projection screen and the tablet reflected the visual display, giving subjects the illusion that the display was in the same plane as the tablet. Lamps situated between the half-silvered mirror and the tablet allowed us to control vision of the hand: Subjects could see the stylus in their hand when the light was on but not when the light was off. Subjects intercepted the virtual targets by sliding the stylus across the drawing tablet. A Macintosh Pro 2.6-GHz Quad-Core computer controlled the presentation of the stimuli and registered the position of the stylus at 200 Hz. The setup was calibrated by aligning the position of the stylus with dots appearing on the screen, which allowed us to later present visual stimuli at any desired position on the tablet.

Subjects

Eleven subjects participated in each experiment after giving written informed consent. Five of them participated in all four experiments. All were right-handed and had normal or corrected-to-normal vision, and none had evident motor abnormalities. They could adjust the height and the position of the chair they were sitting on to ensure they felt comfortable. The study was part of a program that was approved by the local ethical committee.

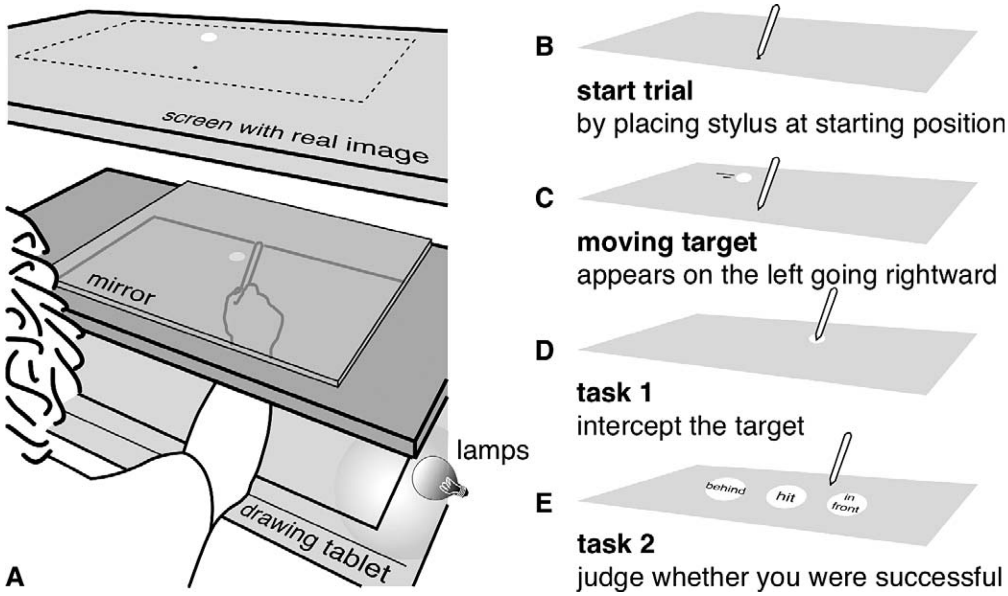

Figure 1. Schematic representation of the equipment and procedure. (A) Images were projected on a screen above a half-silvered mirror. Subjects could see their hand through the mirror only if the lamps beneath the mirror were on. (B–D) Subjects had to intercept a virtual moving target by sliding a stylus across the surface of the drawing tablet. They always saw the target but either saw the stylus in their hand or a cursor representing the stylus. The cursor displayed the stylus's position after a delay and was often presented during only part of the movement. (E) After each interceptive movement, the subject judged whether he or she had hit the target or had passed ahead of it or behind it by moving the stylus to one of three panels (with, from left to right, the texts "hand behind target," "hit," and "hand in front of target").

Procedure and tasks

The general procedure for all experiments is shown in Figures 1B through E. Each trial consisted of two parts: trying to hit the target and indicating whether one was successful. The target that one was trying to hit was an 8-mm-diameter dot that moved from left to right at 30 cm/s. To start each trial, subjects had to move the tip of the stylus (which we will refer to as the stylus) to an indicated starting position (5-mm-diameter blue dot). Using a fixed, small, visible starting point ensures that vision and proprioception are aligned spatially. The trial started once the stylus was within the starting point for a random interval between 300 and 500 ms. At that moment, the starting point disappeared and the moving target appeared. The target's path was 20 cm further away from the subject than the starting point.

Subjects had to try to hit the target. They were free to decide when to start moving and where to hit the target, but they were required to perform a continuous movement without lifting the stylus off the tablet. Once they had finished the hitting movement, three written options appeared on the screen. Subjects had to judge whether they had hit the target or had passed ahead of it or had passed behind it. They indicated their judgment by moving the stylus to one of the three panels on the way back to the starting position (Figure 1E). Subjects received no explicit feedback about their performance on either task, but of course seeing the cursor hit or pass the target provides feedback about the performance. The precision in the subjects' judgments about their performance provides a measure for the quality of such feedback.

In most conditions, the lights beneath the mirror were off, so that subjects could not see their hand or the stylus. In these cases, a 5-mm-diameter white cursor dot could be drawn at the position of the stylus to help guide the hand, both when hitting the target and when indicating one's judgments about one's success and returning to the starting point. The cursor's position was delayed by 60 ms with respect to that of the stylus. Subjects could rest at any moment by not placing the stylus at the starting position. We designed four experiments with different conditions to investigate the importance of visual feedback at different times. Each condition was presented as a block of 200 trials and took about 15 minutes to complete.

Experiment 1: Visual feedback and baselines

In the first experiment, we examined how the temporal precision of hitting and the judgments about one's performance differed between the three basic visual feedback conditions: (a) real visual feedback about the stylus and hand, provided by turning on the light beneath the mirror (hand condition); (2) delayed visual feedback about the stylus, provided by displaying a cursor at the measured stylus position (cursor condition); and (3) no visual feedback at all about the stylus's position during the hitting movement, but delayed visual feedback when indicating how one thought that one had performed and when moving the stylus back to the starting dot (return condition). Feedback from the cursor had a delay of about 60 ms with respect to the actual position of the hand (this value was determined by comparing the positions of stylus and target on trials of the hand condition that were judged by the subjects to have been hits).

When subjects can see their hand (hand condition), we expect them to be precise, and we do not expect them to systematically arrive at the target's path before or after the target. When subjects have no visual information about their movement (return condition), we expect them to be less precise, and we expect individual subjects to have all sorts of biases. The main question is whether providing visual information about the movement through a single cursor that is drawn at the position of the tip of the stylus (cursor condition) is enough for subjects to achieve a similar precision as when seeing the whole hand with the stylus and whether the responses will be adjusted to the delayed visual information so that the hand arrives before the target so that the cursor hits the target. If the hand movements are adjusted to achieve precise timing in hitting the target with the cursor, we can proceed to manipulate the visibility of the cursor in the following experiments. To familiarize subjects with the interception task, the condition with the light on (hand condition) was always performed first. The other two were run in counterbalanced order.

Experiment 2: Varying the amount of feedback

In the second experiment, we examined how reducing the part of the movement for which visual feedback was provided influences performance. The aim of this experiment was to determine when visual feedback starts to help improve the ongoing movement and until when it can still do so. The light beneath the mirror was always off, so subjects had to rely on the cursor for visual feedback about the hand. In the four different conditions, the cursor was drawn until the stylus had reached 2% (first 2% condition), 33% (first 33% condition), 66% (first 66% condition), or 110% (first 110% condition) of the distance from the starting point to the target (i.e., had moved about 4 mm, 7 cm, 13 cm, or 22 cm). Note that in the first 110% condition, the cursor was drawn until after it crossed the target's path, so this is very similar to the cursor condition in Experiment 1. In all four conditions, the cursor reappeared after the movement (when the hand started moving back toward the subject's body) and was visible when making the perceptual judgments and moving to the starting position. Subjects who had not participated in the first experiment completed an additional condition in which the light beneath the mirror was on (hand condition) before being tested in this second experiment, so that they would be familiar with the task (the data from those sessions were not analyzed). The four conditions were performed in counterbalanced order.

We expect the hand to reach the target closer to the time that would make the (invisible) cursor hit the target as more information is provided, both in terms of variability and in terms of the average timing, except perhaps when comparing the two conditions with the most feedback, because we expect there not to be enough time to adjust the ongoing movement when the hand is less than 7 cm away from the target. Finding improved performance when the final part of the movement is visible would suggest that seeing the cursor pass the target, and thereby obtaining more accurate information about one's timing, influences performance on subsequent trials.

Experiment 3: Relevance of seeing the outcome

To more directly test the idea that seeing the cursor pass the target influences performance on subsequent trials, we conducted a third experiment, in which the visual feedback was provided too late for correcting the ongoing movement. Providing feedback around the time at which the cursor crosses the target provides precise knowledge of the outcome of the movement, which could help to time better future movements, as well as provides feedback about the movement at the moment that the hand is moving fastest, so that delays would be most conspicuous. There was a single condition in which we provided feedback during the final 33% of the displacement (last 33% condition). We expected this to be too late to correct the movements, as will be verified in the Results section. All subjects had participated in one or both of the previous experiments, so no additional practice was necessary. The importance of adjusting new actions on the basis of feedback about the timing on previous attempts will become evident by comparing the performance in this condition with the performance in the various conditions of Experiments 1 and 2.

Experiment 4: The role of delayed feedback at other times than during the interception

In the last experiment, we investigated the role of delayed visual feedback when moving the cursor back to the starting point. During the interception, no feedback at all was provided. If delaying the feedback during the interception normally only makes subjects hit earlier on the next trial because they saw the cursor pass behind the target, providing delayed feedback between such movements should not influence performance. However, if the delayed feedback makes subjects change their sense of the synchrony between vision and proprioception, or at least between vision and their own actions, we could expect some influence of delayed feedback provided while moving back to the starting point. The hand and cursor will presumably be moving slowly on the way back to the starting point, and timing is not very critical at that time, so any influence of the delay will probably be less evident than for delays in feedback presented during interception.

There were three conditions that were performed in a fixed order: (a) a condition with the light on beneath the mirror (a repetition of the hand condition of experiment 1), (b) a condition in which feedback about the position of the stylus was given only when the stylus was on its way back to the starting point and even then only when it was completely static (moved less than 1 mm in 25 ms; static condition), and (c) a condition in which the cursor was drawn only when moving back to the starting point after having made the perceptual judgment (after judgment condition). We started with a condition in which subjects saw their hand to ensure that they were all initially exposed to the "true" synchrony between vision and the hand. In the static condition, subjects never saw the cursor move smoothly, so they could never experience the delay in the feedback while moving. The delay manifested itself only in the interval between when the stylus stopped moving and when the feedback appeared and in the interval between when the stylus started moving and the (static) feedback disappeared. We could not remove the feedback altogether because subjects needed information about spatial misalignment to be able to place the stylus at the starting point. The critical question is whether subjects would perform differently in the after judgment condition, in which they were exposed to the temporal delay for a short period of time between trials.

Data analysis

We evaluated subjects' performance by examining variable errors (standard deviations) and two kinds of systematic errors: bias and drift. The bias is the average time between when the center of the target and when the tip of the stylus cross the point at which the stylus crosses the target's path. Drifts are systematic fluctuations in the bias. The delay that we introduced when drawing the cursor (60 ms) is likely to result in a bias in the responses, whereas failures to synchronize vision with the hand may give rise to drifts, which may differ between subjects.

To evaluate the amount of drift in our data, we compared local and global measures of the standard deviation in the timing error (Haeckel & Schneider, 1983). The local standard deviation is derived from successive trials (q, Equation 1), whereas the global standard deviation is derived in the conventional manner (s, Equation 2).

$$q = \sqrt{\frac{1}{2(n-1)}\sum_{i=1}^{n-1}(x_{i+1}-x_i)^2} \quad (1)$$

$$s = \sqrt{\frac{1}{n-1}\sum_{i=1}^{n}(x_i-\bar{x})^2}, \quad \text{where} \quad \bar{x} = \frac{1}{n}\sum_{i=1}^{n}x_i \quad (2)$$

The idea is that if there is no drift, then measuring the variability locally or globally will give the same result. If successive values are independent and randomly distributed around a fixed mean, then the average difference between successive values is $\sqrt{2}$ larger than the average difference between each value and the mean. This is compensated for in Equation 1, so if there is no drift, q and s will be very similar. Gradual systematic changes (i.e., drift) in the value of x will hardly influence q but will clearly increase s, so if there is substantial drift, s will be larger than q.

To visualize the drift, we plot the local standard deviation as a function of the global standard deviation. In such a plot, drift manifests itself as a deviation from the unity line ($s > q$). To get some feeling for the magnitude of the drift, we formulate the following simple model (although we obviously have no evidence that this is really what happens):

$$x_t = a_t + e_t \quad (3)$$

$$a_{t+1} = a_t + \alpha e_t \quad (4)$$

In these equations, x_t is the response on trial t, a_t is the timing that one is aiming for on trial t, e_t is the timing error on trial t (for instance, because of motor noise), and α is a value that indicates the extent to which the timing that one is aiming for is influenced by the previous error. If $\alpha = 0$, subjects aim for a fixed timing and there is no drift. If $\alpha = 1$, the timing that one is aiming for is the timing that was achieved on the previous trial, so the timing follows a random walk. A value of $\alpha = 0.15$ means that after every trial, the timing that one is aiming for shifts in the direction of the error (as in the random walk) but only by 15% of the error. Shifting the aiming point to compensate for errors would give rise to a negative value of α.

To interpret the perceptual judgments, we plotted the cumulative fraction of certain categories of responses as a function of the true timing error and fit cumulative normal distributions to these plots. We did so separately to determine whether the stylus was considered to have passed ahead of the target (using "passed ahead" responses as the category of interest) and to determine whether the stylus had passed behind the target (combining "hit" and "passed ahead" responses into one category). The standard deviations of the two fit distributions were averaged as our measure of the resolution of perceptual judgments.

Results

Figure 2 shows the bias in performance: the average time between when the tip of the stylus crossed the target's path and when the center of the target crossed the position at which it did so. There are different panels for the different experiments. Data are presented for individual subjects. Positive values mean that the stylus arrived before the target. For the cursor to arrive at the same time as the target, the stylus must arrive 60 ms before the target. Figure 3 shows the average variability per condition, both for performance (bars) and for the perceptual judgments (points).

Experiment 1

The conditions in the first experiment (top left panels) are hand (subjects saw the stylus in their own hand), cursor (subjects saw the 60-ms–delayed cursor indicating the stylus's position), and return (subjects only felt their hand when moving to the target but saw the 60-ms–delayed cursor when making their perceptual judgments and moving back to the starting position). When subjects could see their hand, the average standard deviation in their performance was less than 20 ms (gray bars in Figure 3, top left panel, hand condition). When they saw the (delayed) cursor rather than the hand itself, the variability in their performance was slightly larger (same panel, cursor condition), and they tended to cross the target's path about 60 ms too early (Figure 2, top left panel), in accordance with timing a collision between the cursor and the target rather than one between the stylus and the target (the bias in the cursor condition was not significantly different from 60 ms; $t = 0.09$, $p = 0.93$). In both the hand and the cursor condition, the visual judgments (points in Figure 3) were more precise than the performance (bars in the same figure). The standard deviations in the judgments were less than 15 ms.

When no visual feedback was provided during the movement (return condition), both performance and judgments were more variable (Figure 3). Somewhat surprisingly, the subjects' performance was less variable than their judgments about the performance in this condition. The mean bias was not significantly different from 60 ms ($t = -0.21$, $p = 0.84$), although it varied considerably across subjects (Figure 2). It was significantly different from 0 ms ($t = 2.45$, $p < 0.05$). Thus, the first experiment confirms the hypothesis that seeing either the hand or a cursor representing the hand enhances precision, both in performance and in perceptual judgments about the performance. The first experiment also shows that subjects synchronize the arrival of the delayed cursor (the delayed visual information) with the target, rather than synchronizing the arrival of the unseen hand with the target. Note that they even seem to do so when the cursor is not visible during the interceptive movement, in which case they received no visual feedback about their performance. Although half the subjects had performed the cursor condition before the return condition, the other half performed the return condition directly after the hand condition, so for half the subjects, this bias is not even consistent with the past visual feedback that they received about the interception.

Experiment 2

We can observe a gradual transition between the condition with almost no feedback at all (first 2% condition) and the condition with visual information during the whole movement (first 110% condition) in all measures of performance (Figures 2 and 3, top right panels). The mean bias across subjects was about 60 ms in all conditions, but individual subjects' biases differed systematically from 60 ms. These deviations from 60 ms were smaller when more visual feedback was provided. Interestingly, there are differences between the first 66% condition and the first 110% condition. These two conditions differ in that the last part of the movement was performed without visual feedback in the first 66% condition, whereas it was performed with visual feedback in the first 110% condition. This last part of the movement took only 73 ms to complete (on average), and the feedback was provided only after a delay of 60 ms, so the difference in performance cannot arise from online corrections, because visual information takes much longer than 13 ms to be used (Brenner & Smeets, 1997, 2003b). If the difference between the two conditions is not due to correcting the ongoing movement, it is presumably related to the fact that subjects see the cursor pass the target only in the first 110% condition. Thus, seeing the outcome of the movement presumably has an effect on planning the next trials. The similarity between performance in the first 2% condition and the return condition of Experiment 1 and between the first 110% condition

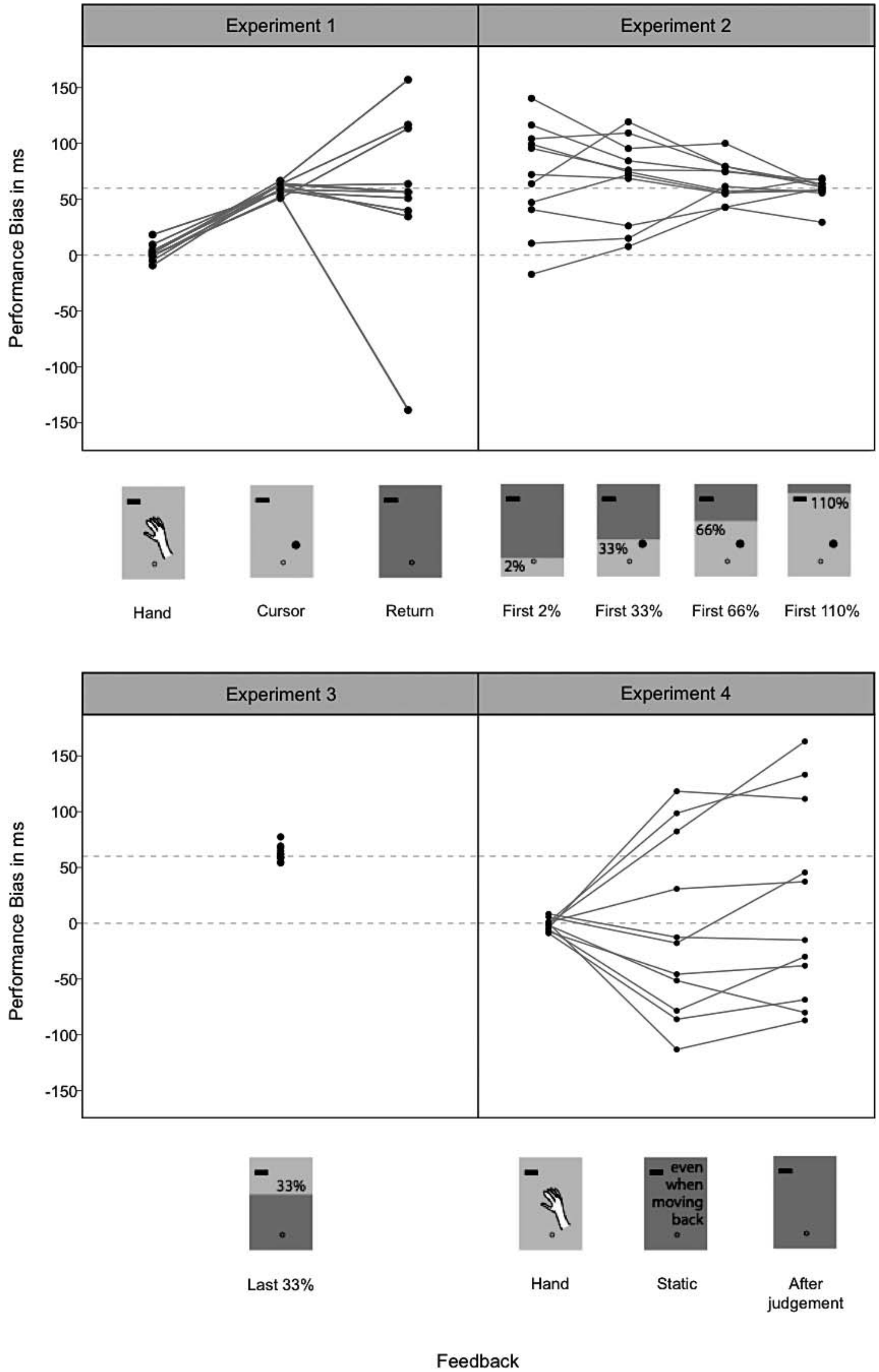

Figure 2. How much ahead of the target the stylus intersected the target's path (average bias in milliseconds) for each subject in each condition. Positive values correspond to the stylus arriving before the target. Each point represents one subject, with lines connecting the subject's values for the different conditions within each experiment. Note that performance is reported relative to the stylus, so there is no bias if the stylus hits the target (dashed line at zero), whereas a bias of about 60 ms is needed for the cursor to hit the target (dashed line at 60).

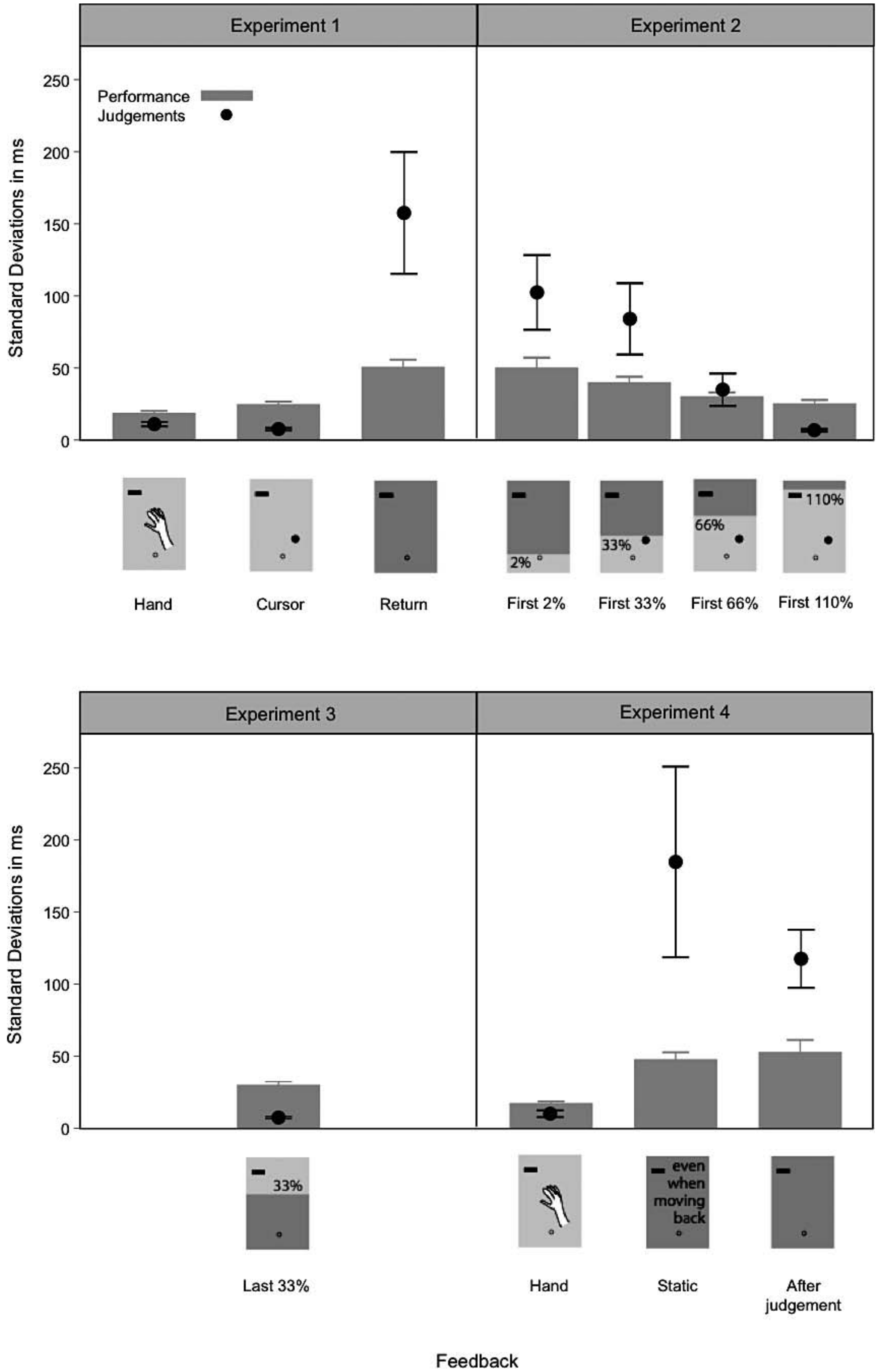

Figure 3. Standard deviations in both performance (gray bars) and subsequent judgments about that performance (black points) for each condition. Values are the means (with standard errors of the mean) of the 11 subjects' standard deviations.

and the cursor condition of Experiment 1 shows that additional experience hardly improves performance.

Experiment 3

The difference between performance in the first 66% condition and performance in the first 110% condition of Experiment 2 was further explored in Experiment 3, which consisted of a single condition in which feedback was provided during only the last 33% of the trajectory (last 33% condition). In this experiment, it took the subjects an average of 65 ms to cover the last 33% of the trajectory toward the target, so they could not have corrected the ongoing movements on the basis of the delayed visual information from the cursor. Seeing the last part of the movement does provide reliable feedback about one's performance, as is evident from the standard deviation in the judgments (point in the bottom-left panel of Figure 3). Interestingly, the standard deviation in performance (bar in the same panel) was almost as small as when the cursor was visible throughout the movement (cursor and first 110% conditions in Experiments 1 and 2). The bias too was similar. Across subjects, it did not differ significantly from the 60-ms delay between the stylus and cursor positions ($t = 1.24$, $p = 0.24$).

These findings suggest that our subjects' performance was primarily achieved by adjusting motor commands on the basis of the perceived sensory outcome on previous attempts to intercept the target. However, performance cannot have been determined only by adjusting the timing of each movement to the error on the previous trial, because there are several conditions in which performance is better than the visual judgments about that performance. To evaluate the role of mechanisms other than a combination of corrections to the ongoing movement and aiming for a different timing on the basis of success on the previous trial, we manipulated the feedback provided between hitting movements.

Experiment 4

In Experiments 1 and 2, there were conditions in which subjects had (almost) no feedback during the interceptive movement. In those conditions, the average biases were 56 ms (return condition of Experiment 1) and 58 ms (first 2% condition of Experiment 2). Thus, the average bias was closer to 60 ms than to 0 ms in these conditions, despite the cursor, and therefore the 60-ms delay, (almost) only being visible between trials. In Experiment 4, we confirmed that vision of delayed motion during the return movement gave rise to this bias. This is important because if a bias can arise from feedback that is presented between the attempts to intercept the target, performance cannot be due only to adjusting the motor commands for the hitting movement to feedback about the success of such movements (in combination with adjustments during the movement). We first repeated the hand condition of Experiment 1 to make sure that there was no initial bias in the subjects' performance. Then, in the static condition, no visual feedback was provided except when the stylus was not moving. In this condition, performance was very variable across subjects, with an average bias of −7 ms (bottom right panel of Figure 2).

In the after judgment condition, (delayed) feedback was provided when moving back to the starting position after having made one's perceptual judgment, thus at a moment that timing is unimportant and the stylus is far from the target's path. Despite the large variability in biases across subjects, almost all of the subjects' biases were slightly larger after seeing the moving cursor. The mean bias was 16 ms. Although this is well below the 60-ms delay of the cursor, it is larger than for the static condition: The difference is significant when tested with a paired t-test ($t = -2.3$, $p < 0.05$). As in the previous conditions without visual feedback during the movement, judgments were more variable than performance (Figure 3, bottom right panel). It may seem obvious that any exposure to the delayed cursor would induce a bias, but note that in this whole experiment, subjects were never exposed to the cursor during the actual interceptive movement, so any effect on the bias must arise from learning the relationship between the hand and the cursor movement on the way back to the starting point.

Drift

As already mentioned, seeing the cursor cross the target seems to be critical for precision in hitting as well as in perceptual judgments. Apparently, feeling the hand cross the visible target provides far less reliable information about the timing. This suggests that a large part of the increase in the standard deviations when visual feedback about the movement is removed may be the result of losing the ability to synchronize one's actions with the target. To examine the extent to which the timing of the movement drifts away from the correct timing, we plot the relationship between the local standard deviation and the global standard deviation for each subject and condition (Figure 4). In such a plot, drift is manifested as a deviation from the unity line (see the Data Analysis section). There is very little drift, if any, in the conditions in which subjects saw their hand or the cursor cross the target's path (blue dots near the unity line). When subjects did not see their hand or the cursor cross the target's path (red dots), the standard deviation increased, with the global standard deviation increasing more than the local standard deviation (points below the unity line), which is consistent with the additional variability being caused by drifts in the timing. The black dashed line in Figure 4 shows the average relationship between the two measures of variability obtained by simulating many 200 trial blocks of trials with Equations 3 and 4 for $\alpha = 0.15$ and normally distributed errors (e_t).

There were no obvious differences between the average reaction times (time between the target appearing and the subject starting to move) and movement times (time between when the subject started to move and when the hand crossed the target's path) for the different conditions within each experiment (Figure 5), although subjects were free to intercept the target anywhere along its path. Neither the differences between the median reaction times nor the differences between the median movement times were significant (tested with repeated-measures analyses of variance within experiments).

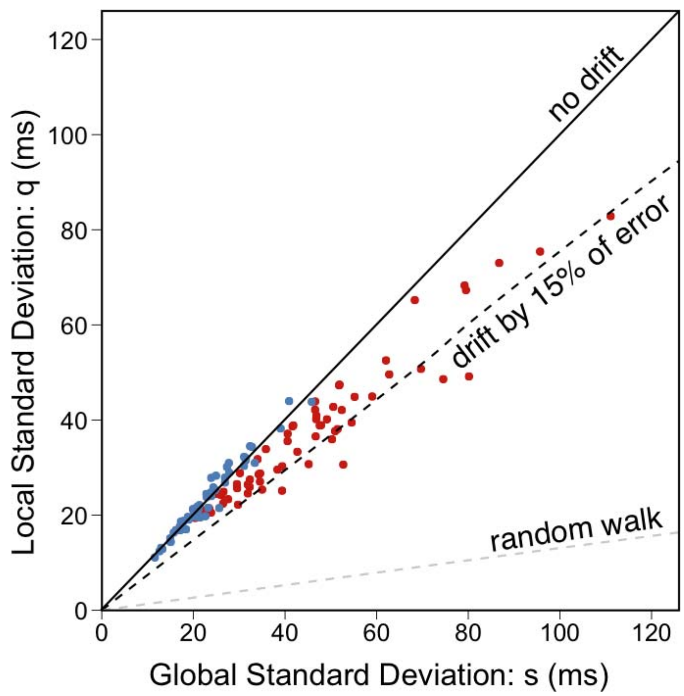

Figure 4. Local and global standard deviations in performance. Each point represents one subject and condition. The points are blue if the hand or cursor was visible when it crossed the target's path, and they are red if it was not visible at that time. The lines indicate where the points are expected to lie if there is no drift in the timing (black solid line), if the timing follows a random walk (gray dashed line) or if the timing shifts by 15% of the error (with respect to the aiming point) on each trial (black dashed line).

Discussion

Previous work involving temporal delays between one's actions and their visual consequences (e.g., Kennedy, Buehner, & Rushton, 2009; Stetson, Xu, Montague, & Eagleman, 2006) has shown that people can adjust their actions in accordance with modest delays. Here we examine how information at different stages of an interception movement, and between such movements, affects such adjustments. We consider three general methods by which such information could improve performance: error correction, online feedback, and learning the delay between the hand and the cursor. We evaluate the contributions of these mechanisms by comparing performance when information was presented at various times. Adjustments based on the errors on previous attempts are expected to rely primarily on seeing the cursor pass the target. Adjustments to ongoing movements should rely primarily on seeing the first part of the cursor's movement toward the target. Neither predicts any influence of feedback provided between the interceptive movements, whereas one could learn about the delay between the stylus and the cursor (i.e., either between one's actions and their visible consequences or between proprioception and vision) on the way back to the starting point.

Error correction

It is well established that perceived errors are used to plan and correct future movements (e.g., Brenner & Smeets, 2011b; Shadmehr & Mussa-Ivaldi, 1994; Shadmehr & Wise, 2005; van Beers, 2009; Wei & Körding, 2009). In support of learning from errors playing an important role in achieving a high precision in our task, performance was clearly best when one could see the cursor or stylus cross the target's path, which is obviously also when perceptual judgments are most reliable (Figure 3). Thus, our subjects may have simply learned to arrive earlier or equivalently to aim ahead (i.e., to the right) of the target, to compensate for the errors that would otherwise arise from the delay that we introduced.

Correcting errors on a trial-by-trial basis could also compensate for any drift in the timing of the movements. A substantial part of the decrease in precision when feedback is removed is due to drift (Figure 4). The results shown in Figure 2 suggest that the fluctuations in the aiming point are less random than is proposed in Equation 4, because individual subjects drifted systematically toward different biases. However, irrespective of the origin of the drift, a decrease in precision associated with drift can be avoided by trial-by-trial corrections, and indeed, seeing the last part of the hitting movement clearly helped our

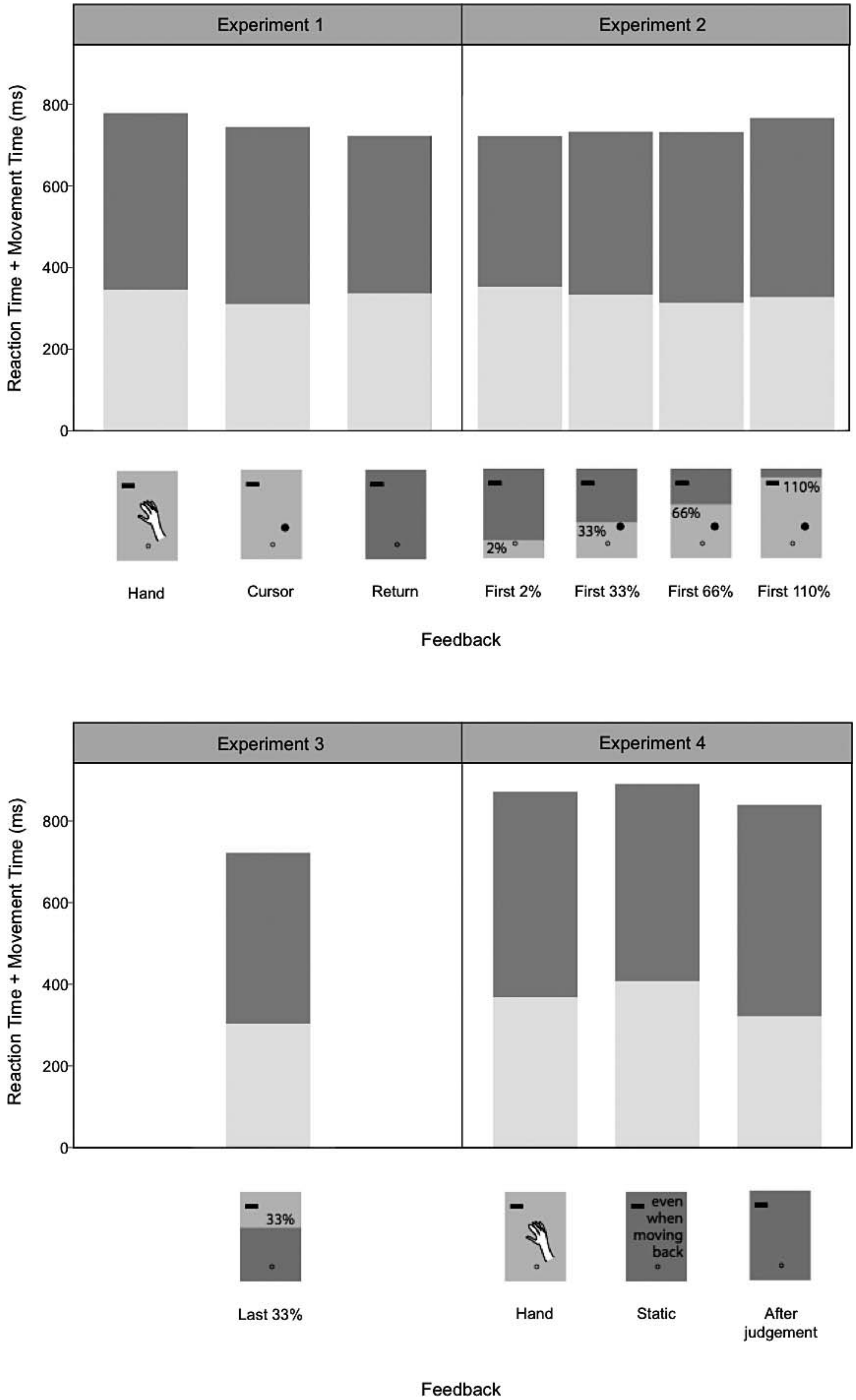

Figure 5. Average reaction and movement times for each condition. The height of each section of the bars is the mean of the 11 subjects' median values. The lower, brighter sections are the reaction times, and the upper, darker sections are the movement times. Each panel represents one experiment, with different bars for different feedback conditions.

subjects synchronize their actions with their anticipated visual consequences (Figure 2).

However, trial-by-trial corrections need not be the only mechanism for using visual information to guide one's movements. One reason to suspect that this may not be the only mechanism involved is that there are several conditions in which performance was better than judgments about how well one had performed. Another reason is that information provided between the attempts to hit the target seems to matter. Nevertheless, the evidence supports this as being the main determinant of temporal precision.

Online feedback

Providing feedback about the stylus's motion during early parts of the movement can be expected to improve performance because it provides the opportunity to correct the ongoing movement (Brenner & Smeets, 2011a). Indeed, with more feedback, the standard deviation in performance and the variability in the bias across subjects were both smaller (Experiment 2; Figures 3 and 4). However, considering that our subjects' judgments about their performance also improved as the duration of the visual feedback was increased (Figure 4; Experiment 2, black points), this effect could also be due to error correction, so the current study does not provide strong evidence for the use of online feedback, although there is also no reason to doubt that it is used when available.

Learning the delay between the hand and the cursor

There are many studies on various aspects of the spatial alignment of vision and proprioception (e.g., DiZio, Lathan, & Lackner, 1993; Pick, Warren, & Hay, 1969; Rodríguez-Herreros & López-Moliner, 2011; Rossetti, Desmurget, & Prablanc, 1995; van Beers, Sittig, & Denier van der Gon, 1996, 1999; Warren & Pick, 1970), including adaptation to experimentally induced offsets (e.g., Harris, 1974; Hay & Pick, 1966; Jakobson & Goodale, 1989; Kitazawa, Kimura, & Uka, 1997; Rock, Goldberg, & Mack, 1966; van den Dobbelsteen, Brenner, & Smeets, 2003) and the senses drifting apart in the absence of feedback (e.g., Brown et al., 2003; Desmurget & Grafton, 2000) in a subject-specific manner (Smeets et al., 2006). There are fewer studies on the temporal alignment of vision and proprioception, where the emphasis has been on the extent to which adapting to experimentally induced temporal delays between one's actions and their visual consequences influences subsequent visual judgments (e.g., Cunningham, Billock, & Tsou, 2001; Heron, Hanson, & Whitaker, 2009; Kennedy et al., 2009; Stetson et al., 2006). The present study confirms that temporal adaptation between one's actions and their visual consequences is easily achieved during an interception task: Subjects readily arrived 60 ms earlier than the target when there was a 60-ms delay between their action (the hand movement) and its visual consequence (the cursor's motion). It does not directly examine whether this adaptation is specific to the task, as it would be if it were the result of adjusting an aiming point, or whether there is some more general component to the adaptation, such as a temporal realignment of vision with proprioception.

The importance of having visual feedback at the moment of the hit does not necessarily argue for error correction rather than temporal realignment, because errors in timing are most apparent when the hand is moving fast and the timing is critical; thus, for temporal alignment, the moment at which the cursor crosses the target is also the most important (spatial alignment should not be a problem in our study because in almost all conditions, feedback about the hand's position was provided throughout the movement back to the starting point). Finding that the bias is shifted toward positive values when feedback is provided only while the hand is moving back to the starting point (Figure 2; Experiments 1 and 4) supports the idea of learning the delay between the hand and the cursor, because it suggests that the temporal relationship between motor commands and their consequences (or between vision and proprioception) is learned while moving back to the starting point and that this influences the hitting movement despite the complete absence of visual feedback during that movement. These results also confirm that what is learned is temporal, rather than spatial, because the temporal delay is independent of the speed and direction of motion, whereas the spatial relationship between the stylus and the cursor depends on the movement and is reversed when the direction of movement is reversed. Thus, although the 60-ms temporal bias could also be considered to be a 1.8-cm lateral bias, we are convinced that the former interpretation is the correct one. However, we cannot tell whether subjects have learned how to move the stylus to move the cursor in a certain way or whether they also perceive their hand to be at the position of the cursor. Of course, the former could be achieved by simple error correction in the manner described above.

Conclusion

Subjects corrected for a delay between the stylus and the cursor by moving their hand earlier to match the cursor's timing with that of the target. We found that the influence of delayed feedback was particularly strong when it was provided as the cursor was passing the target. We suggest that feedback at that time is critical for adapting to a temporal delay because timing is most critical and errors in timing are best detected when the rapidly moving hand is close to the target.

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