The Use of Egocentric and Exocentric Location Cues in Saccadic Programming

PAUL DASSONVILLE,*† JOHN SCHLAG,* MADELEINE SCHLAG-REY*

Theoretically, the location of a visual target can be encoded with respect to the locations of other stimuli in the visual image (exocentric cues), or with respect to the observer (egocentric cues). Egocentric localization in the oculomotor system has been shown to rely on an internal representation of eye position that inaccurately encodes the time–course of saccadic eye movements, resulting in the mislocalization of visual targets presented near the time of a saccade. In the present investigation, subjects were instructed to localize perisaccadic stimuli in the presence or absence of a visual stimulus that could provide exocentric location information. Saccadic localization was more accurate in the presence of the exocentric cue, suggesting that localization is based on a combination of exocentric and egocentric cues. These findings indicate the need to reassess previously reported neurophysiological studies of spatial accuracy and current models of oculomotor control, which have focused almost exclusively on the egocentric localization abilities of the brain.

Spatial localization   Saccade   Visual stability   Eye position signal   Human

INTRODUCTION

For over a century it has been theorized that the brain must monitor its own oculomotor output if it is to make sense of stimulus location information imbedded in the incoming visual signal (see Grüsser, 1986 for a historical review). How else, the theory goes, can the brain distinguish the movement of the visual image caused by an eye movement from that caused by a true displacement of the visual scene? In recent times, several investigations have focused on the accuracy of this self-monitoring ability. Matin and Pearce (1965) asked subjects to perceptually localize a brief flash of light by verbally comparing its location to that of a previously extinguished visual reference. When the target flash was presented around the time of a saccadic eye movement, the subject mislocalized the flash along the axis of the intervening saccade. The pattern of errors displayed by the subjects led Matin and Pearce to conclude that, although the brain was taking into account the presence of the saccade, the internal representation of the saccade moved with a velocity much less than the true velocity of the eye. Several subsequent studies of perceptual localization verified this finding (Bischof & Kramer, 1968; Kennard, Hartmann, Kraft & Glaser, 1971; Monahan, 1972; Mateeff, 1978; Honda, 1989).

Examining the question from an oculomotor viewpoint, Hallett and Lightstone (1976a, b) asked subjects to localize a perisaccadic flash by making an eye movement to its location (also see Gresty & Leech, 1976). Finding that oculomotor localization was accurate, Hallett and Lightstone concluded that, unlike perception, the oculomotor system has access to an accurate, up-to-date representation of eye position. This led to much speculation in the scientific literature as to the significance of, and mechanisms responsible for, this apparent difference between perceptual and motor localization. However, the conclusions of Hallett and Lightstone, and much of the speculation that followed, have been called into question by recent studies from our laboratory (Dassonville, Schlag & Schlag-Rey, 1991, 1992) and that of Honda (1990, 1991), which found that oculomotor localization is indeed based upon a damped representation of eye position similar to that used for perceptual localization.

What might explain the differences between the results of Honda (1990, 1991) and Dassonville *et al.* (1992), and those of Hallett and Lightstone (1976a, b)? Is it possible that the differences were caused by dissimilar paradigms of target presentation? Indeed, many procedural differences did exist, and have been extensively discussed elsewhere (Honda, 1990; Dassonville *et al.*, 1992; see also Howard, 1982). We felt that the simplest manner in which to tease apart the individual contributions of the procedural differences was to test their effects in isolation. In the present study, we compared subjects' localization abilities using the task of our original study (Dassonville *et al.*, 1992) and a version of that task in

*Brain Research Institute, University of California at Los Angeles, Los Angeles, CA 90024-1761, U.S.A.
†Present address: Brain Sciences Center (11B), Minneapolis V. A. Medical Center, 1 Veterans Drive, Minneapolis, MN 55417, U.S.A.

which the timing aspects of visual presentation were altered to be more similar to those of Hallett and Lightstone. In doing so, we found that localization was better with the altered visual presentation; the general pattern of error reduction was consistent with an ability to make use of visual information concerning a target's location with respect to the locations of any visual references that may be present. Although this object-centered (exocentric) localization ability has long been known to exist in conjunction with (and even dominate) egocentric localization in visual perception (Matin, Picoult, Stevens, Edwards, Young & MacArthur, 1982), its role in oculomotor programming has only recently been investigated (Hayhoe, Lachter & Møller, 1992; Honda, 1993). Preliminary results from this investigation have been published elsewhere (Dassonville et al., 1991, 1992; Dassonville, Schlag & Schlag-Rey, 1993).

METHOD

Five normal adults provided written consent to serve as subjects in this study (naive, BWC, MCD, ZSK; non-naive, MSR, PRD), details of which were approved by the Human Subject Protection Committee of the University of California, Los Angeles. A portion of the results presented here were collected during the course of a previously reported investigation performed in our laboratory (Dassonville et al., 1992); further details of this task can be found there. In short, subjects were asked to make saccadic eye movements to brief visual stimuli in the order of appearance; stimuli were small (0.23 deg dia) luminous (15 mcd/m^2) green dots back-projected onto a tangent screen (132 cm from the eyes) by a Tektronix 608 oscilloscope equipped with a wide-angle projection lens. Horizontal and vertical positions of the eye were measured with a monocular scleral search coil (Skalar #3021). A personal computer running the MacProbe software package (Aristometrics) was used to control the timing and position of visual targets, and to digitally sample (1-kHz) eye position information for off-line analysis. Each trial began when the subject's gaze entered an invisible 4 deg window centered on a fixation point [F, Fig. 1(A, B)] located at eye level, 20 deg to the left of screen center (-20 deg). After a 750-msec delay, the fixation point was extinguished and replaced by a brief flash (S_1, 5-msec duration) at the screen center (0 deg). This flash served as the target for a 20 deg rightward horizontal saccade. After a variable, randomly selected delay (50–500 msec) measured from the onset of S_1, a second target (S_2, 2-msec duration) was presented at one of five possible locations (horizontally -15, -10, -5, 0, or $+5$ deg from the screen center, vertically 10° above the screen center). The subject was required to make a subsequent targeting saccade to the location of S_2. No feedback was ever given to the subject concerning movement accuracy or the actual position of S_2. It is important to note that in this paradigm, which we will refer to as the GAP task, a period of complete darkness (45–495 msec duration) intervened between the offset of S_1 and the onset of S_2.
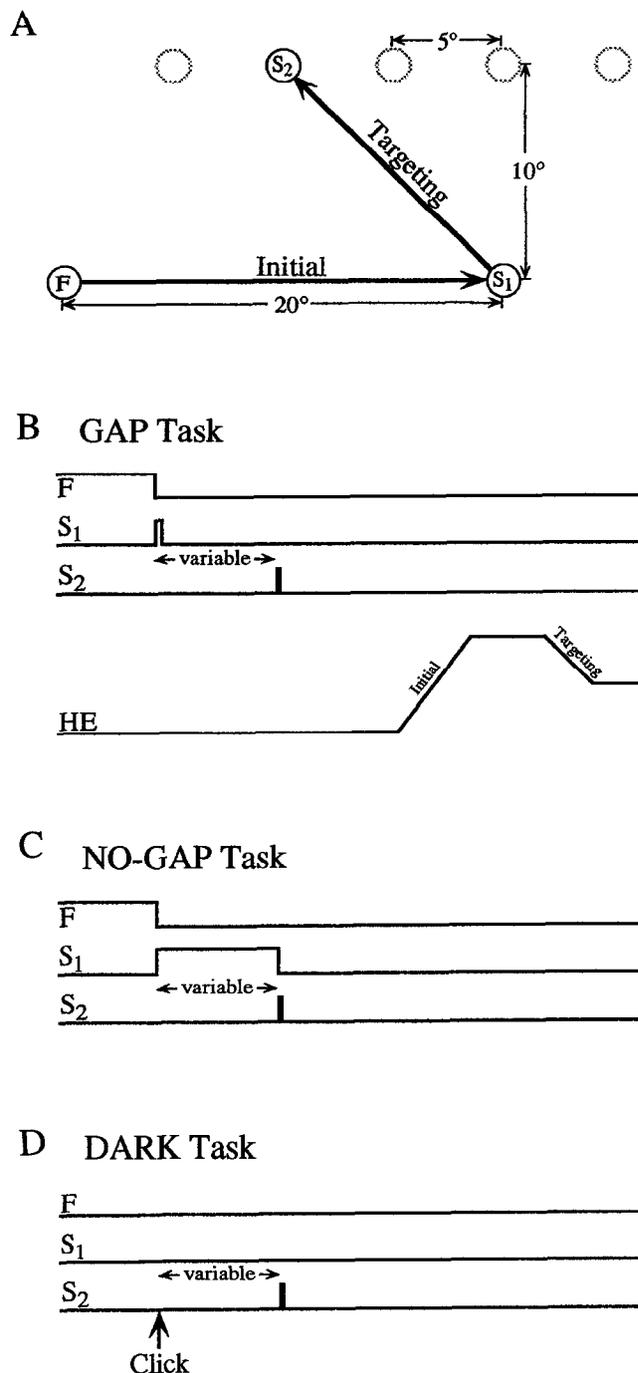

FIGURE 1. Schematic comparison of GAP, NO-GAP and DARK tasks. (A) XY plot of flash locations. F, fixation point; S_1, stimulus No. 1; S_2, stimulus No. 2, randomly located in one of five possible locations (gray circles); initial, initial saccade from fixation point to S_1; targeting, targeting saccade from S_1 to S_2. (B) Timing of stimuli presentations in the GAP task. F = 750 msec; S_1 = 5 msec; S_2 = 2 msec, with a variable onset randomly selected to occur anywhere before, during or after the initial movement; HE, horizontal eye position. (C) Timing of stimuli presentations in the NO-GAP task. F = 750 msec; S_1 = variable duration, offset synchronous with S_2 onset; S_2 = 2 msec, with a variable onset. (D) Timing of stimuli presentations in the DARK task. Click, audible signal for subject to perform a rightward initial movement of 20 deg amplitude; S_2 = 2 msec, with a variable onset; F and S_1 are not illuminated in the DARK task.

The task described above is qualitatively similar to the task of Hallett and Lightstone (1976a, b). The first visual stimulus serves as a fixation point, the second serves to evoke an initial saccade, and the third—presented around the time of the initial saccade—serves as a visual probe. The subject's localization of this probe can be used to deduce the internal representation of eye position at the time of probe onset (see Dassonville *et al.*, 1992). However, our GAP task does differ quantitatively from the task of Hallett and Lightstone in several respects. The difference that we chose to investigate in the present study is that of S_1 duration. Whereas S_1 had a 5-msec duration in our GAP task, the equivalent stimulus of Hallett and Lightstone had a much longer variable duration such that S_1 was extinguished only upon the illumination of S_2 (Hallett & Lightstone, 1976b), or 10 msec before the illumination of S_2 (Hallett & Lightstone, 1976a). This effectively eliminates the period of complete darkness that exists between S_1 and S_2 in the GAP task. Our NO-GAP task, then, is identical to the GAP task with this one exception: S_1 duration is set equal to the variable delay between S_1 onset and S_2 onset [Fig. 1(C)].

The temporal relationships of the visual stimuli in the GAP task were originally designed to minimize the subjects' ability to use exocentric cues to localize the visual target. However, to ensure that the subjects rely only on egocentric cues, the fixation point and S_1 must be eliminated from the task completely. To accomplish this, we used a third paradigm of visual presentation— the DARK task [Fig. 1(D)]—to test three of the subjects (BWC, MCD, and PRD). To begin each trial, the subject was instructed to look, in total darkness, toward the location that the fixation point had occupied in previous experiments using the GAP and NO-GAP paradigms. After a short delay (approx. 1 sec), an audible click was issued from a speaker located directly over the subject's head; this served as the subject's signal to make a spontaneous saccade of the same direction and amplitude (i.e. 20 deg rightward) as those of the initial saccades from the GAP and NO-GAP paradigms. Target S_2 was presented at a pseudorandom delay (50–500 msec) after the click was issued, and the subject was required to make a subsequent targeting saccade to its location. Throughout the 30 min duration of each experimental session with this paradigm, the subject was provided no visual input except the 2 msec flash of S_2. Because of this, the subject sometimes had difficulty in accurately directing his or her eyes to the fixation region to begin the next trial. When this occurred, the experimenter coached the subject with verbal instructions of where to fixate (i.e. by telling the subject to look up, down, left or right). Similarly, the subject was coached on the accuracy of the initial saccade so that appropriate amplitudes and directions were approximately maintained. As in the GAP and NO-GAP tasks, no feedback was provided to the subject concerning the accuracy of the targeting movement or the actual position of S_2.
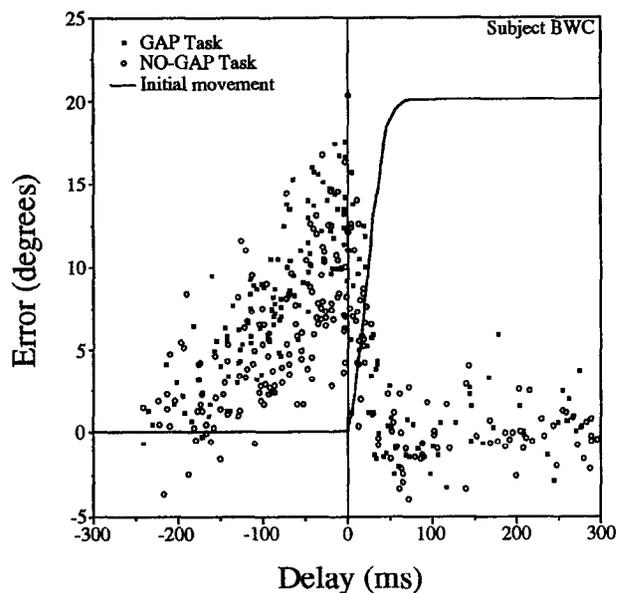

FIGURE 2. Patterns of oculomotor mislocalization in the GAP (■) and NO-GAP (○) tasks, showing for each trial the magnitude of error (ordinate, deg) vs delay (abscissa, msec) between S_2 onset and initial saccade onset (0 msec). Positive error values represent mislocalizations in the direction of the initial saccade; positive delays represent targets occurring after initial saccade onset. The solid curve denotes the mean horizontal component of the initial saccade from this subject.

RESULTS

The results of our previous study (Dassonville *et al.*, 1992) demonstrated a characteristic pattern of localization errors in the GAP task. This same pattern of errors was obvious in the data collected in the GAP, NO-GAP and DARK tasks of the present study (Fig. 2): whereas targets presented well before the movement were localized with relative accuracy, targets presented just before or during the initial movement (i.e. the saccade from the fixation point to S_1) were systematically mislocalized. The direction of this mislocalization was consistently in the same direction as the initial movement, with peak errors occurring for targets presented at the onset of the movement. Targets presented after the initial movement were once again localized accurately, with only random errors scattered about the actual position of the target. As has been previously demonstrated (Honda, 1993; Dassonville *et al.*, 1992), systematic errors were evident only along the axis of the initial movement. For this reason, the analyses that follow address only the errors in localization along the horizontal dimension.

Because our main objective was to compare the magnitude of errors associated with the different tasks, it seemed appropriate to concentrate our analysis on those trials in which the target was presented at or just before initial movement onset—the time at which mislocalizations were greatest. For this purpose, the error magnitudes were averaged for those trials in which target onset occurred within a 30 msec window before initial movement onset. A window duration of 30 msec was chosen as a compromise between the desirability of using the shortest window possible at the time of peak error

with the necessity of having enough trials (approximately 30 for each task condition) to allow for an adequate statistical comparison. To ensure that any differences in the subjects' ability to localize S_2 in the respective tasks were caused by differences in the visual presentation paradigms rather than consistent differences in the initial saccades, the amplitudes of the initial saccades from the NO-GAP and DARK tasks were statistically compared (independent-samples t-test) to those from the GAP task (Table 1). The comparison of the movements in the NO-GAP and GAP tasks revealed a significant difference in only one subject (ZSK, $P < 0.001$); the results from this subject were therefore excluded from the analyses that follow. Significant differences were also noted in the amplitudes of the initial movements collected in the DARK and GAP tasks for two of the three subjects tested (BWC and PRD, $P < 0.001$). Because of this, the results from the DARK task were fully analyzed only for subject MCD. There were no qualitative differences between the results from subject ZSK (and from the DARK task for subjects BWC and PRD) and those reported here.

The bar graphs in Fig. 3 show the mean peak errors from the GAP and NO-GAP tasks for each subject, and from the DARK task for subject MCD. Subjects were most accurate in the NO-GAP condition, with the magnitude of the localization errors significantly reduced from that of the GAP condition in three of the four subjects (independent-samples t-test). Performance of subject MCD was slightly, although not significantly, worse in the DARK task than in the GAP task.

A more detailed examination of the localization errors revealed a significant location-dependent trend in the magnitude of the errors produced in the NO-GAP task for each subject (ANOVA, $P < 0.005$): Errors tended to be smaller for trials in which S_2 was presented near the location of S_1 (i.e. stimulus positions -5, 0 and 5 deg, Fig. 4). No significant trend of this type was evident in the results from the GAP task in three of the four subjects (nor from the DARK task in any of the three subjects tested), but a similar yet smaller trend was
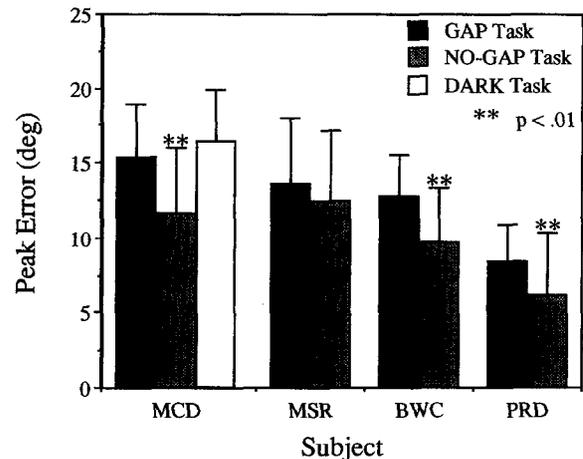

FIGURE 3. Peak error (mean + SD, deg) of S_2 localization in the GAP (solid bars), NO-GAP (gray bars), and DARK (open bars) tasks, computed as the mean localization error for those trials in which S_2 was presented in the 30 msec before initial saccade onset. **Statistically significant ($P < 0.01$) reduction in the peak errors of the NO-GAP task, compared to the values of the GAP task. Peak errors did not significantly differ between the GAP and DARK tasks in subject MCD.

obvious in the results of the GAP task in subject PRD (ANOVA, $P < 0.05$). To further quantify this effect, between-task statistical comparisons (independent-samples t-test) were performed on the magnitude of the errors at each S_2 location. Whereas no significant differences were found between the results of the GAP and NO-GAP tasks when the target was in either of the two leftmost positions, significant differences were common with targets presented in any of the rightmost positions (Fig. 4). Conversely, no differences were seen at any target position when comparing the results of the GAP and DARK tasks in subject MCD.

Whereas Figs 3 and 4 provide a comparison of the localization errors for targets presented immediately before initial movement onset, Fig. 5 allows a comparison for all target delays. Each curve represents the subject's localization of individual targets in the respective tasks, plotted with respect to the delay between initial movement and target onsets (curves represent raw data, smoothed with a locally-weighted least squares algorithm). Thus, the leftmost curve describes the localization of S_2 when presented in the leftmost target location (-15 deg) at different onset delays. If targeting had been perfect for all locations at all delays, the curves would have formed five vertical lines above the five target locations in the lower schematic. Instead, systematic errors were evident when S_2 was presented near the time of the initial movement. Each curve in Fig. 5(A) runs approximately parallel to its neighbors, as is expected from the lack of any location-dependent trends in the subject's performance of the GAP task (Fig. 4). In comparison, the curves in Fig. 5(B), representing data from the NO-GAP task, are somewhat compressed near the time of initial movement onset, with peak errors smaller for targets presented in the rightmost positions. Results from the DARK task [Fig. 5(C)] were similar to

TABLE 1. Initial movement characteristics

Subject	Task	Duration (mean ± SD, msec)	Amplitude (mean ± SD, deg)
MCD	GAP	60.4 ± 4.5	19.1 ± 1.8
	NO-GAP	58.8 ± 3.5	18.2 ± 1.2
	DARK	60.7 ± 7.5	18.7 ± 3.7
BWC	GAP	62.1 ± 5.8	19.3 ± 2.2
	NO-GAP	58.8 ± 2.8	18.4 ± 1.7
	DARK	83.3 ± 9.7	24.3 ± 3.2
PRD	GAP	52.1 ± 3.7	17.7 ± 2.2
	NO-GAP	52.8 ± 4.1	17.9 ± 1.5
	DARK	67.1 ± 9.1	21.4 ± 3.1
MSR	GAP	62.8 ± 5.2	17.5 ± 2.0
	NO-GAP	58.4 ± 2.9	17.9 ± 1.1
ZSK	GAP	79.8 ± 9.6	22.9 ± 1.8
	NO-GAP	70.0 ± 4.7	18.8 ± 1.7

those of the GAP task, with peak errors approximately equal for all target positions. As previously noted (Dassonville *et al.*, 1992), this particular subject (MCD) displays a distinctive bias in target localization: targets presented to the rightmost positions are mislocalized to the right when presented well before the initial movement, and targets presented in the leftmost positions are mislocalized to the left when presented after the initial movement. Because this bias is equally evident in the GAP, NO-GAP, and DARK tasks (Fig. 5), it is obviously not brought about by any particular parameter of the visual presentation in this investigation.

DISCUSSION

The experiments presented here were undertaken in an effort to explain the discrepant results from previous investigations of the oculomotor system's egocentric localization abilities: Recent results from our laboratory (Dassonville *et al.*, 1992) and that of Honda (1990, 1991) found large errors in the localization of perisaccadic flashes, whereas earlier results from Hallett and Lightstone (1976a, b) found no errors. In the present study, we isolated and investigated one of the differences between our original task and that of Hallett and Lightstone—the relative timing of the initial saccade
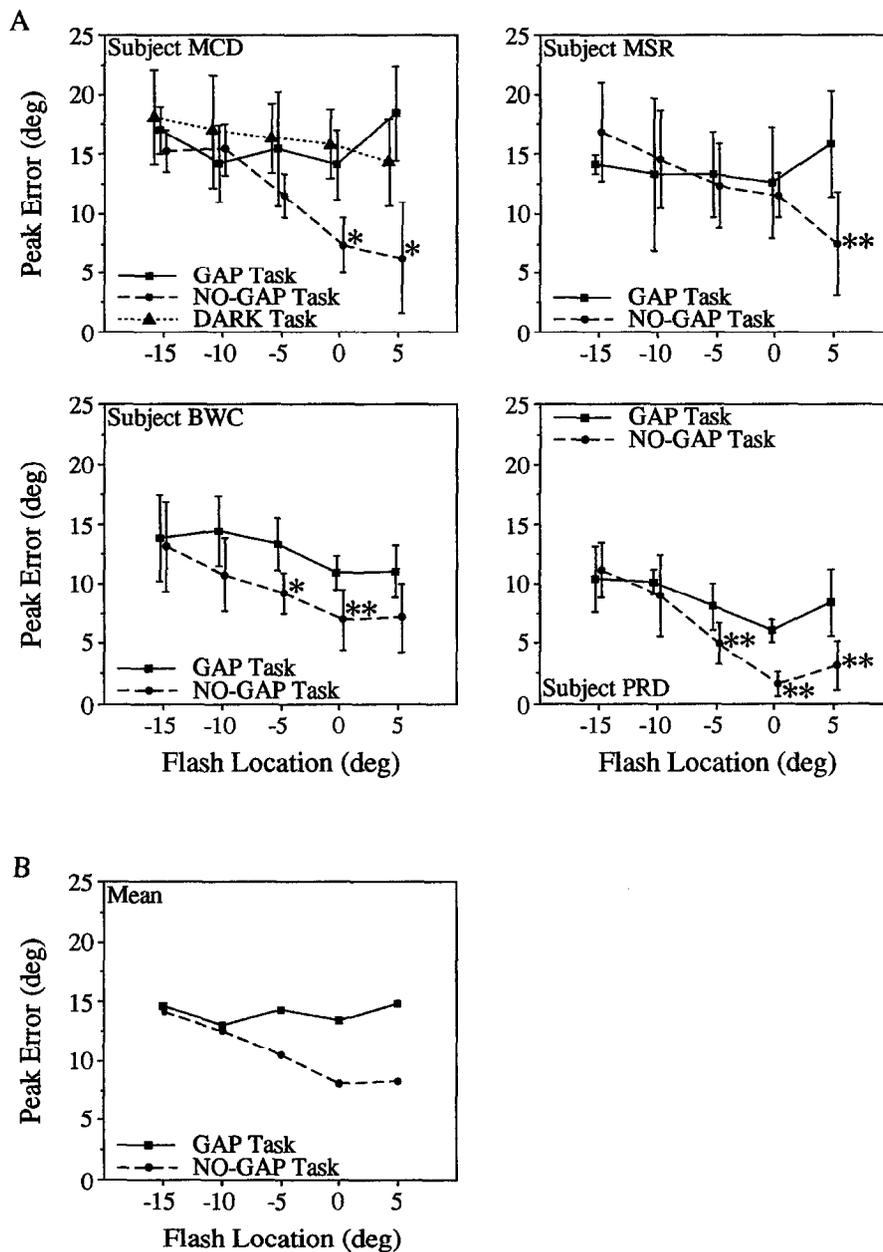

FIGURE 4. Peak errors compared across target locations. (A) Peak errors (ordinate, mean ± SD, deg) in each subject, plotted with respect to each of the five possible S_2 locations (abscissa, values refer to the horizontal distance between S_1 and S_2, deg) for the GAP (■), NO-GAP (●), and DARK tasks (▲). Asterisks denote the positions at which the error magnitudes differed significantly between the GAP and NO-GAP tasks (*$P < 0.02$; **$P < 0.01$). No significant differences were found between the GAP and DARK tasks. (B) Same representation as in (A), showing the peak errors in the GAP and NO-GAP tasks averaged across all subjects.
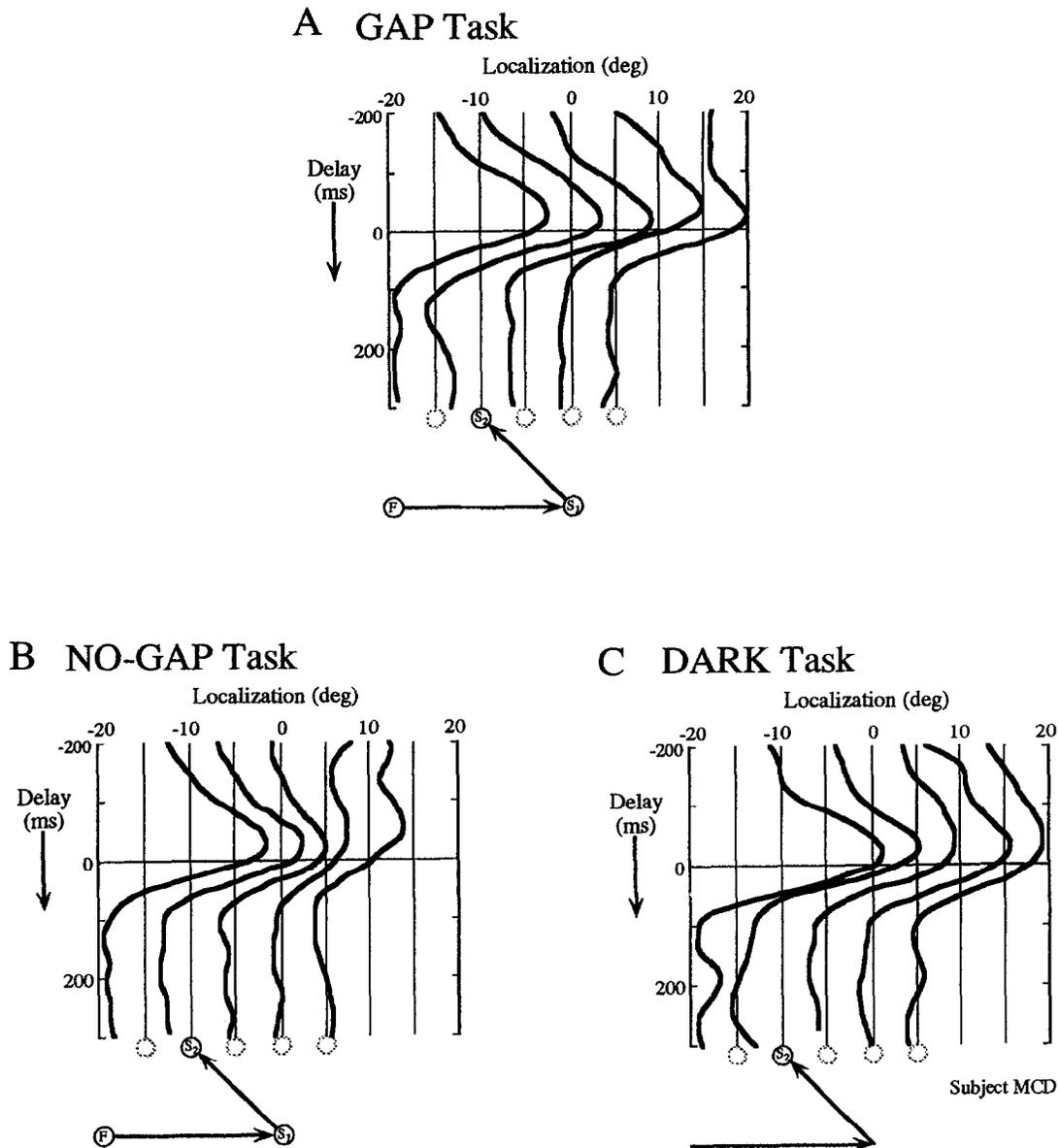
A GAP Task

B NO-GAP Task

C DARK Task

FIGURE 5. Localization of S_2 at all target delays. (A) Localization in the GAP task. Each curve represents the subject's localization of S_2 (abscissa, deg, measured from the horizontal location of S_1) for each of the five possible target locations (shown in the lower schematic), plotted with respect to flash delay (ordinate, msec; initial movement onset is synchronized at 0 msec). Curves were derived by smoothing the raw scatterplots with a locally-weighted least squares algorithm. (B) Localization in the NO-GAP task; same representation as in (A). (C) Localization in the DARK task; same representation as in (A).

target (S_1 in the present study). Upon increasing the duration of this target in the NO-GAP task, we found that the localization of a subsequent visual target (S_2) was improved for trials in which the two targets were spatially proximate. In the DARK task, on the other hand, S_1 and the fixation point were removed so that the subjects only saw the 2-msec flash of S_2. In this type of trial, the subjects' error patterns were similar to those of the GAP task as reported here and in a previous study (Dassonville *et al.*, 1992).

What aspect of the NO-GAP task was responsible for the reduction in errors? Technically, the only difference between the GAP and NO-GAP tasks was the duration of S_1; however, this single difference had several effects.

First, as was discussed above, the longer S_1 duration in the NO-GAP task eliminated the dark period that was present between S_1 and S_2 in the GAP task. Thus, light from the two stimuli was present on the retina at nearly the same moment in time. Second, the increased duration of S_1 in the NO-GAP task caused it to appear brighter than it had in the GAP task. Finally, the appearance of S_2 immediately after the onset of S_1 in the NO-GAP task may have led to a phenomenon of apparent motion. (Although none of the subjects reported experiencing apparent motion between the stimuli, it might have affected localization at a level below that of perception). Perhaps these effects acted singularly or in unison to promote a better localization of S_2 with

respect to S_1. Theoretically, the oculomotor system could achieve accurate localization by using these exocentric or object-centered cues and foregoing the use of the error-prone egocentric cues. For example, the subject might perceive the location of S_2 to be, say, directly above that of S_1. After the initial movement to S_1 is complete, the motor vector of the targeting saccade needs only to match the exocentric relationship of the two targets in order to be accurate. However, our results show only a reduction in localization errors rather than a complete elimination, so it would seem that the oculomotor system relies on a combination of egocentric and exocentric cues.

In addition to an overall decrease in the magnitude of localization errors, what other effects might one observe if a subject has the ability to use exocentric cues to improve saccadic localization? Gogel (1973a, b) has demonstrated a general rule, the adjacency principle, that describes the extent of the brain's ability to use exocentric cues in perceptual tasks. This principle states that the exocentric cues between two nearby objects are more effective than those between two distant objects. Given this, it is not surprising to find smaller localization errors in the NO-GAP task for those trials in which S_1 and S_2 are spatially proximate, and larger errors for those in which S_1 and S_2 are more distant. However, we must also consider an alternate hypothesis concerning the cause of this location-dependent effect: as can be seen in the spatial schematic of the task in Fig. 1(A), the S_2 location closest to S_1 also happened to lie directly above S_1. Perhaps the verticality of the geometric relationship between S_1 and S_2 was responsible for the location-dependent increase in accuracy. Further studies, using paradigms that better dissociate target proximity and geometry, are necessary to determine if the location-dependent effects seen in the NO-GAP task are caused by adjacency, verticality, or a combination of both.

In the three tasks presented here, S_1 was never visible when the target flash was presented, nor when the targeting movement was made. Yet, in the NO-GAP task, the oculomotor system was able to use the relative locations of the two flashes to improve localization. Even the period of complete darkness that existed between the presentations of S_1 and S_2 in the GAP task was apparently insufficient to completely eliminate the use of exocentric cues by subject PRD, as evidenced by a small but significant location dependency in the GAP task. Thus, it seems that simultaneous presentation is not an absolute requirement for the use of exocentric cues. However, this is not to say that presentation timing is of no importance; the results presented here demonstrate that the stimuli must at least be temporally proximate (as they were in the NO-GAP task) in order to have an effect. This leads us to propose the existence of a temporal equivalent to the spatial adjacency principle of Gogel (1973b). One could conjecture that if S_1 were present throughout the duration of each trial, localization accuracy would even surpass that seen here with the NO-GAP task (see also Møller, Hayhoe, Ballard & Albano, 1989).

Sperling (see Sperling, 1990, for a review) and O'Regan (1984) have shown that some perisaccadic mislocalizations can be attributed to a concomitant displacement of extraneous visual images across the retina. The DARK task of the present study was designed to eliminate the possibility that these visual factors play a role, and to isolate the subjects' localization abilities to an egocentric frame of reference. The quantitative similarities between subject MCD's localization abilities in the DARK and GAP tasks, along with the qualitative similarities seen in the results of subjects BWC and PRD, confirm our previous conclusions (Dassonville et al., 1992) that the ability to egocentrically localize a visual target is hampered by the brain's maintenance of an internal representation of eye position that fails to accurately encode the timing and velocity of saccadic eye movements.

Although researchers in many areas of perception have long acknowledged the various roles played by exocentric cues, researchers of the oculomotor and skeletomotor systems have only recently begun to investigate their roles in motor programming. In a study directly related to the role of exocentric cues in oculomotor spatial accuracy, Hayhoe et al. (1992) presented evidence that saccadic programming is based, in part, on exocentric cues. In their study, two short-duration visual stimuli were presented simultaneously while the subject maintained fixation. After a short delay, one of the original stimuli was reilluminated; the subject's task was to saccade first to the reilluminated target, and then to the remembered location of the other stimulus. Hayhoe et al. found that, on trials in which the location of the reilluminated target was imperceptibly shifted up (or down), the subject's localization of the remembered target was similarly shifted up (or down), albeit to a lesser extent than the actual shift of the reilluminated target. Thus, when egocentric and exocentric cues are discordant, it appears that oculomotor localization relies on a combination of the two. Honda (1993) investigated the role of exocentric cues in target localization by presenting perisaccadic flashes (in a task similar to our GAP task) against a visible background composed of a line-drawing of a map of Japan. In summary, Honda found that subjects are slightly more accurate when the background was present, with a pattern of errors that was dependent on target location. The present investigation differed from Honda's in the complexity and timing of the visual references available to the subjects. Our use of a reference composed of a single distinct point of light has provided greater control over the subjects' use of exocentric cues, allowing a more precise investigation of the spatiotemporal limitations of the ability to use these cues in oculomotor programming.

In the past, neurophysiologists (and modelers of the motor systems) have completely ignored the possibility that the brain may be using exocentric cues to calculate the required dimensions of a targeting movement. Indeed, many researchers (i.e. Mays & Sparks, 1980; Gnadt & Andersen, 1988; Goldberg & Bruce, 1990; Barash, Bracewell, Fogassi, Gnadt & Andersen, 1991;

Duhamel, Colby & Goldberg, 1992) have used para-digms much like the NO-GAP task in single-unit studies of what they described as the brain's egocentric localiz-ation abilities. Could some aspect of these unit activities be related to the processing of exocentric cues? The findings of the present investigation lead us to suggest that the results from those studies must be re-examined with an eye toward the role of exocentric cues in spatial accuracy.

There does exist an inherent difficulty in studying the exocentric localization abilities of the perceptual and motor systems: it appears impossible to completely isolate the brain's exocentric abilities from its egocentric abilities. Isolation of the egocentric is relatively simple—one needs merely to eliminate all exocentric cues by presenting only single targets in the absence of all possible visual references (as was done in the present study with the DARK task). But how does one eliminate all egocentric cues? Deafferentation of the extraocular muscles will certainly eliminate proprioceptive infor-mation concerning eye position and velocity, but an overwhelming amount of evidence suggests that the majority of eye position information is derived centrally via a corollary discharge of the brain stem oculomotor command (Guthrie, Porter & Sparks, 1983; Gauthier, Nommay & Vercher, 1990; Bridgeman & Stark, 1991). However, it is possible to investigate the brain's exocentric localization abilities without altogether removing the influence of egocentric cues. In the present study and others (Matin et al., 1982; Shebilske, Karmiohl & Proffitt, 1983; Stark & Bridgeman, 1983; Mateeff & Hohnsbein, 1989; Honda, 1993; Velay, Roll, Lennerstrand & Roll, 1994), the roles of exocentric cues were explored by presenting them at a time at which it was known that the subject's egocentric localization abilities were impaired. Other laboratories have explored the same issue by presenting illusory exocentric cues (Gogel, 1973a, b; Hayhoe et al., 1992).

Although the presence of exocentric cues did not completely eliminate the mislocalizations inherent in the egocentric localization of perisaccadic flashes, the find-ings presented here do show that the oculomotor system is capable of using these cues to assist in programming a more appropriate targeting saccade. This does not completely answer the question as to why discrepant results were generated from our laboratory and that of Hallett and Lightstone (1976a, b), but it does suggest a partial explanation. There are several other procedural differences between the two studies, most notably the amount of feedback provided to the subjects concerning the actual location of the targets (see Howard, 1982; Honda, 1990; Dassonville et al., 1992, for thorough discussions of these differences). Perhaps a full investi-gation of these additional differences will further eluci-date the reasons for the discrepancy.

REFERENCES

Barash, S., Bracewell, R. M., Fogassi, L., Gnadt, J. W. & Andersen, R. A. (1991). Saccade-related activity in the lateral intraparietal area—II. Spatial properties. *Journal of Neurophysiology, 66,* 1109–1124.

Bischof, N. & Kramer, E. (1968). Untersuchungen und Überlegungen zur Richtungswahrnehmung bei willkürlichen sakkadischen Augen-bewegungen. *Psychologische Forschung, 32,* 185–218.

Bridgeman, B. & Stark, L. (1991). Ocular proprioception and efference copy in registering visual direction. *Vision Research, 31,* 1903–1913.

Dassonville, P., Schlag, J. & Schlag-Rey, M. (1991). Human oculomo-tor system uses both exo- and egocentric cues in the localization of successive targets. *Society for Neuroscience Abstracts, 17,* 860.

Dassonville, P., Schlag, J. & Schlag-Rey, M. (1992). Oculomotor localization relies on a damped representation of saccadic eye displacement in human and nonhuman primates. *Visual Neuro-science, 9,* 261–269.

Dassonville, P., Schlag, J. & Schlag-Rey, M. (1993). Direction con-stancy in the oculomotor system. *Current Directions in Psychological Science, 2,* 143–147.

Duhamel, J.-R., Colby, C. L. & Goldberg, M. E. (1992). The updating of the representation of visual space in parietal cortex by intended eye movements. *Science, 255,* 90–92.

Gauthier, G. M., Nommay, D. & Vercher, J.-L. (1990). Ocular musclew proprioception and visual localization of targets in man. *Brain, 113,* 1857–1871.

Gnadt, J. W. & Andersen, R. A. (1988). Memory related motor planning activity in posterior parietal cortex of macaque. *Experimental Brain Research, 70,* 216–220.

Gogel, W. C. (1973a). The organization of perceived space—I. Percep-tual interactions. *Psychologische Forschung, 36,* 195–221.

Gogel, W. C. (1973b). The organization of perceived space—II. Consequences of perceptual interactions. *Psychologische Forschung, 36,* 223–247.

Goldberg, M. E. & Bruce, C. J. (1990). Primate frontal eye fields—III. Maintenance of a spatially accurate saccade signal. *Journal of Neurophysiology, 64,* 489–508.

Gresty, M. & Leech, J. (1976). The assessment of position of stationary targets perceived during saccadic eye movements. *Pflügers Archives, 366,* 83–88.

Grüsser, O.-J. (1986). Interation of efferent and afferent signals in visual perception: A history of ideas and experimental paradigms. *Acta Psychologica, 63,* 3–21.

Guthrie, B. L., Porter, J. D. & Sparks, D. L. (1983). Corollary discharge provides accurate eye position information to the oculo-motor system. *Science, 221,* 1193–1195.

Hallett, P. E. & Lightstone, A. D. (1976a). Saccadic eye movements to flashed targets. *Vision Research, 16,* 107–114.

Hallett, P. E. & Lightstone, A. D. (1976b). Saccadic eye movements towards stimuli triggered by prior saccades. *Vision Research, 16,* 99–106.

Hayhoe, M., Lachter, J. & Møller, P. (1992). Spatial memory and integration across saccadic eye movements. In Rayner, K. (Ed.), *Eye movements and visual cognition* (pp. 130–145). New York: Springer.

Honda, H. (1989). Perceptual localization of visual stimuli flashed during saccades. *Perception & Psychophysics, 45,* 162–174.

Honda, H. (1990). Eye movements to a visual stimulus flashed before, during, or after a saccade. In Jeannerod, M. (Ed.), *Attention and performance XIII: Motor representation and control* (pp. 567–582). Hillsdale, N.J.: Erlbaum.

Honda, H. (1991). The time courses of visual mislocalization and of extraretinal eye position signals at the time of vertical saccades. *Vision Research, 31,* 1915–1921.

Honda, H. (1993). Saccade-contingent displacement of the apparent position of visual stimuli flashed on a dimly illuminated structured background. *Vision Research, 33,* 709–716.

Howard, I. P. (1982). *Human visual orientation.* New York: Wiley.

Kennard, D. W., Hartmann, R. W., Kraft, D. P. & Glaser, G. H. (1971). Brief conceptual (nonreal) events during eye movement. *Biological Psychiatry, 3,* 205–215.

Mateeff, S. (1978). Saccadic eye movements and localization of visual stimuli. *Perception & Psychophysics, 24,* 215–224.

Mateeff, S. & Hohnsbein, J. (1989). The role of the adjacency between background cues and objects in visual localization during ocular pursuit. *Perception, 18,* 93–104.

Matin, L. & Pearce, D. G. (1965). Visual perception of direction for stimuli flashed during voluntary saccadic eye movement. *Science*, *148*, 1485–1488.

Matin, L., Picoult, E., Stevens, J. K., Edwards, M. W., Young, D. & MacArthur, R. (1982). Oculoparalytic illusion: Visual-field dependent spatial mislocalizations by humans partially paralyzed with curare. *Science*, *216*, 198–201.

Mays, L. E. & Sparks, D. L. (1980). Dissociation of visual and saccade-related responses in superior colliculus neurons. *Journal of Neurophysiology*, *43*, 207–232.

Møller, P., Hayhoe, M., Ballard, D. & Albano, J. (1989). Spatial memory and the accuracy of saccades to remembered visual targets. *Investigative Ophthalmology and Visual Science*, *30*, 456.

Monahan, J. S. (1972). Extraretinal feedback and visual localization. *Perception & Psychophysics*, *12*, 349–353.

O'Regan, J. K. (1984). Retinal versus extraretinal influences in flash localization during saccadic eye movements in the presence of a visible background. *Perception & Psychophysics*, *36*, 1–14.

Shebilske, W. L., Karmiohl, C. M. & Proffitt, D. R. (1983). Induced esophoric shifts in eye convergence and illusory distance in reduced and structured viewing conditions. *Journal of Experimental Psychology: Human Perception and Performance*, *9*, 270–277.

Sperling, G. (1990). Comparison of perception in the moving and stationary eye. In Kowler, E. (Ed.), *Eye movements and their role in visual and cognitive processes* (pp. 307–351). Amsterdam: Elsevier.

Stark, L. & Bridgeman, B. (1983). Role of corollary discharge in space constancy. *Perception & Psychophysics*, *34*, 371–380.

Velay, J. L., Roll, R., Lennerstrand, G. & Roll, J. P. (1994). Eye proprioception and visual localization in humans: Influence of ocular dominance and visual context. *Vision Research*, *34*, 2169–2176.