

Eye–Hand Coordination: Oculomotor Control in Rapid Aimed Limb Movements

Richard A. Abrams
Washington University

David E. Meyer and Sylvan Kornblum
University of Michigan

Three experiments are reported in which Ss produced rapid wrist rotations to a target while the position of their eyes was being monitored. In Experiment 1, Ss spontaneously executed a saccadic eye movement to the target around the same time as the wrist began to move. Experiment 2 revealed that wrist-rotation accuracy suffered if Ss were not allowed to move their eyes to the target, even when visual feedback about the moving wrist was unavailable. In Experiment 3, wrist rotations were equally accurate when Ss produced either a saccadic or a smooth-pursuit eye movement to the target. However, differences were observed in the initial-impulse and error-correction phases of the wrist rotations, depending on the type of eye movement involved. The results suggest that aimed limb movements use information from the oculomotor system about both the static position of the eyes and the dynamic characteristics of eye movements. Furthermore, the information that governs the initial impulse is different from that which guides final error corrections.

It has been known for some time that rapid aimed limb movements depend critically on information obtained from the eyes. Beginning with the classic research by Woodworth (1899), numerous investigators have studied various aspects of visual-feedback processing related to the production of aimed limb movements (e.g., Carlton, 1981a, 1981b; Keele & Posner, 1968; Prablanc, Echallier, Komilis, & Jeannerod, 1979; Vince, 1948; Zelaznik, Hawkins, & Kisselburgh, 1983). These studies have provided significant insights about the roles played by different sources of visual feedback (e.g., vision of the effector and the target for a movement) and about the speed with which such feedback is processed. Many issues still remain, however, regarding the detailed nature of coordination between the eyes and limbs during movement production by the ocular and manual motor-control systems (for detailed reviews, see Keele, 1981, 1986).

The present article pursues these issues further. We first discuss current knowledge about the behavior of the eyes during aimed limb movements and outline the various kinds of information that the eyes might provide for controlling the limbs. Next, we discuss some features of aimed limb move-

ments that may provide insight into how information from the eyes is actually used. Then we report the results of three experiments designed to answer several questions about the role of eye movements and visual information in the control of limb movements. The answers to these questions have a number of important implications. In particular, they may lead to a better understanding of the mechanisms that mediate aimed limb movements—a type of behavior that most people produce many times each day. The answers may also help to increase our understanding of the relation between the perceptual and motor systems, which serve as the primary interface between people and their environment.

Oculomotor Activity During Aimed Limb Movements

A considerable amount of work has been done already on eye–hand coordination for movements to visual targets (e.g., Angell, Alston, & Garland, 1970; Biguer, Jeannerod, & Prablanc, 1982; Mather & Fisk, 1985; Megaw & Armstrong, 1973; Posner, Nissen, & Ogden, 1978; Prablanc, Echallier, Jeannerod, & Komilis, 1979; Prablanc, Echallier, Komilis, et al., 1979; Prablanc, Pelisson, & Goodale, 1986). The results of these studies are straightforward: The eyes have been found almost always to start moving toward the target before the hand does. Thus, because eye-movement durations are quite brief, the eyes have also usually been found to arrive at the target before the hand starts to move. This has led some researchers to infer that the information needed for guiding a limb accurately can only be obtained after the eyes have reached the target (Paillard, 1982; Prablanc, Echallier, Komilis, et al., 1979).

However, in each of the preceding studies, the target for the movement appeared suddenly, and subjects were in-

Portions of this article are based on a dissertation submitted by Richard A. Abrams in partial fulfillment of the requirements for the PhD degree at the University of Michigan. Funding was provided by National Institute of Mental Health Grant R01 MH37145 to the University of Michigan. Richard A. Abrams was supported by a traineeship from the National Institutes of Health, Grant T32 EY07022, by a fellowship from the Horace H. Rackham School of Graduate Studies at the University of Michigan, and by a Washington University Faculty Research grant.

The authors thank Carol Huff for technical assistance. Correspondence concerning this article should be addressed to Richard A. Abrams, Department of Psychology, Washington University, St. Louis, Missouri 63130.

structured to minimize the latencies of their eye movements, hand movements, or both. Results from such studies may not permit inferences about the role that eye movements play under more natural, less constrained circumstances in which aimed limb movements are often made, as in everyday life. Eye-movement latencies in the previous studies might have been shorter than limb-movement latencies for reasons that have little to do with acquiring information for limb-movement control. For example, abrupt visual stimulus onsets like those used in previous studies may automatically trigger saccadic eye movements (Todd & Van Gelder, 1979). According to Todd and Van Gelder, such movements are initiated quickly because it is important to inspect areas of the visual field in which new information has just appeared. Sudden stimulus onsets would thus favor immediate eye movements, but not limb movements. Similarly, other research suggests that latencies of saccades are less affected by stimulus uncertainty than are latencies of limb movements (Megaw & Armstrong, 1973; Posner et al., 1978; Todd & Van Gelder, 1979). It may simply be easier (and faster) to program the eyes to look at a target that suddenly appears than it is to program the hand to reach toward such a target.

Another possible reason why eye-movement latencies have been shorter than hand-movement latencies in previous studies is that delays associated with muscle contraction for hand movements exceed those for eye movements (Biguer et al., 1982). Motor commands dispatched simultaneously to the eyes and hand may yield a sequence of overt behavior in which the eyes move first, even though both eye and hand movements may be initiated at the same time centrally. In fact, there is reason to believe that motor commands for concurrent movements are dispatched at approximately the same time when subjects are under pressure to move quickly (Biguer et al., 1982; Kelso, Southard, & Goodman, 1979).

If any of these possibilities hold, then the relative eye-hand movement patterns observed under conditions with time pressure and spatial or temporal uncertainty would not necessarily bear on the role of "free" eye movements in the control of limb movements. Moreover, although it is tempting to attribute some significance to the eyes moving first (e.g., once an eye movement is programmed, then the same information can be used to program a hand movement), there is no reason to believe that eye movements are an essential component of limb movements. Except for the results of a few experiments, one might even conclude that the behavior of the eyes has little or no impact on limb movements (e.g., Mather & Fisk, 1985; Prablanc, Echallier, Komilis, et al., 1979). In those experiments, however, it was found that limb-movement accuracy did suffer when subjects were not permitted to move their eyes.

Consequently, we sought to determine more precisely what the behavior and function of eye movements are during rapid aimed limb movements when there is no temporal or spatial uncertainty about the movement requirements. This should lead to a better understanding of why limb movements suffer when people cannot move their eyes. Such an undertaking may also provide important insights into the nature of the information provided by the eyes to the limb-movement control system. In the following sections, we discuss various

possible forms that this information might take, and we discuss how they might be used during different parts of a limb movement.

Contributions of the Eyes to Limb-Movement Control

There are two types of information relevant for limb-movement control that can be obtained from the eyes: *retinal* and *extraretinal*. Retinal information arises from the patterns of stimulation on the retina such as the location and movement of objects in the environment (including a limb and the target of an aimed movement). In contrast, extraretinal information concerns the position of the eyes obtained from nonretinal sources, including oculomotor commands executed in moving the eyes between different locations and, perhaps, proprioceptive cues transmitted from anatomical structures in the eye muscles. The accurate localization of objects in space relative to one's body requires integrating these two types of information (Helmholtz, 1866/1963).

Retinal information may play several roles in guiding limb movements. For example, immediately before an aimed limb movement, information about the location of a peripheral target can be extracted from the scene falling on the retina. Indeed, without such retinal information, the subject might not know where the target is. Another important role of retinal information is in providing visual feedback about the status of an ongoing movement. In particular, such feedback contains information not only about the current state of the moving limb (Carlton, 1981b), but also about the location of the target and the relative positions of limb and target (Prablanc et al., 1986). Without these sorts of information, movement performance quickly deteriorates. As several researchers have shown, deprivation of visual feedback during a movement usually causes the movement to be considerably less accurate (Carlton, 1981a, 1981b; Keele & Posner, 1968; Meyer, Abrams, Kornblum, Wright, & Smith, 1988; Vince, 1948; Woodworth, 1899).

Extraretinal (eye-position) information may likewise play an important role in aimed limb movements. Evidence from several sources suggests that subjects can guide a limb accurately to a spatial location based solely on extraretinal information about eye position (Hansen & Skavenski, 1977, 1985; Hill, 1972; Morgan, 1978). Given this result, several researchers have hypothesized that such information might be used to localize the target for a rapid aimed movement (Hansen & Skavenski, 1977, 1985; Prablanc, Echallier, Komilis, et al., 1979). However, the contributions of retinal and extraretinal information to localization of the target for a limb movement depend on the position of the eyes during the movement, and it is not yet entirely clear where the eyes actually should or do point at this time.

Phases of An Aimed Movement

Because the eyes may contribute different types of information at different times during an aimed limb movement, one needs to analyze the several distinct phases that a movement may include. Researchers have found specifically that rapid aimed limb movements are composed of three major

component phases: *movement preparation*, *initial impulse*, and *error correction* (e.g., Carlton, 1981a; Kerr, 1978; Meyer et al., 1988; Meyer, Smith, Kornblum, Abrams, & Wright, 1990; Woodworth, 1899). Here we consider the information used during each phase.

Movement-preparation phase. The movement-preparation phase is believed to begin immediately after a decision has been made to produce a limb movement but before the movement commences overtly. During this time, a subject may construct a goal for the movement (i.e., specify the desired spatial and temporal properties of the forthcoming response) and assemble an initial motor program (i.e., set of commands) needed to attain the goal. An entire limb movement need not be specified at this time; only enough preparation is needed to initiate and sustain the movement until additional information becomes available.

Several types of information from the eye may contribute to the preparation phase. If the subject views the limb at the movement-starting position, then both retinal and extraretinal information would be available about the current position of the limb. Prablanc, Echallier, Jeannerod, et al. (1979) showed that such retinal information is important during this phase: Limb movements are more accurate when subjects can see the limb before its movement begins, regardless of whether the limb will be visible during the movement itself.

The eyes may also provide information about the target position during the preparation of a limb movement. A visible target in the periphery can be located via retinal information. If the eyes moved to the target, extraretinal information about eye position can further convey the location of the target. As a number of researchers have shown, people can accurately point to locations in space on the basis of extraretinal eye-position information (Hansen & Skavenski, 1977, 1985; Hill, 1972; Morgan, 1978).

Initial-impulse phase. After movement preparation, the next phase of movement consists of initiating and executing the initial impulse (Woodworth, 1899) or primary submovement (Meyer et al., 1988), which propels a limb toward the target. The initial impulse for a limb movement is typified by a fairly rapid, continuous change in the position of the limb as it traverses most of the distance between the starting position and the final target location (Carlton, 1981a; Crossman & Goodeve, 1963/1983; Woodworth, 1899).

Because the initial impulse of a limb movement is typically ballistic (i.e., it is usually not modified once begun; Carlton, 1981a; Crossman & Goodeve, 1963/1983; Meyer et al., 1988; Woodworth, 1899), the behavior of the eyes during this phase probably would not have an immediate influence on the movement. However, movements of the eyes during the initial impulse may provide information for the next limb-movement phase (i.e., error correction). Indeed, Prablanc et al. (1986) showed that visual information obtained about the target early in a limb movement, during the initial impulse, can ultimately improve the movement's terminal accuracy.

Error-correction phase. After the initial impulse, a limb movement may enter an error-correction phase. Here attempts are made to minimize any apparent discrepancy ("error") between the current position of the limb and the movement goal. This phase corresponds to Woodworth's (1899)

current control and *groping about*, and Meyer et al.'s (1988) *secondary submovement*. Error corrections are typified by discontinuities in the position and velocity of the moving limb (Carlton, 1981a; Meyer et al., 1988, 1990; cf. Pelisson, Prablanc, Goodale, & Jeannerod, 1986).

The error-correction phase depends strongly on the presence of retinal information about the current state of the limb. When the limb's movement remains visible from start to stop, rather than being occluded at some point soon after movement initiation, the ultimate accuracy of such corrections increases markedly (Carlton, 1981a; Keele & Posner, 1968; Meyer et al., 1988; Prablanc et al., 1986; Wallace & Newell, 1983; Woodworth, 1899; Zelaznik et al., 1983). Extraretinal information may also contribute to the error-correction phase. If the eyes are pointing at the target during the error corrections, people may localize the target at least partially on the basis of oculomotor cues about eye position (Prablanc, Echallier, Komilis, et al., 1979).

Overview of Present Experiments

Given that the potential contributions of the eyes to the control of limb movements depend greatly on the eyes' behavior, our first goal is to establish exactly what that behavior is under conditions in which eye movements may occur freely without speed stress, as in many real-world situations. In Experiment 1, we did this by monitoring eye position while subjects performed a wrist-rotation task similar to one used previously by us and by other investigators (Crossman & Goodeve, 1963/1983; Meyer et al., 1988; Wright & Meyer, 1983). Here subjects received no special instructions regarding the behavior of their eyes during the wrist rotations; indeed, they did not necessarily have to make any eye movements at all. This allowed us to determine more precisely what people do with their eyes on an ad lib basis during aimed limb movements. In Experiments 2 and 3, we addressed additional questions about the details of the information provided by the eyes. For this purpose, we gave subjects specific instructions designed to vary the behavior of their eyes and assessed the impact of these instructions on the various movement phases of wrist rotations. An important feature of our approach involves using a movement "parsing" algorithm (Meyer et al., 1988) to separate the initial-impulse and error-correction phases of movement. Analyses of the output from this algorithm reveal that the eyes make significant and distinct contributions to both the initial-impulse and the error-correction phases of aimed limb movements.

Experiment 1

Experiment 1 was designed to determine what relationship, if any, exists between eye movements and rapid aimed limb movements in a natural, unconstrained setting. The motivation for the experiment stemmed from some limitations in past research on eye-hand coordination. Previous studies have found that during simultaneous movements of the eyes and hand, the eyes almost always began to move before the hand did (Angell et al., 1970; Megaw & Armstrong, 1973; Prablanc, Echallier, Komilis, et al., 1979; Prablanc et al.,

1986). However, these findings were obtained under conditions in which there was both temporal and spatial uncertainty about when and where the target for the movements would appear. Also, subjects had to minimize their latencies for movements of the eyes, the hand, or both. It is not certain yet whether the results of such studies would generalize to other, more natural situations, including ones in which subjects know the requirements of the movements beforehand and are not under time pressure to initiate them.

We addressed this issue by recording eye position continuously while subjects produced wrist rotations to prespecified visual targets with no particular instructions regarding the behavior of the eyes. Here subjects were not even requested to produce eye movements at all. The obtained results may therefore tell us more about eye-hand coordination under relatively unconstrained circumstances.

Method

Subjects. Four right-handed undergraduates participated as paid subjects. They had no apparent visual or motor defects. Each subject served in six 50-min sessions, and received \$4/session, plus bonuses based on good performance.

Apparatus. Each subject sat in a dimly illuminated sound-attenuated booth, with his or her right forearm resting on a firm support. The forearm was held parallel to the floor, with the upper arm next to the body. The subject's head was held steady with a dental-impression plate.

Using the right hand, the subject grasped a light wooden handle that fit comfortably in the palm. The hand and handle were hidden from view by a wooden shield. The handle rotated freely along the axis of the forearm. Attached to the handle was a low-inertia angular-position transducer (Brush Instruments Model 33-04), which converted the handle's position to a voltage. This voltage was sampled at a rate of 1000 Hz with a resolution of $\pm 0.05^\circ$ of handle arc. Visual stimuli were presented on a cathode ray tube (CRT; Digital Equipment Corp. Model VR17, with P4 phosphor), located 43 cm directly in front of the subject. The display was viewed binocularly. Auditory stimuli were presented via a loudspeaker located 1 m from the subject. A DEC PDP-11/60 computer controlled the sequence of events and acquisition of data.

We monitored the position of the subject's right eye with a scleral-reflectance device (Gulf & Western Model 200) mounted on a spectacles frame. The analog output from the eye-movement monitor was digitized at a rate of 1000 Hz with a resolution of 0.05° . To calibrate the monitor, samples were taken while the subject fixated at each of 11 evenly spaced points across the CRT. Eye position was computed using piecewise linear interpolation of the calibration points. Calibration was performed at the beginning of each session and was verified before each trial.

At the beginning of each trial, subjects saw a display that included a dot that indicated the starting location for the required movement and the initial eye-fixation point (the home position). Two vertical lines to the right of the home dot defined the target region for the wrist rotation. A small triangle (the cursor) represented the current position of the handle. Clockwise and counterclockwise rotations of the handle produced rightward and leftward movements of the cursor across the screen, respectively. Each degree of handle rotation caused the cursor to move through 0.29° of visual angle. Thus, when the handle was at the home position (10° counterclockwise), the cursor and the home dot were located 2.9° of visual angle to the left of straight ahead. The position of the cursor was updated within 1 ms after any change in the handle position. Thus, when the cursor and

target were visible, the subject had complete visual information about the positions of both the handle and the target.

Procedure. Each trial began with the display described above. When the display appeared, subjects had to fixate their eyes on the home position and turn the handle to align the cursor with the home dot. This required pronating the wrist 10° from a vertical position. After the cursor was steadily aligned at the home position, the dot changed to a plus sign. Then a 600-ms warning period elapsed, followed by four tones, each 50 ms in duration and separated by an interval of 260 ms. The first three tones had a 400-Hz frequency and served as warning signals. The fourth tone, with a frequency of 1000 Hz, served as a response signal.

Immediately before the response signal, the position of the subject's right eye was checked. If the eye position was within 1° of the home dot, then the response signal was presented and the trial proceeded in its normal fashion. Otherwise, after a delay of 600 ms, the count-down sequence of tones was repeated from the beginning. If the subject still appeared to be fixating incorrectly after three such attempts, the eye-monitor calibration routine was automatically invoked.

At the onset of the response signal, the subjects had to rotate the handle and move the cursor from its starting location to the target region as quickly and accurately as possible. This involved a rapid supination (clockwise rotation) of the right wrist. The test movement had to begin anytime within an interval from 60 ms before the onset of the response signal to 440 ms after it. If the movement did not begin during this interval, then an appropriate message (STARTED TOO SOON or STARTED TOO LATE) was presented, and the trial was repeated.

The subjects were not pressured to minimize their movement latency, and there was no overt penalty for early or late starts. However, we rewarded them monetarily for short movement durations, provided that the movement ended inside the target region. Thus, it was advantageous for them to be both fast and accurate once the movement began. Unusually slow movements (durations exceeding 600 ms) caused by oscillation of the handle at the end of the movement were followed by an error message (TOO SLOW) and were repeated. Such errors rarely happened after the first practice session.

Subjects were told that they could "do anything they wanted" with their eyes once they had successfully fixated on the home dot before the presentation of the response tone. We made no specific suggestions regarding movements of the eyes. The output of the eye-movement monitor was recorded starting 260 ms before the onset of the response signal and continuing until 200 ms after the end of the wrist rotation. Except for the fixation check preceding the response tone, the eye-movement monitor output was not evaluated until the end of the experiment. The subjects received no feedback regarding the behavior of their eyes.

After each wrist rotation, the subjects saw a display that showed the home dot, the target region, and the position of the cursor at the moment when the wrist rotation was deemed to have ended. They were also shown a point score earned on that trial. The score was an inverse linear function of the movement duration. For any test movement that ended outside the target region, an error message (MISSED TARGET) appeared, and the subject earned no points. Thus, the subjects always had complete knowledge-of-results about the ultimate spatial accuracy of their wrist rotations.

At the end of each trial block, the subjects saw a display showing the total points earned in that block and the number of trials on which the target was missed. This information was discussed with the subjects. They were continually encouraged to decrease their movement durations while still ending accurately in the target region.

Eye-movement analysis. In order to detect the presence of saccadic eye movements, the signal obtained from the eye-movement monitor on each trial was differentiated and filtered using a low-pass digital filter with an 80-Hz cutoff. The resulting velocity profiles were

analyzed to identify the occurrence of saccades. The beginning of a saccade was defined to be at the first moment in time at which the velocity of the eye exceeded $10^\circ/\text{s}$ and remained above that value continuously for at least 10 ms while subsequently exceeding $35^\circ/\text{s}$. The end of the saccade was defined to be at the first moment in time afterward at which the velocity of the eye fell below $10^\circ/\text{s}$. Using this algorithm, we were able to reliably detect the occurrence of saccades larger than about 0.7° of visual angle.

Wrist-rotation analysis. The trajectories of the wrist rotations were analyzed to determine the start and end of the movements, as well as to locate the transition between the initial-impulse and the error-correction phases. In these analyses, we used a movement parsing algorithm identical to that of Meyer et al. (1988). Here the wrist rotations were first filtered and differentiated to obtain smooth records of velocity and acceleration as a function of time. The beginning of each movement was defined to be at the first moment in time when the angular velocity of the handle exceeded $4^\circ/\text{s}$ and remained above that level for at least the next 20 ms. The end of the initial-impulse phase was defined as the first moment after peak velocity when (a) the velocity changed from positive to negative, (b) the acceleration changed from negative to positive, or (c) a positive-to-negative transition occurred in the derivative of acceleration while the acceleration was negative.

After locating the end of the initial impulse in a wrist rotation, we checked for evidence of error corrections. This involved finding the earliest moment after the end of the initial impulse when the velocity of the handle fell within a range of $\pm 12^\circ/\text{s}$ and remained there continuously for at least 160 ms. The end of the overall movement was temporarily defined as that moment, and the interval between the end of the initial impulse and the overall movement end was temporarily defined as the error-correction phase. The nominal error-correction phase was then checked to determine if it contained any voluntary movements, apart from passive tremor or oscillations that often occur at the end of rapid movements. If this interval had a duration of at least 60 ms, if the movement velocity exceeded an absolute value of $4^\circ/\text{s}$ at some moment in the interval, and if a net distance of 1° or more was traversed during that interval, then the interval was defined as containing an error correction. Otherwise, the overall movement was deemed to contain only an initial impulse, and the end of the initial impulse also served to define the end of the overall movement.

The ends of the initial impulse and overall movement were then adjusted in order to more closely equate their respective stopping criteria. Error-correction endpoints were repositioned to the nearest later moment when an acceleration zero-crossing occurred. Initial impulses that ended according to the first criterion stated earlier (positive-to-negative velocity change) and were not followed by an error correction were repositioned to end at the next moment in time when a positive-to-negative acceleration zero crossing occurred.

Design. Each subject served in six 50-min sessions on separate days over a 2-week period. The first two sessions were considered to

be practice and are not reported here. In each of the four test sessions, subjects produced movements in six to eight blocks of trials. Each block consisted of 10 movements. We included four different target conditions, corresponding to orthogonal combinations of two target distances and two target widths. Target centers were either 10.0° or 39.5° of wrist rotation away from the home position, and the targets were either 2.5° or 4.0° wide. The target condition was the same for all trials within a block, but varied from block to block. Orders of target conditions were counterbalanced within each day, and across days for the 4 subjects, by using a Latin-square design.

Results

Eye movements. Saccadic eye movements were observed on 1,173 of 1,200 total trials (98%). This occurred even though subjects were not told to move their eyes. Corrective saccades were also observed on 36% of the trials that contained primary saccades. Primary saccades often undershot their goal slightly, and the small secondary saccades served to correct that undershooting.

Table 1 shows the mean frequencies, amplitudes, and durations of the primary and secondary saccades as a function of target condition. These data reveal quite clearly that subjects produced saccades directly to the target region. Both the amplitude and the duration of the primary saccades increased with the distance to the center of the target: For amplitude, $F(1, 3) = 4163.0, p < .0001$; for duration, $F(1, 3) = 213.4, p < .001$. However, the width of the target did not affect these variables: For amplitude, $F(1, 3) = 1.1, p > .4$; for duration, $F(1, 3) < 1$. The amplitudes and durations of the secondary saccades, on the other hand, were not influenced by the target distance: For amplitude, $F(1, 3) = 2.7, p > .20$; for duration, $F(1, 3) < 1$. Similarly, secondary saccades were not affected by the target width: For amplitude, $F(1, 3) = 3.7, p > .10$; for duration, $F(1, 3) < 1$. These results suggest that subjects moved their eyes directly to the target region during the limb movements.

Wrist rotations. Features of the wrist rotations are summarized in Table 2 for each combination of target distance and width. Three measures characterize the overall movements: (a) movement time (MT), the mean duration of the wrist rotations; (b) constant error (CE), the mean deviation between the center of the target and the end location of the wrist rotations across trials; and (c) variable error (VE), the standard deviation of the wrist-rotation endpoints in a given condition. Also shown in Table 2 are measures of the mean durations of the initial-impulse and error-correction phases

Table 1
Mean Amplitudes and Durations of Saccades in Experiment 1

Target distance (wrist ^a)	Target width (wrist ^a)	Target distance (visual ^a)	Primary saccade			Secondary saccade		
			Frequency ^a (%)	Amplitude (visual ^a)	Duration (ms)	Frequency ^b (%)	Amplitude (visual ^a)	Duration (ms)
10.0	4.0	2.9	95	2.81	32.9	34	-.11	36.7
10.0	2.5	2.9	97	2.66	33.6	25	1.7	34.4
39.5	4.0	11.3	100	10.94	55.6	43	1.4	34.4
39.5	2.5	11.3	100	10.92	53.9	39	1.9	36.0

^a Percentage of total trials (for each target condition) containing at least one saccade. ^b Percentage of total trials containing two or more saccades.

of movement: the initial-impulse time (T_{ii}) and the error-correction time (T_{ec}).

As shown in Table 2, wrist rotations had much longer durations for the 39.5° targets than for the 10° targets, $F(1, 3) = 277.3$, $p < .001$. Target width did not influence MTs overall, $F(1, 3) = 4.2$, $p > .10$. However, wrist rotations to the 10° targets had longer durations when the targets were narrow (2.5°) than when they were wide (4.0°), yielding an interaction between target distance and target width, $F(1, 3) = 26.6$, $p < .05$. The constant error (CE) and variable error (VE) did not depend on the target distance or width: Constant error for distance, $F(1, 3) = 4.0$, $p > .10$, and for width, $F(1, 3) = 5.5$, $p > .10$; variable error for distance, $F(1, 3) = 1.6$, $p > .20$, and for width $F(1, 3) = 2.4$, $p > .20$. Taken together, these results suggest that subjects were sensitive to the target conditions and that they chose to trade movement speed for a given level of accuracy.

The durations of the initial impulses (T_{ii}) increased with increasing target distance, $F(1, 3) = 20.2$, $p < .05$, but T_{ii} was not affected by the target width, $F(1, 3) < 1$. The proportion of the trials that contained an error-correction phase (p_{ec}) increased somewhat with target distance, $F(1, 3) = 7.1$, $p < .10$, but p_{ec} did not depend on the target width, $F(1, 3) = 1.6$, $p > .20$. Finally, the error corrections that did occur had longer durations (T_{ec}) as target distance increased, $F(1, 3) = 34.6$, $p < .01$, but the durations did not depend on the target width, $F(1, 3) = 3.73$, $p > .10$. These results replicate those reported previously for wrist rotations (Meyer et al., 1988).

Temporal relations between eye and wrist movements. The most interesting results involve the temporal relations between the eye and wrist-rotation movements. Figure 1 shows examples of movement trajectories on two typical trials. In the upper panel are data from a trial on which the eye began to move before the wrist rotation; in the lower panel, the wrist rotation started before the eye movement. For each target condition and subject, Table 3 shows the proportion of trials on which the eye began to move before the onset of wrist rotation. This proportion constituted a majority of the trials (76%), with the mean interval between the onsets of eye movements and wrist rotations equal to 57.3 ms. As is evident in the upper section of Table 3, the relative times of movement onset did not depend systematically on the target condition. However, as the lower section indicates, they did vary considerably from subject to subject. Of the 4

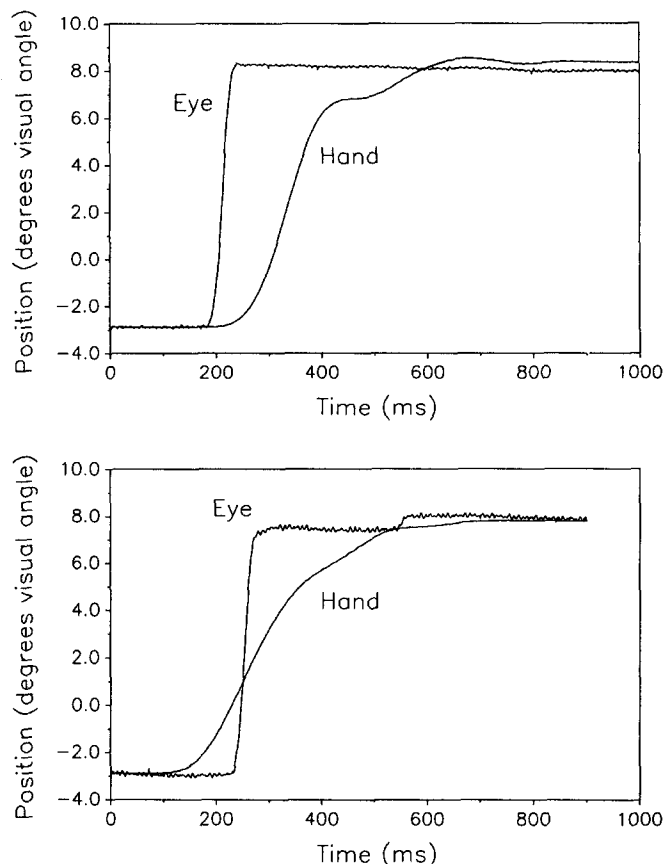


Figure 1. Examples of eye and wrist-rotation trajectories from two typical trials in Experiment 1.

subjects, 3 began to move their eyes before their wrists on most trials; 1 subject began the wrist rotation first most of the time. Within each subject, the relative onsets of movements did not vary across target conditions.¹

Regardless of the precise pattern of movement onsets, both the eyes and wrist began moving fairly closely in time. Only 1 of the 4 subjects initiated the movements more than 100 ms apart on the average. Because the durations of eye movements are generally much shorter than those for wrist rotations, such approximate simultaneous onset would ensure that the eye arrived at the target well before the wrist did (see Figure 1).

Figure 2 shows the time at which the eye movement began and ended relative to (a) the onset of wrist rotation, (b) the end of the wrist-rotation initial impulse (and hence the beginning of error corrections), and (c) the end of the overall wrist rotation. Times in Figure 2 are normalized with respect to the onset of wrist rotation (which occurred at time zero). These data reveal that a considerable amount of time elapsed after the eye movement but before the end of the wrist rotation. On the average, the eye arrived at the target region 224 ms before the end of the wrist-rotation initial impulse and 424 ms before the end of the overall wrist rotation.

¹ We have also observed large individual differences in relative eye and wrist-rotation onset times in several other experiments.

Table 2
Features of the Wrist Rotations in Experiment 1

Dependent variable	10° target distance		39.5° target distance	
	4.0° width	2.5° width	4.0° width	2.5° width
MT	311	359	485	485
CE	.14	.10	-.27	.00
VE	.90	.74	1.6	.86
T_{ii}	190	198	227	224
p_{ec}	.68	.76	.94	.97
T_{ec}	176	212	273	267

Note. MT = movement time (ms); CE = constant error (deg); VE = variable error (deg); T_{ii} = initial-impulse time (ms); p_{ec} = proportion of movements containing an error-correction phase; T_{ec} = error-correction time (ms).

Table 3
Relative Onset of Eye and Wrist-Rotation Movements in Experiment 1

Factor	% eye moved first	M eye lead (ms)
Target distance/width		
10.0/4.0	67	18
10.0/2.5	75	74
39.5/4.0	75	63
39.5/2.5	86	74
Subject		
1	27	-31
2	96	122
3	88	57
4	92	81

Note. M eye lead = Wrist-rotation starting time minus eye-movement starting time. Target distances and widths are in degrees of wrist arc.

To further assess the relation between the eye and wrist-rotation movements, we computed correlations between their temporal features. Because subjects were not pressured to minimize latencies (i.e., the movements could begin anytime within a wide temporal interval), correlations between the eye and wrist movement latencies were very high but not very meaningful. Also, for each target and subject, we found that the interval between the end of the saccade and the end of the wrist-rotation initial impulse was positively correlated with the duration of the initial impulse, mean $r = .62$, all $ps < .01$. In other words, when the wrist-rotation initial impulses were temporally longer, the eyes arrived at the target earlier in relation to the end of the initial impulse. This suggests that the eye and wrist movements were initiated together.

We also evaluated the wrist rotations to determine if they depended on their temporal relation to the eye movements. No differences were observed in the wrist-rotation durations or the means and standard deviations of the wrist-rotation endpoints as a function of whether the eye-movement onset preceded or followed the wrist-rotation onset, $F(1, 3) < 1$.

Spatial relations between eye and wrist movements. Thus far, the reported data show that the eye and wrist-rotation movements were initiated closely together in time and that the eyes arrived at the target well ahead of the wrist. We now turn to the issue of what the eyes did after arriving at the target. To examine this, we compared the mean position of the eyes for each target condition at three moments in time: (a) the end of the primary saccade, (b) the end of the initial impulse, and (c) the end of the overall wrist rotation. The eye position at the end of the primary saccade was on average 0.35° from the center of the target. Eye position changed very little between the end of the primary saccade and the end of the initial impulse (M change = 0.2°), and between the end of the initial impulse and the end of the overall wrist rotation (M change = 0.175°). The positions of the eyes at each of these three moments were all within fractions of a degree of each other, $F(2, 6) < 1$, showing that subjects left their eyes at the target region until after the wrist rotation ended.

The position of the eyes at the end of the initial impulse and the end of the overall wrist rotation was compared with the position of the wrist at these same times for each target

condition. If the position of the eyes provided a signal for controlling the wrist directly, then it might be expected that the eye and wrist positions would be correlated. A relatively short eye-movement distance might lead to a relatively short initial-impulse distance, or a relatively short overall wrist rotation (Prablanc, Echallier, Komilis, et al., 1979; Nemire & Bridgeman, 1987). However, there was no evidence of any such correlation.

This lack of correlation may have occurred for several reasons. First, the foveal region of the retina is approximately 1° to 2° in diameter. In the present task, a 3.5° handle rotation would be required to move the cursor through 1° of visual angle on the CRT, which is quite large relative to the wrist-rotation endpoint variability (i.e., the standard deviation of the wrist-rotation endpoints was on the order of 1° of wrist arc). So the wrist-rotation endpoints were not sufficiently variable to require movements of the eye in order to foveate them. Second, subjects had visual information about the target and the cursor throughout each trial. Thus, they would be aware of any error in their eye movements, and they could adjust the wrist rotations accordingly.

Discussion

Experiment 1 shows that when people produce rapid aimed limb movements, they spontaneously execute a saccade toward the target of their movements. The saccade is closely time locked to the initiation of the limb movement, although its order of occurrence does not seem crucial: Limb movements (e.g., wrist rotations) are equivalent whether they lead or follow an eye movement. Although subjects may have their own preferred strategies regarding the relative onsets of eye and limb movements, 3 out of 4 subjects tested began to move their eyes first on a majority of trials. Regardless of the relative onset of the eye and limb movements, the eye almost always arrived at the target well before the limb (i.e., wrist) did.

This pattern of results differs from the findings of some previous studies (e.g., Biguer et al., 1982; Prablanc, Echallier,

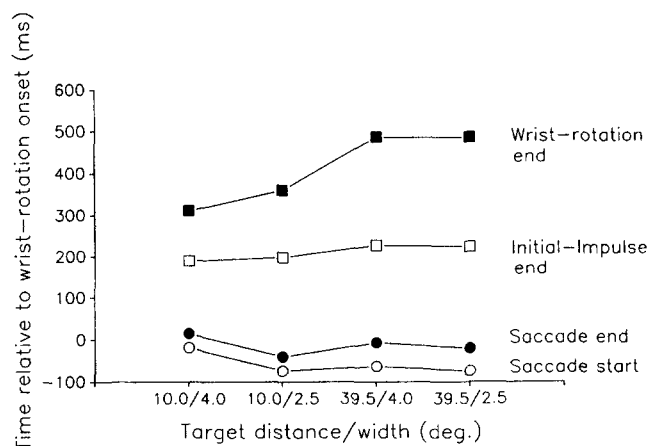


Figure 2. Mean times of events during eye and wrist-rotation movements relative to the onset of the wrist rotations in Experiment 1. (The wrist rotations began at time = 0.)

Komilis, et al., 1979; Prablanc et al., 1986). In those studies, the eye usually completed its movement to the target before the limb ever began to move. There are two possible explanations for this difference. First, in our study there was no uncertainty about the spatial location of the target. Second, subjects were not pressured to minimize movement latencies nor were they even requested to produce eye movements. In contrast, previous studies did involve spatial uncertainty and time pressure. As discussed above, such factors could cause subjects to begin moving their eyes before their limbs.

One question that we cannot answer yet is whether the eye movements in Experiment 1 served any useful purpose for the wrist rotations. The answer to this question is pursued in Experiment 2.

Experiment 2

Experiment 2 was designed to determine whether eye movements like those observed in Experiment 1 play any significant role in the guidance of limb movements, and if so, to examine what that role may be. One possible benefit of moving the eyes to the target is that such movements might provide a centrally registered eye-position signal (extraretinal information) for identifying the location of the target (Prablanc, Echallier, Komilis, et al., 1979). Because the eyes usually arrive at the target before the end of the initial impulse in a limb movement, this signal could be used to control final error corrections. In fact, under some circumstances, people can guide their limbs accurately to specific locations by using only eye-position information (Hansen & Skavenski, 1977, 1985; Hill, 1972; Morgan, 1978).

A second possible benefit of producing saccades to the target is that having the eye at the target before the start of error corrections might improve the visual (retinal) feedback available for them. In Experiment 1, the eyes typically reached the target over 200 ms before the error corrections began (Figure 2). This is well within the time needed to process visual feedback for movement control (Carlton, 1981a; Keele & Posner, 1968; Zelaznik et al., 1983). Furthermore, the duration of the error corrections (200 ms; Figure 2) was sufficiently long for visual feedback obtained at the end of the initial impulses to be incorporated into these corrections before the movements ended.

To determine the relative contributions of retinal and extraretinal information for limb movements, we again had subjects produce wrist rotations like those studied in Experiment 1. That is, on one half of the trials, subjects were permitted to move their eyes as they wished. However, on the other half of the trials, subjects were prohibited from making saccades; instead, they had to maintain eye fixation at the home position throughout each wrist rotation. Also, on one half of the trials in each of these two eye-movement conditions, the image of the cursor disappeared from the display screen at the moment when the wrist rotation began; subjects completed these latter movements without concurrent visual feedback regarding the wrist's position.

The rationale of Experiment 2 is straightforward. If eye movements are not important for achieving accurate limb movements, then there should be no difference in accuracy

between wrist rotations performed under the two different eye movement conditions here. However, if eye movements do play a key role in the production of limb movements, then performance should deteriorate when subjects must keep their eyes fixated at the home position. Furthermore, comparison of movements performed with and without a visible cursor may help distinguish between the various roles that eye movements play. In particular, if eye movements contribute to limb movements solely through visual feedback provided during the movement, then there should be no detrimental effect of constraining the eyes when the cursor is not visible. This is because no visual feedback is available when the cursor is invisible, regardless of the behavior of the eyes. However, if moving the eyes to the target provides an improved sense of the target's location (e.g., through eye-position information), then any benefit derived from producing a saccade may be the same whether or not the cursor is visible.

Method

Subjects. Four right-handed students served as paid subjects. They were drawn from the same pool as those in Experiment 1, but none had served previously. None had any apparent visual or motor deficiencies. Each subject received \$4/h, plus bonuses based on good performance.

Procedure. The procedure was similar to that of Experiment 1. Exceptions are noted below.

Eye-movement conditions. Subjects were studied under two different eye-movement conditions. On one half of the trials (the *saccade condition*), subjects were permitted to move their eyes as they wished during the wrist rotations, as in Experiment 1. On the other half of the trials (the *control condition*), subjects had to maintain eye fixation at the home location throughout the entire wrist rotation. We signaled the control condition to the subject by flashing the plus sign at the home position during the interval between cursor alignment and the beginning of the countdown sequence, and signaled the saccade condition by having the plus sign remain continuously visible. Trials for the saccade and control conditions alternated throughout the experiment. After each trial of the control condition, the eye-monitor output was analyzed to determine whether subjects had complied with the eye-movement restriction. If the position of the eye at the end of the wrist rotation differed by more than $\pm 1^\circ$ of visual angle from its position during the pretrial fixation check, then an error message (EYES MOVED) was presented, and the trial was repeated at the end of the block. There was no penalty for such errors. During each trial of the saccade condition, the position of the eyes was recorded as in Experiment 1.

Visual-feedback conditions. The visual feedback that subjects received during the wrist rotations varied from trial to trial. Each trial involved either a *visible-cursor* or *invisible-cursor condition*. Under the visible-cursor condition, which occurred on one half of the trials, the cursor remained visible throughout the entire trial, as it had in Experiment 1. The visible-cursor condition provided subjects with complete concurrent feedback regarding the progress of their movements. Under the invisible-cursor condition, which occurred on the other half of the trials, the cursor disappeared as soon as the handle moved 0.3° (0.1° of visual angle) to the right of the home position toward the target. The cursor did not reappear until the presentation of the display with the subject's results at the end of the trial. Because subjects could not see their hand or the handle in the invisible-cursor condition, they received no concurrent visual feedback about the progress of the movement. The two cursor conditions were distributed randomly among the trials in a block, subject to the constraint that

one half of the trials in each of the two eye-movement conditions (i.e., saccade and control) were run under each of the two cursor conditions. Thus, subjects did not know beforehand whether the cursor would be visible. The home and target positions always remained visible throughout each trial.

Movement-target conditions. Two target conditions were included here. Target distance was either 10° or 39.5°, and the target width was 2.5°. The target distances corresponded to visual eccentricities of 2.86° and 11.29° between the home and target center, respectively. Only two targets were used so as to maximize the number of observations available for each condition. This had the added benefit of providing subjects with considerable practice in producing the requisite wrist rotations. As a result, effects of eye-movement condition and cursor visibility could be more readily attributed to the loss or degradation of useful concurrent information.

Design. Each subject performed six blocks of 12 trials during each session. The target condition remained constant within a block, but varied from block to block. Within each block, both cursor conditions and both eye-movement conditions were presented (the eye-movement conditions alternated from trial to trial, and the cursor conditions were pseudorandomly assigned, as described earlier). Thus, there were eight different conditions overall: 2 (target conditions) × 2 (cursor conditions) × 2 (eye-movement conditions). Each subject experienced each condition during each session. The order of presentation of target conditions was counterbalanced across blocks within each session and across sessions for each of the 4 subjects.

Results

The most important results involve the effects of eye-movement condition and cursor condition on features of the wrist rotations. We first focus on the overall movements and then describe the initial-impulse and error-correction phases.

In our analyses, it is important to establish that the constraints imposed by the instructions regarding eye movements were successful. We evaluated the mean position of the eye at the beginning and the end of the wrist rotations separately for each eye-movement condition and each target condition. In the control condition, in which no eye movements were permitted, the positions of the eye at the beginning and the end of the wrist rotations were about equal (averaging across the two target conditions, the mean eye position was -3.1° at both the beginning and end of the wrist rotations), $F(1, 3) = 1.3, p > .15$. Subjects successfully inhibited their eye movements when required to do so. In the saccade condition, however, eye movements still occurred frequently, as in Experiment 1.

At the start of the wrist rotations, the mean eye position was slightly more positive (i.e., closer to the target) in the saccade condition ($M = -1.9^\circ$) than in the control condition ($M = -3.1^\circ$). This reflects the fact that some saccades were initiated before the beginning of the wrist rotations. However, these effects were unreliable: There were no significant differences in the position of the eye at the beginning of the wrist rotation as a function of target distance, $F(1, 3) = 1.8, p > .25$, cursor visibility, $F(1, 3) = 7.8, p > .05$, or eye-movement condition, $F(1, 3) = 2.9, p > .15$.

At the end of the wrist rotations, the eyes were much closer to the target in the saccade condition than in the control condition (mean position in the saccade condition = -1.1° and 5.4° for targets centered at 0.0° and 8.4° , respectively),

$F(1, 3) = 36.1, p < .01$. Also, the position of the eyes at the end of the wrist rotations depended on the target distance, $F(1, 3) = 38.2, p < .01$. However, eye position did not depend on the target distance in the control condition, and as a result, the effects of eye-movement condition interacted with target distance, $F(1, 3) = 55.1, p < .01$.²

Target hits. The first row of Table 4 shows the proportion of wrist rotations in each condition that ended inside the target region. As can be seen, wrist rotations were generally more accurate when the target distance was shorter, $F(1, 3) = 11.4, p < .05$, when the cursor was visible, $F(1, 3) = 210.8, p < .001$, and when the eyes were free to move, $F(1, 3) = 8.7, p < .10$.

Movement times. The durations of the overall wrist rotations (MT) are shown in Table 4 separately for each target and condition. As expected, wrist rotations had much longer durations for the longer target distances, $F(1, 3) = 39.8, p < .01$. Movement times did not depend at all on the eye-movement condition, $F(1, 3) = 1.3, p > .4$, and there was no main effect of cursor visibility, $F(1, 3) = 4.8, p > .10$. However, the longer (39.5°) movements had shorter durations when the cursor was invisible than when it was visible, yielding an interaction between the effects of cursor visibility and movement distance, $F(1, 3) = 31.3, p < .05$. As will be discussed later, this occurred because error corrections consume more time for more difficult movements (longer distances), and less time is spent performing error corrections when the cursor is invisible.

Variable errors. The upper panel of Figure 3 shows the VEs of the wrist rotations for each condition. Variable errors increased when the target distance was longer, $F(1, 3) = 56.1, p < .01$, and when the cursor was invisible, $F(1, 3) = 105.4, p < .01$. Furthermore, the increase in VEs caused by the invisible cursor was greater for the longer distances, yielding an interaction between the effects of target distance and cursor visibility, $F(1, 3) = 37.4, p < .01$. This suggests that longer movements depend more on visual feedback than do shorter movements.

There was no main effect of the eye-movement condition on wrist-rotation VEs, $F(1, 3) < 1$. However, the effects of the eye-movement condition and cursor visibility did interact with each other, $F(1, 3) = 18.0, p < .05$. In essence, when the cursor was invisible, VEs were large and did not depend on the position of the eye. However, when the cursor was visible, the requirement to maintain fixation at the home location

² Under the saccade condition, the mean position of the eye at the end of the wrist rotations was somewhat short of the target. This occurred because, on some trials, subjects did not move their eyes from the home position even though they were permitted to do so. Considering only those saccade-condition trials on which a saccade was detected (80% of the total), the mean eye position at the end of the wrist rotation was -0.4° and 7.0° of visual angle for targets centered at 0.0° and 8.4° , respectively—much closer to the target. When queried during debriefing (after completion of the experiment), subjects mentioned that they occasionally forgot to move their eyes on some saccade-condition trials. As a result, subjects in Experiment 3 were continually reminded to keep the eye-movement condition in mind on each trial, and to remember that they could do “whatever they wanted” with their eyes on trials in the saccade condition.

(control condition) increased the endpoint variability, but only for the most eccentric (39.5°) target. We therefore infer that at least one component of the information provided by movements of the eye is retinal information about the state of the moving limb or the target.³

Constant errors. Constant errors of wrist rotations for each condition are shown in the lower panel of Figure 3. First, a main effect of target distance is evident here: On the average, wrist rotations toward the 10° target overshoot its center, whereas wrist rotations toward the 39.5° target undershot it, $F(1, 3) = 24.4, p < .05$. Although the eye-movement condition did not affect the MTs or VEs, it did influence CE. The wrist rotations traveled farther in the control condition than in the saccade condition, producing saccades to a target influences limb movements. Furthermore, the effect of the eye-movement condition did not interact with the visibility of the cursor, $F(1, 3) = 1.7, p > .25$, nor did cursor visibility have a consistent main effect, $F(1, 3) = 6.9, p > .05$.⁴ These results suggest that at least some of the influence of the eye-movement condition stems from processes other than those involved in evaluating visual feedback.

Initial-impulse phase. More detailed information about the wrist rotations comes from separately evaluating the initial-impulse and error-correction phases of movement. Table 4 includes the mean duration of the initial-impulses (T_{ii}) for wrist rotations in each of the conditions. As with the overall MT, T_{ii} was substantially longer for wrist rotations toward farther targets, $F(1, 3) = 12.5, p < .05$, but was not affected by the eye-movement condition, $F(1, 3) = 3.6, p > .15$, or cursor visibility, $F(1, 3) < 1$. The latter (null) result is not surprising, because initial impulses may be essentially ballistic (Woodworth, 1899). Thus, one would not expect them to depend on the presence or absence of visual feedback.

Although the durations of the initial impulses were not affected by either the eye-movement condition or cursor visibility, the distance traveled by the wrist during the initial impulses (D_{ii}) was. The top panel of Figure 4 shows what happened. The initial impulses traveled farther as target distance increased, $F(1, 3) = 169.0, p < .005$. Also, when the eyes remained fixed at the home position in the control condition, the initial impulses traveled significantly more

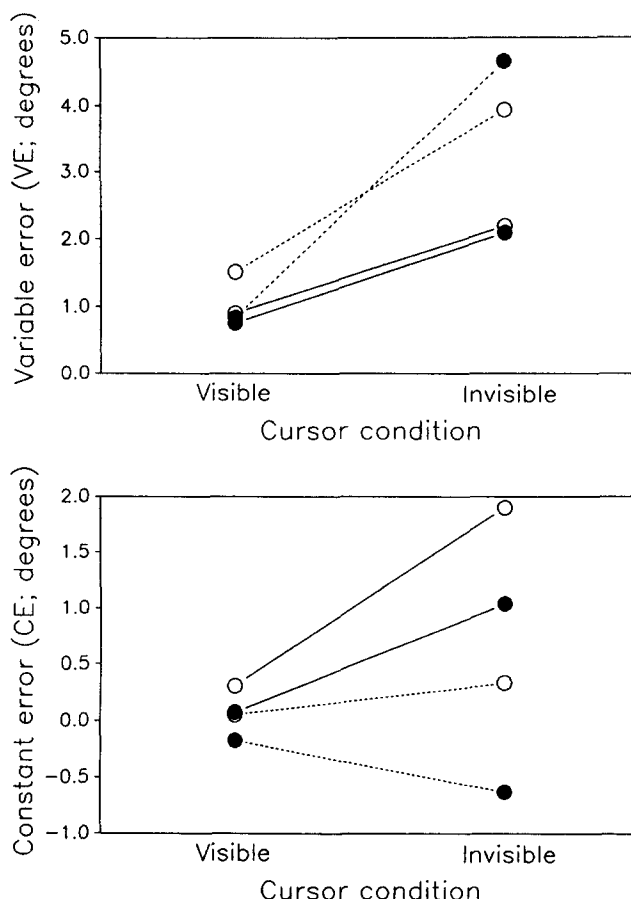


Figure 3. Upper panel: Mean variable error (VE, degrees) for wrist rotations in Experiment 2. Lower panel: Mean constant error (CE, degrees) for wrist rotations in Experiment 2. Positive values denote movements that overshoot the center of the target; negative values denote movements that undershot it. (Filled circles = saccade condition; open circles = control condition; solid lines = 10° targets; dashed lines = 39.5° targets.)

distance than they did in the saccade condition, $F(1, 3) = 32.2, p < .05$. Cursor visibility, on the other hand, had no effect on the D_{ii} s, $F(1, 3) < 1$, as might be expected if a visible cursor served primarily to facilitate error corrections based on visual feedback. These results show that at least some of the effect of the eye-movement condition occurred during the

Table 4
Features of the Wrist Rotations in Experiment 2

Dependent variable	Control condition				Saccade condition			
	10°		39.5°		10°		39.5°	
	VIS	INV	VIS	INV	VIS	INV	VIS	INV
HITS	.84	.34	.61	.21	.87	.41	.84	.23
MT	412	393	630	535	394	394	600	541
T_{ii}	191	197	254	258	192	196	247	242
p_{ec}	.88	.85	.96	.92	.82	.79	.98	.96
T_{ec}	253	230	390	301	244	242	358	309

Note. VIS = visible cursor condition; INV = invisible cursor condition; HITS = proportion of wrist rotations ending inside the target region; MT = movement time (ms); T_{ii} = initial-impulse time (ms); p_{ec} = proportion of movements containing an error-correction phase; T_{ec} = error-correction time (ms).

³ The 10° target, with a visual eccentricity of 2.9°, may have been close enough to the fovea for adequate resolution in the control condition. However, the 39.5° target was 11.3° of visual angle from the home position; acuity at this eccentricity is quite poor.

⁴ The effect of cursor visibility did interact with that of target distance: Wrist rotations toward 10° targets ended farther from the center of the target with an invisible cursor than with a visible cursor, but constant errors of wrist rotations toward 39.5° targets were relatively insensitive to the cursor condition. This may be due in part to the dramatic increase in movement-endpoint variability (VE, Figure 3, upper panel) when the cursor was removed for 39.5° targets. As discussed later, these data can be understood more clearly by examining what happened in the initial-impulse and error-correction phases of the wrist rotations.

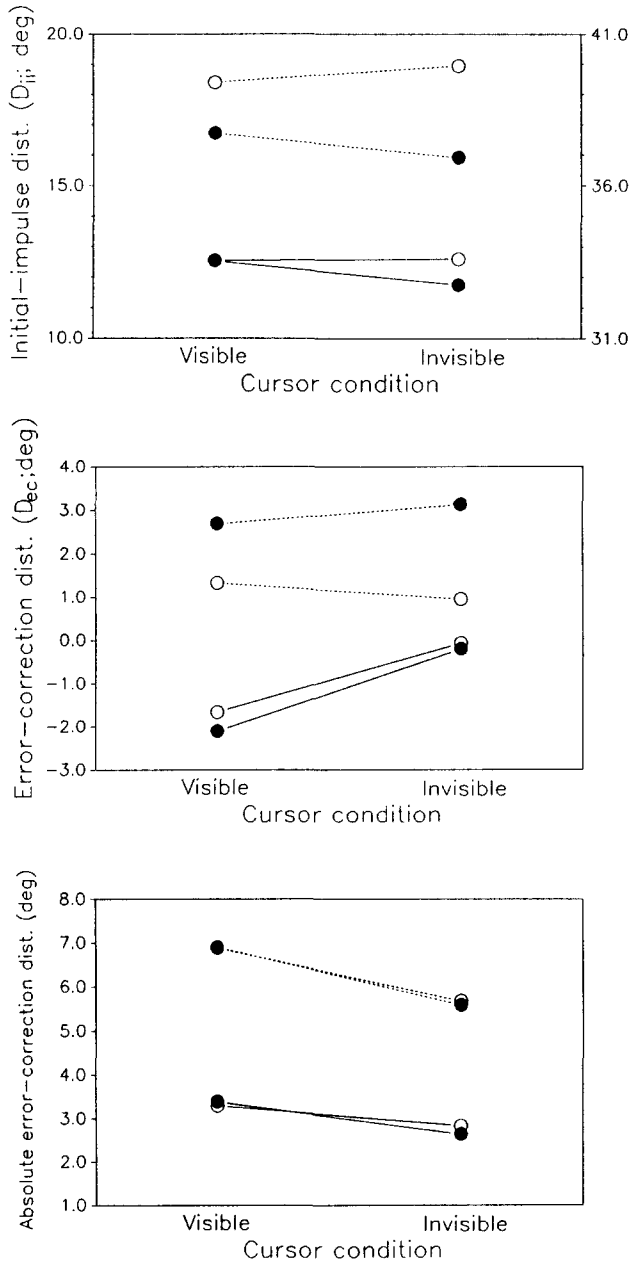


Figure 4. Top panel: Distance traversed during the initial-impulse phase of wrist rotations (D_{ii} , degrees) in Experiment 2. The ordinate on the right applies to the dashed lines. Middle panel: Net distance traveled during error corrections (D_{ec} , degrees) for wrist rotations in Experiment 2. Positive values denote corrections to the right; negative values denote corrections to the left. Bottom panel: Absolute distance (degrees) traversed during error corrections for wrist rotations in Experiment 2. The plotted data are the means of the absolute values of the distance traversed during the error-correction phase on each trial (excluding movements with no error corrections). (Filled circles = saccade condition; open circles = control condition; solid lines = 10° targets; dashed lines = 39.5° targets.)

initial-impulse phase of the wrist rotations and was not limited to processes involved in the error-correction phase. Furthermore, the consistent lengthening of D_{ii} when saccades were prohibited suggests that constraining the eyes may induce a

shift in the perceived location of the target relative to the limb.⁵

Also, the difference between D_{ii} in the control and saccade conditions increased when subjects could not see the cursor, $F(1, 3) = 10.8, p < .05$. As Figure 4 shows, the distance traveled during the initial impulses in the saccade condition (filled circles) was shorter when the cursor was invisible than when it was visible. In the control condition, D_{ii} did not depend on cursor visibility. Because the cursor disappeared at the onset of wrist rotation, this result suggests that subjects may have been more sensitive to the presence or absence of the cursor when their eyes were at the target than when their eyes remained fixed at the home position.

Error-correction phase. There were also some important effects of eye-movement condition and cursor-visibility on the error-correction phase that could provide insight into the source of information used during the error corrections. Table 4 shows the proportion of wrist rotations that contained an error-correction phase (p_{ec}), together with the mean duration of the error corrections when they did occur (T_{ec}). Error corrections were more likely for wrist rotations to farther targets, $F(1, 3) = 10.3, p < .05$. Error corrections tended to occur more frequently when the cursor was visible, but not reliably so, $F(1, 3) = 1.3, p > .3$. However the eye-movement condition did not affect p_{ec} , $F(1, 3) = 1.1, p > .3$.

The durations of the wrist-rotation error corrections (T_{ec}) paralleled the pattern found for p_{ec} : Error corrections had longer durations for farther targets, $F(1, 3) = 272.4, p < .001$; there was a marginally significant reduction in T_{ec} when the cursor was invisible, $F(1, 3) = 4.6, p < .15$; and the eye-movement condition had no effect on the duration of the error corrections, $F(1, 3) < 1$.⁶

Although the frequencies and durations of the error corrections were fairly insensitive to the eye-movement condition,

⁵ Other kinematic features of the wrist rotations showed similar patterns, demonstrating that the differences in the initial impulses as a function of eye-movement condition occurred quite early in the movement. For example, although the mean time at which peak acceleration occurred in the wrist rotations was unaffected by the eye-movement condition, $F(1, 3) < 1$, the mean velocity at that moment was greater under the control condition than under the saccade condition, $123^\circ/\text{s}$ versus $118^\circ/\text{s}$; $F(1, 3) = 10.0, p < .05$. The peak-acceleration time was, on the average, only 60 ms after the beginning of the wrist rotations, suggesting that the initial impulses in the control condition were destined from their outset to travel farther. Similarly, although the mean time of peak velocity was the same under the two eye-movement conditions (114 ms after the onset of movement), $F(1, 3) = 2.4, p > .20$, wrist rotations in the control condition had already traveled farther by then, $F(1, 3) = 11.4, p < .05$. These results suggest that maintaining eye fixation at the home position throughout a limb movement may result in a rescaling of the force parameter for the initial impulses, but not the time parameter for them (cf. Meyer, Smith, & Wright, 1982).

⁶ Further inspection of Table 4 reveals that the reduction in T_{ec} due to cursor invisibility was greater for the 39.5° targets than for the 10.0° targets (69 ms vs. 12 ms). Although just marginally reliable, $F(1, 3) = 9.8, p < .10$, the magnitude and direction of this interaction accounts for the pattern observed earlier in movement times (MTs). The decreases in overall MT under the invisible-cursor condition were 77 ms and 9 ms for the far and near targets, respectively (Table 4).

the nature of the corrections themselves depended on what the eyes did. The middle panel of Figure 4 shows the net distance traversed by the wrist during the error-correction phase (D_{ec}) under each condition. A significant interaction occurred between the effects of target distance and cursor visibility: For 10° targets, D_{ec} was much closer to zero when the cursor was invisible than when it was visible, $F(1, 3) = 14.7$, $p < .05$, whereas cursor visibility had little effect on D_{ec} for 39.5° targets. The magnitude of D_{ec} presumably reflects subjects' perception of the error in the initial impulses, and according to this interpretation, the interactive effects of target distance and cursor visibility suggest that the perception of such errors was unaffected by cursor visibility for longer movements. This is not surprising, because the initial-impulse endpoints were much more variable for longer movements, and thus the interaction may simply reflect a threshold in error detection.

In addition, two marginally reliable trends are apparent in the middle panel of Figure 4. First, D_{ec} was positive for 39.5° targets but negative for 10° targets, $F(1, 3) = 3.1$, $p < .2$. This would be expected if subjects attempted to correct initial impulses that were perceived to have undershot or overshot their goal, respectively. And indeed, this was the direction of the errors in the initial impulses of the wrist rotations (see Figure 4, top panel). Second, D_{ec} was closer to zero under the control condition than under the saccade condition, $F(1, 3) = 8.3$, $p < .10$. The error corrections performed under the control condition yielded less net change in the position of the wrist. This suggests that the information on which error corrections were based in that condition was degraded.

These conclusions are further supported by an evaluation of the absolute distances traversed by the wrist during the error-correction phase, as shown in the bottom panel of Figure 4. Here it appears that error corrections traveled farther (absolutely) for movements to more distant targets, $F(1, 3) = 54.8$, $p < .01$. Similarly, error corrections traveled farther when the cursor was visible than when it was invisible, $F(1, 3) = 12.0$, $p < .05$, suggesting that a visible cursor is perceived to provide useful information for the corrections. However, the total amount of distance traveled during the error corrections did not depend on the eye-movement condition, $F(1, 3) < 1$. Thus, the position of the eye at the end of the initial impulse had little bearing on the attempted error corrections.

When these data are considered together with those concerning D_{ec} (Figure 4, middle panel), an important picture emerges: Although just as much absolute wrist-rotation movement occurred during the error corrections under the saccade and control conditions, the movement under the control condition was less beneficial. It yielded less net change in the position of the wrist and hence a smaller reduction in the wrist-rotation error for the same duration and total amount of distance traveled.

Discussion

The main finding of Experiment 2 is that rapid aimed limb movements (wrist rotations) were less accurate when subjects were prohibited from making saccades during the movements. Although limb-movement times and variable errors were

unaffected by constraining the eyes, signed constant errors increased significantly when the eyes remained fixed at the home position (i.e., the wrist rotations traveled farther). This happened regardless of the cursor visibility, suggesting that eye movements, when permitted, did more than simply provide better retinal information about the moving limb. Rather, the eye movements also appeared to provide extra-retinal information about the location of the target.

An analysis of the initial-impulse and error-correction phases of movement yielded additional details regarding the relationship between the eye and limb movements: Constraining the eyes affected both phases of wrist rotation. The initial impulses traveled faster and farther under the control (no saccade) condition, even though their durations did not change. This implies that the representation of the target used to produce the initial impulses depended on the eye-movement constraint. In particular, when the eyes remained at the home position, the target was apparently perceived to be farther away than when eye movements were permitted.

The error-correction phase of limb movement was also influenced by the eye-movement condition. During error corrections, the net distance traveled was closer to zero when eye movements were prohibited (control condition). Thus, although subjects attempted to perform the same amount of error correction regardless of the eye-movement condition, the resulting error corrections were less effective when the eyes remained at the home position than when they moved to the target. Because this happened regardless of cursor visibility, it cannot be attributed entirely to the degradation of retinal information about the cursor (visual feedback) when the eyes remained at the home position.

Cursor visibility did have some effect, however. When subjects could see the cursor, the variability of the wrist-rotation endpoints decreased and the proportion of target hits increased. Although features of the initial impulses stayed the same regardless of cursor visibility, the distance traveled by the wrist during the error corrections was smaller when the subject did not receive visual feedback from the cursor.

Thus, Experiment 2 demonstrates that both retinal and extraretinal information contribute to the production of rapid aimed limb movements. Because much prior work has investigated details of visual-feedback processing based on retinal information (e.g., Carlton, 1981a, 1981b; Prablanc, Echallier, Komilis, et al., 1979), we chose instead to focus our efforts next on understanding the role of extraretinal eye-position information in movement control. This issue is pursued in Experiment 3.

Experiment 3

There were two major differences between the saccade and control conditions of Experiment 2 that might explain why wrist rotations were more accurate under the saccade condition than under the control (no saccade) condition. First, when the error corrections began in the saccade condition, a saccade had just recently been executed from the home position to the target region. Second, in the saccade condition, the eyes were pointing at the target during the final error corrections. Neither of these events occurred in the control condition. Either (a) extraretinal information about a recently

produced saccade to the target, for example, knowledge of the commands used to produce the eye movement, or (b) extraretinal information about the current position of the eyes when at the target may have provided important cues used during the wrist rotations. Experiment 3 was therefore designed to examine these possibilities.

We consider three specific hypotheses here. According to the first, important extraretinal information comes from having the eyes gaze at the target before the end of the limb movement, but the actual movement of the eyes per se to the target is unimportant. This is referred to as the *position-only hypothesis*. Another hypothesis is that producing a saccadic eye movement from the home position to the target provides all the extraretinal information used for producing a limb movement (e.g., wrist rotation); no explicit evaluation of eye position after the saccade is required. This is referred to as the *movement-only hypothesis*. Finally, a third (hybrid) hypothesis is that extraretinal information about both the movement of the eyes and their final position at the target is used for a limb movement. This is referred to as the *movement-plus-position hypothesis*.

To test these hypotheses, we had subjects produce wrist rotations under a new eye-movement condition, in addition to the ones previously studied. Here, subjects had to produce a smooth-pursuit eye movement from the home position to the target before beginning a wrist rotation, and then their eyes had to remain fixated on the target throughout the entire wrist rotation. This *pursuit condition* provides a situation in which subjects can gaze at the target during the wrist rotation without having executed a saccade to do so.⁷

The three hypotheses just outlined make different predictions about the quality of wrist rotations under the pursuit condition. According to the position-only hypothesis, wrist rotations under the pursuit condition should be identical to those performed under completely unconstrained conditions (i.e., the saccade condition) because, for both conditions, subjects will be gazing at the target throughout much of the wrist rotation. Having the eyes directed at the target is supposedly all that matters, not how the eyes reach the target. Such a pattern would extend previous research that has shown equally accurate pointing after both saccadic and pursuit eye movements (Hansen, 1979; Hansen & Skavenski, 1977; Honda, 1985).

The movement-only hypothesis, however, makes a different prediction. According to that hypothesis, producing a saccade to the target is crucial, and imposing any constraints on the behavior of the eyes will have detrimental effects on subsequent limb movements. A strong version of this hypothesis further maintains that smooth-pursuit eye movements would not produce any beneficial information beyond what is available under the control (no saccade) condition, in which subjects' eyes must remain fixated at the home position throughout an entire limb movement. Thus, wrist rotations in the pursuit condition would then be the same as those performed under a control condition, as in Experiment 2. Such a finding would fit with previous demonstrations that reveal differences in the perceived final gaze location after saccadic and pursuit eye movements (Festinger & Canon, 1965; Honda, 1984, 1985; Mack & Herman, 1972; Miller, 1980).

Any other pattern of results would support the hybrid movement-plus-position hypothesis. That is, if wrist rotations produced under conditions in which subjects make smooth-pursuit eye movements to the target are not exactly the same as those under either the control or saccade condition, then the contribution of saccadic eye movements could not be attributed solely to either the movement of the eyes or the position of the eyes per se. Instead, mechanisms that extract extraretinal information about *both* movement and position would be implicated.

Method

Subjects. Six right-handed students served as paid subjects. They had not served previously. Each was paid \$4/hr, plus bonuses based on good performance.

Procedure. The procedure was similar to that used in Experiments 1 and 2. Exceptions are noted below.

Cursor-visibility and eye-movement conditions. Both cursor conditions (visible-cursor and invisible-cursor) and both eye-movement conditions (saccade and control) studied in Experiment 2 were included here. Furthermore, one more eye-movement condition (pursuit) was added. Trials under each of the three eye-movement conditions began the same way: Subjects aligned the cursor with the home dot, which was then replaced by a plus sign that subjects fixated visually. (In the control condition, the plus sign flashed, indicating that subjects should remain fixated there throughout the wrist rotation.)

In the pursuit condition, when the plus sign appeared, the dot at the home position began to drift smoothly toward the target region. It moved with a sinusoidally varying velocity (half a cycle) that had a mean of 5°/s. Subjects had to follow the dot with their eye until it came to rest in the center of the target. After the eye arrived at the target, the pursuit eye movement was evaluated (as described in the next paragraph), the subjects received the countdown sequence, and they produced a wrist rotation as in Experiments 1 and 2. However, their eyes had to remain fixated at the target location until the wrist rotation was completed. Because it was necessary to include a visible fixation point in the pursuit condition, the dot remained at the center of the target throughout the wrist rotation. To match the displays in the other conditions, a dot was also added to the target there.

Evaluation of pursuit eye movements. After the dot had drifted to the target, but before the countdown sequence began, the pursuit eye movements were evaluated to determine whether subjects had accurately tracked the dot's motion. Three features of the eye movements were inspected. First, the mean eye position during the first 150 ms of pursuit had to be within $\pm 2^\circ$ of the home position. Second, the mean eye position during the last 100 ms of the pursuit had to be within 2° of the target center. Third, no saccades greater than 2° in amplitude were allowed during any portion of the pursuit.

If any of these criteria failed to be met, then the dot returned to the home position, and subjects received another chance to smoothly

⁷ Previous investigators have found that subjects consistently underestimate the extent of smooth-pursuit eye movements compared with saccades of the same magnitude (Honda, 1984, 1985; Mack & Herman, 1972; Miller, 1980). However, the underestimation of smooth pursuits only occurs reliably when people must perceptually estimate the extent of movement; when they have to point at the end location of an eye movement (a motor response), they can do so accurately after both saccades and smooth pursuits (Hansen, 1979; Hansen & Skavenski, 1977; Honda, 1985). Because Experiment 3 involves motoric responses, it is possible that people would perform as accurately after both saccadic and pursuit eye movements.

follow the dot to the target. After five unsuccessful attempts, the eye-monitor calibration routine was automatically invoked, and the trial was repeated from the beginning. If all three criteria were successfully met, then the sequence of countdown tones was initiated, and the trial proceeded. As in the other conditions, before the response signal was presented, we checked whether fixation was within 1° of the required location. In the pursuit condition, the required fixation was at the center of the target; in the other conditions, it was at the home position.

After each trial in the pursuit and control conditions, a check was also made to verify that subjects had complied with the fixation requirement. If the position of the eye at the end of the wrist rotation differed by more than 1° from its position during the pretrial fixation check, then an error message (EYES MOVED) was presented, and the trial was repeated at the end of the block.

Movement-target conditions. The targets for the wrist rotations were the same as in Experiment 2 (2.5° wide, centered 10° and 39.5° from the home position). However, to enhance any possible effects of retinal eccentricity, the visual distances between the images on the CRT were increased by a factor of 1.3. As a result, 1° of handle rotation produced 0.372° of cursor movement, compared to 0.286° in Experiments 1 and 2. Correspondingly, the visual eccentricity between the home position and the center of the target region was 3.7° and 14.7° for targets requiring wrist rotations of 10° and 39.5°, respectively. The visual width of the target was also increased proportionately. Although subjects viewed the display from the same distance as in Experiments 1 and 2, the effect of increasing the visual gain was the same as if the display were simply moved closer to them. What subjects needed to do with their wrists in order to move the cursor to the target remained the same.

Design. Each subject performed six blocks of 12 trials during each of four sessions. The target remained constant within a block, but varied from block to block. Within each block, both cursor-visibility conditions and all three eye-movement conditions were presented. The eye-movement condition varied sequentially, and cursor visibility was determined randomly on each trial, subject to the constraint that equal numbers of trials in each eye-movement condition were performed with a visible and invisible cursor (as in Experiment 2). Thus, there were 12 different conditions studied in Experiment 3: 2 (target conditions) × 2 (cursor conditions) × 3 (eye-movement conditions). Each subject experienced each condition in each session. The order of presentation of target conditions was counterbalanced across blocks within each session, and across sessions for the 6 subjects.

Results

Eye-movement constraint. The position of the eyes at the beginning of the wrist rotations depended on both the eye-

movement condition, $F(2, 10) = 231.2, p < .0001$, and the target condition, $F(1, 5) = 730.5, p < .0001$. In the control condition, the eyes were at the home position (-3.7° visual angle) at the beginning of the wrist rotation (mean eye position = -3.9° , for both the short and long target distances); in the pursuit condition they were at the target (mean eye position = -0.1° and 11.0° , for targets with visual eccentricities of 0.0° and 11.0° , respectively); and in the saccade condition, they were near the home position but on their way to the target (mean eye position = -2.6° and -1.1° , for the short and long targets). Not surprisingly, the effects of target distance also interacted with those of eye-movement condition, $F(2, 10) = 927.2, p < .0001$. Cursor visibility marginally affected the position of the eye, $F(1, 5) = 4.2, p < .10$.

At the end of the wrist rotations, the eyes were still at the home position in the control condition (mean eye position = -4.0° , for both the short and long target distances), whereas they were at the target in both the saccade condition ($M = -0.4^\circ$ and 10.0° , for targets at 0.0° and 11.0° of visual angle, respectively) and pursuit conditions ($M = -0.2^\circ$ and 10.9°), $F(2, 10) = 993.8, p < .0001$. Post-hoc analyses revealed no reliable differences between the position of the eye at the end of the wrist rotations in the saccade and pursuit conditions, so any differences in wrist rotations across these two conditions cannot be attributed to differences in static extraretinal eye-position information (at least not after the saccades in the saccade condition had ended). The position of the eye at the end of the wrist rotations also depended on the target distance, $F(1, 5) = 1948.5, p < .0001$, and the effects of target distance interacted with those of eye-movement condition, $F(2, 10) = 497.2, p < .0001$. Cursor visibility had no effect, $F(1, 5) < 1$.

Target hits. The proportion of wrist rotations that ended inside the target region for each condition is shown in the top row of Table 5. Wrist rotations generally ended in the target more often when the cursor was visible, $F(1, 5) = 127.7, p < .0005$, and when the target distance was short (10°), $F(1, 5) = 12.6, p < .05$. Moreover, the eye-movement condition also influenced the proportion of target hits, $F(2, 10) = 21.4, p < .0005$. Post hoc tests revealed no reliable differences between the proportion of hits in the saccade and pursuit conditions, but movements in the control condition did hit the target less frequently than those in the other conditions.

Movement times. Movement times for wrist rotations in each condition are shown in Table 5. Movement times were much longer with the farther targets, $F(1, 5) = 86.2, p < .0001$.

Table 5
Features of Wrist Rotations in Experiment 3

Dependent variable	Control				Saccade				Pursuit			
	10°		39.5°		10°		39.5°		10°		39.5°	
	VIS	INV	VIS	INV	VIS	INV	VIS	INV	VIS	INV	VIS	INV
HITS	.60	.26	.46	.20	.64	.36	.77	.24	.72	.42	.74	.22
MT	387	339	543	497	350	333	561	495	379	347	553	493
T _{ii}	194	210	273	267	194	196	272	272	205	199	272	268
T _{ec}	232	203	288	244	226	202	303	250	222	207	289	255
p _{ec}	.83	.67	.94	.94	.72	.69	.96	.90	.79	.72	.97	.89

Note. VIS = visible cursor condition; INV = invisible cursor condition; HITS = proportion of movements landing inside the target region; MT = movement time (ms); T_{ii} = initial-impulse time (ms); T_{ec} = error-correction time (ms); p_{ec} = proportion of movements containing an error-correction phase.

.0005. They were also longer with a visible cursor, $F(1, 5) = 13.6, p < .05$. The eye-movement condition did not influence MTs overall, $F(2, 10) < 1$, but MTs for 10° targets in the control and pursuit conditions were elevated somewhat over MTs for 10° targets in the saccade condition, $F(2, 10) = 6.6, p < .05$. As will be seen, this outcome can be attributed to an increase in the relative frequency of error corrections, combined with a trend toward increased initial-impulse durations for the conditions with the elevated MTs.

Variable errors. Variable errors of the wrist rotations are shown in the upper panel of Figure 5. Movement endpoints were much more variable for farther (39.5%) as opposed to nearer (10°) targets, $F(1, 5) = 195.5, p < .0001$. Greater endpoint variability also occurred when the cursor was invisible than when it was visible, $F(1, 5) = 51.8, p < .001$. Furthermore, the effects of these two factors (i.e., target distance and cursor condition) interacted: Endpoints of movements to farther targets were more affected by cursor

invisibility than were those of movements to nearer targets, $F(1, 5) = 54.0, p < .001$. Variable errors did not depend on the eye-movement condition, $F(2, 10) < 1$. These patterns are the same as those observed in Experiment 2 (Figure 3, upper panel).

Constant errors. The CEs of the wrist rotations are shown in the lower panel of Figure 5. As in Experiment 2, wrist rotations to the 10° target tended to overshoot the target center, whereas those to the 39.5° target fell short of it, $F(1, 5) = 12.5, p < .05$. Overall, there were no reliable effects of either cursor visibility, $F(1, 5) = 4.8, p > .05$, or eye-movement condition, $F(2, 10) = 3.2, p > .05$. However, Figure 5 shows that for each target condition and cursor condition, wrist rotations tended to travel farther under the control condition. This is what occurred in Experiment 2. Furthermore, there were no apparent differences between CEs of wrist rotations in the saccade and pursuit conditions. Thus, these results replicate those from Experiment 2, at least qualitatively, suggesting that the requirement to remain fixated at the home position in the control condition induced a change in the perceived location of the target. On the other hand, it appears that subjects' perception of the target's location was similar in the saccade and pursuit conditions.

Given the pattern observed in the wrist-rotation CEs, it is possible to tentatively eliminate the movement-only hypothesis. According to that hypothesis, producing a saccade to the target is crucial for accurate wrist rotations, and there should not be any differences between the control and pursuit conditions, because subjects were not permitted to produce saccades in either of these conditions. However, the results in Figure 5 suggest that the wrist rotations under the pursuit condition differed from those under the control condition.

Initial-impulse phase. The mean durations of the wrist-rotation initial impulses (T_{ii}) are shown in Table 5. As in Experiment 2, T_{ii} s were much longer for far targets than for near targets, $F(1, 5) = 23.9, p < .005$, but they did not depend on cursor visibility, $F(1, 5) < 1$, or on the eye-movement condition, $F(2, 10) < 1$.

The mean distances traveled during the initial impulses (D_{ii}) are shown in the upper panel of Figure 6. Like the initial-impulse times, D_{ii} was much longer for wrist rotations to the far target, $F(1, 5) = 1731.5, p < .0001$. Furthermore, cursor visibility, which did not influence T_{ii} , also had no effect on D_{ii} , $F(1, 5) = 2.3, p > .15$. As in Experiment 2, however, some major differences did occur in the D_{ii} s that were not reflected by T_{ii} . Most important, the eye-movement condition dramatically affected the distance traveled during the initial impulses, $F(2, 10) = 16.4, p < .001$. D_{ii} was much greater under the control condition than under the saccade condition. Furthermore, the initial impulses traveled *shorter* distances under the pursuit condition. There was also an interaction between the effects of target distance and eye-movement condition: The differences between D_{ii} in the eye-movement conditions were larger for wrist rotations to the farther target, $F(2, 10) = 8.1, p < .01$. This is what we would expect if the forces associated with the initial impulses were simply being rescaled proportionately in the various conditions. Thus, it appears that the behavior of the eyes around the time of the wrist rotations

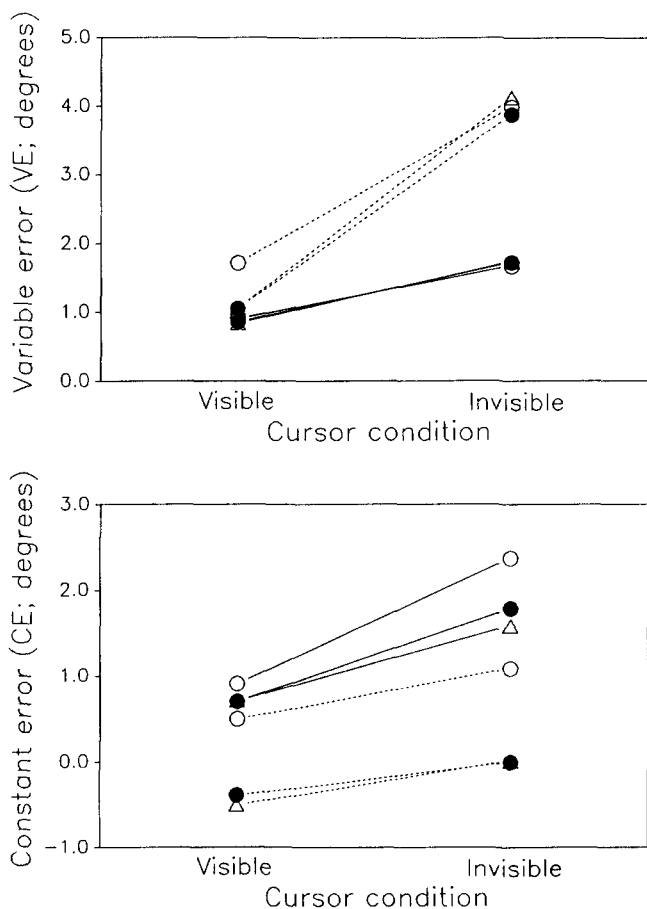


Figure 5. Upper panel: Mean variable error (VE, degrees) of wrist rotations in Experiment 3. The data points for the 10° targets fall on top of each other. Lower panel: Mean constant error (CE, degrees) of wrist rotations in Experiment 3. Positive values denote overshoots; negative values denote undershoots. (Filled circles = saccade condition; open circles = control condition; triangles = pursuit condition; solid lines = 10° targets; dashed lines = 39.5° targets.)

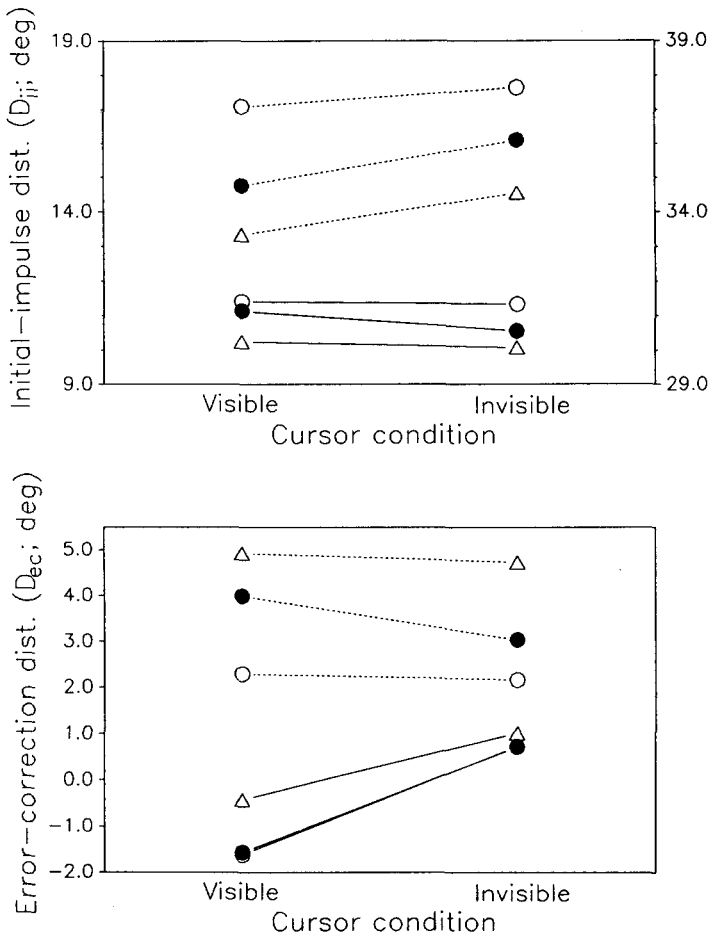


Figure 6. Upper panel: Distance traversed during the initial impulse (D_{ii} , degrees) of wrist rotations in Experiment 3. The ordinate on the right applies to the dashed lines. Lower panel: Net distance moved during error corrections (D_{ec} , degrees) for wrist rotations in Experiment 3. Positive values denote corrections to the right; negative values denote corrections to the left. The data for wrist rotations in the saccade and control conditions with 10° targets fall on top of each other. (Filled circles = saccade condition; open circles = control condition; triangles = pursuit condition; solid lines = 10° targets; dashed lines = 39.5° targets.)

had a consistent, systematic influence on the form of the initial impulses.⁸

These results allow one to distinguish further between the three different hypotheses outlined earlier. The position-only hypothesis maintains that eye movements per se provide no useful information for the performance of the wrist rotations; all that matters is having the eyes fixated at the target position. As long as the eyes are fixated at the target beforehand, there should be no differences in wrist rotations performed under the saccade and pursuit conditions. However, the distances traveled by the initial impulses (D_{ii}) in Experiment 3 revealed differences between these two conditions. Thus, the position-only hypothesis cannot be correct; the mechanisms underlying the production of rapid aimed limb movements receive and use extraretinal information about eye movements per se.⁹

Error-correction phase. Further evidence for a distinction between wrist rotations performed under the saccade, pursuit, and control conditions comes from evaluating the error-correction phase of movement. Table 5 shows the proportion of wrist rotations that contained an error correction in each condition (p_{ec}). Wrist rotations to the far target (39.5°) contained more error corrections, $F(1, 5) = 20.7, p < .01$. Error corrections occurred somewhat less frequently when the cursor was invisible than when it was visible, $F(1, 5) = 4.2, p < .10$. There were no differences in p_{ec} for the different eye-

⁸ As in Experiment 2, other analyses of the movement trajectories further support the conclusion that differences in the eye-movement conditions led to a rescaling of the initial impulses in the force domain but not the time domain. For example, the time interval from movement onset until the moment of peak acceleration did not depend on the eye-movement condition, $F(2, 10) < 1$, but the eye-movement condition reliably influenced the position, $F(2, 10) = 11.9, p < .005$, and the velocity, $F(2, 10) = 12.5, p < .005$, of the wrist at that moment. (Cursor visibility had no effect, for wrist position: $F[1, 5] = 3.9, p > .10$; for wrist velocity: $F[1, 5] = 1.5, p > .25$.) The directions of the differences were exactly what would be expected from an evaluation of D_{ii} : Movements under the control condition were traveling faster and had already covered more distance than those under the saccade condition; movement positions and velocities under the saccade condition exceeded those under the pursuit condition. The time at which all of these differences were apparent was 69 ms after the onset of movement. The times, positions, and velocities at the moment of peak velocity (126 ms after movement onset) show precisely the same pattern.

⁹ Before accepting the conclusion that saccades provide extraretinal information different from what is available after smooth pursuits, an alternative interpretation of the effects on D_{ii} must be considered. Inspection of the upper panel of Figure 6 reveals that D_{ii} under the saccade condition fell between those under the pursuit and control conditions. Because subjects here began to move their eyes before their hands on 43% of the trials in the saccade condition, it is possible that the eyes were sometimes at the target when the initial impulse began, and sometimes they had not yet left the home position. Thus, the saccade condition may simply be a mixture of two types of trials: trials on which the wrist rotations began before the eyes moved (as in the control condition) and trials on which the eyes moved to the target first (as in the pursuit condition). If this were true, then the differences in D_{ii} between conditions could be entirely a result of differences in the position of the eyes, and have nothing to do with eye movements per se. However, two sources of evidence directly suggest that trials in the saccade condition were not equivalent to a mixture of trials from the other two conditions. First, trials in the saccade condition were partitioned according to the order in which the eye and wrist movements occurred. This analysis revealed no differences in D_{ii} between the two types of trials, $F(1, 5) = 3.1, p > .10$. Second, if saccade trials had consisted of a mixture, then the endpoints of the initial impulses should have been more variable under the saccade condition than under the other two conditions. However, the standard deviation of the initial-impulse endpoints was not affected at all by the eye-movement condition, $F(2, 10) = 1.5, p > .25$. Indeed, the standard deviation was greater for longer (39.5°) wrist rotations, as would be expected, $F(1, 5) = 102.9, p < .0005$. These data reject the possibility of a mixture, whereas they bolster the claim that the manual motor system has access to some extraretinal information about movements of the eye per se.

movement conditions, $F(2, 10) < 1$. These patterns are the same as those obtained in Experiment 2.

As in Experiment 2, the durations of the error corrections (T_{ec}) paralleled the pattern obtained for p_{ec} . These are shown in Table 5. T_{ec} was longer when the cursor was visible than when it was invisible, $F(1, 5) = 16.5, p < .01$. T_{ec} was also longer when the target was farther away, $F(1, 5) = 27.7, p < .005$. The eye-movement conditions did not influence T_{ec} , $F(2, 10) < 1$.

Although the eye-movement conditions did not influence the frequency and duration of the wrist-rotation error corrections, there were differences in the nature of the error corrections that did depend on the eye-movement condition. The lower panel of Figure 6 shows the net distance moved by the wrist during the error-correction phase under each condition (D_{ec}). The first noteworthy feature of these data is that D_{ec} differed for the two target conditions, $F(1, 5) = 15.2, p < .05$. Generally, D_{ec} was negative for wrist rotations to the 10° target, and positive for wrist rotations to the 39.5° target. These differences are precisely what would be needed to compensate for the initial impulses that, as shown in the upper panel of Figure 6, overshoot or undershot the target, respectively.

The next salient feature of Figure 6 is that the magnitude of D_{ec} depended on the eye-movement condition, $F(2, 10) = 21.7, p < .0005$. The differences were larger for wrist rotations to the far (39.5°) target. As a result, the effects of target distance and eye-movement condition interacted, $F(2, 10) = 5.7, p < .05$. Note that D_{ec} was much greater (more positive) in the pursuit condition than in the saccade (and control) conditions. The difference between the pursuit and saccade conditions is particularly revealing because the position of the eye throughout the error corrections was the same under both conditions. Furthermore, the directions and magnitudes of the differences in D_{ec} were sufficient to compensate for the differences between the initial-impulse endpoints in the saccade and pursuit conditions. Consequently, the final endpoints of the wrist rotations in the saccade and pursuit conditions were equivalent (see Figure 5, lower panel). This happened regardless of whether or not the cursor was visible, $F(1, 5) = 2.5, p > .10$.

Discussion

Experiment 3 allows us to distinguish between several alternative hypotheses regarding the role of eye movements during aimed limb movements. Certain salient aspects of the wrist rotations made here were systematically influenced by constraints imposed on the behavior of the eyes during the movements, whereas other aspects of the wrist rotations were unaffected. In particular, the endpoints of the wrist rotations in the saccade and pursuit conditions (in which the eyes were fixated on the target before the end of the limb movement) were equally accurate, whereas wrist rotations in the control condition (in which the eyes remained at the home position) were significantly less accurate. Moreover, differences between wrist rotations in the saccade and pursuit conditions were evident from the internal structure of these movements: Wrist-rotation initial impulses traveled shorter distances in the pursuit condition than in the saccade condition, whereas the error corrections traveled longer distances.

Taken overall, the data support the hybrid movement-plus-position hypothesis. The importance of extraretinal eye-position information is documented by our findings that wrist rotations in the pursuit condition were as accurate as those in the saccade condition.¹⁰ The importance of extraretinal information from saccadic eye movements is documented by differences between the dynamic structures of the wrist rotations in the saccade and pursuit conditions. These results suggest that the manual motor-control system receives and uses extraretinal information about both the *movement* and the *position* of the eyes for guiding the hand.

General Discussion

Our research has yielded several insights into the role of the eyes during the production and control of rapid aimed limb movements. In Experiment 1, subjects spontaneously executed a saccade to the target for a wrist rotation. The initiation of these saccades was closely time locked to the onset of limb movement, although the precise temporal order of the two movements differed between subjects and was unrelated to movement accuracy. Experiments 2 and 3 showed that even without visual feedback, the position of the eyes during wrist rotations influenced the subjects' ability to reach the target accurately, whereas how the eyes reached the target influenced the dynamic structure of the wrist rotations.

Implications for Limb-Movement Control

Perhaps the most important result of this study is that the initial-impulse and error-correction phases of wrist rotations were differentially affected by manipulations of subjects' eye movements before and during the wrist rotations. This pattern suggests that the information obtained from the oculomotor system for guiding limb movements may be different for the different movement phases. Such a possibility is consistent with a considerable amount of previous research on spatial localization and manual motor control, which we discuss in the following sections for each movement phase.

Programming the initial impulse. In Experiments 2 and 3, the distances traversed during the wrist-rotation initial impulses (D_{ii}) depended on the eye-movement condition. Both experiments showed that the initial impulses in the control (no saccade) condition traveled farther than those in the saccade condition. These differences are consistent with the work by Hill (1972) and Morgan (1978), which showed that people underestimate the extent to which their eyes are oriented away from straight ahead. Given such underestimation, when the eyes were fixed at the home position in the control condition (to the left of straight-ahead), any object opposite the direction of eye orientation (i.e., to the right)

¹⁰ An alternative interpretation of this result is that the benefit of having the eyes at the target arises from enhanced retinal information about the target when the target can be viewed in central vision. Some evidence does exist that there are important differences between the visual processing of central and peripheral stimuli (Paillard, 1980). Nevertheless, this alternative cannot explain the differences that we observed between the movement trajectories in the saccade and pursuit conditions.

would appear farther away than it actually was. As a result, wrist-rotation initial impulses would be expected to travel farther under the control condition than under the saccade or pursuit conditions, which is exactly what we found.

In Experiment 3, initial impulses of wrist rotations made under the pursuit condition traveled less far than those under the saccade condition. This result is also consistent with earlier work. There have been numerous demonstrations that people consistently underestimate the velocity, and hence the extent, of a smooth-pursuit eye movement relative to a saccade of the same size (Festinger & Canon, 1965; Honda, 1984, 1985; Mack & Herman, 1972; Miller, 1980). Thus, our data support the hypothesis that the spatial goal for the initial impulses involved assessing the distance that the hand had to move. Fixing the eye at the home position in the control condition presumably caused a relative overestimation of that distance, and moving the eye to the target smoothly in the pursuit condition caused a relative underestimation (compared with the saccade condition).

Controlling error corrections. We also found that wrist rotations in Experiment 3 ended with equal accuracy in the saccade and pursuit conditions despite differences between their initial impulses, but wrist rotations in the control condition ended less accurately. This may be explained by a position-seeking mechanism whose goal for the error corrections is defined by a final desired location in space, not by the distance needed to reach that location. Such an approach could allow the wrist (and hand) to attain the final desired location accurately regardless of where the error corrections begin (i.e., regardless of the endpoints of the initial impulse). The results of Experiments 2 and 3 suggest that these position-seeking error corrections may be performed more accurately when the eyes are pointing at the target than when they are at the home position. We therefore infer that extraretinal information about eye position contributes significantly to selecting the spatial goal for the error corrections.

Relation to Models of Limb-Movement Control

Our results have some other important implications concerning models for the mechanisms that underlie the control of limb movements. Several researchers conceive rapid aimed limb movements to involve a preprogrammed burst of activity in agonist muscles with well-defined force-time relationships (e.g., Meyer et al., 1988; Meyer, Smith, & Wright, 1982; Schmidt, Zelaznik, Hawkins, Frank, & Quinn, 1979). According to these conceptions, the amplitude and duration of the force pulse that moves a limb may be programmed from the outset to achieve a particular movement distance. Different movement distances supposedly require force pulses of different amplitudes and durations. This is consistent with the idea that an initial impulse relies on assessing the distance between the initial limb position and the target location. Manipulations that affect the perceived distance (such as the current position of the eyes and the type of eye movement just executed) should then influence the initial impulses, just as we found (Experiments 2 and 3).

Other models of motor control have emphasized the position-seeking characteristics of limb movements. There is evidence that, in many situations, commands to the muscles

directly specify the desired end location of a limb movement (Polit & Bizzi, 1979; Sakitt, 1980). One way that this may be done is by adjusting the desired resting lengths or stiffnesses of opposing muscle pairs. Through such adjustments, limb movements could still stop accurately, regardless of their starting points and regardless of any perturbations encountered along the way. These characteristics are consistent with the hypothesis that error corrections may be programmed to move a limb to a particular location in space; hence, limb movements may end with equal accuracy, despite differences in the endpoints of their initial impulses.

Viewed as a whole, our results suggest that rapid aimed limb movements involve mechanisms based on both types of control (i.e., distance and position programming). The first movement phase (initial impulse) exhibits properties corresponding to impulse-variability models of distance (force-time) programming. The second phase (error correction) exhibits properties corresponding to position-programming (mass-spring) models. The conclusion that both of these types of models are relevant for aimed limb movements has been suggested by Keele (1981) and other investigators (e.g., Abrams & Landgraf, 1990; Meyer et al., 1982; 1990).

Relation to Oculomotor Control Mechanisms

The present work also bears further on oculomotor control mechanisms. Several researchers have claimed that important similarities exist between the mechanisms for controlling saccadic eye movements and the mechanisms for controlling limb movements (e.g., Abrams, Meyer, & Kornblum, 1989). Our conclusions about limb-movement control are consistent with such claims. Like limb movements, saccades are believed to include two phases: an initial *pulse* of force that moves the eyes rapidly toward a target area and a subsequent *step* change in resting muscle lengths that holds the eyes at the desired new location (Bahill, Clark, & Stark, 1975; Robinson, 1981). In some situations, the pulse and step have been observed to be inappropriately matched (Bahill et al., 1975; Easter, 1973). The result of this mismatch is a final slow gliding movement of the eyes (a glissade) after the brief pulse that moves the eyes toward the location specified by the step. Thus, the underlying control mechanisms for saccades do not necessarily preclude a mismatch occurring between the sizes of the pulse and the step. Similarly, we have found that one can separately influence the pulse and the step of an aimed limb movement (initial impulse and error correction, respectively) by varying the information available to the manual motor system.

Relation to Research on Spatial Localization

Finally, our results bear on the mechanisms that underlie spatial localization. Several researchers have found that the manual motor system is immune to manipulations of visual stimuli that affect the perceived spatial location of objects (Bridgeman, Kirch, & Sperling, 1981; Bridgeman, Lewis, Heit, & Nagle, 1979; Honda, 1985). In these studies, subjects pointed accurately to stimuli that were perceptually mislocalized. Our results suggest, however, that the manual motor system may not be entirely free from the effects of such

perceptual manipulations. Rather, localization by the motor system might depend on how the limb movement endpoint is determined (e.g., one might define the end of an overall movement in the same way as we defined the end of the initial impulse), or on other motoric requirements of a response. These conclusions accord well with the results of Abrams and Landgraf (1990) and Honda (1985), which showed that perceptual mislocalizations can affect limb-pointing accuracy to varying degrees, depending on where the pointing movement begins in space.

Conclusion

In conclusion, our results support a hybrid model of rapid limb-movement control in which initial impulses are programmed to traverse a specific distance, and error corrections are designed to arrive at a specific final location. The assessment of distance is influenced by the current position of the eyes as well as how the eyes arrive at this position. The specification of the final end location depends only on where the eyes are pointing.

References

- Abrams, R. A., & Landgraf, J. Z. (1990). Differential use of distance and location information for spatial localization. *Perception & Psychophysics*, *47*, 349–359.
- Abrams, R. A., Meyer, D. E., & Kornblum, S. (1989). Speed and accuracy of saccadic eye movements: Characteristics of impulse variability in the oculomotor system. *Journal of Experimental Psychology: Human Perception and Performance*, *15*, 529–543.
- Angell, R. W., Alston, W., & Garland, H. (1970). Functional relations between the manual and oculomotor control systems. *Experimental Neurology*, *27*, 248–257.
- Bahill, A. T., Clark, M. R., & Stark, L. (1975). Glissades—Eye movements generated by mismatched components of the saccadic motoneuronal control signal. *Mathematical Biosciences*, *26*, 303–318.
- Biguer, B., Jeannerod, M., & Prablanc, C. (1982). The coordination of eye, head, and arm movements during reaching at a single visual target. *Experimental Brain Research*, *46*, 301–304.
- Bridgeman, B., Kirch, M., & Sperling, A. (1981). Segregation of cognitive and motor aspects of visual function using induced motion. *Perception & Psychophysics*, *29*, 336–342.
- Bridgeman, B., Lewis, S., Heit, G., & Nagle, M. (1979). Relation between cognitive and motor-oriented systems of visual position perception. *Journal of Experimental Psychology: Human Perception and Performance*, *5*, 692–700.
- Carlton, L. G. (1981a). Processing visual feedback information for movement control. *Journal of Experimental Psychology: Human Perception and Performance*, *7*, 1019–1030.
- Carlton, L. G. (1981b). Visual information: The control of aiming movements. *Quarterly Journal of Experimental Psychology*, *33A*, 87–93.
- Crossman, E. R. F. W., & Goodeve, P. J. (1983). Feedback control of hand-movement and Fitts' law. *Quarterly Journal of Experimental Psychology*, *35A*, 251–278. (Original work presented at the meeting of the Experimental Psychology Society, Oxford, England, July 1963).
- Easter, S. S. (1973). A comment on the "glissade". *Vision Research*, *13*, 881–882.
- Festinger, L., & Canon, L. K. (1965). Information about spatial location based on knowledge about efference. *Psychological Review*, *72*, 373–384.
- Hansen, R. M. (1979). Spatial localization during pursuit eye movements. *Vision Research*, *19*, 1213–1221.
- Hansen, R. M., & Skavenski, A. A. (1977). Accuracy of eye position information for motor control. *Vision Research*, *17*, 919–926.
- Hansen, R. M., & Skavenski, A. A. (1985). Accuracy of spatial localizations near the time of saccadic eye movements. *Vision Research*, *25*, 1077–1082.
- Helmholtz, H. von. (1963). *A treatise on physiological optics*: Vol. 3 (J. P. C. Southall, Ed. and Trans.). New York: Dover. (Original work published 1866).
- Hill, A. L. (1972). Direction constancy. *Perception & Psychophysics*, *11*, 175–178.
- Honda, H. (1984). Functional between-hand differences and outflow eye-position information. *Quarterly Journal of Experimental Psychology*, *36A*, 75–88.
- Honda, H. (1985). Spatial localization in saccade and pursuit-eye-movement conditions: A comparison of perceptual and motor measures. *Perception & Psychophysics*, *38*, 41–46.
- Keele, S. W. (1981). Behavioral analysis of movement. In V. Brooks (Ed.), *Handbook of physiology: The nervous system: Vol. 2. Motor control* (pp. 1391–1414). Baltimore, MD: American Physiological Society.
- Keele, S. W. (1986). Motor control. In K. Boff, L. Kaufman, & J. Thomas (Eds.), *Handbook of perception and human performance* (pp. 30-1–30-60). New York: Wiley.
- Keele, S. W., & Posner, M. I. (1968). Processing of visual feedback in rapid movements. *Journal of Experimental Psychology*, *77*, 155–158.
- Kelso, J. A. S., Southard, D. L., & Goodman, D. (1979). On the coordination of two-handed movements. *Journal of Experimental Psychology: Human Perception and Performance*, *5*, 229–238.
- Kerr, B. (1978). Task factors that influence selection and preparation for voluntary movements. In G. E. Stelmach (Ed.), *Information processing in motor control and learning* (pp. 55–69). New York: Academic Press.
- Mack, A., & Herman, E. (1972). A new illusion: The underestimation of distance during pursuit eye movements. *Perception & Psychophysics*, *12*, 471–473.
- Mather, J. A., & Fisk, J. D. (1985). Orienting to targets by looking and pointing: Parallels and interactions in ocular and manual performance. *Quarterly Journal of Experimental Psychology*, *37A*, 315–338.
- Megaw, E. D., & Armstrong, W. (1973). Individual and simultaneous tracking of a step input by the horizontal saccadic eye movement and manual control systems. *Journal of Experimental Psychology*, *100*, 18–28.
- Meyer, D. E., Abrams, R. A., Kornblum, S., Wright, C. E., & Smith, J. E. K. (1988). Optimality in human motor performance: Ideal control of rapid aimed movements. *Psychological Review*, *95*, 340–370.
- Meyer, D. E., Smith, J. E. K., Kornblum, S., Abrams, R. A., & Wright, C. E. (1990). Speed-accuracy tradeoffs in aimed movements: Toward a theory of rapid voluntary action. In M. Jeannerod (Ed.), *Attention and performance XIII* (pp. 173–226). Hillsdale, NJ: Erlbaum.
- Meyer, D. E., Smith, J. E. K., & Wright, C. E. (1982). Models for the speed and accuracy of aimed movements. *Psychological Review*, *89*, 449–482.
- Miller, J. M. (1980). Information used by the perceptual and oculomotor systems regarding the amplitude of saccadic and pursuit eye movements. *Vision Research*, *20*, 59–68.

- Morgan, C. L. (1978). Constancy of egocentric direction. *Perception & Psychophysics*, 23, 61-68.
- Nemire, K., & Bridgeman, B. (1987). Oculomotor and skeletal motor systems share one map of visual space. *Vision Research*, 27, 393-400.
- Paillard, J. (1980). The multichanneling of visual cues and the organization of a visually guided response. In G. E. Stelmach & J. Requin (Eds.), *Tutorials in motor behavior* (pp. 259-279). Amsterdam: North-Holland.
- Paillard, J. (1982). The contribution of peripheral and central vision to visually guided reaching. In D. Ingle, M. Goodale, & R. Mansfield (Eds.), *Analysis of visual behavior* (pp. 367-385). Cambridge: MIT Press.
- Pelisson, D., Prablanc, C., Goodale, M. A., & Jeannerod, M. (1986). Visual control of reaching movements without vision of the limb: II. Evidence of fast unconscious processes correcting the trajectory of the hand to the final position of a double-step stimulus. *Experimental Brain Research*, 62, 303-311.
- Polit, A., & Bizzi, E. (1979). Characteristics of motor programs underlying arm movements in monkeys. *Journal of Neurophysiology*, 42, 183-194.
- Posner, M. I., Nissen, M. J., & Ogden, W. C. (1978). Attended and unattended processing modes: The role of set for spatial location. In H. Pick & E. Saltzman (Eds.), *Modes of perceiving and processing information* (pp. 137-157). Hillsdale, NJ: Erlbaum.
- Prablanc, C., Echallier, J. F., Jeannerod, M., & Komilis, E. (1979). Optimal response of eye and hand motor systems in pointing at a visual target: II. Static and dynamic visual cues in the control of hand movement. *Biological Cybernetics*, 35, 183-187.
- Prablanc, C., Echallier, J. F., Komilis, E., & Jeannerod, M. (1979). Optimal response of eye and hand motor systems in pointing at a visual target: I. Spatio-temporal characteristics of eye and hand movements and their relationships when varying the amount of visual information. *Biological Cybernetics*, 35, 113-124.
- Prablanc, C., Pelisson, D., & Goodale, M. A. (1986). Visual control of reaching movements without vision of the limb: I. Role of retinal feedback of target position in guiding the hand. *Experimental Brain Research*, 62, 293-302.
- Robinson, D. A. (1981). Control of eye movements. In V. Brooks (Ed.), *Handbook of physiology: The nervous system: Vol. 2. Motor control*. Baltimore, MD: American Physiological Society.
- Sakitt, B. (1980). A spring model and equivalent neural network for arm posture control. *Biological Cybernetics*, 37, 227-234.
- Schmidt, R. A., Zelaznik, H., Hawkins, B., Frank, J. S., & Quinn, J. T., Jr. (1979). Motor-output variability: A theory for the accuracy of rapid motor acts. *Psychological Review*, 86, 415-451.
- Todd, J. T., & Van Gelder, P. (1979). Implications of a transient-sustained dichotomy for the measurement of human performance. *Journal of Experimental Psychology: Human Perception and Performance*, 5, 625-638.
- Vince, M. A. (1948). Corrective movements in a pursuit task. *Quarterly Journal of Experimental Psychology*, 1, 85-103.
- Wallace, S. A., & Newell, K. M. (1983). Visual control of discrete aiming movements. *Quarterly Journal of Experimental Psychology*, 35A, 311-321.
- Woodworth, R. S. (1899). The accuracy of voluntary movement. *Psychological Review*, 3, (2, Whole No. 13).
- Wright, C. E., & Meyer, D. E. (1983). Conditions for a linear speed-accuracy trade-off in aimed movements. *Quarterly Journal of Experimental Psychology*, 35A, 279-296.
- Zelaznik, H. N., Hawkins, B., & Kisselburgh, L. (1983). Rapid visual feedback processing in single-aiming movements. *Journal of Motor Behavior*, 15, 217-236.

Received February 17, 1989

Revision received June 5, 1989

Accepted June 12, 1989 ■