

Oculocentric Coding of Inhibited Eye Movements to Recently Attended Locations

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Results are reported for experiments that examined eye movements directed toward recently cued objects. In 1 experiment participants were slower to initiate saccades toward the earlier location of an object that had been cued, even though the cued object had subsequently moved away from that location. Other experiments involved exploring the reference frame within which the inhibited eye movements are encoded. These experiments revealed that the eye movement that is inhibited is encoded in an oculocentric—rather than an environmental—reference frame. However, simple detection as indexed by manual keypress responses is encoded in an environmental reference frame. The results have implications for inhibition of return, for the link between eye movements and attention, and for the nature of the spatial reference frames in which both covert and overt movements of attention are encoded.

During the normal course of scanning their visual worlds, people repeatedly move their attention from one location to another. Exploration of complex scenes might be facilitated if a person could maintain some record of the locations to which they had recently attended. Indeed, people are slower to detect and respond to events occurring at recently attended locations (Abrams & Dobkin, 1994a, 1994b; Oonk & Abrams, 1998; Posner & Cohen, 1984; Pratt, 1995; Pratt & Abrams, 1995; Rafal, Calabresi, Brennan, & Sciolto, 1989; Reuter-Lorenz, Jha, & Rosenquist, 1996). The mechanism that accomplishes this has come to be known as *inhibition of return*.

Considerable research has been conducted recently to learn more about the detailed properties of inhibition of return. The belief is that the inhibitory mechanisms play a central role in guiding or assisting interactions with the visual world, and an enhanced understanding of them would be beneficial. Researchers have examined the extent to which inhibition of return affects discrimination responses as opposed to detection responses (Lupianez, Milan, Tornay, Madrid, & Tudela, 1997; Pratt, 1995; Terry, Valdes, & Neill, 1994); whether inhibition will affect stimulus attributes other than spatial location (Kwak & Egeth, 1992; Law, Pratt, & Abrams, 1995); and the extent to which the to-be-inhibited entity is a location in space or a specific object (Muller & von Muhlenen, 1996; Tipper, Driver, & Weaver, 1991; Weaver, Lupianez, & Watson, 1997).

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Coordinate Systems for the Inhibition

We are especially interested in prior research that has examined the spatial reference frames within which the inhibition operates. Maylor and Hockey (1985) told their participants to move their eyes after the appearance of an initial attentional cue but before the presentation of a to-be-detected target. They found that the inhibition did not move with the eye but instead remained at the environmental (physical) location at which the cue had been presented. A similar result was reported by Posner and Cohen (1984). These findings suggest that the inhibition operates on a representation that is coded in environmental coordinates¹—an important attribute if the inhibition is to be useful in guiding one's interactions with the world. In this way, to-be-inhibited objects would remain inhibited even as a person moves through the environment.

Although Posner and Cohen (1984) and Maylor and Hockey (1985) did have their participants make eye movements between cue and target presentation, they studied fixed targets. Thus, their results are consistent with either an environment-based reference frame for inhibition of return or an object-based one. Tipper et al. (1991) examined the possibility that the inhibition is encoded in an object-centered reference frame. They first cued a visual object (a small square) with a luminance change, then they moved the square while the participants remained fixated, and finally they presented a target to be detected at one of several possible locations. Participants were indeed slower to detect the target when it appeared in the previously cued square even though the square had moved to a new location. Those results show that at least a component of inhibition of return is encoded in an object-based representational system.

¹ An environmental reference frame is also an *exocentric* one, in which locations are coded relative to some reference that is not on the actor's body. Reference frames in which locations are coded relative to a person's eyes or head or other body part are called *egocentric*.

Subsequent work by Tipper, Weaver, Jerreat, and Burak (1994) has shown that both object-based and environment-based components can operate simultaneously. Oonk and Abrams (1998) also recently showed that a new perceptual object can invoke inhibition of return, further underscoring the important role of objects in the phenomenon.

Inhibited Eye Movements

There is also evidence that inhibition of return affects not only covert movements of attention, but overt movements of the eye as well. Abrams and Dobkin (1994a) found that participants were slower to move their eyes to a previously attended location—even when the imperative signal was a centrally presented arrow and not a peripheral signal that required detection. Because the signal was presented centrally, inhibited perception or attention at the cued location cannot explain the slower eye movements.² Instead, Abrams and Dobkin (1994a) argued that the results indicate the presence of a separate component of inhibition of return—an eye movement component. This component inhibits the production of eye movements to recently attended locations, in addition to any inhibition of attention or detection that might also be present.³

Coordinates for the Inhibited Eye Movements

Interestingly, unlike inhibition for target detection, the inhibited eye movements are not encoded in an object-based representational system. To study this, Abrams and Dobkin (1994a) asked participants to make eye movements to objects that had been previously cued but had since moved from the location at which they had been cued. No inhibition was found for the initiation of eye movements under those circumstances (even though Abrams and Dobkin were able to confirm Tipper et al.'s, 1991 finding that inhibited detection did move with the cued object). Thus, the inhibited eye movements appear to be encoded not in an object-centered reference frame but in some alternate reference frame. The purpose of the present study was to learn more about the reference frame in which the inhibited eye movements are encoded.

Our interest in this question is twofold. First, we are interested in learning more about inhibitory mechanisms in general and inhibition of return of visual attention in particular. By studying the frame of reference for the inhibited eye movements, we hope to learn more about basic attentional and inhibitory processes. Second, we are also interested more generally in oculomotor mechanisms and hope, through the present investigation, to learn more about some of the basic principles underlying the planning and production of eye movements. By learning more about the reference frame in which inhibited eye movements are encoded, we may be able to better evaluate current models about how people plan and program saccades generally.

Our specific goal was to distinguish between two alternative reference frames for the inhibition: oculocentric and environmental. In an oculocentric reference frame, locations are specified relative to the eye, or relative to the current

direction of gaze. This is also sometimes referred to as a retinocentric or retinally based reference frame. In an environmental reference frame, locations are specified with respect to some origin external to the observer. In such a representation, a fixed location in space would have the same representation regardless of the position of the observer or of their eyes.⁴

There is already some support for the use of each of these alternative possible reference frames for the inhibited eye movements. For example, as noted earlier, inhibited target detection is encoded in environmental coordinates (Maylor & Hockey, 1985; Posner & Cohen, 1984). Thus, we might expect inhibited eye movements to also be encoded in environmental coordinates. Such a result would be consistent with evidence that indicates that saccades are specified in terms of the final desired position of gaze and not exclusively in terms of the movement needed relative to the current fixation. The presence of eye-position-dependent cells in the superior colliculus (SC), a part of the brain important in generating saccades, is also consistent with the idea that an environmental frame of reference is involved in the production of saccades (Van Opstal, Hepp, Suzuki, & Henn, 1995).

On the other hand, there are also some reasons to posit an oculocentric coordinate system for the inhibited saccades. First, Posner & Cohen (1984) showed that the initial facilitatory effect of exogenous cuing was mapped in retinal coordinates. Thus, it might be that at least some aspect of the inhibition (i.e., the inhibited eye movements) would also be

² Vaughan (1984) reported similar results for saccades to suddenly appearing targets. Thus, it is not possible to determine the extent to which the slower latencies in his study reflected inhibited detection of the saccade target as opposed to inhibited production of the required saccade.

³ It is important to consider the possibility that the results of Abrams and Dobkin (1994a) may not reflect purely oculomotor inhibition. That possibility might be so if a movement of attention to a saccade target was a necessary prerequisite to an eye movement. If the attention movement was delayed (perhaps by the more familiar type of inhibition of return), that might in turn delay the saccade. We think this alternative is unlikely for two reasons. First, although there is evidence that attention often does move to a target prior to an eye movement (e.g., Shepherd, Findlay, & Hockey, 1986), it has not been demonstrated that a delay in the attention movement would also affect saccade latency. Second, Stelmach, Campsall, and Herdman (1997) questioned the initial Shepherd et al. conclusion and described some additional circumstances under which people can produce saccades apparently without any movement of visual attention at all.

⁴ Of course, there are additional reference frames that we are not considering here. For example, Brotchie, Andersen, Snyder, and Goodman (1995) showed that neurons in the posterior parietal cortex encode locations of visual stimuli in a body-centered representation. The response of the studied cells depended not only on the retinal position of the stimulus but also on the position of the eyes in the head and the position of the head relative to the body. In our study, the participants' heads remained fixed, so we cannot address issues about this sort of body-centered representation nor can we consider some alternate possible reference frames.

retinally coded (i.e., oculocentric). Also, there is some evidence that, at least at some level, saccades are planned in terms of the direction and distance they are to travel, that is, involving a retinally centered coordinate system (Abrams & Jonides, 1988). There is also a considerable body of evidence indicating the presence of a motor map in the SC (e.g., Wurtz & Goldberg, 1972). The motor map codes the vector of the saccade needed to move the eyes from the current position to the desired position—in other words, a retinally centered specification of the movement that is needed.⁵

Overview of Experiments

In the first experiment, we confirm that the inhibited eye movements are not encoded in an object-based reference frame but instead must be encoded in either an oculocentric or environment-centered reference frame. In subsequent experiments, we show that the eye movements that people are slower to initiate are encoded in an oculocentric reference frame, and we also show that the inhibited detection of visual events is in an environmental reference frame (as Maylor & Hockey, 1985, showed).

Experiment 1

Abrams and Dobkin (1994a) confirmed Tipper et al.'s (1991) earlier finding of object-based inhibition of return.⁶ In particular, participants were slower to initiate eye movements to an object that had been previously cued but had since moved to a new location. However, this effect only occurred when the imperative stimulus was a sudden onset in the object itself. If the imperative stimulus was a centrally presented arrow, then no inhibition was observed. Abrams and Dobkin (1994a) concluded that the former case, with peripheral stimuli, reflected a reduced ability of the participant to actually detect the stimulus when it appeared in the previously cued object, whereas the results in the latter case with central stimuli showed that the oculomotor system itself was no slower to produce the required movement. Hence, the conclusion that the eye movement component of inhibition of return is not object centered.

Although Abrams and Dobkin (1994a) found that the inhibition to initiate eye movements did not move when the cued object moved, they did not show what happened to the inhibition. Presumably, after the cued object moved, participants would have been slower to look to its original location. However, that condition was not included in the earlier work. In the present experiment, our goal was to determine whether participants are indeed slower to look to the location at which the initial cue had been presented, even after the cued object has since moved from that location. Note that, to measure the ease of looking, we employed central arrows as imperative stimuli in this and other experiments. Thus, any differences in latencies between conditions cannot be attributed to the ease or difficulty with which participants can perceive peripheral stimuli.

Method

Participants. Fourteen Washington University students participated in one 1-hr session and received \$7 for their time. Participants were naive with respect to the hypotheses under investigation.

Apparatus and procedure. Testing was conducted in a dimly illuminated, quiet room. Participants sat in front of a cathode-ray-tube display with their heads steadied by means of a chinrest-headrest combination. They wore a scleral-reflectance eye movement monitor mounted on a spectacle frame. The sequence of events is illustrated in Figure 1. Participants began by fixating on a cross at the center of a display that contained four boxes, each 0.8° per side and centered 7° from fixation. After 300 ms, the cross changed to a dot, which participants were required to fixate on. Eight hundred milliseconds later, we presented a cue in one of the boxes by illuminating an asterisk for 300 ms. Two hundred milliseconds after the offset of the asterisk, the fixation dot was replaced by an asterisk and the boxes were rotated clockwise 90° so that each box stopped in a location previously occupied by another box. The rotation appeared smooth and was accomplished by presenting 15 frames, each for 20 ms (the refresh rate of the monitor was 50 Hz). Thus, the total duration of the box rotation was 300 ms. The asterisk at fixation was turned off and then on again once during the rotation, and it was replaced by a dot when the rotation ended. One hundred sixty milliseconds after the end of the box movement, an arrow, pointing either to the left or to the right, replaced the fixation dot. The direction of the arrow indicated the direction in which participants were to move their eyes, and they were to do so as soon as possible after presentation of the arrow. A total of 960 ms elapsed between the presentation of the cue (asterisk) and that of the imperative stimulus.

Eye movement monitoring. The participant's eye position was digitized and recorded at a rate of 1000 Hz during critical portions of the trial. The eye movement monitor was calibrated at the beginning of each session by having the participants fixate on each of five evenly spaced points on the display. Subsequent eye positions were determined by linear interpolation of the digitized signal from the device. Calibration was confirmed at the beginning of each trial, before presentation of the peripheral cue. During this time, participants were supposed to be fixating on the dot at 0°. If the output from the eye movement monitor indicated that fixation was within 1.5° of the correct position, then the trial proceeded as described earlier. However, if the output was not within the specified range, the calibration procedure was automatically invoked, and the trial was repeated from the beginning.

Eye position was also examined at two moments during the trial to ensure that participants were not moving their eyes in response to the initial peripheral cue. A sample was saved from the eye movement monitor (a) immediately after the offset of the cue (i.e., 300 ms after its onset) and (b) immediately before the onset of box rotation (i.e., 500 ms after the onset of the peripheral cue). The eye

⁵ Note that the alternative frames of reference are not necessarily mutually exclusive. It is quite possible that saccades might be encoded in retinal coordinates at one level of the oculomotor system, yet be mapped in environmental coordinates at another (see Abrams, Van Dillen, & Stemmons, 1994, for some discussion of this issue). Our interest in the present study is to learn more about the coordinates of a planned (or to-be-inhibited) eye movement at the level at which inhibition of return operates.

⁶ Recently there has been some controversy surrounding the existence of this phenomenon (Muller and von Muhlenen, 1996; Weaver, Lupianez, & Watson, 1997). The present experiments do not bear directly on this issue.

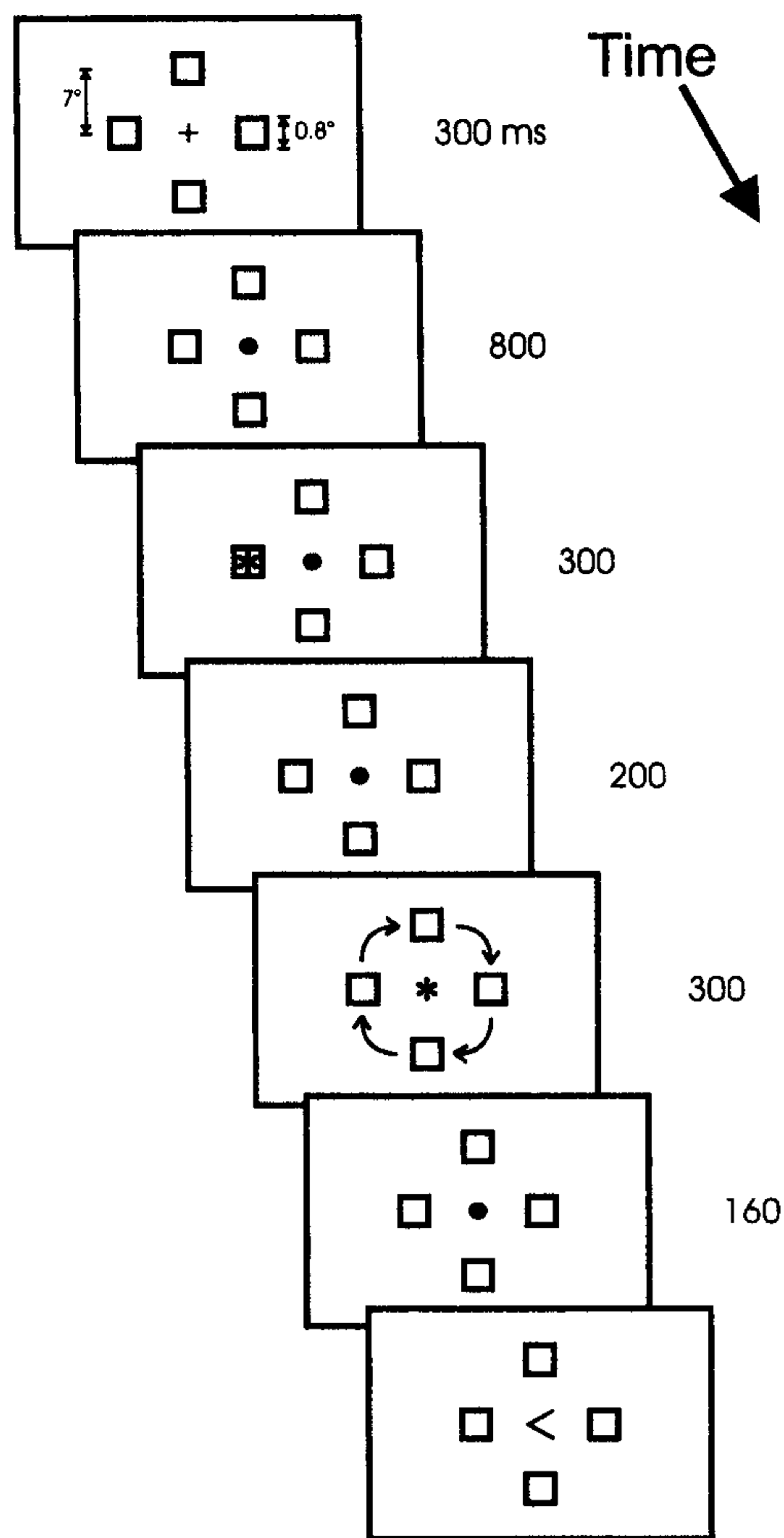


Figure 1. Sequence of events in a trial in Experiment 1. See Method section of Experiment 1 for detailed description of this sequence.

position during each of these samples was required to be within 3° of straight ahead, otherwise the trial was rejected. (When eye movements are made in response to the cue, they are almost always much larger than 3° in amplitude.)

To identify eye movements, we digitally filtered and differentiated the eye position signal to obtain a smooth record of velocity. An eye movement was defined to begin at the first moment in time at which the velocity exceeded $10^\circ/s$, subject to the constraint that the velocity remained above that value for at least 10 ms and subsequently exceeded $35^\circ/s$. These are the same criteria that we used previously (e.g., Abrams & Dobkin, 1994a).

Design. Participants performed an initial practice block of 8 trials, followed by eight test blocks of 32 trials each. In the test blocks, each of the four boxes was cued equally often, and each of the two horizontal boxes was equally likely to be the target of the eye movement response. The relation between the cue and target defined one of four conditions: If the top or bottom box had been cued, then, after the rotation had stopped, participants would be asked to look to either the cued object or an uncued object. (Note that the cued object would now be in a location other than that in which it had been when cued.) If the left or right box had been cued, then participants would be asked to make an eye movement toward either the cued location or the uncued location. (Note that at the

time of the response, the cued object would have moved away from the cued location.) Participants completed eight trials in each of these four conditions (four to the left and four to the right) in each block of trials.

Results

Mean latencies to initiate saccadic eye movements are shown in Figure 2, plotted as a function of condition. Overall, latencies on cued trials were longer than on uncued ones, consistent with an overall inhibition of return effect, $F(1, 13) = 7.5, p < .05$. However, this effect was due entirely to what happened on the cued-location and uncued-location trials. As can be seen, participants were slower to look to the location at which the cue had been presented (cued-location condition) compared with the opposite side (uncued-location condition). Yet, there was no inhibition to look to the cued object when it had moved from its original location (compare cued-object vs. uncued-object conditions). This pattern resulted in an interaction between cuing (cued vs. uncued) and trial type (object vs. location), $F(1, 13) = 18.6, p < .005$.

The overall error rate was 10%, and errors did not depend at all on cue type or trial type, nor did the effects of those factors interact. The breakdown of error is as follows: Saccade latencies were less than 50 ms or more than 550 ms on 1.2% of the trials; the saccade did not end within 3° of the target on 4.2% of trials; and the participants were not accurately fixating when required to do so on 4.6% of the trials. Participants did make slightly fewer errors when looking to the right on uncued-object and uncued-location trials and when looking to the left on cued-object and cued-location trials, resulting in a marginally significant interaction between those factors, $F(1, 13) = 4.8, p < .05$.

Discussion

In the present experiment, participants were slower to initiate eye movements to the spatial location at which an earlier cue had been presented, even though the cued object had since moved away from that location and another object

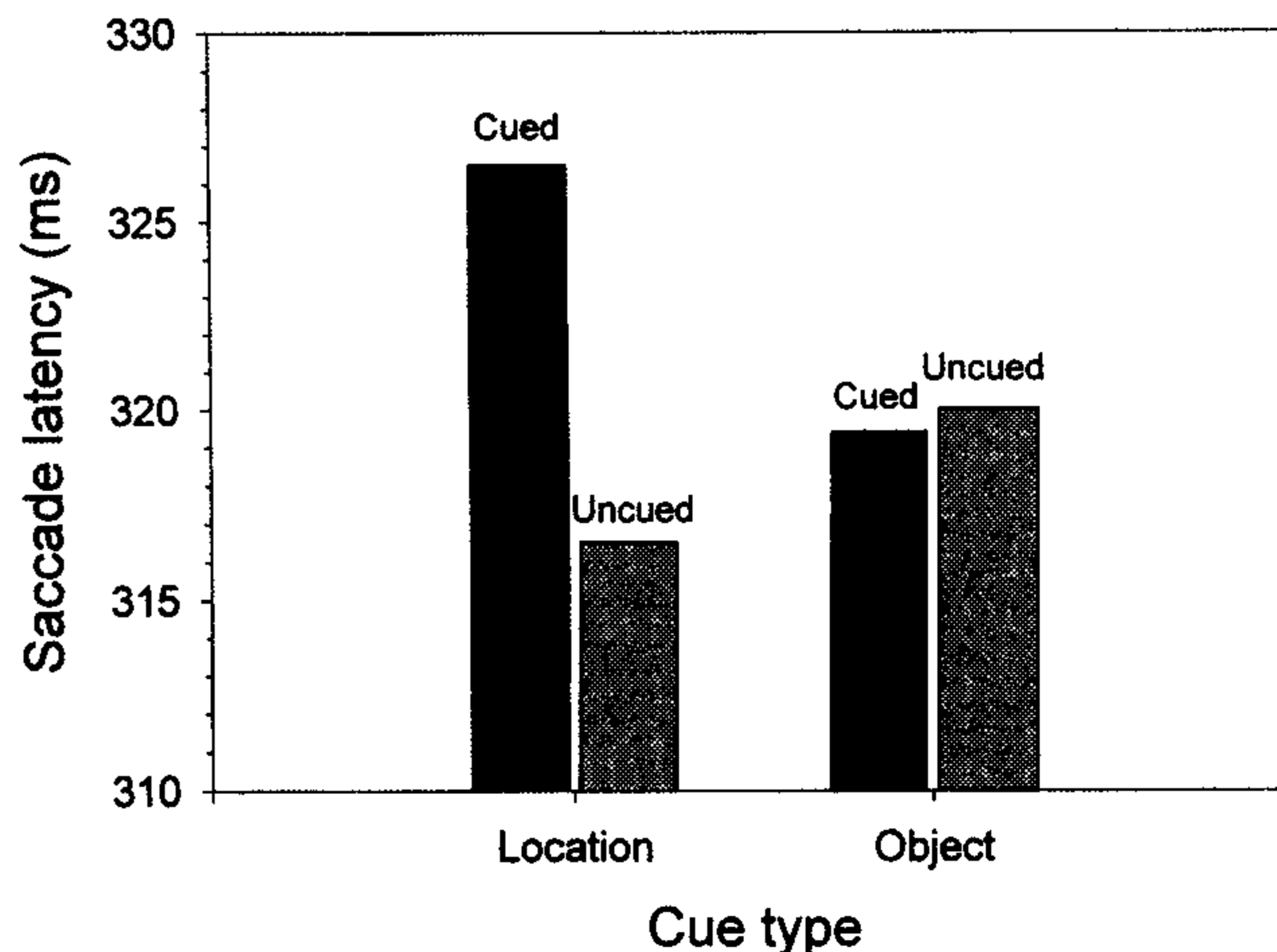


Figure 2. Mean saccade latencies as a function of type of cue in Experiment 1.

had replaced it. These results, combined with those of Abrams and Dobkin (1994a), show that the inhibition of return that affects the oculomotor system is not object centered but rather location based. It remained to be seen what the precise reference frame was in which that location was encoded. That was the purpose of the next experiments.

Experiment 2

Having established that participants are slower to initiate eye movements to the location of the earlier cue, our next goal was to determine whether that location is encoded in environmental coordinates or oculocentric coordinates. As noted earlier, the inhibition of return that has typically been studied involves inhibited *detection* of peripheral visual stimuli as measured by keypress latencies. Posner and Cohen (1984) and Maylor and Hockey (1985) reported evidence showing that such inhibition of return is coded in an environmental reference frame. Tipper et al. (1991) further showed that participants were inhibited in detecting stimuli in a cued object even after it had moved from the location at which the cue had been presented.

It is, however, not clear what reference frame is used to encode the to-be-inhibited eye movements. In the present experiment, we attempted to distinguish between a retinally based, oculocentric reference frame and an environmentally based one. To distinguish between these two possibilities, we had participants in the present experiment make an intervening smooth-pursuit eye movement after the presentation of the initial attentional cue but before that of the subsequent, imperative central arrow signal.

Method

Participants. Eighteen students from Washington University participated in this experiment. They were each paid \$7 for serving in one 45-min session. They were naive with respect to the hypotheses under investigation, and none participated in Experiment 1.

Apparatus and procedure. The procedure used in this experiment is illustrated in Figure 3. Participants viewed a display that contained four boxes, 0.8° on each side, centered at the corners of an imaginary 7° by 14° rectangle. Participants began each trial by fixating on a cross at the center of the display that was aligned with the bottom boxes. Three hundred milliseconds later, the cross was replaced with a dot that remained visible for 800 ms. During this time the calibration of the eye movement monitor was verified. The dot then disappeared and reappeared centered between the two upper boxes, and participants were to make a saccade to its location. An additional delay of 750 ms then transpired, after which we presented a cue by illuminating an asterisk in one of the four boxes for 300 ms. Two hundred milliseconds after the offset of the cue, the dot at the fixation point moved smoothly from a position between the two upper boxes to a position centered between the two lower boxes. This motion consisted of 15 steps, each of which consumed 20 ms, for a total drift time of 300 ms. Participants understood that they were to follow the moving dot by eye.⁷ After an additional 400-ms delay, the fixation point was replaced by an arrow pointing either to the left or to the right. The participants understood that they were to make a saccade as quickly as possible to the box (in the bottom row) to which the arrow pointed.

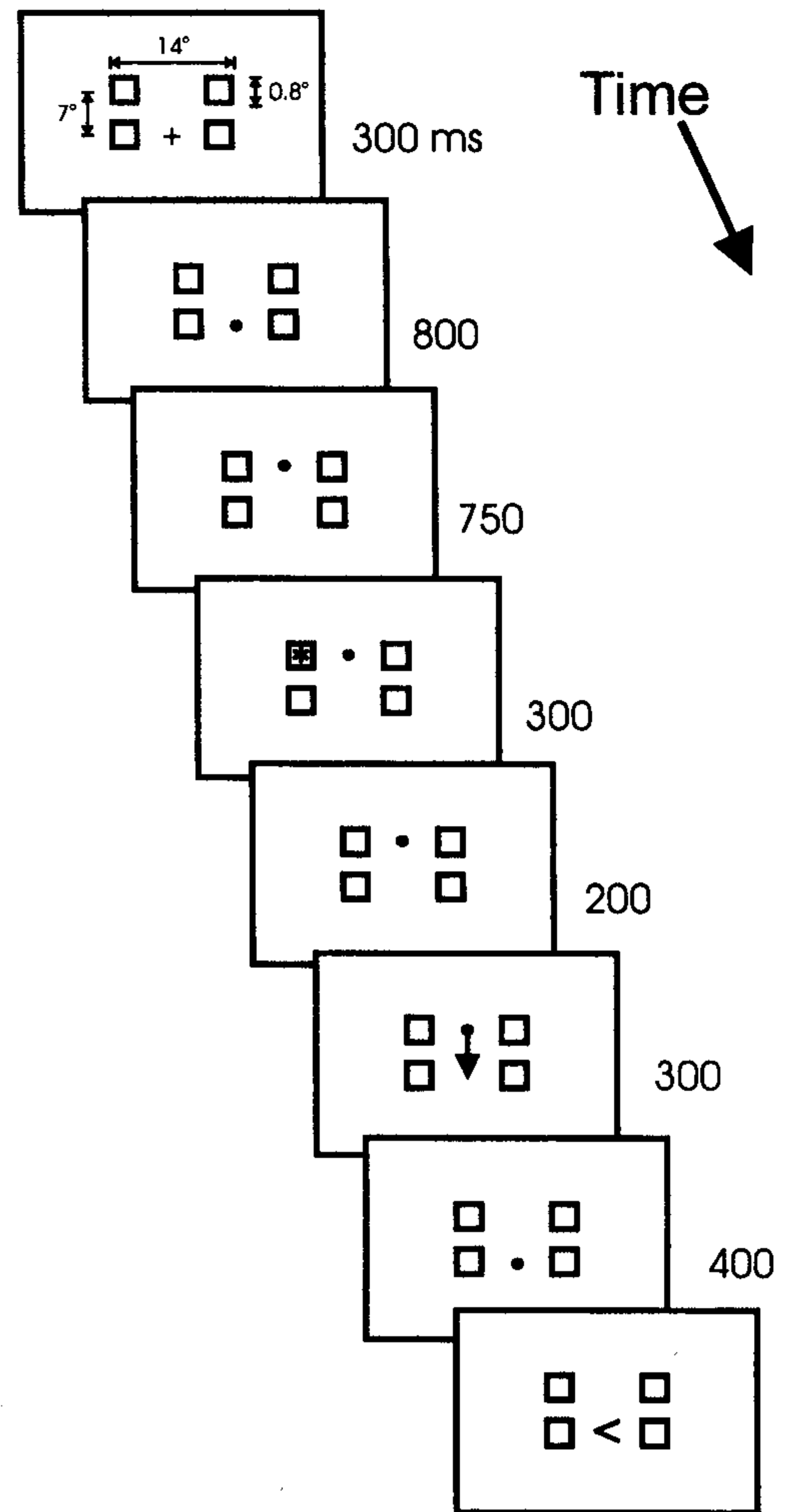


Figure 3. Sequence of events in a trial in Experiment 2. See Method section of Experiment 2 for detailed description of this sequence.

Design. The design was very similar to that of Experiment 1. After a practice block of 8 trials, participants performed in 8 blocks of 32 trials each. In each block, each of the four boxes was equally likely to be cued, and each of the two lower boxes was equally likely to be the target for the saccade. Four different conditions were defined by the relationship between cued and target boxes. There were two possibilities when a box in the bottom row had been cued: In the environmental-cued condition, participants made a saccade to the same box that had been cued (i.e., the box at the same environmental location). At the time the saccade was made, however, the box occupied a different retinal location from the one that it had occupied when it was initially cued. The environmental-uncued condition occurred when a bottom box had been cued but participants were asked to look to the box on the opposite side. Two

⁷ We used a smooth-pursuit movement to change the position of the participant's gaze because the sudden onset of a saccade target, or possibly even the production of an endogenous saccade, might be expected to attract or otherwise activate the attention system and thus disrupt the inhibition that had been established by the initial cue. This issue is explored further in the General Discussion.

additional conditions were studied when boxes in the top row had been cued. In the oculocentric-cued condition, participants looked to the box on the same side as the cue (but in the bottom row, and hence at a different environmental location). In the oculocentric-uncued condition, participants looked to the side opposite the location of the cued box.

Results

Mean reaction times in each of the conditions are shown in Figure 4. There was no overall effect of cuing (cued vs. uncued), $F(1, 17) = 1.9$, *ns*, because cuing had very different effects on the oculocentric-cued and oculocentric-uncued trials compared with the environmental-cued and environmental-uncued trials, resulting in an interaction between the two factors, $F(1, 17) = 6.4$, $p < .05$. As can be seen in Figure 4, participants were slower to initiate saccades to the cued location relative to the uncued location only when the saccade location shared the same oculocentric (i.e., retinal) coordinates as that of the initial attentional cue (oculocentric-cued condition vs. oculocentric-uncued condition). To examine these results more closely, we performed an analysis of variance on the oculocentric trials only (the analysis included target direction, left or right, as a factor). That analysis revealed that oculocentric-cued trials were indeed slower than oculocentric-uncued trials, $F(1, 17) = 7.6$, $p < .05$.

The overall error rate was 9.1%, and errors did not differ as a function of type of cue, coordinate system, or target direction, $F_s(1, 17) < 1.4$, $p_s > .25$. The breakdown of error is as follows: Saccade latencies were less than 50 ms or more than 550 ms on 2.0% of the trials; the saccade did not end within 3° of the target on 4.1% of trials; and the participants were not accurately fixating when required to do so on 2.9% of the trials.

Discussion

The present experiment provides at least a tentative answer regarding the reference frame within which people

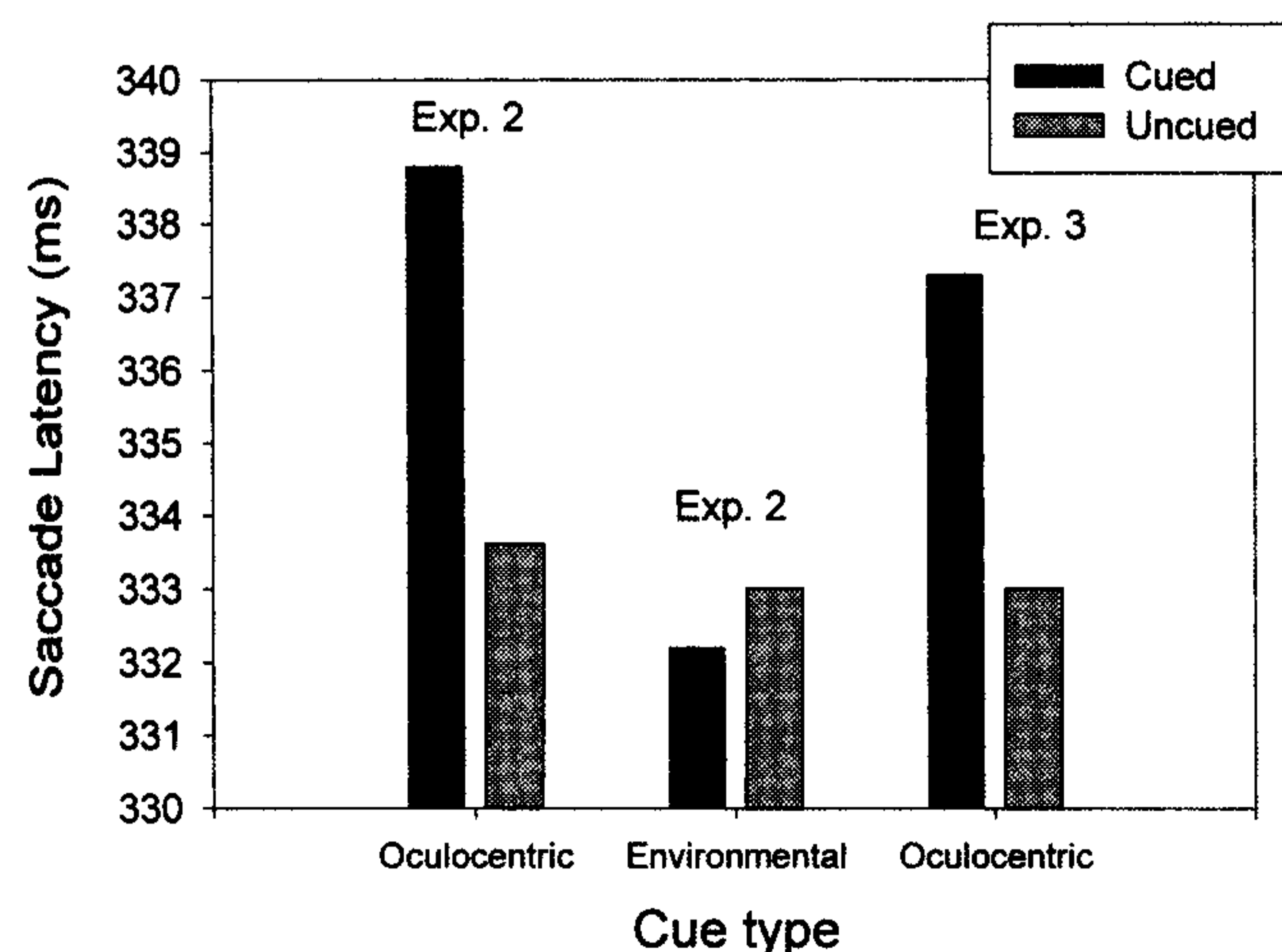


Figure 4. Mean saccade latencies in Experiments (Exp.) 2 and 3 as a function of type of cue.

encode to-be-inhibited eye movements: The inhibited eye movements are encoded in a retinal, or oculocentric, reference frame. This conclusion is possible because, in the present experiment, participants were slower to initiate an eye movement to a target with the same oculocentric coordinates as an earlier attention cue (relative to a location that had not been cued earlier) even though the target was in a different environmental location, and indeed was a different object. It is important to note that inhibition of return, as typically measured by detection keypresses, operates in an environmentally centered reference frame, not an oculocentric one (Maylor & Hockey, 1985; Posner & Cohen, 1984). The implications of these differences are considered in the General Discussion.

Experiment 3

In the previous experiment, participants were slower to initiate saccades to the same oculocentric (retinal) location as an earlier attention cue. Although the difference was reliable, it was somewhat small and different from the pattern that has been typically observed for detection-related inhibition of return. For those reasons, it seemed worthwhile to conduct a replication. In the present experiment, we repeated the oculocentric-cued and oculocentric-uncued conditions from the preceding experiment with a new group of participants.

Method

Participants. Ten individuals who had not participated previously and who were naive with respect to the issues under investigation participated in one 45-min session for which they were paid \$7.

Apparatus, procedure, and design. All aspects of this experiment were identical to the previous one with the exception that only the oculocentric-cued and oculocentric-uncued conditions were included here. After a practice block of 8 trials, participants performed in eight blocks of 32 trials each. Each block contained an equal number of trials in each condition with movements to the left and the right.

Results and Discussion

Mean latencies to initiate saccades are shown in the rightmost two bars in Figure 4. As can be seen, the latencies closely resembled those obtained in the previous experiment. As was true there, participants were slower to initiate saccades to the oculocentric location at which the previous cue had been presented, even though that was now a different environmental location, $F(1, 9) = 11.4$, $p < .01$. These results provide further support for the conclusion that the inhibited eye movements are encoded in a reference frame that differs from that in which inhibition of return for detection operates.

The overall error rate was 7.5%, with participants making slightly more errors on cued trials (8.7%) compared with uncued trials (6.4%), $F(1, 9) = 5.2$, $p < .05$; thus, a speed-accuracy trade-off cannot account for the latency difference observed. The breakdown of error is as follows:

Saccade latencies were less than 50 ms or more than 550 ms on 1.0% of the trials; the saccade did not end within 3° of the target on 2.8% of trials; and the participants were not accurately fixating when required to do so on 3.7% of the trials.

Experiment 4

Results of Experiments 2 and 3 indicate that people are inhibited in making eye movements to recently attended locations, and the eye movement that is inhibited is the one whose target shares the same oculocentric location as that of the initial attentional cue. However, as noted earlier, inhibition of return as indexed by detection keypress responses is believed to be encoded in environmental coordinates (Maylor & Hockey, 1985; Posner & Cohen, 1984). The presence of two distinct reference frames for these two different types of inhibition of return could have important implications, but first we wanted to confirm our assumption that inhibited detection is environmentally based. To this end, we conducted an experiment very similar to Experiment 2. The present experiment included an attentional cue, followed by a smooth-pursuit eye movement, and then the presentation of a target at either the environmentally cued (or not cued) location or the oculocentrically cued location. In this case participants were required to detect the onset of a peripheral visual target and indicate that event by pushing a button. Hence, the latency of the response should reflect the component of inhibition of return involved in the detection of visual stimuli, not the inhibition to make saccades.

Method

Participants. Ten students who had not previously participated were paid \$7 for participating in one 45-min session.

Apparatus, procedure, and design. This experiment was very similar to Experiment 2 with the exceptions of the nature of the imperative stimulus and the type of response required. In the present experiment, the imperative stimulus consisted of the appearance of a dot in the box to the left or right of fixation (as opposed to the presentation of a leftward or rightward pointing arrow, as had been used previously). Upon detection of the dot, participants were to respond as quickly as possible by pushing one of two keys with the index fingers of their right or left hands. The response required was the one that was spatially compatible with the stimulus. Participants completed eight blocks of 32 trials each, after performing in a practice block of 8 trials.

Results and Discussion

Mean reaction times for the keypress responses are shown in Figure 5. Cued trials were slower overall compared with uncued trials, $F(1, 9) = 10.8, p < .01$. As can be seen, participants were much slower to detect the target when it appeared in the environmental location of the initial cue (compared with the uncued environmental location), even though such a location was now at a different position on the retina. No such pattern was observed for the oculocentrically cued location, resulting in an interaction between cuing and reference frame, $F(1, 9) = 9.4, p < .05$.

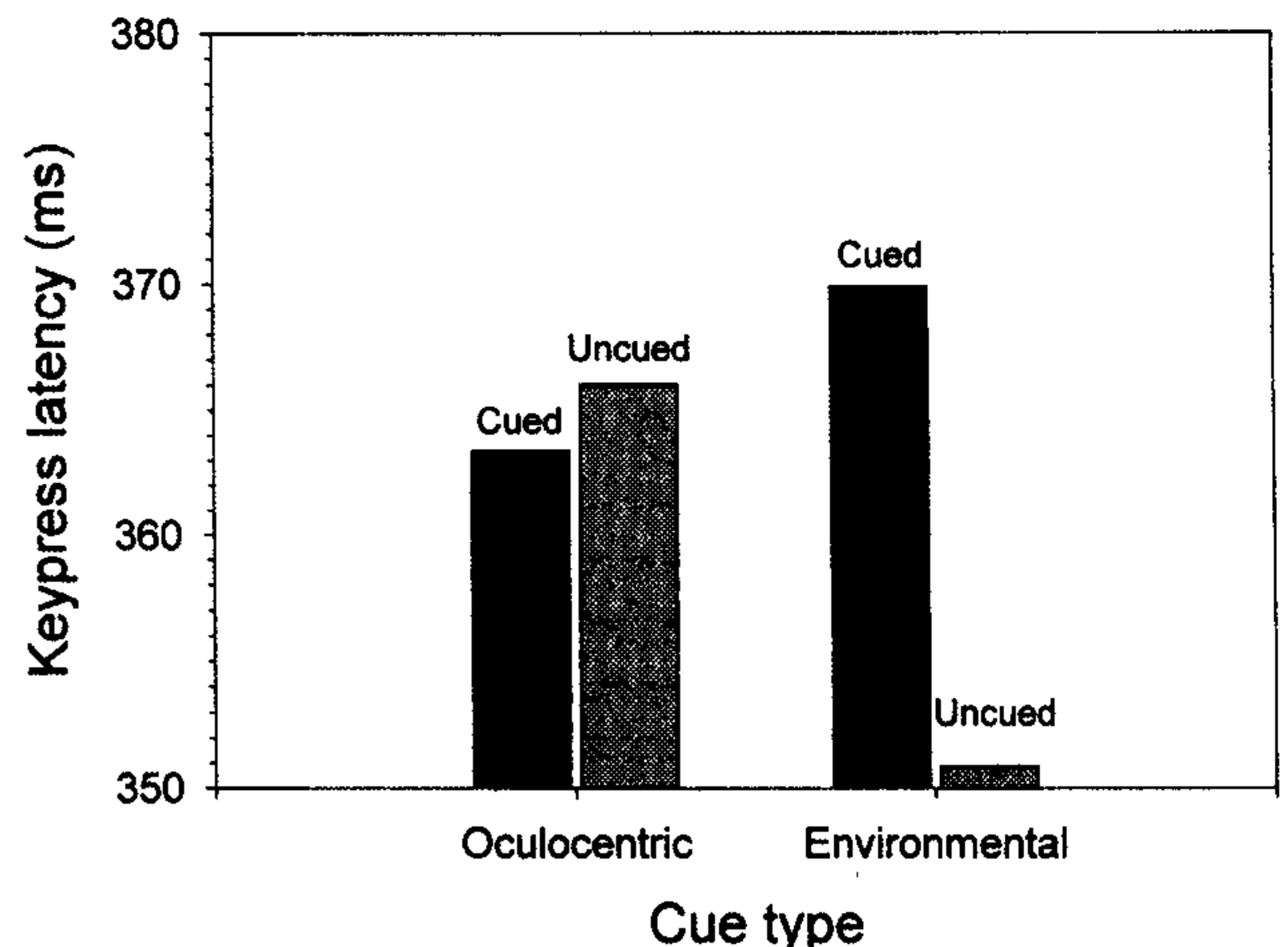


Figure 5. Mean keypress latencies in Experiment 4 as a function of type of cue. The imperative signal was a sudden onset in the periphery.

The overall error rate was 20%, and errors did not depend at all on the type of cue or the nature of the coordinate system, $F_s(1, 9) < 1.9, p > .2$. The somewhat higher error rate can be attributed to a difficulty in inhibiting eye movements in response to the peripheral flash. (In each of the other experiments reported, participants made eye movement responses to centrally presented arrows. Inappropriate eye movements occurred on 11.4% of the trials in the present experiment, inaccurate fixation on 8.4%, and latency less than 100 or more than 1,000 ms on 0.2% of trials.) Nevertheless, we repeated the analysis of the latencies, this time including all trials. Exactly the same pattern was observed: There was a 12-ms inhibition of return effect for the environmentally cued location (compared with 17 ms with the errors removed), and a small, 3-ms effect in the direction of facilitation for the retinally cued location (compared with 2.5 ms with error trials excluded). Thus, we can be confident that the results were not caused by some unusual strategy that the participants were using.

In the present experiment, with peripherally appearing targets and keypress responses, participants were slower to detect targets that appeared in the previously cued environmental location, replicating the findings of Maylor and Hockey (1985) and of Posner and Cohen (1984).

General Discussion

In the present study, we have examined saccadic eye movements that were under the influence of inhibition of return. The inhibition of return was induced by the brief presentation of a peripheral cue, and the saccades studied were directed to peripheral targets by centrally presented arrows. Experiment 1 showed that the saccades that were affected by inhibition of return are ones directed toward the location at which the attentional cue had initially been presented, even though the object that was cued had since moved from that location. Experiment 2 revealed that the location to which saccades are inhibited is encoded in an

oculocentric reference frame, not an environmental one, and those results were confirmed in Experiment 3. In Experiment 4, manual keypresses in response to peripheral target flashes were studied. Unlike eye movements, detection of peripheral targets was slower when the target appeared in the environmental location that had been cued (as opposed to the oculocentric location), confirming earlier results of other investigators. The results are consistent with the view that inhibition of return serves to facilitate inspection of the environment by inhibiting repeated movements of attention or, as shown here, of the eyes to recently attended objects or locations.

Two Types of Inhibition of Return?

An important aspect of our results is that there appear to be two types of inhibition of return, each operating in a different reference frame and affecting a different type of orienting behavior.⁸ First, detection of visual stimuli, thought to be an index of covert orienting, is slower for stimuli appearing on recently attended objects. The inhibition moves with the object when the object moves. (That result was initially reported by Tipper et al., 1991). Second, overt eye movements are also slowed. However, they are slower when directed to the oculocentric location of the object that had initially been attended. Can these two seemingly different types of inhibited responding be reconciled within a common framework? We assume that the brain may bring inhibition to bear on a number of different behaviors at different times, and the reference frame most appropriate for the inhibition would depend on the task involved. In particular, when it is important to inhibit covert orienting, an object-based reference frame is invoked perhaps because there is extensive use of such a reference frame in a variety of different covert-orienting situations (e.g., Abrams & Law, in press; Duncan, 1984; Kahneman, Treisman, & Gibbs, 1992; Tipper et al., 1991). When the task involves overt eye movements, a reference frame is used that is consistent with the manner in which eye movements are coded—relative to the retina, or oculocentric (e.g., Wurtz & Goldberg, 1972; additional discussion of this issue follows in a later section), as we have reported here. Likewise, if a hand movement is to be suppressed, then appropriate inhibition would be in a hand-centered or action-centered reference frame (e.g., Pratt & Abrams, 1994; Tipper, Howard, & Jackson, 1997; Tipper, Lortie, & Baylis, 1992). According to this view, inhibition of return describes a general principle that underlies selection of targets for attention and action.⁹

Utility of Oculocentric Inhibition

Our focus in the present work is on the oculocentric inhibition observed for eye movements. We think that such inhibition can play an important role in assisting searches in cluttered environments. As we noted previously (Abrams & Dobkin, 1994a), inhibiting an unnecessary eye movement to a recently attended location may be even more beneficial to an ongoing visual search than inhibition of an unnecessary attention movement. The reason is that eye movements

consume more time than attention movements. Why, however, is the inhibition oculocentric? On the surface, oculocentric coding would seem inefficient and implausible. For example, it might cause a zone of inhibition to move across the visual field when the eye moved, falling on an as yet unattended and not to be inhibited area. However, there are several reasons why oculocentric coding need not be detrimental and why it would be very feasible to implement. First, the presumed moving zone of inhibition would not exist if inhibition of return had a limited duration or limited capacity for previously attended objects and locations. In fact, we have recently reported that the brain mechanisms responsible for inhibition of return have a very limited memory for recently attended locations (Pratt & Abrams, 1995; see also Tipper, Weaver, & Watson, 1996, and Abrams & Pratt, 1996). As a result, a saccade away from a fixated location, or merely a movement of attention elsewhere, might cause a reduction or elimination of any inhibition of return established during the prior fixation. And there would not be a moving zone of inhibition that might inappropriately affect areas not to be inhibited.

A second reason that oculocentric coding need not result in undesirable inhibition in inappropriate places is that the representation involved in the inhibition may be sensitive to saccadic eye movements. That is, a location to be inhibited could be encoded in an oculocentric reference frame yet still be updated after each saccade. Precisely such a representation exists in the lateral intraparietal area of the posterior parietal cortex (LIP). Colby, Duhamel, and Goldberg (1995) showed that neurons in the LIP code the locations of saccade targets oculocentrically, yet the activity of these cells is updated along with (and sometimes before) saccadic eye movements.

Despite the foregoing comments, in our experiments we did observe a movement of the inhibition after an eye movement. However, the eye movement involved was a smooth-pursuit eye movement, not a saccade, and it is quite possible for a representation to be updated after one type of movement but not the other. Indeed, several reports show that the information available for localization of visual targets is poorer after smooth-pursuit movements compared with saccades (Abrams, Meyer, & Kornblum, 1990; Honda, 1985, 1990; Mack & Herman, 1972; Miller, 1980).

It is also important to note that oculocentric coding of a to-be-inhibited eye movement would be very easy to implement because the nervous system uses oculocentric coding extensively, and hence provides many opportunities for eye movements to be inhibited in an oculocentric reference frame. For example, visual stimuli that will be the target of a saccade are encoded oculocentrically in the SC (Wurtz & Goldberg, 1972), in the LIP (Andersen, Bracewell, Barash, Gnadt, & Fogassi, 1990), as well as in the frontal and supplementary eye fields (Russo & Bruce, 1996). In addi-

⁸ Abrams and Dobkin (1994a) had identified a separate eye movement component of inhibition of return, but their experiments did not establish the reference frame in which it operates.

⁹ We thank an anonymous reviewer for calling our attention to this perspective.

tion, cells in the SC that respond to auditory (Jay & Sparks, 1987) and somatosensory (Groh & Sparks, 1996) stimuli also code them oculocentrically. Thus, oculocentric coding is extensively used in the brain. As a result, there are many opportunities for an eye movement to be inhibited in an oculocentric reference frame.

Distinct Reference Frames for Attention and Eye Movements

Our findings may also have implications for the ongoing debate regarding the extent to which eye movement and attention systems share common processes. On the one hand, our results are consistent with the ample evidence that shows close links between attention and eye movements. In particular, a number of researchers have shown enhanced perception near the target of an eye movement before any movement of the eye (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Shepherd, Findlay, & Hockey, 1986). Others have shown changes in saccade metrics as a result of prior attentional allocation (Sheliga, Riggio, and Rizzolatti, 1994). Similarly, we have shown that prior attentional allocation can affect the latency of subsequent saccades to the attended location. Such results are consistent with the proposal that movements of attention are accomplished using many of the same mental mechanisms that are involved in the production of saccades (Rizzolatti, Riggio, Dascola, & Umiltà, 1987; Sheliga et al., 1994). According to such a "premotor theory," attention movements are prepared eye movements that have not been executed.

Nevertheless, our results also show that there are important differences between eye movement and attentional systems. In particular, we found that inhibition of return involves different reference frames for the inhibition of attention (environmental, object based) and of eye movements (oculocentric). As a result, people might be inhibited in returning their attention to one location, yet at the same time they could be inhibited in making an eye movement to another location—both the result of a single, prior attentional cue.¹⁰ Different reference frames for the inhibition of saccades and attention would be inconsistent with premotor theories of attention mentioned previously. Several other researchers have also reported evidence inconsistent with such theories (Klein, 1980; Klein & Pontefract, 1994; Hodgson & Muller, 1995; Stelmach, Campsall, & Herdman, 1997).

How are we to resolve the conflicting results? Logically, if overt and covert orienting were controlled by two separate systems, they might occasionally, or often, target the same spatial location, consistent with several reports noted above. However, a dissociation between the two systems, such as that demonstrated in the present study, could not be accomplished if the two systems were identical. Of course, because the eyes and not attention must be controlled by muscles, systems underlying the two types of orienting must diverge at some point, so perhaps the only point of contention involves how early in processing the two systems do indeed diverge. Our results show that they diverge at least as early

as the level at which an attended spatial location can be remembered for subsequent eye or attention movements.

Neural Basis for the Inhibited Eye Movements

Although it is obviously too early to identify specific neural mechanisms underlying the phenomenon that we have reported, there are a number of reasons to propose a central role for the SC in the inhibited eye movements, as well as in inhibition of return for detection responses. First, Posner, Rafal, Choate, and Vaughan (1985) showed reduced inhibition of return in patients with progressive supranuclear palsy, a disease that affects midbrain structures such as the SC. Next, Rafal et al. (1989) found enhanced inhibition of return for targets presented in temporal as opposed to nasal visual hemifields, consistent with greater temporal input to midbrain oculomotor mechanisms and the purported role of the SC in inhibition of return. Finally, Abrams and Dobkin (1994b) found that the effects of inhibition of return interacted with the effects of advance fixation-point offset (the "gap" effect). The gap effect is an oculomotor phenomenon thought to be mediated by collicular mechanisms. Thus, the interaction suggests shared mechanisms for the two phenomena and further implicates the SC as having a role in inhibition of return.

There are also a number of additional details regarding the gap effect that may permit further insight into the inhibited eye movements that we have identified here. The gap effect is thought to arise at least in part from a reduction in the activity of fixation cells in the SC. When active, the fixation cells serve to inhibit the production of eye movements (Dorris & Munoz, 1995; Sparks & Mays, 1983). In the gap paradigm, the offset of the fixation point is the event that results in a reduction in the activity of these fixation cells and, as a result, disinhibition in the SC, thus permitting shorter latency eye movements when the saccade target appears. We think it is possible that the fixation cells may also play an important role in the inhibited eye movements that we have identified. Indeed, it is the activity of these fixation cells that inhibits saccades in a gap paradigm, and it may also be activity in these cells that inhibits saccades to recently attended locations.

There is, however, an important difference between the effects of active fixation in the gap paradigm and the type of inhibition that we have reported here. In the gap paradigm, the reduced activity of the fixation cells has a nonspecific effect, facilitating saccades to any target (Dorris, Pare, & Munoz, 1997). But in our studies, the inhibition of return slowed saccades only to a specific (and oculocentrically coded) location. Is it possible that the fixation cells, or other inputs to the SC, could inhibit saccades selectively? Although there is not presently direct evidence showing

¹⁰ A similar conclusion was reached by Maylor (1985) on the basis of temporal order judgments. She noted that a person might be inhibited to respond to a target in one location yet perceive it as occurring earlier than a target in another location. We also made a similar conclusion on the basis of our earlier work (Abrams & Dobkin, 1994a).

selective inhibition, there are a number of observations that are consistent with spatially specific coding in the SC related to the gap effect. For example, Dorris et al. reported that in addition to reduced activity of fixation cells, the gap effect also involves spatially specific enhancement of saccade-related neurons associated with movements to the anticipated target location. And Rohrer and Sparks (1993) showed that practice in a gap paradigm can reduce saccade latencies to the anticipated target—but only when the eye begins from the same initial position as that practiced. In other words, the practice benefit accrues in oculocentric coordinates.¹¹

The SC is also ideally situated to receive spatially specific input related to inhibited saccades. It receives a strong projection from the LIP, in which planned movements are coded oculocentrically (Andersen et al., 1990; Colby et al., 1995). Perhaps even more important, the parietal lobe is thought to play a crucial role in the guidance of visual-spatial attention (Petersen, Corbetta, Miezin, & Shulman, 1994). Thus, parietal input from the LIP to the SC would be a natural means by which spatial attention systems could influence eye movements. The recent finding of parietal activity related to the gap effect further strengthens this proposal (Csibra, Johnson, & Tucker, 1997).

Another feature of SC activity that suggests an important role in inhibition of return is the predictive nature of its activity. Walker, Fitzgibbon, and Goldberg (1995) showed that neurons in the SC respond predictively, in advance of an impending eye movement, to reflect the consequence of the stimulation that is expected to be present after the eye movement has been completed. This ability to predict an upcoming movement suggests an important role in the planning, and hence the inhibition, of such movements. Because a similar predictive response has been observed in the LIP (Colby et al., 1995) and because the LIP projects strongly to the SC, Walker et al. (1995) concluded that it was likely that the predictive SC activity was a result of the projection from the LIP. As noted before, the key role of parietal cortex in spatial attention fits well within this scheme.

The SC also receives projections from the frontal eye fields, the supplementary eye fields, and the prefrontal cortex in the frontal lobe (see Pierrot-Deseilligny, Rivaud, Gaymard, Muri, & Vermersch, 1995, for a review), so it is possible that mechanisms there are also involved in the inhibited saccades that we have reported. Frontal mechanisms are also thought to be involved in spatial memory (Goldman-Rakic, 1990)—a function that would be needed to ensure inhibition of the correct saccade. More important, the prefrontal cortex plays a role not only in the guidance of desired saccades, but also in the inhibition of unwanted ones (Funahashi, Chafee, & Goldman-Rakic, 1993). Thus, frontal mechanisms seem well suited to contribute to the inhibition of saccades to recently attended locations that we have identified here.¹²

Finally, it is worth noting that the SC also receives projections from the substantia nigra pars reticulata. This nucleus in the basal ganglia is known to be active during saccades to remembered target locations (Hikosaka & Wurtz, 1983). The basal ganglia are also thought to play a

crucial role in inhibiting undesired movements (Mink, 1996). Thus, it is possible that the basal ganglia also play a role in the inhibited eye movements that we have reported.

One feature of our results that we cannot yet accommodate in this scheme is the finding that attention movements and eye movements are inhibited in different reference frames. Of course, this would require that spatial information from the attention system be provided to the oculomotor system at a point that is prior to that at which the attentional representation is updated by movements of the eye. Pinpointing the mechanisms involved will require more work, but the effort would be likely to reveal key features of the attention and eye movement systems.

Implications for Models of Perception and Action

Our results also have general implications for models of perception and action. In particular, the conclusion that attention and eye movements are inhibited in different reference frames is consistent with neuroanatomical and other evidence indicating a distinction between brain mechanisms involved in perception and those involved in action (e.g., Goodale & Milner, 1992). Nevertheless, recent findings from several laboratories also suggest close links between limb movements and attentional systems. For example, Deubel and colleagues (Deubel & Schneider, 1996; Deubel, Schneider, & Paprotta, 1998) have shown that stimulus identification is enhanced near the target location of both eye and hand movements. Also, Bekkering, Pratt, and Abrams (1996), studying the gap effect, found that latencies for some types of aiming hand movements were affected by the gap much like latencies for eye movements were. Such results may help link our present findings regarding saccades and inhibition with studies of movement planning and control in a more general way. In particular, it may be that saccades are best regarded as one of a number of different types of movements, all of which can be affected by attention but which are also in many ways independent of the attention system.

Oculomotor Activation and Inhibition of Return

Several researchers have suggested that inhibition of return is a consequence of activation of the oculomotor system (Rafal et al., 1989; Reuter-Lorenz & Rosenquist, 1996). Such activation is assumed to occur when a peripheral flash automatically attracts one's attention (e.g., as in Posner & Cohen, 1984) and when a centrally presented arrow indicates a potential target for a saccade, even if the saccade is never executed (Rafal et al., 1989), but not when an endogenous arrow signals a target to be attended (as in

¹¹ In a related result, Albano (1996) showed that an oculocentric framework describes the rapid saccadic adaptation that accompanies repeated mismatches between saccade and target amplitude.

¹² As noted earlier, neurons in both the supplementary eye fields and frontal eye fields code saccade targets oculocentrically (Russo & Bruce, 1996), consistent with this possibility.

Posner & Cohen, 1984; Rafal et al., 1989).¹³ The present results provide additional support for the special role of the oculomotor system in inhibition of return, yet they also raise some interesting questions. For example, preparation and then cancellation of a saccade has been shown to yield inhibition of return, but the inhibition has been determined by measuring keypress responses to peripherally presented stimuli (Rafal et al., 1989). It is not known whether such saccade preparation will also yield inhibition of saccades, like that studied in the present paper. Even more intriguing is the possibility that the saccades that are inhibited as a consequence of saccade preparation, might be those that share the same retinal coordinates with the planned saccade even though the attentional inhibition would presumably be coded in environmental coordinates. Our goal is to learn more about these and other questions about inhibited movements of the eyes and attention.

¹³ At this point it is also worth considering an alternative interpretation of the present results. We assumed that the saccades that we observed were inhibited as a result of a prior movement of attention to, and then away from, the initial cue. However, it may be possible that the inhibited eye movements are instead caused by a purely oculomotor phenomenon. According to this alternative, participants might engage in some sort of cancellation or suppression of an eye movement to the initial cue, and some of the inhibition would still remain when the test eye movement is eventually required. We thank Greg Zelinsky (personal communication, October 1998) for calling our attention to this alternative. Of course, at one level it may not be possible to distinguish between an attentional and an oculomotor effect. Indeed, some researchers have suggested that movements of attention are produced by, and hence indistinguishable from, activation of the oculomotor system (e.g., Sheliga et al., 1994). Nevertheless, Zelinsky offers a way to distinguish between the attention and oculomotor possibilities. According to him, an attentional phenomenon should be limited only to the saccade vector directed to the specific oculocentrically inhibited location, whereas a carryover of motor suppression would be spatially more general, affecting saccades both shorter and longer than the oculocentrically specified one and, we assume, also saccades with slightly different directions. (Some support for a broad spatial effect of saccades comes from work by Chelazzi et al., 1995.) Evidence ruling out the oculomotor alternative comes from the environmental-cued condition of Experiment 2, where participants were not slower to look to a target on the side that had been cued when its oculocentric coordinates were different from those that defined the initial cue. This shows that the phenomenon in question affects a narrowly defined set of saccades, which, according to Zelinsky, is consistent with the attentional explanation.

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