

The Duncker Illusion and Eye–Hand Coordination

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Soechting, John F., Kevin C. Engel, and Martha Flanders. The Duncker illusion and eye–hand coordination. *J Neurophysiol* 85: 843–854, 2001. A moving background alters the perceived direction of target motion (the Duncker illusion). To test whether this illusion also affects pointing movements to remembered/extrapolated target locations, we constructed a display in which a target moved in a straight line and disappeared behind a band of moving random dots. Subjects were required to touch the spot where the target would emerge from the occlusion. The four directions of random-dot motion induced pointing errors that were predictable from the Duncker illusion. Because it has been previously established that saccadic direction is influenced by this illusion, gaze was subsequently recorded in a second series of experiments while subjects performed the pointing task and a similar task with eye-tracking only. In the pointing task, subjects typically saccaded to the lower border of the occlusion zone as soon as the target disappeared and then tried to maintain fixation at that spot. However, it was particularly obvious in the eye-tracking-only condition that horizontally moving random dots generally evoked an appreciable ocular following response, altering the gaze direction. Hand-pointing errors were related to the saccadic gaze error but were more highly correlated with final gaze errors (resulting from the initial saccade and the subsequent ocular following response). The results suggest a model of limb control in which gaze position can provide the target signal for limb movement.

INTRODUCTION

The perceived direction of the motion of an object is affected by motion of the background. For example, a target moving straight down, displayed against a background moving to the left, appears to move downward and to the right. This illusion, first described by Duncker (1929), also influences the saccadic eye-movement system. Saccades to remembered targets are displaced in the direction opposite to the direction of background motion (Zivotofsky et al. 1996), suggesting that the target position is encoded relative to the background. However, smooth pursuit eye movements are affected to a much lesser extent, if at all (Collewyn and Tamminga 1986). Thus the eye can accurately track a small target through a moving background, even in cases where the saccadic system exhibits illusory responses.

The initial purpose of the present study was to determine whether or not targeted arm movements are also influenced by the Duncker illusion. To this end, we presented subjects with a moving target that could disappear behind a band of moving random dots, and asked them to point to the spot where the target would re-emerge. When we found that hand interception

was indeed influenced, we initially supposed that this result implied that extrapolated (or imagined object motion) was also subject to the Duncker illusion. However, the subjects often began to move to the expected point of re-emergence even before the target disappeared from view, suggesting that the perceived direction of target motion may be affected by background motion even when the target is not within the field of the background.

Therefore we also examined the eye movements during the course of the hand-interception task, to determine the time frame in which subjects predicted the target's emergence. This more detailed examination of subjects' behavior in this task led to new conclusions concerning role of gaze in encoding information about target location for limb motion. In this paper, we will describe the pattern of eye movements and the extent to which eye and hand motions are coordinated in an interception task.

METHODS

Visual display

Subjects sat in front of a 20-in computer video monitor (Mitsubishi Diamond Scan 20 M) with a resolution of 640×480 pixels (34.8×26.0 cm) and a 60-Hz refresh rate. The room was illuminated normally, and the screen was at a comfortable reaching distance, the distance from the head to the screen being about 50 cm. The subjects were presented with the display illustrated schematically in Fig. 1A. In the middle of the screen, there was a band (640×200 pixels) of random dots. Each of the 200 random dots was rendered as a square 3×3 pixels. Eighty percent of the dots moved coherently (at a speed of 300 pixels/s or 16.3 cm/s) from one frame to the next in one of four directions: up, down, left, or right. The direction of motion of the other 20% of the pixels was random from one frame to the next (also at a speed of 300 pixels/s). We used the procedures developed by Newsome and Paré (1988) to generate the random-dot pattern. From one frame to the next, each dot had an 80% probability of moving coherently, and, as dots reached the edge of the frame, they were extinguished and replaced by a new dot, positioned to maintain a uniform dot density.

At the start of each trial, a square target (10×10 pixels) appeared at the top center of the screen. The color of the target (cyan) was the same as the color of the random dots. The target moved at a constant speed (200 pixels/s) in 1 of 14 directions, ranging from ± 5 to $\pm 35^\circ$ from vertical downward in 5° increments. As soon as the target reached the border of the random-dot pattern, it disappeared from view.

The subject's head was not restrained in these experiments. Typi-

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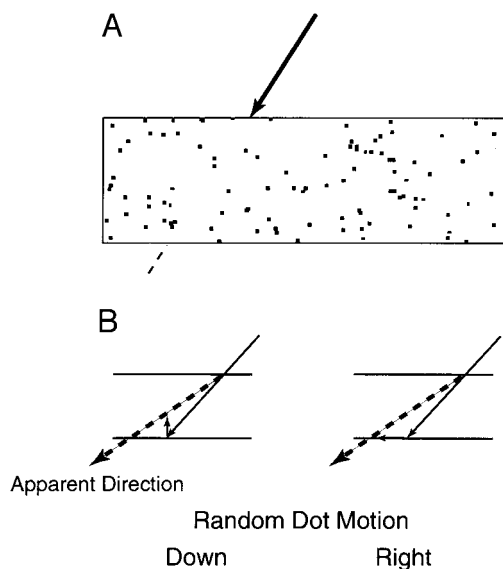


FIG. 1. *A*: schematic of the experimental paradigm. The target appears in the middle of the top border of the monitor and moves obliquely downward, in the direction indicated \downarrow . When the target reaches the central portion of the screen, it is occluded by a band of moving random dots. (The band of dots was not enclosed by a solid frame, as suggested by the diagram.) *B*: predictions of the Duncker illusion. ---, the apparent motion of the target. Downward random dot motion should add an upward component to the target's actual motion (*left*) and rightward random dot motion should add a leftward component (*right*). In both instances, there should be a rightward bias of the target's apparent motion.

cally, the eyes were about 45 cm away from the monitor screen and accordingly, a displacement of 100 pixels is equivalent to about 6.9° of visual angle.

Experimental design (interception task)

In the first experiment, subjects were instructed to touch the screen at the position, and at the time, they expected the target to emerge from behind the occlusion. (The target did not emerge, to prevent the possible effects of learning. This precaution was probably unnecessary because preliminary experiments in which the target did emerge gave qualitatively and quantitatively similar results.) The subjects also were instructed not to attempt to track the target with their hand. With the exception of this caution, they were given no other specific instructions as to how they were to accomplish the task. They initiated each trial by pressing the space bar on the computer keyboard. The time and the place of finger contact were recorded using a touch-sensitive screen (Elo Touch Systems) mounted on the monitor, at a spatial resolution of better than 0.2 pixels and a temporal resolution of 10 ms (Engel and Soechting 2000).

Trials were presented in random order, with eight repetitions for each condition (4 directions of random dot motion \times 14 directions of target motion), for a total of 448 trials. Eight subjects participated in this experiment. The procedures were reviewed by the Institutional Review Board of the University of Minnesota and the subjects gave informed consent.

Recording of gaze direction

In a second series of experiments, we also recorded gaze direction during this task. The experimental design in this series was similar to the first with some minor differences. To limit the length of the experiment, we reduced the number of target directions to five: 0, ± 10 , and $\pm 20^\circ$. Target speed in this experiment was 180 pixels/s, as was the speed of the random dots. Finally, to standardize the gaze at

the start of the trial, a fixation point (located at the center of the screen, 20 pixels from the upper edge) was provided before the onset of each trial.

In 100 trials (5 repetitions \times 5 target directions \times 4 directions of random-dot motion), the instructions to the subjects were the same as for the first experiment. Thus subjects were to intercept an imagined target with the hand. No explicit instructions were given concerning eye movements except to regard the fixation point at the onset of the trial.

In another 100 trials (randomly interleaved), we asked the subjects to track the target with their eyes only. To facilitate tracking, we decreased the width of the band of random dots from 200 to 100 pixels and had the target re-appear after it had traversed the random-dot occlusion. At the onset of these trials, subjects were instructed to place their index finger in a box at the lower right-hand corner of the monitor screen and to maintain it there throughout the trial. A fixation point, located in the center of the top of the screen, was also provided. The fixation point disappeared as soon as the trial began with the appearance of the target. Five subjects participated in this second series of experiments. All five also took part in the first experimental series.

Gaze position was recorded by means of head-mounted video cameras (SMI Eye Link System). Two cameras, operating in the infrared range, recorded eye position, relative to the head, with a spatial resolution of better than 0.1° at a sampling rate of 250 Hz. The third camera recorded the motion of the head at the same sampling rate. The system was calibrated at the onset of the experiment and periodically throughout the series of trials. Gaze-position signals from the two eyes were averaged to increase the signal to noise ratio.

RESULTS

Distortion of perceived target trajectory

A moving occlusion affects target interception in the manner predicted by the Duncker illusion. Figure 1A illustrates the experimental paradigm. A random-dot pattern was in motion in a central region of the display. A target that appeared at the top middle of the monitor moved downward at an oblique angle and disappeared from view when it reached the region encompassed by the random-dot pattern. Subjects were instructed to put their finger at the point where the target was expected to re-emerge as indicated in Fig. 1A (---).

The predicted errors are illustrated in Fig. 1B and are based on the assumption that a component of the background motion sums vectorially with the actual target motion to produce the illusion. For example, if the random-dot motion is downward (Fig. 1B, *left*), the illusory component would be upward (opposite to the direction of background motion) and the apparent motion of the target would be more oblique than the actual trajectory. Conversely, upward random-dot motion should produce the illusion of a target motion closer to vertical. Random-dot motion to the right (Fig. 1B, *right*) would be expected to produce an illusory shift of target motion in the opposite direction, i.e., to the left, whereas leftward random-dot motion would be expected to produce a shift to the right.

Pointing errors

The experimental results, shown in Fig. 2, were in accord with these predictions. The panels in Fig. 2 show the horizontal error in pointing position (distance error, *left*) and timing (time error, *right*). A positive pointing error (expressed in pixels) implies that the subject touched the screen to the right of where

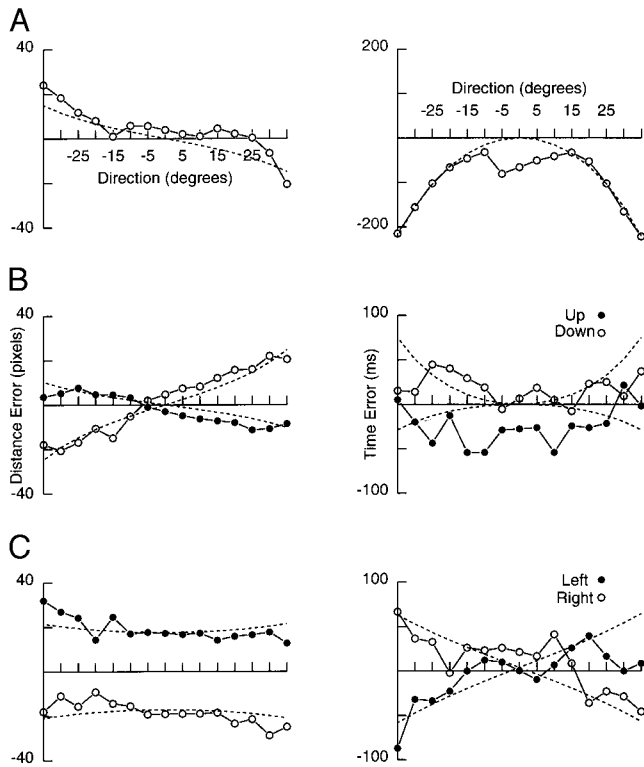


FIG. 2. Average errors in pointing occasioned by random-dot motion. *A*: the pointing error along the horizontal axis (*left*) and the timing error (*right*), averaged over the 4 conditions of random-dot motion. ---, the fit of a model (described in RESULTS) to the data. *B*: pointing errors induced by upward (●) and downward (○) random-dot motion. Errors are computed relative to the mean errors depicted in *A*. *C*: pointing errors induced by leftward (●) and rightward (○) random-dot motion. For distance errors, ---, predictions of a model assuming summation of target velocity and a vector directed oppositely to the direction of random-dot motion. For timing errors, the model in *A* assumes a constant time after target disappearance, and the model in *B* and *C* assumes that apparent changes in direction produce changes in the timing estimate. Data are averages for 8 subjects.

the target would have emerged. A negative timing error implies that the subject touched the screen prior to the time that the target would have emerged from behind the occlusion.

The *top panels* (Fig. 2*A*) show the results averaged over all four conditions of random-dot motion and all subjects plotted as a function of target direction, negative target directions being to the left of vertical. There was a consistent bias in the average errors; subjects tended to point to a spot that was closer to the midline than the actual and in anticipation of the time of emergence.

The results of simple models fitted to the data are shown (· · ·). The model for distance error assumed

$$\theta_p = a_1 + a_2\theta_a \quad (1)$$

where θ_p and θ_a are the predicted and the actual directions of target motion. According to this model, $a_2 = 0.92$ gave the best fit to the data ($r^2 = 0.997$). The model for timing error assumed that subjects struck the screen at an interval that was constant relative to the disappearance of the target and that their estimate for the time elapsed for a target traveling straight downward was veridical.

There were some differences among the responses of individual subjects. Regarding the distance error, five of the eight subjects conformed to the average pattern shown in Fig. 2*A*.

One other subject had uniformly small positional errors for all directions of target motion, whereas the remaining two subjects tended to overestimate the slant of most targets, errors generally being negative for targets in negative directions and positive for targets in positive directions. Concerning errors in timing, seven of the eight subjects conformed to the mean pattern shown in Fig. 2*A* in the sense that they anticipated the emergence of more obliquely directed targets to a greater degree than the emergence of targets moving close to vertical. However, the extent to which they anticipated the expected emergence of the targets varied widely. For targets close to vertical, timing errors ranged from -200 to $+100$ ms. For the remaining subject, timing errors were uniform for all directions.

The extent to which the direction of the moving random dots influenced the pointing errors made by the subjects is shown in Fig. 2, *B* and *C*, *left*. These errors, computed after subtracting the mean effects for all four directions of random-dot motion (presented in Fig. 2*A*), are in accord with the Duncker illusion. When the random dots moved downward (○, Fig. 2*B*), subjects overestimated the obliqueness of the target's motions (see Fig. 1*B*), with negative errors for targets directed to the left of vertical and positive errors for targets directed to the right of vertical. The opposite pattern was found when the random dots moved upward (●, Fig. 2*B*). Rightward random dot motion induced a leftward bias to the results (○, Fig. 2*C*) and leftward random dot motion induced a rightward bias (●, Fig. 2*C*). Note that these errors could be as large as 1 cm or more (18.4 pixels/cm). Furthermore this behavior was very consistent for all subjects. For the 14 directions of target motion times four directions of background motion, the average standard error (SE) of the pooled data was 2.51 pixels, ranging from 1.36 to 3.78 for different directions.

Distance errors were well accounted for by a model that assumed vectorial summation of a velocity component directed oppositely to the motion of the random dots and the target motion (see Fig. 1*B*). The model's predictions are indicated (---) in Fig. 2, *B* and *C*, *left*. For horizontally directed random dots, the amplitude of this illusory component was the same for leftward and rightward random-dot motion (8.8% of target velocity for leftward moving random dots and 8.5% for dots moving to the right). However, when the random dots moved vertically, the effect was asymmetrical (5.5% for random dots moving up and 17% for random dots moving down).

The same model was not able to account for errors in timing, however. For random dots moving vertically, this model predicts that subjects should strike the screen earlier (at negative times) when the dots move up and later when they move down. The results in Fig. 2*B*, *right*, are in qualitative accord with the prediction but not in quantitative agreement. For downward random-dot motion, assuming the same weighting of background motion as for the distance errors, the model predicted a delay in excess of 150 ms, clearly not in accord with the data. Furthermore for horizontally moving random dots, there should be no timing errors according to the vectorial model, in disagreement with the data in Fig. 2*C*, *right*. (An ANOVA showed significant effects at $P < 0.05$ for the more obliquely directed target motions, such as $\pm 35^\circ$.)

More generally, the variability in timing was much greater than the variability in location of pointing. For timing, the SE

for the error in timing averaged to 22.5 ms with a range from 16.5 to 39.1 ms.

The model that best accounted for errors in timing was the following: the time to transit is computed as if the speed does not change but the direction does. The predictions of this model are given in Fig. 2, *B* and *C*, *right* (---). This model does account reasonably well for timing errors when random dots moved horizontally but less well so when the random dots moved vertically. Furthermore it is contrary to the assumption used to predict the average time error (Fig. 2*A*), namely that direction is not taken into account in predicting the transit time of the target. Thus there seem to be several different influences on the timing of interception, and timing was much more variable than was the spatial locus.

In summary, subjects made consistent errors in indicating the point where the target should emerge from behind the occlusion. These errors were in accord with predictions of the Duncker illusion and could be predicted by assuming a vectorial model. However, this model did not account for timing errors that were also made by the subjects.

Eye-hand coordination in interception tasks

We observed that some subjects began to move the hand to the monitor screen even before the target disappeared from view, suggesting that they might have begun to predict the target's trajectory at the onset of limb motion. To get a better appreciation of when and how subjects formed the decision about where the target would emerge from behind the occlusion, we decided to obtain records of the subjects' gaze during this task. We repeated the experiment described above, restricting the direction of target motion to five directions: 0, ± 10 , and $\pm 20^\circ$. Figure 3 shows two representative examples from one subject in trials in which the target moved 10° to the left with a random dot motion down (Fig. 3*A*) and up (Fig. 3*B*). Gaze location is shown in the *top panels* (saccades being indicated by ---) and gaze velocity is shown in the *bottom panels*. The target disappeared at about 1.1 s as indicated by | (*bottom*), and it remained behind the occlusion for more than 1 s.

In both trials, the subject saccaded to the target shortly after it appeared and then tracked the target at the target's speed (compare gaze speed with the target speed of 180 pixels/s, Fig. 3, *bottom*, —). Also in both trials, the subject made a saccade to the lower border of the occlusion band around the time at which the target disappeared from view. Saccade onset coincided almost exactly with the target's disappearance in the trial at left and preceded it slightly in the other trial. The subject maintained fixation at the lower border of the occlusion zone for 500 ms or more before touching the screen.

The behavior illustrated in Fig. 3 was typical. Generally subjects began to track the target and then, around the time of the target's disappearance, made one or more saccades anticipating the target's motion. Sometimes the saccades were directed to the lower border as in the examples in Fig. 3. In other instances, subjects made a saccade to a point in the middle of the occlusion zone, followed by a second saccade to the lower border. More rarely, they directed their gaze down to the lower border, then back up and then back down again.

The saccade directions were clearly influenced by the motion of the random dots, and they were in the direction of the Duncker illusion in accord with observations by Zivotofsky et al. (1996). This is evident in the examples shown in Fig. 3—when the random dots moved downward (*left*), the saccade was directed more obliquely than the true direction of target motion (cf. Fig. 1*B*), whereas the saccade direction was closer to the vertical when the random dots moved up (*right*).

Most strikingly, there was high degree of correlation between the gaze direction and the point on the screen touched by the finger. This can be seen in the two examples in Fig. 3 in which gaze position has been plotted from the trial's onset until the time that the finger made contact with the screen. The point of contact is indicated by ● at the lower boundary of the occlusion zone. In both trials, the subject made a second saccade, directed down and to the left, and then maintained fixation. The error made in pointing with the finger corresponds closely with the horizontal error in gaze position around the time that the subject's finger contacted the monitor screen.

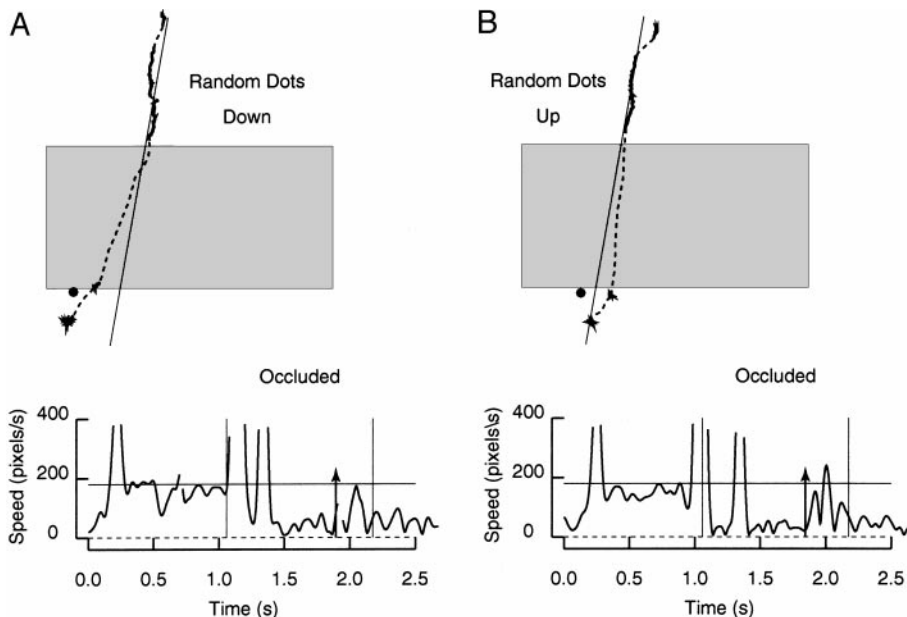


FIG. 3. Gaze direction during the interception task. —, target direction; ■, the zone of random dots in which target motion is occluded. The target disappeared behind the occlusion and did not reappear. —, epochs of smooth pursuit; ---, saccade trajectories. *Bottom*: traces depict gaze velocity during the trial. |, the time at which the target disappeared from view (at 1.1 s) and the time at which the target would have emerged from the occlusion band (at 2.2 s). —, target speed (180 pixels/s). ↑, the time at which the finger touched the screen at the location indicated by ●. Note that saccades are biased in the direction predicted by the Duncker illusion. Note also the close correspondence between finger contact and gaze.

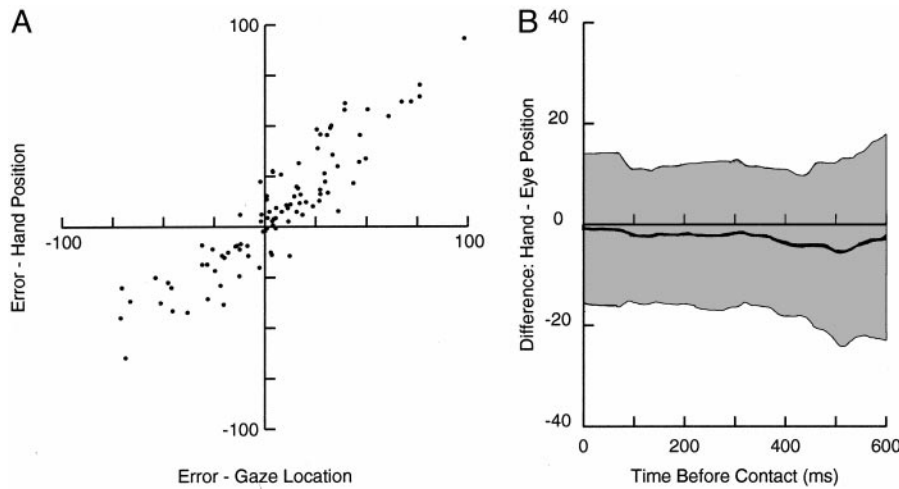


FIG. 4. A: errors in hand position plotted as a function of the error in gaze location. Data are for all trials in 1 subject. For each variable, error (in pixels) is defined as the difference between the horizontal location of the finger (or gaze) and the point at which the target would emerge from behind the random-dot occlusion. B: average (—) and standard deviation (■) of the difference between horizontal hand and gaze location. Gaze location was computed at various times before finger contact with the screen. Data are for all trials from the same subject as in A.

(The time of contact is indicated by the upward arrow in the bottom panels and the time at which the target would have reappeared is denoted by the second vertical line, at about 2.2 s. In both trials this subject anticipated the target's reemergence.)

In general, the direction of gaze along the horizontal was an excellent predictor of where the finger contacted the screen. This can be appreciated in Fig. 4, which shows the errors in gaze location and in the position of the hand for all of the trials from one subject (*subject E*, also illustrated in Fig. 3). The errors plotted on the two axes indicate the horizontal difference in the location of the gaze and the hand relative to the point at which the target would have reemerged from the occlusion band. For this subject, there was a high degree of correlation between these two parameters ($r^2 = 0.83$, and a slope of hand re eye = 0.99, Fig. 4A and Table 1). The results for this subject were typical, correlation coefficients ranging from 0.58 to 0.86 for the five subjects (Table 1). Furthermore for none of the subjects did the slope of the relationship between hand position error and gaze error differ significantly ($P < 0.05$) from unity.

The values in Table 1 are based on the gaze error determined 120 ms prior to the contact of the hand with the screen. This time interval was chosen somewhat arbitrarily partly because

TABLE 1. Slopes and coefficients of determination for the relation between gaze and pointing errors

	Error Hand Position vs. Error Gaze Location			
	Gaze: 120 ms Before Contact		Gaze: Saccade End	
	r^2	Slope	r^2	Slope
A	0.66	1.10 (0.16)	0.62	0.76 (0.11)
B	0.80	0.92 (0.10)	0.59	0.80 (0.11)
C	0.86	1.06 (0.11)	0.88	0.80 (0.08)
D	0.58	1.16 (0.16)	0.28	1.00 (0.17)
E	0.83	0.99 (0.10)	0.77	0.88 (0.10)
Mean	0.75 ± 0.05	$1.05^{**} \pm 0.04$	0.63 ± 0.10	$0.81^{**} \pm 0.05$

Gaze error was computed either by gaze location 120 ms prior to finger contact with the monitor (*left*) or by gaze location at the end of the last saccade prior to finger contact (*right*). Values in parentheses denote the 95% confidence limits of the slope of the regression of pointing error on the indicated gaze error. All r^2 values are statistically significant. The bottom line shows the mean \pm SE for all 5 subjects. $**P < 0.01$ (paired t -test).

this value corresponds to the visuomanual reaction time (cf. Soechting and Lacquaniti 1983). Furthermore the r^2 values generally did not change appreciably when the time interval was varied over the range of 0–200 ms. (Recall that subjects generally maintained fixation for about 500 ms before striking the screen.) For *subject E* (Fig. 4), r^2 ranged from 0.77 to 0.84 for time intervals between 48 and 200 ms, being substantially lower (0.28) for time intervals of 0 and 24 ms. The lower r^2 values for shorter time intervals are due to the fact that this subject sometimes initiated a saccade away from the lower border of the occlusion just prior to the time the hand contacted the screen. Figure 4B illustrates the average and the standard deviation of the difference between hand position at contact and gaze position at various times prior to contact for *subject E*. The mean and the variance of the difference were relatively constant over a long time interval, i.e., for gaze locations ranging from about 100 to about 300 ms prior to contact of the hand with the screen. The result shown in Fig. 4B is to be expected if gaze is maintained constant for a period of time.

If gaze is indeed maintained constant, then one might also expect the error in pointing to be highly correlated with the gaze at the end of the last saccade before the time the hand touched the screen. As can be ascertained from the summary in Table 1, hand-pointing error was in fact significantly correlated with saccadic error with values of r^2 ranging from 0.28 to 0.88. For one subject (*D*), the coefficient of determination was significantly less for hand versus saccadic error than it was for hand versus gaze error at a slightly later time (i.e., 120 ms prior to contact). For the other four subjects, the coefficients of determination did not differ significantly for these two regressions. When the error in pointing was regressed on gaze error at the end of the saccade, the slope of the relation between hand error and gaze error was significantly less than 1.0 for four of the five subjects (Table 1).

As might be surmised from the statistical analysis in Table 1, there was not always a perfect correspondence between gaze at the end of the last saccade (typically 500 ms before hand contact) and the gaze at later times. When the random dots moved up or down, fixation was generally maintained, as shown in the two examples in Fig. 3. However, this was generally not the case when the random dots moved horizontally, as demonstrated by illustrative examples from two sub-

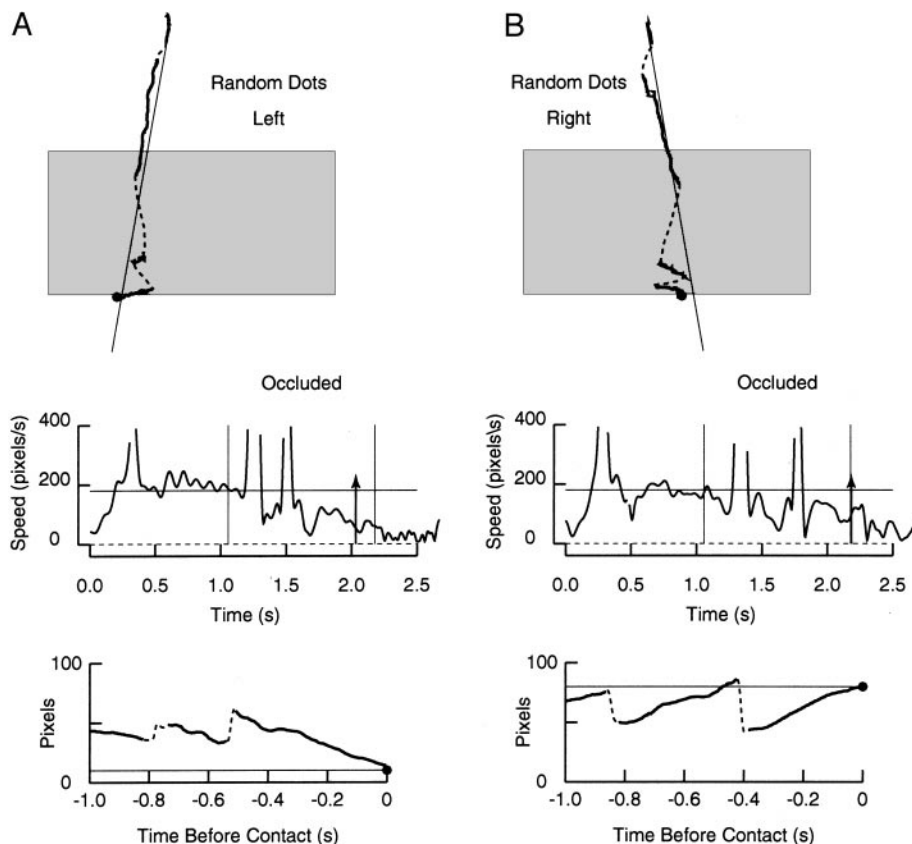


FIG. 5. Gaze direction during interception task with horizontally moving random dots. *Top*: the same format as in Fig. 3. *Bottom*: the horizontal motion of gaze as a function of time before finger contact with the screen. The horizontal line and (●) denote the location of finger contact along the horizontal. ---, saccades.

jects in Figs. 5 and 6. When the dots moved to the left (Figs. 5A and 6A), there was a rightward bias to saccade direction when the target was occluded (consistent with the Duncker illusion). Similarly, rightward moving dots induced a leftward bias to the saccades (Figs. 5B and 6B). However, in none of the four examples in Figs. 5 and 6 is there a good correspondence between gaze at the end of the saccade and the location of finger contact with the screen. This can be appreciated in Figs. 5 and 6, *top*, which show the locus of the gaze positions in space, and also in the *bottom panels* of these figures, which depict the time course of horizontal gaze position. (In both panels, ● depicts hand location.)

In each of the examples in Figs. 5 and 6, it is clear that there is a slow drift of gaze in the direction of the random dots. Sometimes (as in Fig. 5), this slow drift is interrupted by a saccade in the opposite direction and at other times this slow drift proceeds uninterrupted (as in Fig. 6). Such obvious ocular following responses (Miles et al. 1986) were obtained for horizontally moving random dots in three of the five subjects. As in the examples shown in Figs. 5 and 6, the hand location generally correlated much better with gaze position at or shortly before the time of hand contact than with gaze position at the end of the saccade. This was true irrespective of whether we considered the first saccade after the target had entered the occlusion zone or the last saccade before the finger struck the screen.

As was mentioned in the preceding text, the slope of hand-position error regressed on gaze error at the end of the saccade was significantly less than unity in four of the five subjects (Table 1), implying that saccadic gaze error was larger than

pointing error. Since ocular following responses were in the direction opposite to the Duncker illusion (see Figs. 5 and 6), they tended to reduce the error in gaze. Accordingly, the slope of pointing error relative to gaze error 120 ms before contact was always larger. Moreover, it never differed significantly from unity (Fig. 4 and Table 1). This implies that the hand is directed to the gaze location near the time of impact when gaze is the result of a combination of saccadic and ocular following responses.

We attempted to arrive at a better estimate of the temporal relations between gaze and pointing location by computing the mean difference between gaze and final hand position (Fig. 4B), restricting our analysis to only those trials in which the background moved horizontally, i.e., those trials in which ocular following was likely to occur. The results of this analysis are shown in Fig. 7 for the two subjects for which the SD of the difference increased the most as a function of time before contact (*B* and *D*). Note that these are also the two subjects for which the coefficient of determination (r^2) is much less when the error on hand position is regressed on gaze at saccade end (Table 1). For *subject B* (Fig. 7A), it appears that the SD is relatively constant over the interval from 0 to 120 ms before contact, suggesting that gaze at any time within this interval could have provided the target for hand pointing. For the other subject (*D*, Fig. 7B), the SD appears to decrease throughout the interval from 0 to 300 ms. Trends for the other three subjects were weaker than those shown in Fig. 7. Thus our data are inconclusive on the issue of the precise timing between gaze signals and the control of limb pointing.

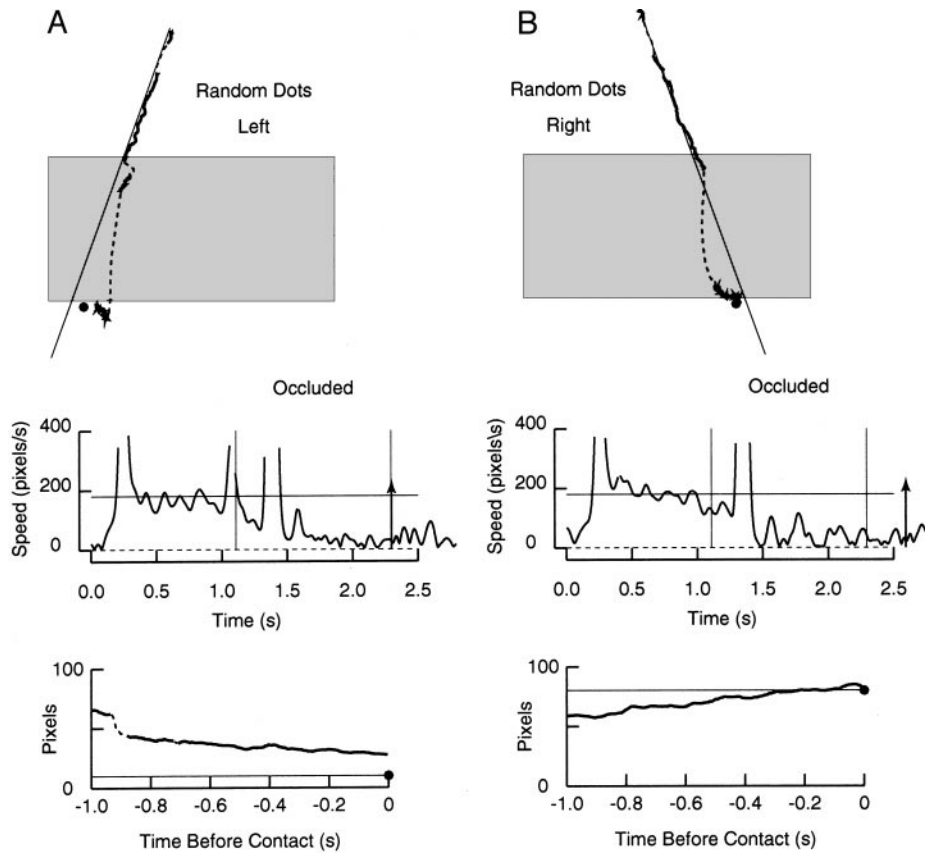


FIG. 6. Gaze direction and finger pointing in trials with horizontally moving random dots. The data are plotted in the same format as those in Fig. 5 but are from a different subject.

Tracking a target through the occlusion

As was shown in the previous section, pointing movements of the hand were influenced by two countervailing tendencies of the contemporaneous eye movements: saccades were influenced by the Duncker illusion, but ocular following responses in the direction of the random dot motion also affected the hand's target location. These same two countervailing tendencies were also observed when subjects were instructed to track (with the eyes only) the target through the occlusion zone. Figures 8 and 9 show examples obtained from two subjects in this task.

As can be ascertained from the traces of gaze velocity in Figs. 8 and 9, *bottom*, these subjects were able to continue pursuit of the target even when it had disappeared from view. In the examples shown, there was a saccade shortly after the onset of target motion, bringing gaze into coincidence with the location of the moving target. Thereafter gaze velocity corresponded well to the target's velocity (180 pixels/s). Pursuit tracking was well maintained until about the time the target disappeared from view (indicated by the first vertical line at about 1.2 s in Figs. 8 and 9, *bottom*). Thereafter smooth pursuit speed declined slowly to a value of about 50–60% of target

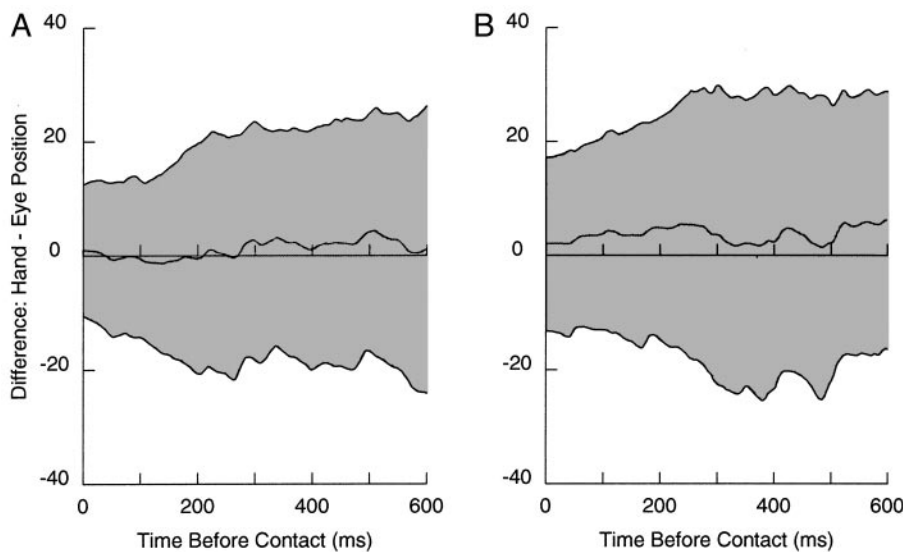


FIG. 7. Average (—) and standard deviation (■) of the difference between horizontal hand and gaze location for trials in which the background moved either to the left or to the right. Gaze location was computed at various times before finger contact with the screen.

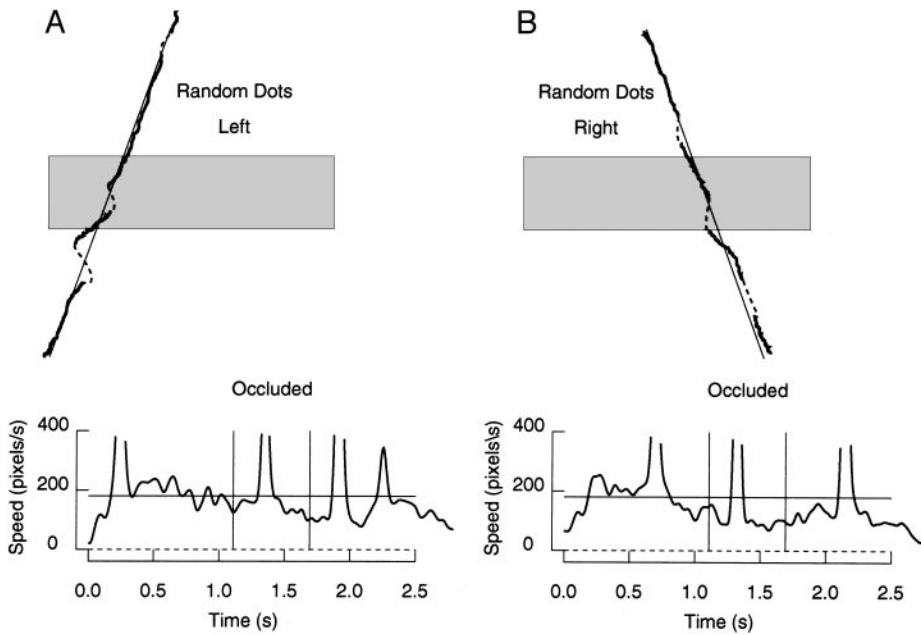


FIG. 8. Eye tracking of an occluded target in the presence of random-dot motion. —, the target trajectory; - - -, target motion being occluded when the target is within the band of moving random dots. *Bottom*: gaze velocity. Note the deviation of saccades in a direction opposite to the direction of motion of the random dots. Also note that smooth pursuit gaze velocity shows a deviation in the opposite direction.

speed. Smooth pursuit tracking was usually interrupted by a saccade when the target was out of view. After the target had reappeared from view, there was a second saccade, bringing gaze back on target.

Saccades occurring while the gaze was within the occlusion zone were clearly affected by the Duncker illusion. Thus when the random dots were moving left, saccades showed a rightward bias. Leftwardly moving random dots introduced a rightward bias to the saccades. In brief, saccade directions during the tracking task showed the same biases as did saccades when subjects were instructed to intercept the moving target with their hand, i.e., when they did not attempt to pursue the target through the occlusion.

However, the direction of smooth pursuit (and/or ocular following) movement showed a bias opposite to that of the saccades when the target was occluded: a leftward drift when the random dots were moving leftward and a rightward drift for

rightward moving dots. This bias was sometimes observed to develop slowly and gradually after gaze had entered the occlusion zone, as in the examples shown in Figs. 8A and 9A. On other occasions, as in the example shown in Fig. 8B, the directional bias was already present before the target had disappeared from view.

The examples shown in Figs. 8 and 9 were representative of tracking behavior in the four subjects who performed the task adequately. (The 5th subject did not pursue the target through the occlusion and generally made saccades to its lower border.) This can be appreciated from Figs. 10 and 11, which show averaged results obtained from the four subjects. Each panel shows averaged values of gaze speed (*left*) and gaze direction (*right*) for one direction of target motion. Data obtained for random dots moving left (thin lines) or right (thick lines) have been superimposed in Fig. 10, and the results for vertical background motion are reported in Fig. 11. These data were

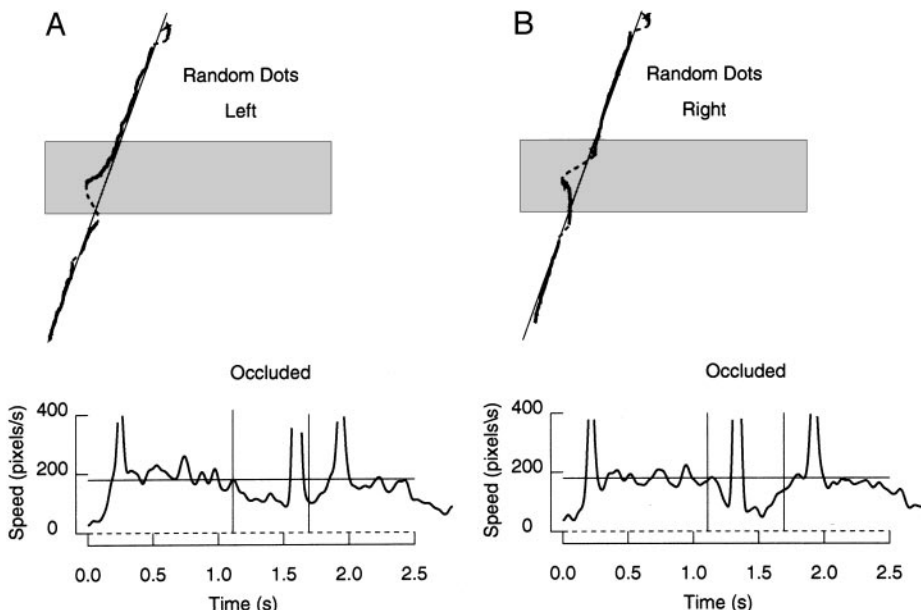


FIG. 9. Tracking an occluded target in the presence of random-dot motion. Data are plotted in the same format as in Fig. 8 but are from a different subject.

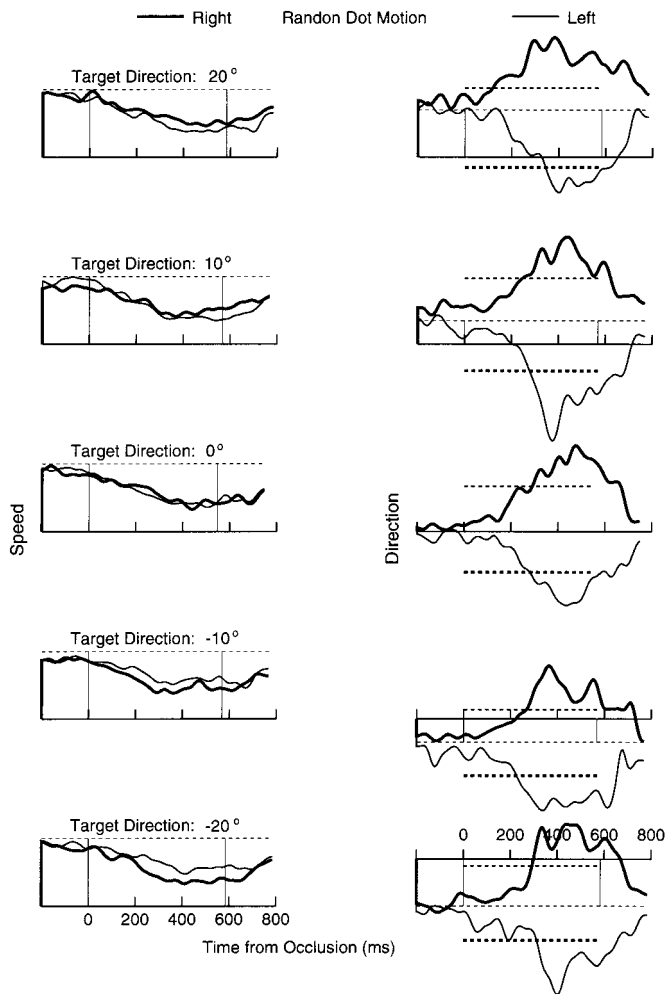


FIG. 10. Average speed and direction of smooth pursuit in tracking a target obscured by a moving random-dot pattern. Data are averages of all trials obtained from 4 subjects; saccadic intervals were removed by interpolation. The heavy traces, results for trials in which the random dots moved to the right; lighter traces, for trials in which they moved to the left. Averages are aligned on the time at which the target disappeared from view (0); the 2nd vertical line (slightly before 600 ms) indicates the time at which the target reappeared. The horizontal dashed lines in the left panels denote the target speed (180 pixels/s), and the dashed lines in the panels on the right denote the direction of target motion. Right: the heavy and light dashed lines, extending over the time at which the target was occluded, denote the average saccadic direction during this interval.

obtained by removing the saccades from individual trials, interpolating horizontal and vertical velocity components through the saccadic interval and then averaging to obtain smooth pursuit speed and direction.

As was already apparent in individual trials, pursuit speed declined gradually from the target speed (indicated by the horizontal dashed line) after the target disappeared behind the occlusion, reaching a minimum of about 50% of target speed 400–500 ms after the target disappeared at *time 0*. There appears to be an effect of the random-dot motion on the pursuit speed during the interval that the target was occluded. For target motion to the right (10 and 20°), pursuit speed was faster when the random dots were also moving to the right. Conversely, for targets moving to the left, pursuit speed was faster when the random dots were also moving to the left. This result is consistent with a vectorial addition of smooth pursuit with an

ocular following response in the direction of the random dot motion. However, a statistical analysis (see following text) showed that this effect did not reach statistical significance.

The direction of pursuit velocity was clearly affected by the direction of random-dot motion as can be seen in Fig. 10, right. In each panel, the direction of target motion is indicated by the long horizontal dashed line. Before the target disappeared, the direction of smooth pursuit was close to this direction. Shortly after the target disappeared, the direction of gaze velocity began to deviate in the direction of the motion of the random dots: in a positive, rightward direction for random dots moving to the right and conversely for leftward random dot motion. This deviation reached a peak 300–450 ms after the target disappeared and began to decline before the target re-emerged (at shortly before 600 ms, indicated by the 2nd vertical line in each panel).

Saccadic eye movements showed a bias in the opposite direction. The shorter horizontal dashed lines (spanning the time the target is occluded) denote the average saccadic direction in these trials, heavier dashed lines for random dots moving rightward, and the lighter dashed lines for trials in which the random dots moved to the left. It is clear that the gradual deviation in smooth pursuit was opposite to the deviation in the direction of the saccades.

Random dots moving up or down did have an effect on the

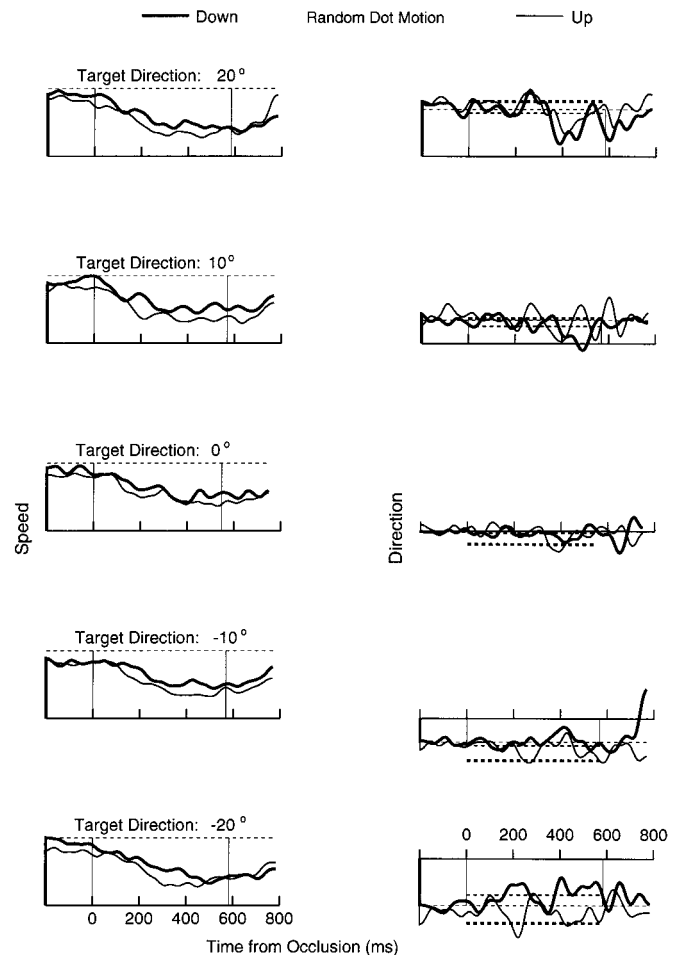


FIG. 11. Average speed and direction of smooth pursuit in tracking a target obscured by a random-dot patterns moving up or down. The data are plotted in the same format as those in Fig. 10.

speed of smooth pursuit during the interval in which the target was occluded (Fig. 11). Pursuit speed was consistently larger when the random dots moved downward, in the same direction as the target. However, there was no apparent effect of the vertically moving random dots on the direction of smooth pursuit (Fig. 11, *right*). In agreement with the effect on saccadic eye movements observed when subjects were asked to point to the spot where the target was to emerge (Fig. 3), the direction of saccadic eye movements was affected by vertically moving random dots, at least when target motion was oblique ($\pm 20^\circ$). For example, saccades were directed to the left of the target when the target moved 20° to the left (*bottom*) and the random dots moved down (thick dashed line), and they were directed to its right when the random dots moved up (thin dashed line). A similar effect was also observed when the target moved 20° to the right (*top*). For intermediate target directions, biases on saccade directions were either absent or less clear cut.

To delineate these effects more precisely, we computed average values for pursuit speed and direction for each subject and experimental condition (direction of target and of background motion), binning the data in 20-ms intervals. We then subjected these data (at 100-ms intervals) to a two-way ANOVA for the effect of the direction of background and of target motion. For pursuit speed, there was no significant effect of target motion nor was there any significant interaction between the direction of target and background motion ($P > 0.05$). The direction of background motion did have a significant effect on the speed of pursuit ($P < 0.05$) at *time 0* ($F_{3,60} = 3.77$), 200 ms after target disappearance ($F_{3,60} = 9.16$), and for the average speed during the time the target was occluded ($F_{3,60} = 3.62$). Post hoc analysis showed that in each case, the pursuit speed was less when the background moved upward but that there was no significant difference in pursuit speed between rightward and leftward background motion.

A similar analysis for the direction of smooth pursuit showed significant main effects for the direction of target motion and for the direction of background motion but no significant interaction between these two effects at any point from 0 to 500 ms. For the effect of background motion, the F values computed at 100-ms intervals ranged from $F_{3,60} = 10.20$ ($P < 0.01$) at $t = 0$ to a maximum at $t = 400$, $F_{3,60} = 40.37$ ($P < 0.01$). A post hoc analysis showed that at each point in time, the direction of smooth pursuit for rightward and leftward background motions differed significantly from each other and also sometimes from the direction of smooth pursuit for upward or downward background motions. At none of the times did the direction of smooth pursuit differ for upward compared with downward target motions.

We also performed a statistical analysis on saccade direction for saccades occurring while the target was occluded. For this analysis, we used the data for individual trials and found significant effects for background as well as target direction as well as a significant interaction between these two main effects ($P < 0.01$). We therefore did a regression analysis of saccade direction as a function of target direction for each of the four conditions of target motion. The results of this analysis are reported in Table 2. It is clear that rightward background motion imparts a leftward (negative) bias to the saccades and vice versa for leftward background motion (compare the constants c_1 for these 2 conditions). When the background motion

TABLE 2. Regression analysis on the direction of saccades during tracking through the occlusion zone

Background	Saccadic Direction vs. Target Direction	
	Constant (c_1), degrees	Slope (c_2)
Down	-3.53 (1.32)	1.30 (0.09)
Up	-0.49 (1.07)	0.89 (0.08)
Right	-16.62 (1.60)	0.57 (0.11)
Left	16.26 (1.04)	0.95 (0.07)

Values in parentheses are SE.

is vertical, the constant c_1 does not differ appreciably but the slope (c_2) does. The slope is greater than unity (1.30) when target motion is down, and it is less than unity when the background moves up (0.89). These results are in accord with the Duncker illusion described in Fig. 1.

DISCUSSION

The results show that the Duncker illusion influences goal-directed pointing movements to a visually defined target in space. In contrast to previous reports of the Duncker illusion, where motion of the target was against a moving background, in our experiments, the illusory stimulus influenced the predicted target trajectory as the target disappeared behind a moving occlusion. When subjects were asked to touch the spot at which they expected the target to emerge, they typically initiated a saccade at or before the time the target disappeared from view. These saccades were biased in the direction predicted by the Duncker illusion, indicating that the apparent direction of target motion is already altered before the target enters the band of moving dots. This should not be surprising. Coding of the direction of motion involves neurons in the medial temporal (MT) as well as medial superior temporal (MST) areas of visual cortex, and neurons in these areas, especially in MST, typically have large receptive field sizes (cf. Britten et al. 1992; Duffy and Wurtz 1995; Maunsell and Van Essen 1983; Tanaka et al. 1986; Zeki 1974).

We did not test the subjects' perception of the direction of the occluded target motion, and thus we do not know if it too is subject to the illusion and, if so, whether the illusory effects are comparable in magnitude or greater than the effects we found for pointing errors. Thus our results do not contribute directly to resolving the controversy of whether or not perceptual and motor systems are similarly biased by illusory stimuli (cf. Bridgeman and Huemer 1998; Bridgeman et al. 1979; Goodale and Milner 1992; Pavani et al. 1999). However, our results do emphasize some of the subtleties that need to be attended to in interpreting results of pointing errors, especially in light of the hypothesis (which we will develop in the following) that extraretinal gaze signals can provide the target for limb pointing. Perceptual and motor tasks are not easily dissociated. Specifically, we would expect eye movements similar to the ones we have described here during an experiment where subjects are engaged in a strict cognitive task, such as reporting whether the target moved to the left or to the right. In many of the experiments reporting a dissociation between visual illusions and pointing performance, eye movements are not described (e.g., Bridgeman et al. 1979) and the results of limb pointing performance can be accounted for by the possi-

bility of a veridical gaze signal afforded by the experimental design.

As an extension of previous observations (Wong and Mack 1981; Zivotovsky et al. 1996, 1998), we showed that saccadic eye movements are affected by the illusory stimulus, both when subjects attempted to track the target through the occlusion (Figs. 8 and 9) and when they saccaded to the expected point of emergence of the target (Figs. 5 and 6). However, pursuit eye movements were not affected by this illusion, also in agreement with previous observations (Collewijn and Tamminga 1986; Zivotovsky et al. 1996). In fact, smooth pursuit eye movements sometimes showed a bias in the opposite direction. Specifically, pursuit eye movements were veridical and initially followed the direction of target motion but were gradually combined with an ocular following response in the direction of the background motion (Figs. 8–10). Such an ocular following response was also sometimes elicited when subjects attempted to fixate gaze near the lower border of the occlusion band (Figs. 5 and 6). Thus this task appears to present an exception to the conclusion that saccadic and smooth pursuit eye movement systems are similarly influenced by perceptual and cognitive stimuli (Krauzlis and Stone 1999).

We found a high degree of correlation between the errors in gaze and the errors in manual pointing in this experiment (Fig. 4 and Table 1), and in the remainder of this discussion, we wish to focus on the implications of this observation. Clearly, the observation points to a high degree of hand–eye coordination in this task of pointing to a remembered/extrapolated target location. Thus the present results support the conclusion of Flanders et al. (1999). These authors also found a high degree of correlation between pointing errors to remembered targets and gaze direction (inferred from head posture) in a task that required stepping and reaching. Our results are also in accord with observations on eye movements by Epelboim et al. (1995, 1997) in a task in which subjects were required either to tap a specified sequence of targets or merely to gaze at them. These authors found that the characteristics of gaze shifts depended on whether or not the subjects executed targeted limb movements, leading them to conclude that limb and ocular movements were not independent. A similar conclusion was reached previously by Levine and Lackner (1979) based on an investigation of gaze and limb movement errors when an illusory limb displacement was induced by muscle vibration.

However, the present results do not appear to be compatible with a model in which a common input drives both the (saccadic) oculomotor and the limb motor systems. This conclusion is based on the observation that, sometimes, eye position began to drift away from its position at the end of the saccade, exhibiting an ocular following response (Figs. 5 and 6). In those instances, the error in pointing was better correlated with the gaze position a short time before contact than it was with the gaze position at the end of the saccade (Table 1 and Figs. 5–7). If there were a common input providing the target for the eyes and the limb, one would expect the error in hand pointing to be best correlated with the eye position at the end of the saccade and not to be influenced by the ocular following response. (Ocular following should in fact degrade the correlation.) Instead we propose that the target signal for the arm in our task is provided by a gaze position signal, derived from extraretinal signals such as efference copy of the input to ocular motoneurons (Lewis et al. 1998), irrespective of the

source of the signal governing gaze (i.e., saccadic, smooth pursuit, or ocular following).

Such an interpretation is supported by recent results of Batista et al. (1999), who found that reach-related neurons in posterior parietal cortex (a presumptive locus for spatial planning of limb movements) were tuned in an eye-centered frame of reference. The receptive fields of these neurons shifted if there was an intervening saccade between the flashed presentation of the target and the onset of limb movement, providing for spatial constancy of the coding of the target location for limb movement (Duhamel et al. 1992). Because the ocular following response causes a breakdown of the spatial constancy (i.e., the hand would follow the eye and no longer point to the correct locus in space), we would predict that the receptive field locus of posterior parietal cortical neurons should not change when an ocular following response is elicited.

While we propose that a gaze signal can provide the target for a limb movement, we do not mean to imply that such a signal is obligatory. Clearly, accurate arm movements can be performed even when the target is not foveated (cf. Crawford et al. 2000) although pointing error does depend on retinal eccentricity (Henriques and Crawford 2000). Furthermore under unconstrained behavioral conditions involving sequences of movements of the hand, the target is first fixated by the eyes (as in our experimental paradigm), but, by the time the hand reaches the target, the eyes have already saccaded to the next target in the sequence (Johansson and Flanagan 1999).

Whereas the present results suggest that gaze produces a target for the hand, there is also a considerable body of evidence that hand motion can affect eye movements. For example, it has been reported that smooth pursuit movements are facilitated when there is concomitant manual tracking of the target (Gauthier and Mussa Ivaldi 1988; Gauthier et al. 1988; Sarchilli and Vercher 1999). Ocular tracking of hand motion, be it passively or actively generated, is even better (Mather and Lackner 1980). Furthermore saccadic latency is greater than normal when the target shifts away from the goal of a pointing movement prior to its completion (Neggers and Bekkering 2000). Taken together, all of these results and the results of our investigation point to the conclusion that the control of hand movements and the control of eye movements are not effected by two separate and autonomous neural circuits. The control of eye and hand movements is intimately linked, and it appears that sometimes, such as in the present experiments, the eye controls the hand, and that at other times, the hand may also control the eye.

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