The Use of Egocentric and Exocentric Location Cues in Saccadic Programming

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

Received 21 June 1994; in revised form 13 December 1994

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.

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
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 & Möller, 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/m²) 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 (S₁, 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 S₁, a second target (S₂, 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 from the location of S₁. No feedback was ever given to the subject concerning movement accuracy or the actual position of S₂. 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 S₁ and the onset of S₂.

FIGURE 1. Schematic comparison of GAP, NO-GAP and DARK tasks. (A) XY plot of flash locations: F, fixation point; S₁, stimulus No. 1; S₂, stimulus No. 2, randomly located in one of five possible locations (gray circles); initial, initial saccade from fixation point to S₁; targeting, targeting saccade from S₁ to S₂. (B) Timing of stimuli presentations in the GAP task. F = 750 msec; S₁ = 5 msec; S₂ = 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; S₁ = variable duration, offset synchronous with S₁ onset; S₂ = 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; S₁ = 2 msec, with a variable onset; F and S₁ 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 $S_2$ duration. Whereas $S_2$ had a 5-msec duration in our GAP task, the equivalent stimulus of Hallett and Lightstone had a much longer variable duration such that $S_2$ was extinguished only upon the illumination of $S_3$ (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: $S_2$ 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 egocentric cues to localize the visual target. However, to ensure that the subjects rely only on egocentric cues, the fixation point and $S_2$ 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 fixation point to $S_1$ on the subject concerning the accuracy of the targeting movement or the actual position of $S_2$.

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 $S_2$) were systematically mislocalized. The direction of this mislocalization was consistently in the same direction as the initial movement, with peak errors occurring after 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 slight, 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 of the GAP task in subject PRD (Fig. 4). Conversely, no differences were seen at any target position when comparing the results of the GAP and DARK 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 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).

### TABLE 1. Initial movement characteristics

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

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 S1 locations (abscissa, values refer to the horizontal distance between S1 and S2, 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.
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).

First, as was discussed above, the longer $S_2$ 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 $S_2$ 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

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.
respect to $S_r$. 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 $S_r$ to be, say, directly above that of $S_t$. After the initial movement to $S_t$ 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 $S_t$ and $S_r$ are spatially proximate, and larger errors for those in which $S_t$ and $S_r$ 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 $S_t$ location closest to $S_r$ also happened to lie directly above $S_r$. Perhaps the verticality of the geometric relationship between $S_t$ and $S_r$ 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, $S_t$ 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 $S_t$ and $S_r$ 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 $S_t$ 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 skeletonmotor 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 fromHonda'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;
Dassonville, Colby & Goldberg, 1992) have used paradigms much like the NO-GAP task in single-unit studies of what they described as the brain’s egocentric localization 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 egocentric abilities from its exocentric 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 information 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; Shebiliske, Karmiohl & Proffitt, 1983; Stark & Bridgeman, 1983; Mateeff & Hohnsbein, 1989; Honda, 1993; Velay, Roll, Lenerstrand & 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 findings 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 investigation of these additional differences will further elucidate the reasons for the discrepancy.

REFERENCES


Acknowledgements This research was supported by USPHS grant EY05879, as well as Graduate Fellowships from the National Science Foundation and ARCS Foundation, Inc., and an NIH Mental Health Training Grant to P. Dassonville. We thank Henry Sanchez for his assistance in data processing and analysis.