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Oculomotor localization relies on a damped representation of saccadic eye displacement in human and nonhuman primates

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Abstract

The oculomotor system has long been thought to rely on an accurate representation of eye displacement or position in a successful attempt to reconcile a stationary target's retinal instability (caused by motion of the eyes) with its corresponding spatial invariance. This is in stark contrast to perceptual localization, which has been shown to rely on a sluggish representation of eye displacement, achieving only partial compensation for the retinal displacement caused by saccadic eye movements. Recent studies, however, have begun to cast doubt on the belief that the oculomotor system posseses a signal of eye displacement superior to that of the perceptual system. To verify this, five humans and one monkey (*Macaca nemestrina*) served as subjects in this study of oculomotor localization abilities. Subjects were instructed to make eye movements, as accurately as possible, to the locations of three successive visual stimuli. Presentation of the third stimulus (2-ms duration) was timed so that it fell before, during, or after the subject's saccade from the first stimulus to the second. Localization errors in each subject (human and nonhuman) were consistent with the hypothesis that the oculomotor system has access to only a damped representation of eye displacement—a representation similar to that found in perceptual localization studies.

Keywords: Spatial localization, Visuomotor integration, Psychophysics, Saccade, Eye movement

Introduction

Although it was once thought that oculomotor localization could be guided using only the retinal location of a target, it has become generally accepted that the saccadic system must be capable of combining retinal error and eye displacement (or eye position) information if accurate eye movements are to be made under certain conditions. Indeed, the work of Hallett and Lightstone (1976*a, b*) was instrumental in swaying many of the advocates of retinal localization (e.g. Robinson, 1973) to acknowledge the oculomotor system's need for a spatial localization ability (Robinson, 1975). To test the oculomotor performance of normal human subjects, Hallett and Lightstone employed a double-step stimulus: the subject's task was simply to follow the stimulus as it was stepped to different parts of the screen. By timing the second stimulus step to occur just after the onset of the saccade toward the first step location, Hallett and Lightstone were able to dissociate the retinal and spatial locations of the second step. Finding that the oculomotor system was capable of compensating for intervening eye movements when programming a subsequent targeting saccade, they concluded that the oculomotor system combines retinal and eye-position information to localize the stimulus in head- or body-centered coordinates. Furthermore, the finding that accurate saccades could be made to a stimulus presented *during* an eye movement led to the conclusion that the oculomotor system uses an accurate, up-to-date eye displacement or position signal (EPS, used henceforth to denote the oculomotor system's internal representation of eye displacement or eye position).

In contrast to these findings on oculomotor localization, perceptual studies have long demonstrated the considerable mislocalizations inherent to perisaccadic stimulus presentations (Matin & Pearce, 1965; Bischof & Kramer, 1968; Kennard et al., 1971; Monahan, 1972; Mateeff, 1978; Honda, 1989). Each of these studies found that flashes presented just before a saccade were perceptually mislocalized in the same direction as the saccade, whereas flashes presented just after were sometimes mislocalized in the opposite direction. Flashes presented well before or well after the saccade were accurately localized. These studies suggest that, although eye displacement is taken into account in perceptual localization, the EPS is not veridical around the time of a saccade (see also Grüsser et al., 1987).

The dichotomy of results seen with perceptual *vs.* oculomotor localization would lead to an apparent paradox: a subject would look in one (appropriate) direction to foveate a flash per-

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ceived to be in another (inappropriate) direction. This paradox has prompted several authors to suggest explanations and mechanisms underlying the perceptual/motor discrepancy (Bridgeman et al., 1979; Gresty & Leech, 1976; Hershberger, 1987; Hallett, 1976; Hallett & Lightstone, 1976*b*; Skavenski & Hansen, 1978; Hansen & Skavenski, 1985; Skavenski, 1990).

Could it be, however, that the dichtomy is not one of perceptual *vs.* motor abilities, but is, instead, one of methodological differences between the two types of studies? Recent investigations of oculomotor localization suggest that this may be the case. Honda, studying horizontal (1989, 1990) and vertical saccades (1991), used a modified double-step stimulus presentation to test the oculomotor system's ability to localize perisaccadic flashes. His results show that oculomotor localization is very similar to perceptual localization: errors occur when stimuli are presented in the time span from 100 ms before to 100 ms after movement onset. In another approach, using microstimulation studies of primate frontal eye fields, Dassonville et al. (1990*b*, 1992) found indirect evidence that similarly pointed to the oculomotor system's use of an inaccurate EPS.

Because this recent evidence refutes a long-accepted conclusion on the accuracy of the internal representation of eye displacement used by the oculomotor system, and in light of the considerable effort put forth by many authors in explaining the apparent perceptual/motor dichotomy, it is important to verify just how accurately the oculomotor system can compensate for intervening saccades. In addition, since a portion of the refuting evidence originates from a microstimulation study of monkey cortex, we felt it necessary to compare the localization abilities of humans to those of nonhuman primates. A brief summary of a portion of this study has been presented elsewhere (Dassonville et al., 1990*a*).

Methods

Five adult humans (naive: BWC, MCD, ZSK; nonnaive: MSR, PRD) served as subjects in this study, details of which were approved by the UCLA Human Subject Protection Committee. During the experimental sessions, eye position was measured with a monocular scleral search coil (#3021, Skalar, Delft, Netherlands). Sinusoidal currents flowing through paired vertical and horizontal coils (63-cm diameter), positioned around the subject's head, created magnetic fields of 40 and 80 kHz. These magnetic fields induced, in the search coil, the signal used to measure eye position (Robinson, 1963). Each subject wore his or her own spectacles to correct acuity to near normal levels, and a bite plate was used to stabilize the subject's head. Visual stimuli, which were viewed binocularly, consisted of low intensity (15 mcd/m^2), small (0.23-deg diameter) luminous green dots back-projected onto a tangent screen by a Tektronix 608 oscilloscope equipped with a wide-angle projection lens. The tangent screen measured 61 deg horizontal by 50 deg vertical, and was placed 132 cm from the eyes. For each trial, eye and target positions were digitally sampled online (1 kHz) by a personal computer.

Because of the low intensity and short duration of the visual stimuli used in this study, it was necessary to allow the subject to become dark adapted before the experimental trials began. This period of adaptation lasted 15-20 min, after which a short (5-10 min) training session was performed to accustom the subject to the task. Immediately after the training session, the eye was anesthetized with proparacaine hydrochloride 0.5%, and the scleral search coil was inserted. After calibration of the eye-position signal, the experimental session began, with approximately 200 trials performed. At the end of this period, calibration of the signal was verified, and the coil was removed from the eye. The coil never remained in the subject's eye for more than 30 min.

Fig. 1 provides a schematic representation of the task, showing the spatial (A) and temporal (B) relationships of the visual stimuli. Whereas Hallett and Lightstone (1976*a,b*) referred to their task as having used only a single stimulus stepped to different parts of the visual field, differences in the timing of our experimental task made it more sensible to refer to three visual stimuli: a fixation point, F, and two subsequent saccade targets, S1 and S2. In every trial, F was placed at eye level, −20 deg (i.e. 20 deg to the left) from the screen center. Each trial began when the subject's gaze entered a 4-deg window centered about F. After a 750-ms delay, F was extinguished, and target S1 was illuminated for a duration of 5 ms. The location of S1 was consistent across trials, always presented at the screen center. Onset of S1 was the cue for the subject to make a 20-deg rightward *initial saccade* from F to S1. At a variable, randomly selected time (50-500 ms) after S1 onset, S2 appeared for 2 ms in one of five possible locations: 10 deg above eye level and −15, −10, −5, 0, or +5 deg from the screen center. Variability of S2 onset time ensured that the flash would be presented either before, during, or after the initial movement. The dependent variable in this study was the accuracy of the *targeting saccade* made from S1 to S2.

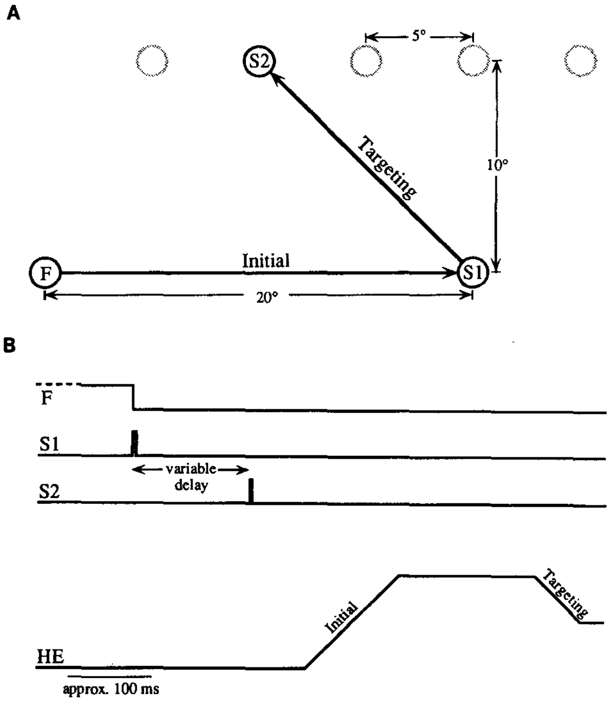

Fig. 1. Schematic diagram of a single trial. A: *XY* plot of flash locations. F = fixation point; S1 = flash #1; S2 = flash #2, randomly located in one of five possible locations (grey circles); *initial* = initial saccade from fixation point to S1; *targeting* = targeting saccade from S1 to S2. B: Timing of stimuli presentations. F = 750 ms; S1 = 5 ms; S2 = 2 ms, with a variable onset randomly selected to occur anywhere before, during, or after initial movement; HE = horizontal eye position.

The 10-deg vertical displacement of S2 allowed for an easy discrimination between the initial and targeting saccades – initial saccades were in a horizontal direction, whereas targeting saccades had an upward component of approximately 10 deg. Although the row of possible target positions lay along the axis of the initial movement in earlier studies (Hallett & Lightstone, 1976*a, b*; Honda, 1989, 1990, 1991), we felt a vertical displacement of S2 necessary for two reasons. First, subjects occasionally made more than one saccade in acquiring S1: it would have been difficult to distinguish between the second "initial saccade" and the targeting saccade without the vertical displacement of S2. Second, Honda (1989, 1990) describes trials in which no targeting saccades were made (and, similarly, Hallett and Lightstone [1976*a,b*] describe trials in which the targeting movement was withheld until after the target was re-presented): with no S2 displacement present, it was unknown whether these null trials represented (1) occasions in which the targeting saccade simply failed to be evoked, or (2) instances in which the target was obtained with the initial saccade alone. In the present study, these confusions were avoided by simply displacing S2 10 deg upward.

In some experimental sessions, the fixation point F was a red LED placed behind the projection screen, rather than a spot projected from the Tektronix 608 oscilloscope. Intensity of the LED was comparable to that of the projected stimuli, and no differences were seen between sessions using either type of fixation point. In an additional variation of the task, S2 was occasionally triggered, after a random delay (0–400 ms), by the online computer detection of initial movement onset. This allowed the presentations of S2 to occur at consistent intervals during or after the initial movement.

It was explained to the subject that the first two flashes (F and S1) would always occur in the same locations, and that the third would occur "somewhere above the first two." The subject was instructed to look, as accurately as possible, to the locations of the three successive stimuli, and to maintain fixation of the third stimulus location for approximately 1 s. In addition, the subject was instructed to note (by pressing a switch) any trial in which he or she was not reasonably certain of the flash location. In the subsequent analyses, these trials (1.3% of all trials; range over all subjects: 0.0–2.6%) were eliminated from consideration.

Because of the importance of having initial movements of consistent amplitude for intertrial comparisons, subjects were verbally warned by the experimenter after trials in which the location of S1 was achieved with two or more saccades. These trials (11.2% of all trials, range over all subjects: 6.5–19.5%) were also eliminated from subsequent analyses. All experimental and training sessions were carried out in complete darkness, and at no time did the subject receive any type of feedback, visual or otherwise, concerning the actual location of S2 or the accuracy of the targeting movement. After the experimental session was complete, the subject was asked if he or she had noticed anything peculiar about flash locations, intensity, timing, etc. Even though S2 could occur only in five possible locations, the naive subjects never reported any awareness of this; indeed, even the nonnaive subjects felt incapable of pinpointing which of the five flash locations was used in individual trials.

In addition to the human subjects, one female adult monkey (*Macaca nemestrina*, monkey Z) was tested. A monocular search coil (Robinson, 1963) was surgically implanted in monkey Z according to the method described by Judge et al. (1980). Wire leads from the coil were secured to a pedestal of dental cement anchored by screws to the animal's skull. An additional surgery was later performed to implant a stainless-steel chamber over the arcuate sulcus, used for single-unit recording experiments unrelated to the present study (see Dassonville et al., 1992). All surgical procedures were performed while the monkey was under deep sodium pentobarbital anesthesia; all aspects of this and other studies dealing with monkey Z were approved by the UCLA Chancellor's Animal Research Committee.

During both training and recording sessions, the monkey sat in a primate chair placed in the same experimental setup used to test the human subjects. To immobilize the animal's head, the pedestal was attached with bolts to the back of the chair. Because this monkey had undergone previous oculomotor experiments, it was already well-trained in simple saccade tasks (see Schlag et al., 1990, and Dassonville et al., 1992, for descriptions of previously learned tasks). It had not, however, experienced any task involving double-step stimuli. Additional training sessions were provided so that the monkey could learn the task necessary for the present study. The training task was similar to the human experimental task described above, with only a single modification – presentation of S2 was always delayed 500 ms after the onset of the initial movement from F to S1. A juice reward was contingent on the accuracy of the targeting saccade toward S2: the movement was required to end within a window of 8 deg centered around the location of S2 (the imposed delay of 500 ms ensured that the change in the EPS had sufficient time for completion, and would therefore not be a source of mislocalization). This training task was quickly learned, and the monkey was able to perform the subsequent experimental sessions with ease. The experimental task was identical to that of the human subjects. Whereas the juice reward was contingent on saccade accuracy in the training sessions, it was contingent only on making a targeting saccade with the proper vertical amplitude to acquire S2 in the experimental sessions – horizontal accuracy was ignored in order to avoid providing feedback concerning the actual horizontal position of the stimulus. Since the monkey was very willing to work for the juice reward, neither food nor water deprivation was required.

The accuracy of the targeting movements, in monkey and human subjects, was determined by measuring the horizontal distance between the location of S2 and that of the final fixation position, even though this final position was often achieved with two or more saccades from the location of S1. Thus, when the "targeting movement" is discussed below, we are referring to the package of 1–3 saccades between the location of S1 and that of the final fixation position.

Results

Fig. 2 shows, from four typical trials (subject MSR), the accuracy of saccadic localization of target S2. In each of these trials, S2 was presented 10 deg to the left of the initial target S1 (as depicted in the schematic of Fig. 1A); however, S2 onset time was varied across trials so that it was presented either before (A,B), during (C), or after (D) the initial saccade. Whereas targeting movements to flashes presented well before (A) or well after (D) the initial saccade were reasonably accurate, mislocalizations could be seen with flashes timed to occur near the initial movement onset (B,C). The long latencies of the targeting saccades shown in Fig. 2 were typical for this subject, but not for all subjects, as shown by Table 1. To provide further detail, Table 1 also shows the mean targeting saccade latency for the

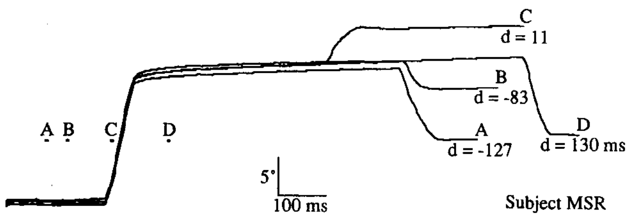

Fig. 2. Horizontal components of initial (first movement in each trace) and targeting saccades (second movement in each trace) from four typical trials, synchronized on initial saccade onset (subject MSR). Note the large inaccuracy when S2 is presented near the onset of the initial saccade in trial C. Labeled dashes (A, B, C, D) = S2 timing and location (10 deg left of screen center, letters correspond to appropriate traces), *d* = delay (ms) between onset of initial movement and S2 (negative delay is before movement onset).

subset of trials in which S2 was presented in the 30-ms window before initial saccade onset, as well as for the subset in which S2 was presented in the 30-ms window after initial saccade offset. This allows a comparison of the latencies for trials having the largest errors (S2 before initial saccade, see Fig. 3A) and the smallest errors (S2 after initial saccade). Although the saccadic latency to a flash presented immediately before the initial saccade was generally longer (35.2 ms average across subjects) than that to a flash presented immediately after, the trend was not consistent for all subjects (i.e. the trend was reversed in subject ZSK and was very small in monkey Z).

For each subject, the time course of mislocalization was assessed by plotting the magnitude of errors (ordinate, Fig. 3A, data shown only from subject PRD) with respect to the time delay (abscissa) between initial movement (0 ms) and S2 onsets. Errors of localization were scattered about 0 deg for flashes presented well before (delay < -100 ms) initial movement onset, began to increase in the direction of the initial movement with flashes occurring just before onset (-100 ms $<$ delay $<$ 0 ms), peaked at onset (delay = 0 ms), and returned to near 0 deg around the time of initial movement offset (delay = 55 ms). In five subjects (BWC, MCD, PRD, ZSK, and monkey Z), biphasic error curves were obtained, with those presented at or just after initial movement offset mislocalized a very small amount in the direction opposite that of the initial saccade (peak postsaccadic errors were less than 1/4 peak presaccadic errors in all subjects). Errors returned to near 0 deg shortly thereafter (delay > 100 ms). In the other subject (MSR), the error curve appeared monophasic—systematic errors were seen with flashes presented before or during the initial saccade.

As mentioned in the Introduction, it has been hypothesized

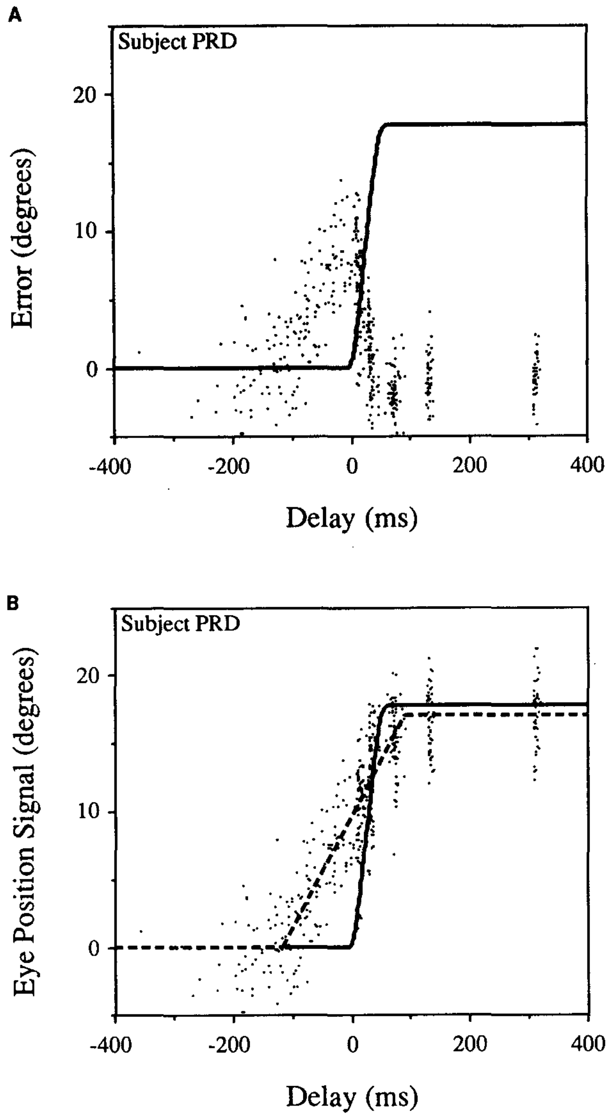

Fig. 3. Pattern of oculomotor mislocalizations of S2 and the representation of eye displacement used by the oculomotor system (subject PRD). A: Magnitude of error (*ordinate*, degrees) *vs.* delay (*abscissa*, ms) between S2 onset and initial saccade onset. Errors begin to increase with flashes presented approximately 100 ms before the initial saccade, peaking with flashes at movement onset. Solid curve = horizontal component of typical initial saccade. B: Representation of eye displacement used by the oculomotor system to localize S2, derived by subtracting retinal error vector from endpoint of targeting saccade. Solid curve = horizontal component of typical initial saccade; and dashed curve = best-fit three-segment curve describing EPS data from this subject.

Table 1. *Targeting saccade latencies (ms, measured from S2 onset to targeting saccade onset)*

Subject	BWC	MCD	MSR	PRD	ZSK	Monkey Z
All trials (mean ± s.d.)	320.2	381.0	505.6	431.7	551.9	316.7
	±111.3	±113.4	±170.0	±115.4	±122.5	±147.6
S2 occurring 0–30 ms *before* initial movement *onset*	276.4	330.0	526.4	461.7	470.2	299.3
	±65.9	±54.1	±127.0	±71.4	±83.2	±101.2
S2 occurring 0–30 ms *after* initial movement *offset*	239.4	285.1	459.6	373.6	497.0	297.9
	±77.3	±34.3	±114.9	±49.3	±87.5	±101.3

that the oculomotor system localizes a stimulus by combining a signal encoding its retinal location with one encoding eye position or displacement (EPS). Thus, to obtain a graphic description of the EPS, one has only to subtract the vector of retinal error (retinal error = S2 position − eye position at flash onset) from the endpoint of the targeting saccade (see Mateeff, 1978; Honda, 1990, for further discussion). Fig. 3B shows the result of this subtraction for subject PRD, demonstrating the time course of the EPS—a damped (or low-pass filtered) version of the actual saccade.

The dashed curve in Fig. 3B depicts the best-fitting nonlinear approximation of the data, using a model composed of three linear segments. A statistical software package (Systat 5.0) was used to iteratively estimate the location of the *onset* inflection point as well as the *duration* and *amplitude* of the EPS change (Table 2). Admittedly, this three-segment model is biologically simplistic, but it had a tighter fit to the data, both visually and statistically for each of the subjects, than a seemingly more plausible exponential filter (with best-fit time constants ranging from 51–172 ms). Additionally, the three-segment model is quite useful in allowing a comparison between the average velocities of the saccade itself (solid curve) and its EPS. Because our intent here is to adequately describe the data rather than to derive the oculomotor system's internal transfer function, we feel the use of this model is justified.

Fig. 4 provides a graphic comparison of the best-fitting EPS approximations for four of the human subjects (BWC, MSR, PRD, and ZSK; dashed curves) and monkey Z (dotted curve), with amplitudes normalized to assist comparisons. The damped nature of the EPS can also be noted in Table 2, by comparing its average velocity (average velocity = amplitude ÷ duration) to that of the respective initial saccade (EM; solid curve in Fig. 4 depicts a typical saccade from subject PRD). It is not known whether the slight amplitude differences (shown in Table 2) for the initial saccade and its EPS are systematic differences, are caused merely by random error, or are byproducts of the curve-fitting approach.

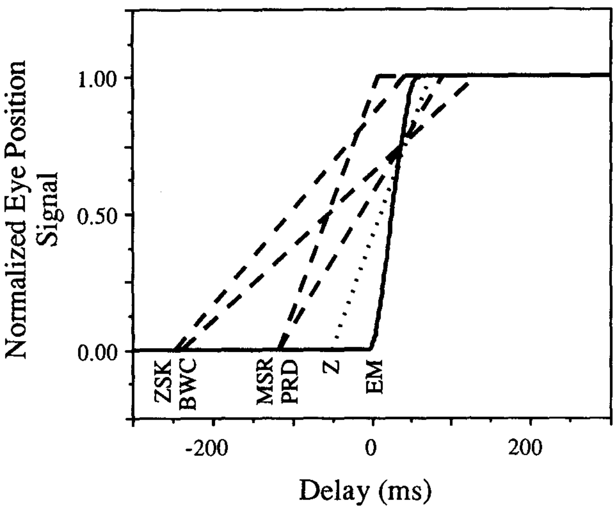

Fig. 4. Best-fit curves describing EPS data from subjects BWC, MSR, PRD, ZSK, and monkey Z. Solid curve (EM) = normalized horizontal component of typical initial saccade (subject PRD); dashed curves = normalized EPS in four human subjects; and dotted curve = normalized EPS in monkey Z.

The EPS was qualitatively similar in the monkey and human subjects in that each was a damped version of the actual saccade, but quantitative differences did exist. Whereas mislocalizations began to increase 114–247 ms before movement onset in the human subjects, the inflection point in monkey Z was only 51 ms before movement onset. Additionally, the average EPS velocity was also somewhat slower in the human subjects (54–136 deg/s) than in the monkey (169 deg/s). It is impossible to tell from this small sample if these dissimilarities reflect interspecies differences, or are, instead, the result of the same intersubject differences evident among the human subjects.

In the subject not depicted in Fig. 4 (MCD), it appeared that an additional source of error was confounding the attempt to accurately localize S2: each of the possible locations of S2 was associated with a unique curve of mislocalization. The five curves presented in Fig. 5A represent the errors (smoothed with a distance-weighted least-squares algorithm) associated with the oculomotor localization of S2 in each of the five possible flash locations. Thus, flashes at the +5-deg position, presented even *well before* initial movement onset, were mislocalized in the direction of the initial movement; flashes at the −15-deg position, presented *well after* the initial movement, were mislocalized in the opposite direction. This effect was not evident in the other four human subjects or monkey Z, as demonstrated in Fig. 5B

Table 2. *Parameters of saccade (EM) and best-fit eye position signal (EPS) for each subject, allowing intrasubject comparisons of EM and EPS, and interspecies comparison of EPS from human and nonhuman primates*

Subject	BWC $n = 191$	MCD $n = 156$	MSR $n = 315$	PRD $n = 486$	ZSK $n = 259$	Monkey Z $n = 284$
EM onset (ms)	0.0	0.0	0.0	0.0	0.0	0.0
EM duration (ms)	62.7	60.4	65.5	55.2	77.1	57.3
EM amplitude (deg)	19.1	18.9	17.3	17.7	20.9	21.4
EM average velocity (deg/s)	304.6	312.9	264.1	320.7	271.1	373.2
EPS correlation coefficient R^2	0.954	[a]	0.948	0.954	0.910	0.957
EPS onset (ms)	−236.6	[a]	−116.0	−114.3	−246.7	−50.8
EPS duration (ms)	368.5	[a]	125.0	203.7	289.7	124.1
EPS amplitude (deg)	19.9	[a]	17.0	17.0	19.4	21.0
EPS average velocity (deg/s)	54.0	[a]	135.9	83.3	67.0	169.1

[a] Curves were not fit to data from MCD. See text.

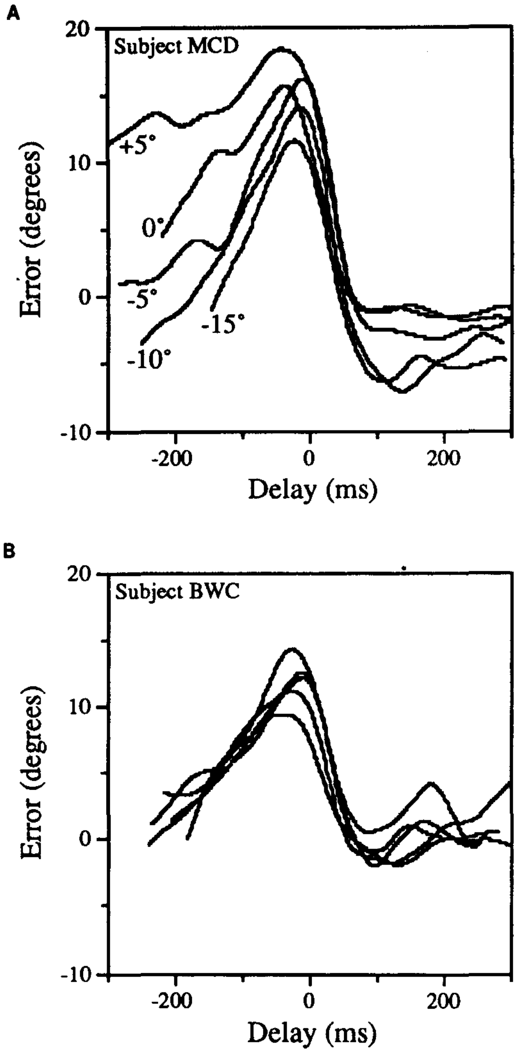

Fig. 5. Comparison of mislocalization curves for each of the five flash locations (−15, −10, −5, 0, or +5 deg from screen center). A: Curves of mislocalization for subject MCD, demonstrating faulty localization of flashes presented well before and well after the initial movement. Each curve is a smoothed version of the actual data (distance-weighted least squares algorithm). B: Curves of mislocalization for subject BWC, with accurate localization of flashes presented well before or well after the initial movement.

for subject BWC. The pattern of errors in MCD seems to be consistent with an overestimation of retinal error gain. Indeed, a similar (although smaller) overestimation was seen in subject MCD when making simple visually evoked saccades directly to the location of S2, bypassing the initial saccade to S1. Because of this, no attempt was made to find the best-fit curve for the EPS in this subject. It is possible that this effect is related to that seen in the perceptual localization study of Bischof and Kramer (1968), in which the shape of the mislocalization curve was also dependent on the retinal location of the target stimulus. In any event, it is obvious from Fig. 5A that a damped EPS was used by the oculomotor system of MCD, just as in the other subjects.

Discussion

The results presented here do serve to verify the main point of the study by Hallett and Lightstone (1976*a*, *b*)—the brain does appear to combine an EPS with a retinal error signal in order to localize visual stimuli. If this were not true, *all* flashes presented before the initial movement would be mislocalized by an amount equal to the initial movement amplitude. The present study did not find, however, that the oculomotor system uses an accurate EPS when computing stimulus location, as Hallett and Lightstone had claimed. Instead, the EPS is a damped version of the actual saccade, leading to a mislocalization of flashes presented in the period just before and after each saccade. This verifies the findings of Honda (1989, 1990), and is reminiscent of the many studies utilizing perceptual localization (Matin & Pearce, 1965; Bischof & Kramer, 1968; Kennard et al., 1971; Monahan, 1972; Mateeff, 1978; Grüsser et al., 1987; Honda, 1989, 1990).

An additional finding of the present study is the general similarity of spatial localization abilities in human and nonhuman primates: in each, a damped EPS is used by the oculomotor system. The dissimilarities seen here, in EPS onset times and rates of change, may be genuine differences between humans and monkeys, just as differences exist between the two regarding, for instance, latency (Boch et al., 1984) and peak velocity (Robinson, 1981) of simple visually evoked saccades. However, additional work must be completed in order to verify that the dissimilarities in spatial localization abilities are more than simple intersubject differences.

Could it be that the mislocalizations seen in the present study are caused, not by an inaccurate EPS, but, instead, by an inaccurate visual representation? Indeed, several possible sources of visual representation errors have been identified by prior studies; three of these are discussed below:

1. Gnadt et al. (1991) describe, for saccades to remembered locations, an inaccuracy which increases as a function of saccade latency. However, this effect does not seem to be the cause of the mislocalizations seen in the present study for three reasons. First, the majority of the latency-dependent error described by Gnadt et al. was in the vertical direction; conversely, the errors associated with the present study were in the direction of the initial saccade (i.e. horizontal). Second, when examining only those trials in which S2 occurred in the 30-ms window before initial movement onset (i.e. when mislocalizations were largest), no consistent relationship was found between targeting saccade latency and the amount of localization error. Third, while it is true that there was a slight increase (35.2 ms averaged across subjects) in targeting saccade latency if S1 occurred just before the initial saccade onset (as opposed to just after, Table 1), this small difference could not account for the large mislocalizations seen here, especially since the latency-dependent errors of Gnadt et al. took approximately 300 ms to grow to only 5 deg in the vertical direction (their Fig. 6).

2. Averaging saccades have been shown to occur when two targets are presented in close spatial and temporal proximity (Becker & Jürgens, 1979; Findlay, 1982). Indeed, in the present study, for trials in which S2 occurred very early (more than 100 ms before initial saccade onset), subjects MSR, ZSK, and monkey Z occasionally showed this type of

saccade averaging (a similar report is made by Honda, 1990). However, the effect was only manifest in the initial saccade trajectory (i.e. the initial saccade had a larger-than-normal upward component due to the upward shift of S2); no differences in S2 localization could be seen among trials (with approximately equal stimuli timing) showing various degrees of averaging on the initial saccade. Furthermore, a target presented at initial movement onset (i.e. the condition of maximum mislocalization) is too late to induce any averaging effects with the initial saccade. Finally, an *averaging* effect, by definition, could be responsible for only those targeting saccades ending *between* the locations of S1 and S2, not for those ending *beyond* S1 and S2 (as does example C in Fig. 2).

3. Sparks et al. (1987) have described a phenomenon in which the metrics of an impending saccade are gradually specified over a period of 100–200 ms (see also Stanford et al., 1990). In their study, visually evoked saccades were evoked prematurely by microstimulation of the paramedian pontine reticular formation in monkeys. These prematurely evoked saccades were found to be hypometric, presumably because the gradual specification of target location had not had time to reach its final value. Since the targeting saccades in the present study all had latencies of more than 200 ms, it is unlikely that this phenomenon is the cause of the mislocalizations seen here. Even if one were to argue that the presence of the initial saccade could possibly interrupt a gradual specification of the target location, it seems that the associated errors would be in the direction opposite the initial saccade (coinciding with the hypometric premature saccades seen by Sparks et al.), not, as they are here, in the same direction as the initial saccade.

Conceivably, some other – as yet unidentified – errors in visual representation may have contributed to the mislocalizations seen in the present study. There is no evidence, however, suggesting that this is so. Therefore, the most parsimonious hypothesis is that the oculomotor system does, indeed, use a damped representation of eye position or displacement in its attempt at spatial localization.

An obvious question that arises concerns the causes behind the differences found in the results of this study (as well as that of Honda, 1989, 1990) and those of Hallett and Lightstone (1976*a*, *b*). There are actually many methodological differences between the studies that could account, at least in part, for the differences. The first two of these have already been addressed by Honda (1990) and Howard (1982), but will be briefly reiterated here:

1. In the experiment of Hallett and Lightstone, the location of the final target step was reilluminated after a delay of 250–500 ms, giving the subject valuable feedback concerning actual stimulus location and task performance. This may have allowed the subject to learn one or several strategies for minimizing the errors (this possibility was also discussed by Hallett, 1976). A related factor is the variable duration (1–300 ms) of the final target step in the study by Hallett and Lightstone: trials having long duration flashes may have provided additional opportunities to develop error-minimization strategies.
2. Hallett and Lightstone always presented the target flash after a fixed delay beyond the detection of initial movement onset. As seen in Fig. 2 of the present study, the magnitude of the localization error is dependent on the presentation time. Holding the delay constant eliminates this variable, and could potentially allow the subject to correct for the mislocalizations by adding a simple biasing term to the compensation computations. Furthermore, with a fixed delay, one incurs the risk of always presenting the stimulus at a time at which the EPS is fortuitously veridical.
3. The amplitude of the initial saccade in our study (20 deg) was much larger than those used in the study of Hallett and Lightstone (3.8 or 7.6 deg). However, Honda (1989, 1990) found results similar to ours when using an initial saccade amplitude (8 deg) comparable to that of Hallett and Lightstone.
4. The stimuli employed by Hallett and Lightstone were more intense than those used in the present study. Our subjects, however, were allowed to become dark adapted before the experiment began, and informal observations demonstrated the subjects' ability to clearly see the stimulus with direct foveation (where visual threshold is highest). As further proof that visibility was not a problem, in only 1.3% of all experimental trials did the subjects report any uncertainty concerning the location of the 2-ms flash, S2. Finally, Honda (1989, 1990) used target flashes much brighter (40 cd/m^2) than those in the present study (15 mcd/m^2), yet found similar results.

A fifth possible explanation for the discrepancy between the results of this study and that of Hallett and Lightstone (1976*a*, *b*) lies in the different timing relationships of the visual stimuli or steps. In the experimental design of Hallett and Lightstone, timing was such that the offset of the first target step was synchronous with the onset of the second. In the design of the present study, the duration of S1 was always 5 ms, so that a variable gap of complete darkness (45–495 ms) existed between S1 offset and S2 onset. This particular design was chosen to minimize the possibility that the subjects would use the exocentric (allocentric) orientation cues between S1 and S2 when programming their targeting saccades (Hayhoe et al., 1990). It is possible that the subjects of Hallett and Lightstone were using these exocentric cues to minimize the inherent errors in egocentric localization. Although Hallett (1976) discussed the possibility of exocentric cues influencing the targeting saccades, he deemed the possibility unlikely since the only continually lit landmark was the almost invisible near-infrared light source used for recording eye position. However, preliminary experiments performed in our laboratory, using a timing relationship similar to that of Hallett and Lightstone, suggest that landmarks need not be continually lit to be used as exocentric cues (Dassonville et al., 1991).

According to most current models of brain-stem oculomotor control, an accurate representation of eye position (or displacement or velocity) is necessary to stop a saccade when its final position is achieved. Since this accurate EPS is theoretically available, why does the oculomotor system use a damped version in its computation of a target's spatial location? Is there any advantage in using a damped version? To answer these questions, one must first look at what type of eye-position representation would be necessary to achieve perfect localization. Obviously, the first requirement is that its time course very closely match that of the eye movement, even during the period of peak velocity (more than 500 deg/s in humans, and more than 800 deg/s in monkeys). However, a further requirement is necessary: to account for the afferent delay of early visual processing (much of which occurs in the retina), the EPS should also be delayed (Schlag et al., 1989). This delay must equal that of early visual processing, so that the appropriate eye-position information is combined with the late-arriving retinal information. Even if it were possible for the brain to accurately delay its EPS, there must be some mechanism to vary the delay to accommodate for the fluctuations in afferent processing time caused by different stimulus intensities or retinal eccentricity. This last requirement certainly seems an insurmountable obstacle, and failing to meet it would allow mislocalizations as large as the initial movement itself. If it is impossible to delay an accurate representation of eye displacement by the appropriate sensory duration, the next best solution is to dampen the EPS. In this way, the oculomotor system can at least minimize the size of the errors encountered; the drawback, of course, is a slightly increased time window in which errors will occur (see also Schlag et al., 1991).

Finally, why do mislocalizations occur with flashes presented *before* a saccade? Does this imply that the EPS begins to change even before the saccade begins? Not necessarily. One must remember that, as mentioned above, light reaching the retina at one point in time will not be combined with an EPS until a second, much later point in time. Thus, a damped EPS that begins changing immediately upon saccade onset will yield a curve of mislocalizations shifted, in time, by an amount equal to this afferent processing delay. A prediction can be made, then, that a stimulus of brighter intensity (or one presented on the central retina) will yield a mislocalization curve that begins changing later than that from a dimmer (or more peripheral) stimulus. Thus, saccades to brighter flashes will tend to have smaller presaccadic mislocalizations, and larger postsaccadic mislocalizations in the direction opposite the saccade (see also Mateeff, 1978). This may account for some of the timing and shape differences of the error curves found in various perceptual studies (Matin & Pearce, 1965; Bischof & Kramer, 1968; Kennard et al., 1971; Monahan, 1972; Mateeff, 1978; Grüsser et al., 1987; Honda, 1989). Additionally, if the visual-processing delays vary between subjects, they may account for the intersubject differences found in the present study.

In recent literature, there has been much discussion of the discrepancy between perceptual and oculomotor localization abilities. While there are some examples where this dichotomy in ability is still probably valid (blind sight: Pöppel et al., 1973; saccadic suppression of displacement: Bridgeman et al., 1979; visual masking: Fehrer & Biederman, 1962), the results presented here preempt some of these discussions: oculomotor and perceptual localization abilities do appear to rely on similarly damped representations of eye position or displacement. Still under dispute is the accuracy of arm movements toward perisaccadic flashes—Hansen and Skavenski (1985) have demonstrated the motor system's use of an accurate EPS, whereas Miller (1989) has demonstrated the use of an inaccurate EPS. One wonders if methodological differences can also account for this discrepancy.

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