

Keith S. Karn · Per Møller · Mary M. Hayhoe

Reference frames in saccadic targeting

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Abstract We attempt to determine the egocentric reference frame used in directing saccades to remembered targets when landmark-based (exocentric) cues are not available. Specifically, we tested whether memory-guided saccades rely on a retina-centered frame, which must account for eye movements that intervene during the memory period (thereby accumulating error) or on a head-centered representation that requires knowledge of the position of the eyes in the head. We also examined the role of an exocentric reference frame in saccadic targeting since it would not need to account for intervening movements. We measured the precision of eye movements made by human observers to target locations held in memory for a few seconds. A variable number of saccades intervened between the visual presentation of a target and a later eye movement to its remembered location. A visual landmark that allowed for exocentric encoding of the memory target appeared in half the trials. Variable error increased slightly with a greater number of intervening saccades. The landmark aided targeting precision, but did not eliminate the increase in variable error with additional intervening saccades. We interpret these results as evidence for a representation that relies on knowledge of eye position with respect to the head and not one that relies solely on updating in a retina-centered frame. Our results allow us to set an upper bound on the standard deviation of an eye position signal available to the saccadic system during short memory periods at 1.4° for saccades of about 10° .

Key words Reference frames · Saccade · Eye position · Spatial memory · Spatial representation

Introduction

Remembering the locations of objects is essential in many perceptual and motor tasks, but we know little about the reference frames in which such memories are stored. We often search for or reach toward a previously seen object that is no longer visible. There are at least three schemes that we can use to remember the location of such a target: (1) in a retina-centered reference frame (e.g., *30° to the left of where I'm currently looking*); (2) in a head- or body-centered reference frame (e.g., *straight ahead of me and 20° below eye level*); or (3) with respect to other visible objects or landmarks in what we call an exocentric or object-centered reference frame (e.g., *on the porch, under the door mat*). It is not known how we store the locations of objects in short-term memory. In this paper we investigate whether locations are remembered in a retina-centered or head-centered reference frame when exocentric cues are unavailable. We also examine the role of exocentric cues made possible by the availability of a landmark.

Under normal conditions, a target casts an image on the retina in a location that is directly related to the saccade required to fixate the target. Thus, a retina-centered representation (i.e., the location of the target's image on the retina) seems to be all that is needed to direct eye movements to targets in a scene. Since information in other reference frames is usually consistent with a retina-centered representation, it is difficult to separate their possible contributions to the planning and execution of eye movements. However, in the laboratory these different reference frames can be teased apart by systematically limiting their use or putting them into conflict with each other. In a classic experiment using the "double-step" paradigm, Hallett and Lightstone (1976) separated the retinal and head-centered locations of a target. In this task the observer fixates each of a series of targets briefly flashed in rapid succession in the dark. While preparing or executing the first movement (to target 1), target 2 is flashed. Thus, the first eye movement intervenes between the presentation of target 2 and the eye movement

K.S. Karn (✉) · M.M. Hayhoe
Center for Visual Science and Department of Brain and Cognitive
Sciences, University of Rochester, Rochester, NY 14627-0270,
USA

P. Møller
Department of Physiology, Medical School, Framlington Place,
Newcastle-upon-Tyne NE2 4HH, UK

to it. The second eye movement required to land on target 2 accurately is, therefore, no longer proportional to the distance and direction of the target's retinal image relative to the fovea. To fixate the location of the second target accurately, the observer must account for the eye movement that intervened between the presentation of the target and the movement to it. In such a task, observers generally saccade accurately to this second target despite the intervening eye movement and do not make the systematic errors that would be associated with a simple retina-centered representation.¹ Sparks and Mays (1983) performed a similar experiment in monkeys, but used electrical stimulation of the superior colliculus rather than a visible target to produce an intervening saccade. When such an induced saccade interrupted planning or execution of a saccade to a flashed visual target, the eyes were deviated, but then moved to the goal previously specified by the visual target. Together, the results of Hallett and Lightstone (1976) and Sparks and Mays (1983) provide evidence against a simple retina-centered encoding scheme and generally have been accepted as evidence that target locations are coded in a head-centered reference frame for eye movement control. These and similar results have been interpreted as support for control system models of saccadic programming in which saccades are programmed in a head-centered reference frame (Young and Stark 1963; Robinson 1973; Zee et al. 1976). These models were a shift away from the long-held view that saccades are simply programmed using a retinal error signal, which is uniquely correlated with the eye movement necessary to fixate a visible target (Lotze, 1885). Note that, by definition, storing the location of a target in a head-centered representation requires a combination of the location of the target's image on the retina as well as the position of the eye with respect to the head² at the time the target is presented. Similarly, using information stored in a head-centered representation to direct the eyes to a remembered location at any given time requires continuous access to the position of the eye with respect to the head, independent of the recent history of movements (e.g., via a proprioceptive signal). See Bridgeman et al. (1994) for a review.

Despite the acceptance of a head-centered representation, recent physiological evidence has revealed a number of ambiguities. Experiments by Goldberg and his colleagues and Sparks and his colleagues require us to reconsider the concept of a retina-centered reference frame. The work of Goldberg and colleagues (e.g., Goldberg and Colby 1989; Goldberg and Segraves 1989; Goldberg and Bruce 1990) reveals neurons in the frontal eye fields (FEF) of monkeys that seem to encode the lo-

cation of visual targets in a retina-centered frame and to compensate for eye movements which intervene between the presentation of a target and a later targeting movement to its remembered location.³ The retina-centered representation is updated after each intervening movement, made either purposely or spontaneously, by what appears to be a vector subtraction of the target's retinal image position and the last saccade made. Note that these neurons need information about each eye movement rather than the continuous read-out of eye position required by a head-centered representation. Such neurons could provide the neurological substrate for behavior in the double-step task discussed above without transforming the target location information into a head-centered representation. Droulez and Berthoz (1991) have proposed a model of a spatial short-term memory for control of orienting movements that relies on such an updated retina-centered representation. Certain neurons in the monkey parietal cortex appear to perform a similar updating of target location, but in advance of an impending eye movement (Duhamel et al. 1992b). In humans, the right frontoparietal areas appear to be related to this updating as lesions here results in an inability to complete the double-step task when the first saccade is into the left hemifield (Duhamel et al. 1992a; Heide et al. 1993).

Sparks and his colleagues (e.g., Sparks and Nelson 1987; Jay and Sparks 1984; Sparks 1986) have proposed a slightly different version of an updating mechanism. They refer to a representation in *motor* coordinates (the movement required to fixate the target). Under most conditions, this theory yields identical predictions to Goldberg's updated retinal coordinates. Sparks and his colleagues have been able to identify a motor-coordinate representation in the intermediate layer of the superior colliculus by using a task involving saccades to auditory targets. We will not attempt to distinguish between updated retina-centered representations and motor representations beyond this point.

Other neurophysiological evidence indicates coding of visual targets in a head-centered reference frame. Andersen and his colleagues have reported neurons in posterior parietal cortex that have both retinal specificity and modulation by eye position (Andersen et al. 1990; Andersen et al. 1985). Networks of such cells are capable of encoding the position of a target in a head-centered frame (Zipser and Andersen 1988) and transcranial magnetic stimulation of the posterior parietal cortex has been shown to disrupt memory-guided saccades (Oyachi and Ohtsuka 1995). Recent reports reveal individual cells that appear to encode visual spatial information in a head-centered reference frame in the premotor cortex (Fogassi et al. 1992; Gentilucci et al. 1983) and in parietal cortex (Galletti et al. 1993). The simultaneous influence of multiple stimulus dimensions on a single cell

¹ There is a brief period around the time of the first saccade in which presentation of the second target produces eye movement targeting errors (Dassonville et al. 1992b) and perceptual misjudgements (Honda 1989; Matin and Pearce 1965), but when the second target is presented outside of this interval, saccades are quite accurate

² This eye in head signal would be the rotational position of the eye within the orbit

³ The frontal eye fields have been proposed as the site of an updating mechanism (Goldberg and Segraves 1989) or as slightly preceding it (Dassonville et al. 1992a)

make it difficult to study information encoding in neural populations. However, recent advances in recording from neurons in awake behaving animals have led to the discovery that neurons in many visual areas of the brain previously thought to carry spatial information in a retina-centered code are also influenced by eye position when firing rates are measured quantitatively. These areas include the lateral geniculate nucleus (Lal and Friedlander 1989), primary visual cortex (Weyand and Malpeli 1993), and area V3a (Galletti and Battaglini 1989). Taken as a whole, these findings suggest that eye position information may affect visual receptive field properties in the very early stages of visual processing. Haber (1985) has gone so far as to suggest that retina-centered coding may be unnecessary for the representation of visual space.

Both retina-centered and head-centered reference frames are classified as *egocentric* since their origins are within the observer's body. Whenever the axes of a reference frame move, a target's location must be recalculated. Thus, a memory representation in a retina-centered frame must account for each eye movement, and a head-centered representation must account for each head movement, which intervenes between the presentation of a target and a later movement to its remembered location. If a retina-centered reference frame is used for storing the location of a target, errors should accumulate with each intervening eye movement due to a loss of precision associated with this updating process. Psychophysical investigations to test this hypothesis provide conflicting results. Skavenski and Steinman (1970) reported that even after 30 large saccades over a period of 40 s, human observers could still re-fixate a remembered location with good precision and accuracy. Even when not permitted to fixate a flashed target initially, observers could compensate for a single intervening saccade and make an accurate targeting eye movement to its remembered location more than 2 s later (Viviani and Velay 1987; Møller et al. 1989a,b; Hayhoe et al. 1990). However, Nemire and Bridgeman (1987) and Honda (1984) showed that a series of eye movements did produce increased errors in subsequent targeting saccades.

In our experiments we examined the question of whether intervening eye movements lead to cumulative errors in saccadic targeting to remembered targets. We reasoned that if the nervous system updates the remembered locations of targets in a retina-centered frame, there should be some error associated with this updating process each time it is used to account for an eye movement during the memory period. Use of a retina-centered frame should lead to cumulative error after a series of intervening saccades when exocentric encoding is prevented. Alternatively, if the target is stored in a head-centered representation, intervening eye movements, without head movement, should have no effect on targeting errors. To test these alternatives, we studied targeting eye movements of human observers who made a saccade to the remembered location of a target a few seconds after it had appeared briefly in a random location. We asked observ-

ers to vary the number of eye movements made during the memory delay period with head fixed, and we studied the effects on targeting precision.

Exocentric representations (in a reference frame centered outside the body) are based on the relationships between two or more objects. Exocentric representations have the computational advantage that they do not need to be updated to deal with intervening movements of the observer. Note from the example used earlier that a description of an object's location in an exocentric frame such as *on the porch, under the door mat* does not change as the observer moves within the scene. In the laboratory, the availability of exocentric information can be eliminated by presenting a single target in otherwise complete darkness such that no landmarks can serve as visual references. It is well known that a great variety of species use landmarks and relational knowledge about the locations of targets (Gallistel 1990; McNaughton et al. 1991; Balda and Kamil 1992; Cheng and Sherry 1992). Although it seems logical that we must often rely on landmarks to provide exocentric cues to remembered locations and to aid our spatial memory, little is known about what situations prompt the use of exocentric cues in either directional judgments or orienting actions. Møller and his colleagues (Møller et al. 1989a,b; Hayhoe et al. 1990) and Dassonville et al. (1991, 1995) demonstrate, through careful control of exocentric cues, that landmarks can improve precision of saccade targeting. These exocentric cues might allow for recalibration of the saccadic system or might be used directly for saccadic programming. Similarly, little is known about the physiological basis of exocentric encoding. Olson and Gettner (1995) have recently provided some of the first evidence of neurons that carry object-centered information related to initiation of saccadic eye movements.

In our experiments we take advantage of the exocentric representation's freedom from the requirement for updating to contend with intervening movements by the observer. We systematically control the availability of exocentric encoding by displaying a landmark on half the trials. The presence of the landmark permits the use of an exocentric reference frame (i.e., remembering the relationship between target and landmark) and typically eliminates the reliance on eye position information in related tasks (Matin 1986). Since we expect no increase in error associated with updating after a series of intervening saccades in a memory-guided saccade task when a landmark is present, the trials with a landmark serve as a control condition.

In experiment 1 observers made either 2 or 5 intervening saccades to flashed targets between the presentation of a memory target and a targeting eye movement to its remembered location 3.5 s later. On half of the trials, a visible landmark could be used to help guide the final targeting eye movement, and in the other trials the target was presented alone – with nothing else visible. In experiment 2, observers performed similar tasks, but the intervening saccades were made in complete darkness (i.e., without visible intervening targets). Both experiments

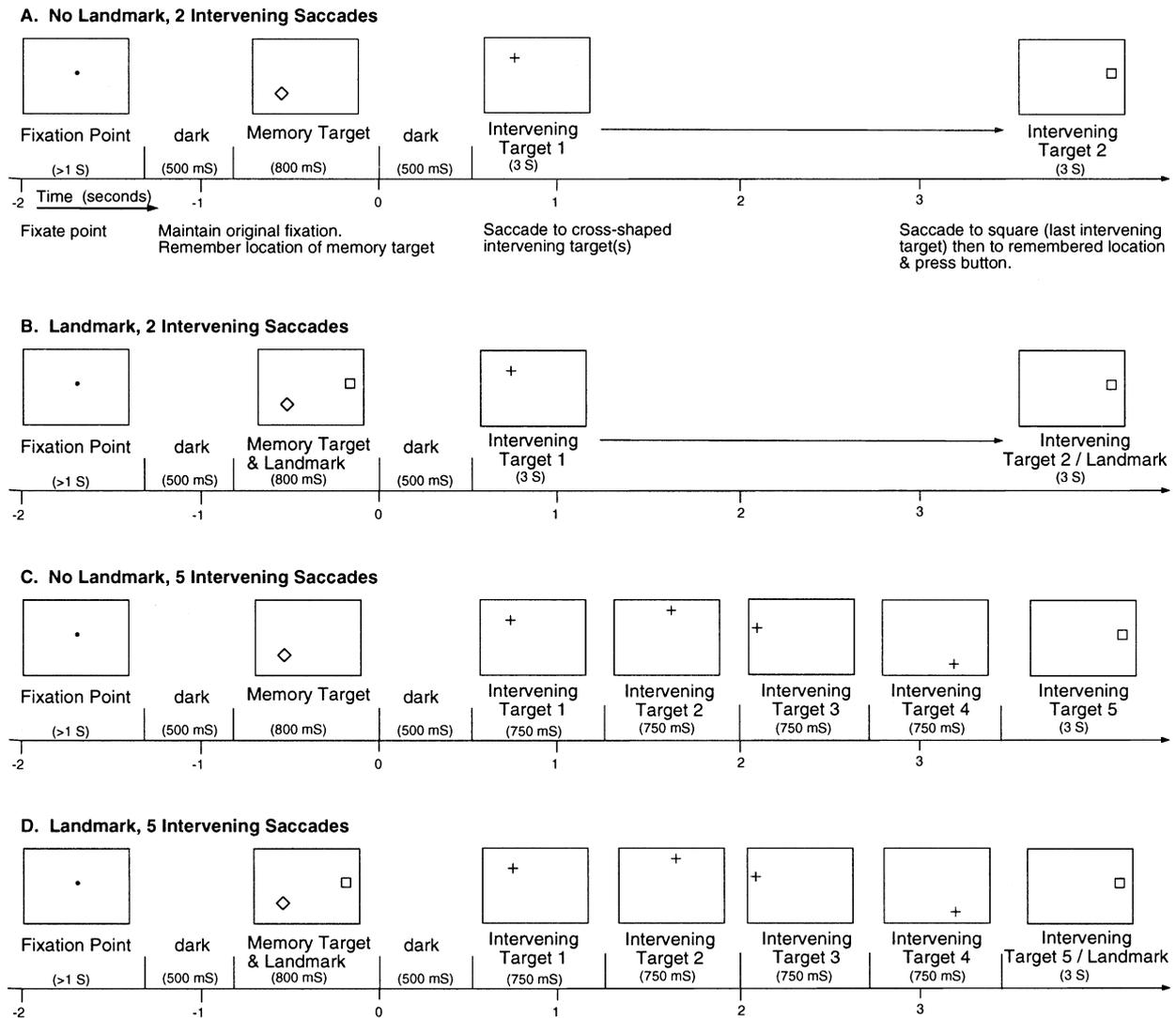


Fig. 1A–D Time lines showing the sequence of events for the four conditions. Stimuli for individual trials varied in two ways: (1) presence or absence of a visual landmark as a basis for exocentric encoding and (2) number of targets for intervening saccades (two or five). **A** no-landmark, two intervening saccades, **B** landmark, two intervening saccades, **C** no-landmark, five intervening saccades, **D** landmark, five intervening saccades. The schematics above each time-line represent the observer's view of the display. Instructions provided to the observer during training are written below panel A

had a 2×2 design with either 2 or 5 intervening saccades and either with or without a landmark (i.e., permitting or prohibiting exocentric encoding). Brief reports of portions of this work have been reported elsewhere (Karn et al. 1991, 1993).

Experiment 1. Intervening saccades to visible targets

Methods

Observers

Three women and two men all with uncorrected 20–20 vision or better and no other known visual abnormalities served as observ-

ers. They ranged in age between 20 and 42 years. Two of the observers were naive to the purpose of the experiment. The authors served as the other observers.

Sequence of events

All stimuli were presented in an otherwise completely dark room. A time line representing the sequence of events for the four trial types is depicted in Fig. 1. The observer sat with head stabilized on a bite-bar viewing a cathode ray tube display that was approximately aligned at eye level, 67 cm in front of the observer's right eye. The left eye was patched. The position of the right eye was monitored with a generation-V, dual-Purkinje image eyetracker (Crane and Steele 1985). Each trial started with a fixation point randomly located near the center of the display. The trial did not proceed until the observer fixated within a radius of 0.5° of this point for 1 s. The screen was then blanked and the observer was in complete darkness for 0.5 s. In the next interval, a diamond-shaped memory target was presented for 800 ms. In half of the trials the memory target appeared alone, and in the other trials a square-shaped landmark appeared simultaneously near by. In all cases the observer was required to maintain the original direction of gaze during this presentation. The screen was again blanked, and the observer was in complete darkness for another 0.5 s. Then a cross-shaped intervening target appeared in a random location on the screen. In trials with only two intervening saccades, this first intervening target stayed illuminated for 3 s. In trials with five intervening saccades, this first cross-shaped intervening target

stayed on for 750 ms, and then immediately the second, third and fourth cross-shaped intervening targets appeared sequentially for 750 ms each. In both types of trial, the final intervening target was a square. The observer was instructed to make an eye movement to each of the cross-shaped intervening targets, then to the square (the last intervening target) and then immediately to the remembered location of the memory target, which was no longer visible. In landmark trials, the final (square) intervening target was visually identical (e.g., same location, shape, etc.) to the previously presented landmark. The observer was encouraged to use the relative information about the location of the target with respect to the landmark, when available, to help remember the target's location. The observer pressed a button when looking to the remembered location of the memory target.

A digital computer controlled the presentation of the stimuli and recorded the position of the eye as determined by the eye tracker and the time of the button-press. Note that the time between the extinguishing of the memory target and the cue to saccade to its remembered location was 3.5 s in all conditions. The observer had an additional 3 s from the presentation of the final (square) intervening target to attempt to fixate the remembered target location and press the button. The trial ended after this 3-s interval or the press of the button, whichever came first. Observers could pace the trials by looking away from the fixation point, thereby delaying the start of a trial, but rarely did so.

Stimuli

We used 12 different memory target locations. Each memory target was paired with a set of 2 and a set of 5 intervening targets. The final intervening target was the same for a given memory target in both the 2 and the 5 intervening saccade conditions. This ensured that the 12 intended targeting vectors were identical in the 2 and the 5 intervening saccade conditions. These 12 targeting vectors (from final intervening target to memory target) are shown in Fig. 2. These targeting vectors ranged in length from 8 to 13° (mean: 10.3°) and represented a variety of directions. All of the intended targeting saccades crossed the observer's midline, but were largely centripetal movements with the intended endpoint (the memory target location) closer to the central position than the starting point of this final saccade. All the memory targets were within 3.5° of the screen's center. These targeting

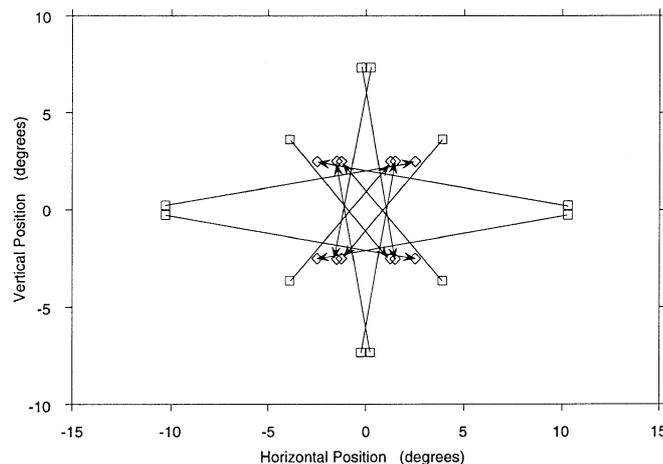


Fig. 2 Vectors representing the magnitude and direction of the twelve intended final targeting saccades. The *diamond shapes* represents the intended landing point of the targeting saccades (i.e., memory target) and the *squares* represent the starting point of the targeting saccades (i.e., the final intervening target). Note that on half the trials the final intervening target doubled as the landmark. The origin represents the screen center which was at eye level and aligned in front of the observer's right (viewing) eye

movements were selected to provide a broad range of directions and amplitudes, while keeping the eye within the range of the eye tracker's best performance. In addition, these memory targets allowed for the comparison of saccades made from different directions to similar locations. The final intervening target served as the landmark in half the trials, appearing initially with the memory target and then again as the final intervening target and the cue to look to the remembered location. The landmark was intentionally extinguished during the intervening saccades so that visual information was not available to update the knowledge of eye position. Since the same 12 combinations of memory target and final intervening target were used in each of the 4 conditions, there were a total of 48 trials that were run in randomly mixed blocks. A brief rest period was given halfway through the block. Each observer completed 12 to 17 blocks over a period of approximately 3 weeks.

The initial fixation points presented at the start of each trial also varied with each of these vectors within $\pm 1.9^\circ$ horizontally and vertically from the center of the display. These fixation points were paired with memory targets in such a way that the distance between the fixation point and the memory target ranged between 4.5 and 5.3° (mean: 5.0°), and the distance between the fixation point and the landmark ranged between 4.3 and 9.2° (mean: 6.5°). Observers easily discriminated the memory target and landmark (both 0.8° on a side) at these eccentricities based on their orientation (landmarks appeared as squares, memory targets as diamonds). The cross-shaped intervening targets subtended 0.5°. They appeared in pseudo-random locations on the screen within $\pm 7.5^\circ$ horizontally and $\pm 6.9^\circ$ vertically from the screen's center. These required the observers to make intervening saccades in a variety of directions and amplitudes (range: 5.3 to 15.8°, mean: 8.8°).

Eliminating visual references

Eliminating all visual references, aside from those provided by the landmark, was critical to the experiment. Stimuli appeared on a vector cathode ray tube (CRT) display with a short persistence (P31) phosphor in a dark room. Observers viewed the display through a long wavelength cut-off filter, which approximately equated rod and cone sensitivity. The CRT intensity was adjusted to be approximately 1 log unit above threshold. In a separate experiment we determined that stimuli presented in this manner are undetectable a few milliseconds after offset⁴ (see Hayhoe et al. 1991). The visible portion of the eye tracker's infrared measuring beam was attenuated with an interference filter with a central wavelength of 940 nm, half bandwidth of 10 nm, and a blocking range into the Far IR. After 24 trials, the experimenter questioned the observer and the data were discarded if the observer reported any stray light. This happened only on a few occasions when light seals were not properly in place. Finally, at each rest break (after every 24 trials), the observer light-adapted by exposure to daylight or bright incandescent light⁵. Together these precautions ensured that the observers saw nothing except the stimuli.

Eyetracker calibration

Before the start of each half-block of 24 trials, the eye tracker was calibrated by asking the observer to sequentially fixate 25 points in a regular $10^\circ \times 10^\circ$ array in the central portion of the display. A two-dimensional linear regression was fit to the vertical and horizontal eye position data for calibration.

⁴ In this test, the observer viewed the stimulus on the CRT through a shuttered aperture. The shutter was opened a variable amount of time after the stimulus signal was turned off. When the shutter was opened 5 or more ms after the signal was turned off, the observer was at chance in detecting the presence or absence of the stimulus

⁵ This ensured that the IR beam from the eyetracker was always below threshold

Practice

After each session, we graphically examined the eye movement trace from each trial to ensure that the observers performed the task as requested. Each observer needed between 1 and 3 half-blocks (24 to 72 individual trials) of practice to attain criterion performance of 16 out of 24 acceptable trials in each half-block. Our criteria for accepting a trial were:

- Maintenance of initial fixation during the presentation of the memory target (no drift more than half way toward the landmark or memory target or halfway toward the line that would connect these two targets).
- Saccades toward each of the intervening targets (note: accuracy of these intervening saccades was not assessed).
- No obvious extra saccades aside from small corrective saccades.
- Fixation within 1.6° of the center of the final (square) intervening target before saccading to the remembered location.
- Depressing the button within 3 s of the appearance of the final intervening target.

We discarded any half-block in which the observer performed acceptably on fewer than 16 of the 24 trials. This was rarely the case after the initial practice.

Results

Figure 3A shows a typical eye movement trace for a single observer for a single trial. Note that the 3 s between presentation of the final intervening target and the end of a trial allowed sufficient time for corrective saccades before pressing the button to designate the estimated memory target location. We used the position of the eye at the time of the button-press as the endpoint of the targeting movements. Figure 3B shows a scatter plot of the endpoints of these targeting eye movement on several trials from a single observer for one stimulus sequence with five intervening saccades for both the landmark and the no-landmark conditions.

Analysis of saccade landing point variable error

We expected that any errors resulting from an updating mechanism would show up in the variability of the targeting eye movements (i.e., the spread of the data points in a scatter plot such as that shown in Fig. 3B), not as constant errors. We calculated the standard deviation in the direction of the intended targeting saccade and in the perpendicular direction (Van Opstal and Van Gisbergen 1989). In order to represent the scatter of these two-dimensional data⁶ as a single number, we averaged the standard deviation values from the two directions.⁷ These combined measures of variable error are averaged across all 12 vectors and plotted individually for the five observers and averaged across observers in Fig. 4. The pattern of results was similar across observers. There are at least three noteworthy features of the data in Fig. 4. First, the overall precision seems quite good, considering that similar saccades to visible targets (without the 3.5-s memory period and without any intervening saccades) have only slightly greater precision (i.e., $SD \cong 0.75^\circ$) (Becker 1989; Møller et al. 1989a,b; Van Opstal and Van Gisbergen 1989).

Secondly, the data also suggest slightly lower variable error when exocentric encoding is allowed by the presence of the landmark (average: 1.15°) compared to the no-landmark condition (1.31°), as previously shown (Dassonville et al. 1995; Hayhoe et al. 1990; Møller et al. 1989a), although this effect did not reach statistical significance. Thirdly, there was a small (approximately

⁶ The individual components of the variable error are shown in Table 1

⁷ We also performed all the analyses with the square root of the sum of the squares of the two orthogonal components of the landing point error. The results were similar to those for the average of the two components, which are reported here

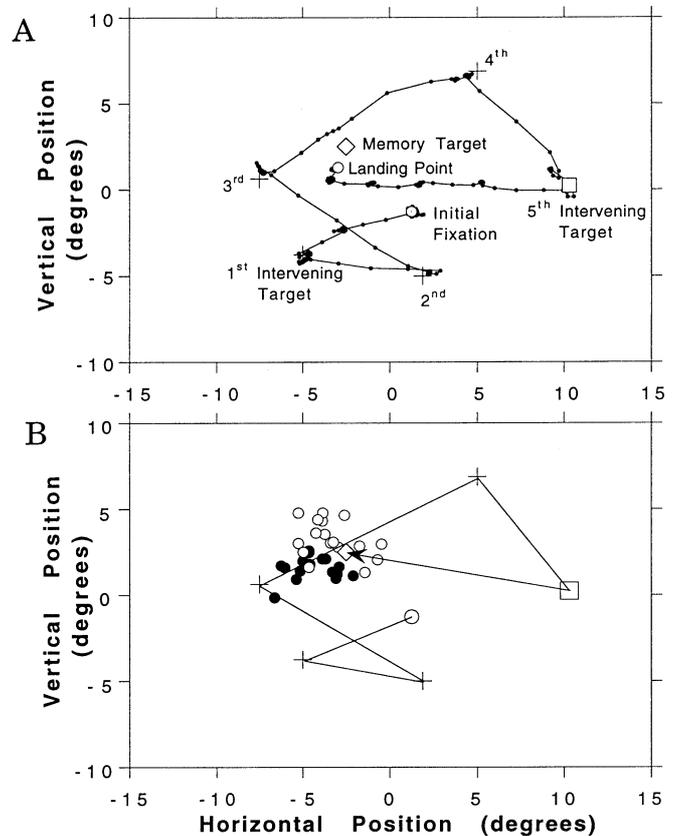
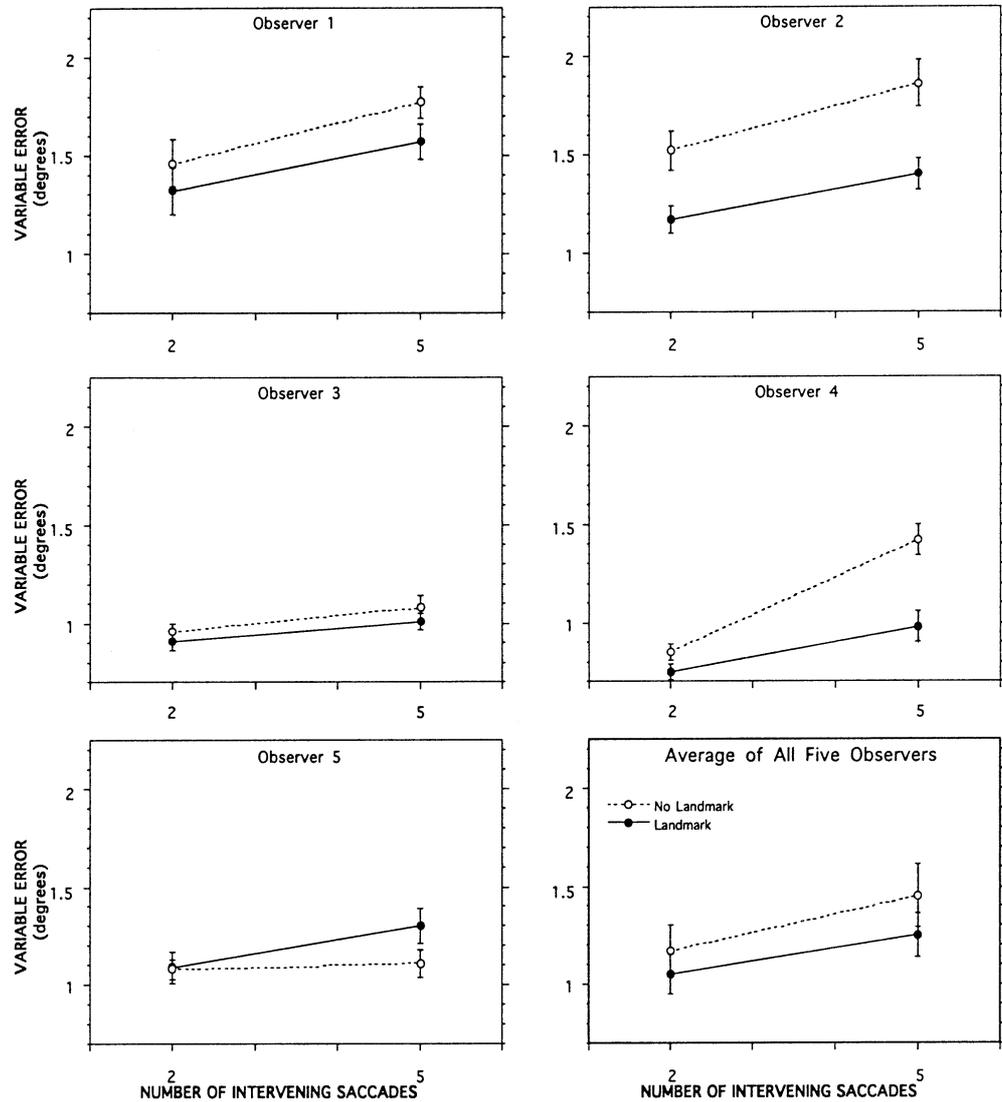


Fig. 3A, B Typical eye movement records. The origin represents the screen center, which was at eye level and aligned in front of the observer's right (viewing) eye. **A** Eye movement trace from a trial with five intervening saccades. The diamond represents the memory target (presented briefly and extinguished before intervening saccades and targeting movement), crosses are intervening targets, square is final intervening target and cue to saccade to remembered location of memory target (it also serves as a landmark on half the trials). **B** Scatter-plot of several trials for one observer for the same stimulus sequence for both landmark (filled symbols) and no-landmark (open symbols) conditions

$1/4^\circ$) but significant increase in variable error from two intervening saccades ($SD: 1.11^\circ$) to five intervening saccades (1.35°). This increase in variable error with more intervening saccades was about the same in the landmark and the no-landmark conditions. Recall that a mechanism for updating the target's location in a retina-centered frame would predict increasing variable error with an increasing number of intervening saccades, but only when exocentric encoding is prohibited (i.e., the no-landmark condition). Alternatively, if the location of the memory target is stored in a head-centered reference frame, we would expect no increase in variable error with more intervening saccades. In fact, we observed neither of these patterns in a three-way repeated measures analysis of variance (number of saccades \times landmark \times vector). The interaction predicted by the retina-centered hypothesis between the number of intervening saccades and landmark availability was not significant in the analysis of variance as ($F_{1,4}=0.66, P=0.46$). A significant main effect of the number of intervening saccades ($F_{1,4}=18.79, P=0.01$) argues against the head-centered hypothesis. The main effect of landmark was not significant in this experiment ($F_{1,4}=3.46, P=0.14$). We will present possible explanations for this pattern of results in the discussion.

Fig. 4 Results of experiment 1. Variable error for the targeting saccades is shown for the four conditions (combinations of landmark (*filled symbols*) or no-landmark (*open symbols*) and two or five intervening saccades) individually for each observer, as well as for the average across all five observers. The measure of variable error is the average of the standard deviation in the direction of the intended targeting saccade and the standard deviation in the orthogonal direction. *Error bars* indicate standard error of the mean between the 12 different targeting vectors for the plots of individual observers and between observers for the group average data



Learning effects

To check out whether observers were learning the locations of the 12 memory targets over the course of repeated trials, we examined the total unsigned error (distance between landing point and memory target location) across blocks of trials. Figure 5 shows these results averaged across observers. A linear regression line fit to these data shows a small but significant effect. The slope of this regression line is $-0.03/\text{block}$. The result is that on average, observers' targeting saccades landed 0.4° closer to the memory target at the end of the experiment compared to the start. Inspecting the data separately for each observer reveals that this effect is mainly due to two observers (one a naive observer and one an experimenter). It does not appear that the observers relied heavily on a long-term memory representation of the target locations. Targeting movements are instead largely determined by events occurring within a single trial.

Since there was no dark interval between the successive presentation of the visible intervening targets, we reasoned that the observers may have been able to encode the location of each intervening target relative to the preceding target. Such temporally integrated exocentric cues have been shown to be helpful in guiding targeting eye movements (Dassonville et al. 1995). Additionally, we could not be sure that differences between the two and the five intervening saccade conditions were due to the additional eye

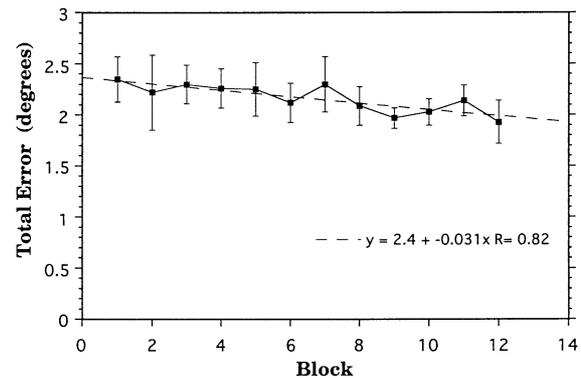


Fig. 5 Learning curve. Total unsigned error plotted across each block of 24 trials averaged for all five observers. Note that these data do not include 12 to 36 trials (0.5 to 1.5 blocks) of practice in the initial introduction to the task during which some learning may have occurred. Error bars represent ± 1 standard error of the mean between observers

movements, and not merely to the presentation of the additional intervening targets (i.e., the additional intervening targets might serve to mask the memory target). To be sure that the no-landmark trials truly represented a condition in which only egocentric cues for target location were available, and to be sure that additional saccades were the only difference between the two and the five intervening saccade conditions, we conducted experiment 2 in which the intervening saccades were made in complete darkness rather than to visible targets.

Experiment 2. Intervening saccades in the dark

Methods for experiment 2

Observers

Four of the observers from experiment 1 participated in experiment 2, along with one other for a total of five (three women and two men). All of the observers had experience with the task either from participation in experiment 1 or similar experiments. All had uncorrected 20–20 vision or better and no other known visual abnormalities. Two of the observers were naive to the purpose of the experiment.

Sequence of events

The timing and presentation of the stimuli and the observer's task were identical to that of experiment 1 except that a short audio tone replaced the visible cross-shaped intervening targets of experiment 1. A fixed source (i.e., the computer terminal to the observer's left) emitted the clearly audible tone. Each tone served as a cue to make an intervening saccade in a direction and magnitude of the observer's choice. The final intervening saccade was still to a visible square target, which also served as the cue to begin the movement to the memory target location. The experimenter instructed the observer to attempt to make the intervening saccades in the dark approximately the same length as those made in the previous experiment and to vary the direction of the saccades as much as possible. The eye tracker provided audible feedback associated with track loss when the observer made an eye movement outside of its operating range (approximately $\pm 8^\circ$ horizontally and $\pm 10^\circ$ vertically). Normal tracking resumed when the eye was brought back within range. This feedback helped observers learn to keep eye movements within range. Aside from the difference of eliminating the cross-shaped intervening targets, observers performed in the same four conditions as experiment 1. Since all but the last of the visible intervening targets were eliminated in this experiment, we simplified the observer's task. We did this by blocking trials such that all 24 trials in a half-block had the same number of intervening saccades (either two or five) rather than the mixed trial blocks in experiment 1. Landmark and no-landmark trials were still randomly mixed.

Results of Experiment 2

Without visible intervening targets, the eye movements in experiment 2 differed slightly from those in experiment 1. In the trials with only two intervening saccades, some observers had a tendency to drift during the 3-s fixation in the dark. Also, since the observers chose the directions and amplitudes of the intervening saccades in experiment 2, they tended to be slightly larger and more variable than those in experiment 1.

Since there were no visible intervening targets, it was difficult to assess the observer's performance in executing the intervening saccades. We visually inspected a graphical trace of each eye movement and used the following criteria for accepting a trial.

- Maintenance of initial fixation during the presentation of the memory target (no drift more than half way toward the land-

mark or memory target or halfway toward the line that would connect these two targets).

- In the two intervening saccade condition, the observer must make only one saccade prior to the saccade to the visible intervening target, though drifts up to 2° are permitted.
- In the five intervening saccade condition observers must make at least three saccades, which are larger than the typical re-fixation saccades for that observer in the dark (greater than 2° for all of our observers).
- Fixation within 1.6° of the center of the final (square) intervening target before saccading to the remembered location.
- Pressing the button within 3 s of the appearance of the final intervening target.

We again discarded any half-block in which the observer performed acceptably on fewer than 16 of the 24 trials. This was rare after a few blocks of practice trials.

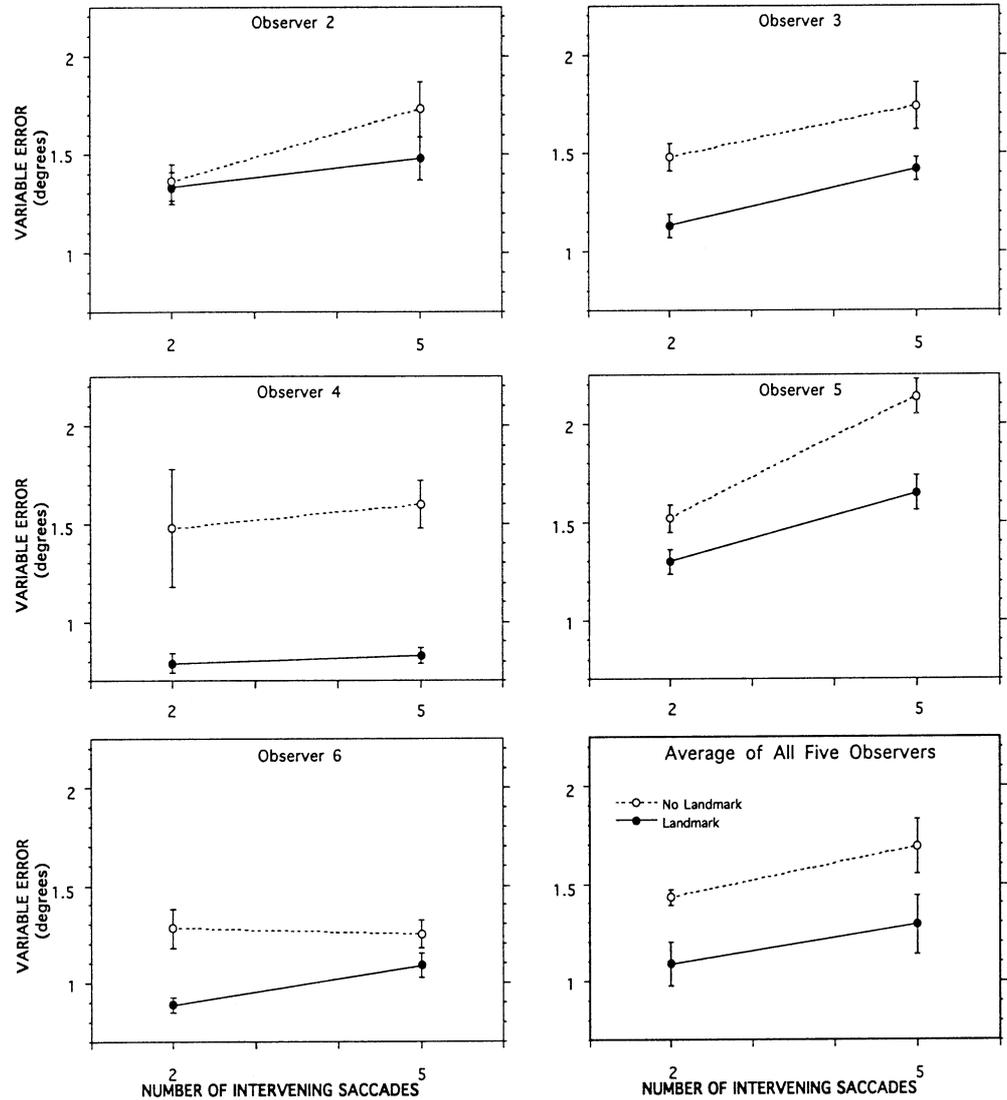
Analysis of saccade landing point variable error

The results of experiment 2 are similar to those of experiment 1 (see Fig. 6). Observers again had greater precision (lower variable error – measured as average standard deviation) in targeting eye movements when use of an exocentric reference frame was permitted by the presence of a landmark (1.19°) compared to trials without a landmark (1.56°). This main effect of the landmark was significant in a repeated measures analysis of variance ($F_{1,4}=13.92$, $P=0.02$). As in experiment 1, targeting eye movements were slightly but significantly less precise after five intervening saccades (1.49°) than after two intervening saccades (1.26°) ($F_{1,4}=10.18$, $P=0.03$). This increase in variable error with a greater number of intervening saccades again appeared even in the landmark trials as indicated by the insignificant interaction between the number of intervening saccades and presence of the landmark ($F_{1,4}=0.40$, $P=0.56$). Remember, the updating hypothesis predicts that an interaction would be found. When the results of experiments 1 and 2 are compared, the main difference shows up in greater variable error in the no-landmark conditions when the intervening saccades are made in the dark, without visible intervening targets (experiment 2). Results from the landmark condition were almost identical in the two experiments. When the data from the two experiments are combined into a four-way repeated measures analysis of variance (number of saccades \times landmark \times vector \times experiment), experiment is not a significant factor, but the landmark ($F_{1,4}=11.52$, $P=0.043$) and the number of intervening saccades ($F_{1,4}=112.52$, $P=0.002$) are significant. Again, none of the interactions are significant.

Analysis of saccade landing point constant error

Analysis of the constant errors can provide some information about the mechanisms underlying the source of the targeting errors. The arrangement of our stimuli makes it possible to compare the accuracy of targeting saccades from two or three different directions to memory targets which were close to each other (see again Fig. 2). This allows us to see if constant errors are related either to the memory target location or to the direction of the targeting saccade to this location. Any systematic deformation of visual space (due to a memory decay of the target's location) would produce the same constant error in the mean landing points for nearby targets, even when the saccades to this target region were from quite different directions. Conversely, the mean landing points would be quite different for saccades coming from different directions to the same region in space if the source of the error is associated with the vector of the saccade. To investigate these issues, we compared the landing points for pairs of different intended saccade vectors which had near-by memory target goals. Figure 7 shows one such pair of saccade vectors and the associated landing-point scatter plots for two observers. Note that observer 5 (Fig. 7A) shows a clear position bias (i.e., the two different targeting saccades produce almost the same mean landing point error).

Fig. 6 Results from experiment 2. As in Fig. 4, variable error for the targeting saccades is shown for the four conditions (combinations of landmark or no-landmark and two or five intervening saccades) individually for each observer as well as for the average across all five observers. Error bars represent ± 1 standard error of the mean between observers. The measure of variable error is the average of the standard deviation in the direction of the intended targeting saccade and the standard deviation in the orthogonal direction



Observer 4 (Fig. 7B) shows a clear vector bias (i.e., this observer lands in one place when making an upward saccade to this region in space and lands in another place when making a leftward saccade to this same general region). It was common to see both of these types of error patterns. All five observers showed some vector bias in at least some regions of space. Four of the five observers showed some position bias in some areas of space. Combinations of these two classifications of constant error in eye movement targeting were common. Although the landing points shown in Fig. 7B could be simply classified as hypermetric, some patterns of landing points were more complicated, showing combinations of direction and amplitude errors.

Discussion

In these experiments observers made targeting eye movements to remembered targets after a memory period of a few seconds. During this memory period, observers made either two or four intervening saccades. In order to discriminate between a neural mechanism that updates the location of a target in a retina-centered frame after each eye movement and a mechanism that stores the tar-

get's location in a head-centered reference frame, we looked for an accumulation of error when the observer made more intervening saccades during the memory period. We measured the precision of targeting eye movements and compared this performance with and without a visual landmark present to manipulate the availability of an exocentric cue. The availability of the landmark consistently resulted in decreased variable error (increased precision) of the targeting movements. Although intervening saccades resulted in increased variable error, this increase was small and approximately equal in landmark and no-landmark conditions. These results do not fit perfectly with either of the predicted outcomes. However, the simplest explanation is that the egocentric representation is in a head-centered frame and independent of an updating process. The increase in variable error associated with more intervening saccades is attributed to a non-specific interference with spatial memory (Logie 1995), as discussed below.

Table 1 Comparison with results from related experiments. Relevant parameters of each experiment are summarized. Trial-to-trial variation of saccade landing points in the direction of the targeting saccade and in the perpendicular direction are given for closely related experiments and the current experiments

Reference	Memory period (ms)	Intervening saccades	Targeting saccade	Standard deviation in direction of saccade	Standard deviation perpendicular to saccade
Miller (1980)	400 ^a	(1) Number: 1 Target: visible Amplitude: ^b varied, (to 16°)	Re-fixation of previous point. Amplitude: varied, (to 16°, mean 8°)	1.3°	0.9°
		(2) Target: none (dark)	Same as above	1.7°	1.1°
Viviani and Velay (1987)	2,350	Number: 1 Target: visible Amplitude: 10°	Amplitude: 8–20°	2.6°	1.0°
Current Expt. 1	3,500	(1) Number: 2 Target: visible Amplitude: 5–16° (mean 8.8°)	Amplitude: 8–13° (mean 10.3°)	1.2°	1.1°
		(2) Number: 5	Same as above	1.5°	1.4°
Current Expt. 2	3,500	(1) Number: 2 Target: none (dark) Amplitude: varied (~3–18°)	Amplitude: 8–13° (mean 10.3°)	1.5°	1.3°
		(2) Number: 5	Same as above	1.7°	1.7°

^a Time to make intervening saccade is not included in Miller's memory period

^b Direction of intervening and targeting saccades varied in all of these experiments

Summary and comparison of results

Our measurements of variable error in this memory saccade task are in line with those found by others under similar conditions (see, for example, Miller 1980; Viviani and Velay 1987). Together these studies indicate that the standard deviation for saccades of about 10° to locations remembered over a period of a few seconds is approximately 1.4° (see Table 1). Differences can be accounted for by slight variations between tasks.⁸

Possible explanations

Disruption unrelated to updating

As mentioned previously, if the target were represented in a head-centered frame when no landmark is available for exocentric encoding, we would expect targeting variable error not to increase with the additional intervening saccades. Trials with a landmark present to provide an exocentric cue are expected to be immune to any effects of intervening eye movements regardless of the egocentric reference frame used. Therefore, the similar increase we found in variable error with additional intervening saccades in both the landmark and no-landmark condi-

tions indicates that the eye movements made during the memory period disrupt spatial memory for target location independent of an updating mechanism and independent of the use of exocentric cues. It is well known that tasks performed simultaneously with a memory task are more disruptive when they are similar to the memory task (Wickens 1984; Logie 1995). Spatial tasks have been shown to interfere with visual spatial memory, but not with other aspects of short-term memory (Baddeley 1992). For example, Baddeley and Lieberman (1980) showed that eye movements made in pursuit of an auditory target in the dark interfered with the use of spatial imagery used as a mnemonic coding system, but not with basic auditory memory span unaided by the spatial mnemonic code. Thus, it seems reasonable to conclude that the increase in variability of the targeting eye movements is not caused by an updating mechanism associated with a retina-centered frame, but rather by another form of spatial memory interference due to intervening spatial tasks which affect egocentric and exocentric representations similarly.

Updating in a retina-centered frame

The updating mechanism proposed by Goldberg and his colleagues (Goldberg and Colby 1989; Goldberg and Segraves 1989) and Sparks and his colleagues (Sparks and Nelson 1987; Jay and Sparks 1984; Sparks 1986) posits that the memory target is held in a retina-centered (or *motor*) frame and updated after each intervening sac-

⁸ Results of Gellman and Fletcher (1992) differ dramatically. It is probable that the difference is due to their presentation of the memory target very close in time to the start of a saccade when the eye position signal is inaccurate (Matin and Pearce 1965; Dassonville et al. 1993; Dassonville et al. 1992b)

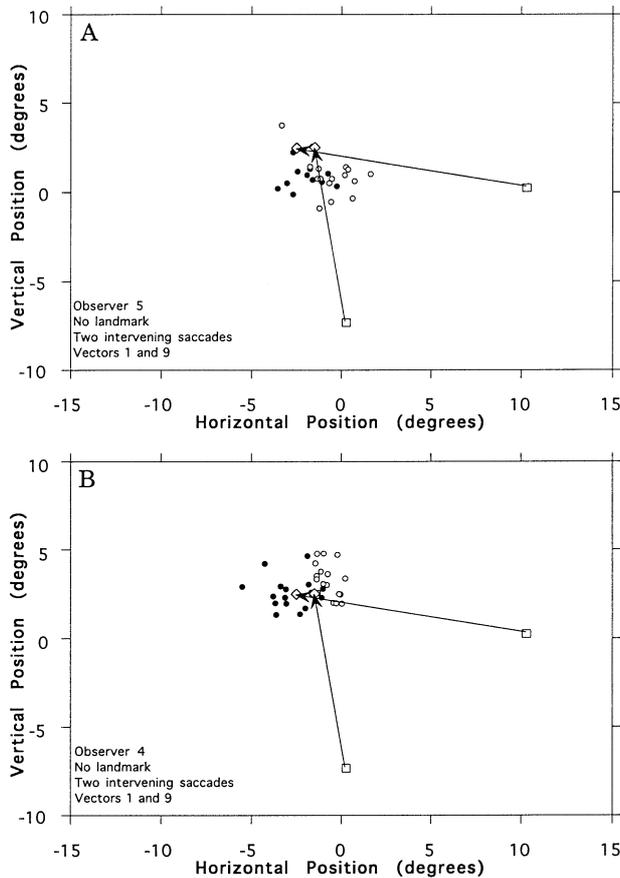


Fig. 7A, B Comparison of constant errors. *Filled circles* represent the landing points of the horizontal (leftward) saccades and *open circles* represent the vertical (upward) saccades. **A** Landing point scatter-plots for one observer, for two intended targeting saccade vectors with nearby memory target goals. Note that the two different saccades produce almost the same mean landing point error for the two memory targets, which are close in space. **B** Landing point scatter-plots for a different observer, for the same two intended targeting saccade vectors as in **A**. Note that this observer had different mean landing points for the two saccade vectors, even though the memory targets were close to the same location

cade. We expect that such an updating process, which amounts to a vector addition of the previous retinal error and the last saccade made, would add noise to the representation of the remembered location of the target with each saccade. Thus, if this retina-centered updating mechanism were in use, we would expect there to be greater variability in the targeting movements after five intervening saccades than after two intervening saccades. Although we see this effect in our no-landmark (egocentric only) condition, the increase in variable error is similar in the landmark condition (in which both egocentric and exocentric cues are available). Since the exocentric representation is expected to be independent of any sort of updating mechanism, it seems unlikely that the small increase in variable error associated with the greater number of intervening saccades is attributed to such an updating mechanism. Because the increases in standard deviation with the additional intervening saccades are

small and similar in the landmark and no-landmark conditions (0.20° and 0.26° respectively), the interpretation suggesting that memory interference is independent of an updating mechanism seems most plausible. In addition, attributing these results to an updating mechanism would imply an unlikely degree of precision of the eye position signal, as discussed later.

Previous studies of disruption of saccadic targeting performance

Previous studies that have looked at the effect of intervening activity on saccade targeting accuracy and precision have been inconsistent. Nemire and Bridgeman (1987) demonstrated a disruption in both eye and hand movements to remembered targets by 40 large, horizontal, intervening saccades.⁹ Honda (1984) found that after a rapid sequence of saccades in the dark, human observers tend to make manual pointing errors in a manner indicating that only the largest of the saccades is registered. On the other hand, Skavenski and his colleagues (Skavenski and Steinman 1970; Skavenski 1971; Hansen and Skavenski 1977) conclude that the ability to re-fixate a previously fixated location in the dark is relatively independent of intervening activity.¹⁰ The experiments, including our own, that have found some disruption by intervening saccades differ from the re-fixation experiments of Skavenski and his colleagues in that our observer is attempting to fixate a remembered target location that was initially presented peripherally; not fixated. It could be that the re-fixation task draws more on memory of proprioceptive signals or tonic oculomotor commands.

Skavenski and Steinman (1970) found that prolonged fixation in the dark resulted in increasing constant errors, but no increase in short-term variability. They interpreted this as evidence for a decay of spatial memory (i.e., drift of the remembered location) with a continued precise comparison between eye position and the inaccurately remembered target location. Gnadt et al. (1991) propose that an anisotropic decay of spatial memory occurs during delay periods as short as 800 ms in a memory-guided saccade task in which no eye movements intervene. Remember that the memory period was held constant in our experiments. Recent evidence indicates that this distortion in saccade targeting performance to remembered targets may be attributed to oculomotor output mechanisms, not in a higher level representation (Barton and Sparks 1993; White et al. 1993; Stanford and Sparks

⁹ The effect was seen in constant error (more undershooting) and not in variable error. The lack of a significant change in variable error may be attributed to two things: (1) intervening eye movements were only horizontal saccades and (2) eye-position-monitoring equipment they used apparently lacked necessary precision, as indicated by unusually large variability while fixating a visible target (Bridgeman 1994, personal communication)

¹⁰ Intervening tasks used by Skavenski and colleagues included 30 large saccades; a smooth eye movement produced by passive head rotation; or 15 min of free eye, head, and body movement

1994). If there was a systematic drift in the remembered location of the target in our experiments, we would expect similar constant errors for saccades from different directions to the same target region. Although this result occurred for some observers in some areas of visual space, we also frequently saw biases specific to the saccade vector. Our intervening activity may have prevented or masked this effect.

Precision of an eye-position signal

Remember that with each eye movement, the image of a stationary visible object sweeps across the retina. To use this changing retinal image to guide our everyday hand, head, and body movements, we must know something about either the position or the movement of the eye within the orbit (see Sparks and Mays 1990 for a review). Although such signals must clearly exist, little is known about their nature. Potential sources of an eye position signal include proprioception from the extraocular eye muscles or an outflow signal (e.g., efference copy) which is calibrated during development by correlating specific eye positions with the tonic activity in the gaze-holding mechanism. An eye movement signal could come directly from an efference copy of the eye movement command.¹¹ One of the difficulties in making conclusions from the current results stems from a general confusion in the literature about what can be inferred about eye movement and eye position signals from such data. In planning targeting movements to visual targets in the absence of exocentric cues, the central nervous system could have access to an eye-position signal, an eye-movement signal or both. If both sources of information are available, the system might combine the two or use only the more precise of the two signals.

Several research teams have estimated (either explicitly or implicitly) the precision of an eye position signal based on the assumption that this signal was the limiting factor in a fixation task. Matin and Kibler (1966) measured the standard deviation of the eye position signal by a vernier acuity task where the two targets were presented in the dark with a delay of up to 3 s between them. They found that the variability of the eye position signal increased with time to about 1° for a 3 s delay. By measuring variability in eye position during 38 s of fixation in the dark (straight ahead or 10° to the left or right), Skavenski and Steinman (1970) estimated that the standard deviation of the eye position signal is about half a degree. Hansen and Skavenski (1977) subtracted variances in manual targeting (striking a stationary visible target with a hammer) in lighted and dark conditions, thereby computing the decrease in variance attributable to the additional visual (exocentric) cues and apparently misinterpreted this as a measure of the precision of the eye posi-

tion signal. Our current data provide an estimate of the precision of the eye-position signal if we assume, for the moment, that performance in our current memory saccade task is limited by an eye-position signal (i.e., uses a head-centered reference frame). Given this assumption, the variation in the landing points of targeting saccades in the two intervening saccade, no-landmark condition (see Fig. 6) can be used to set an upper bound for the standard deviation of the eye position signal at 1.4°. In addition to the studies cited above, others have provided measures of the standard deviation of the eye-position signal, some as high as 5° (see Matin 1986 for a review). Differences in the reported precision of the eye position signal may be due, at least in part, to differences in conditions under which the measurements were taken such as position of the eye within the orbit, duration of time in the dark, and the observer's task. Inferences about an eye-position signal, which are based on microsaccades during attempted fixation in the dark, may not be relevant when considering the signal needed to compute a much larger saccade from an eccentric eye position (Matin and Kibler 1966), especially given the differences in eye movement patterns between fixation in the dark and fixation of a visible target (Cornsweet 1956; Nachmias 1961).

Precision of an eye movement signal

Alternatively, if we assume for the moment that saccadic targeting performance in our current experiments is limited by an eye-movement signal (i.e., a retina-centered representation holds target location during the memory period), the representation of the memory target must be updated after each intervening eye movement. We can describe the variability of the final targeting saccade landing point as the sum of the underlying sources of variability that contribute to performance. Sources of variability might include error in localizing the target image on the retina, memory decay during the delay period, and motor error in the targeting movement itself. If a retina-centered representation is used to hold the target location in memory, added variation would be expected to result from the updating of this representation with each eye movement during the memory period. The premise of the additivity of variances can be useful in dissecting sources of variation in this memory saccade task. We call the total variance of targeting eye movements σ_{total}^2 and regard it as the sum of variances from different sources including the updating process as shown here:

$$\sigma_{\text{total}}^2 = \Sigma \sigma_i^2 + \sigma_m^2$$

where

$\Sigma \sigma_i^2$ = added variation from sources such as retinal error, motor error and memory decay.

σ_m^2 = added variation due to updating with each eye movement.

¹¹ An eye-movement signal could also be derived by computing the difference between pre- and post-saccadic eye position, but we consider this a use of eye position rather than movement information

If the system performs an update of the target's position in a retina-centered frame after each movement, the variance with five intervening saccades is given by:

$$\sigma_{\text{total}}^2 = \Sigma \sigma_i^2 + 5\sigma_m^2$$

The variance with two intervening saccades is given by:

$$\sigma_{\text{total}}^2 = \Sigma \sigma_i^2 + 2\sigma_m^2$$

Using results from the no-landmark condition in experiment 2 (see Fig. 6) we can read the value for σ_{total} from the graph. With five intervening saccades:

$$\sigma_{\text{total}} = 1.7^\circ$$

To make the most conservative (largest) estimate of the variability of the eye movement signal, we use results from the landmark condition for σ_{total} in the two intervening saccade condition. This avoids a possibly inflated value of σ_{total} due to drift of the eye in the dark in the condition with two intervening saccades where the observer was required to maintain fixation without a target. Therefore, with two intervening saccades we have:

$$\sigma_{\text{total}} = 1.1^\circ$$

Solving the two equations above yields:

$$\sigma_m = 0.75^\circ$$

Thus, if we assume that increased variable error with more intervening saccades is due to updating the memory target location in a retina-centered frame, we can set an upper bound on the standard deviation of the eye-movement signal of 0.75° .

There are relatively few estimates of the precision of an eye-movement signal for comparison to this value. If we assume that observers hold the location of a pre-saccadic target in memory using a retina-centered reference frame, one such estimate can be inferred from Matin's (1986) data on position judgments for a post-saccadic target relative to a pre-saccadic fixation point. Matin found a standard deviation of 1.5° for saccades in the range of 2 to 8° . We can apply the technique for dissecting variation used above to Miller's (1980) saccadic eye-movement data to previously fixated targets. If we subtract the average variances in his *Retinal* and *Dark* conditions, we get a measure of the standard deviation of the eye movement signal of 1.1° .

Another useful comparison can be made to the precision of saccades to *visible* targets. Under conditions which are otherwise similar to those in our current experiments, the standard deviation of saccade landing points to visible targets is 0.75° (Møller et al. 1989a; Hayhoe et al. 1990). Given that our estimate of the standard deviation of an eye movement signal is no larger than this, the underlying assumption that performance is limited by updating in a retina-centered frame seems unlikely. Thus, we favor the interpretation of these results as evidence supporting a process that does not rely on updating to ac-

count for changes in eye position after each saccade, but rather on a continuously available eye position signal and a head-centered representation for remembered targets.

Exocentric cues used by the saccadic system

In these experiments, the presence of a landmark, which provides an exocentric localization cue, resulted in less trial-to-trial variation (greater precision) of the targeting movements. This result demonstrates that the motor system can use exocentric information (i.e., the spatial relationships between two or more objects) and confirms earlier results from this laboratory (Møller et al. 1989a,b; Hayhoe et al. 1990) and those of Dassonville and his colleagues (Dassonville et al. 1991, 1995). In addition, the difference in performance in the no-landmark conditions between experiments 1 and 2 appears to indicate use of an exocentric reference frame. It seems that observers were able to integrate visual information from the intervening targets to aid performance in experiment 1 compared with similar conditions and intervening activity but without the visual targets present (experiment 2). This may indicate a temporal integration of sequential exocentric cues by establishing the relationship between one visible target and the next to improve the representation of the memory target and to aid final targeting performance.¹² Alternatively, the observer might use the visual information to improve knowledge of eye position. This would be consistent with Miller's (1980) suggestion that the representation of post-saccadic eye position may be more precise after saccades to visible targets than after saccades made in the dark due to the use of the pre-saccadic retinal error signal.

Most research in the planning and control of biological movement to visual targets and the associated physiological underpinnings has focused on the use of egocentric reference frames. Recent work by Dassonville et al. (1995), Olson and Gettner (1995), previous work from our laboratory, and our present results expand the understanding of motor planning and control to include the use of exocentric reference frames as well. Exocentric cues are recognized as playing a critical role in object identification and recognition, but typically not considered relevant to guiding movements to visual targets. Note that the exocentric information available in our landmark condition was minimal (a single target of less than 1° , which disappeared during the intervening saccades and reappeared prior to the targeting saccade). This landmark seems trivial in contrast to the rich visual environment that is normally available for use in establishing relationships between objects in the real world. Although these findings deal only with movements to locations remembered over brief periods, Dassonville et al. (1995) have shown similar results in immediate movements to visible

¹² We also point out that part of the added variable error in the no-landmark condition of experiment 2 compared to experiment 1 could be due to slightly larger intervening saccades in the dark without visible intervening targets

targets. It is not yet clear how these findings may generalize to other movements such as reaching and locomotion, although cumulative errors have been demonstrated in sequential pointing movements made without sight of the arm or hand (Bock and Arnold 1993).

Elaborating models of the saccadic system

Our data suggest representations of target location in at least two reference frames: egocentric (most likely head-centered) and exocentric. We presented in the introduction evidence for neural representations of target location in retina-centered, head-centered, and object-centered (exocentric) reference frames.¹³ Although others have argued that evidence for a representation in one reference frame is evidence against representation in another, it seems simpler to suppose that the brain holds representations of a target in multiple reference frames that are normally mutually supportive. Evidence for these multiple representations is provided by Møller and his colleagues (Møller et al. 1989a,b; Hayhoe et al. 1990; Hayhoe et al. 1992) and Dassonville et al. (1995) from oculomotor performance¹⁴ and by Abrams et al. (1990, 1994) and Smeets and Brenner (1995) from limb movements. Some system models of spatial representation for motor control contain representations of the target in both retina-centered and head-centered reference frames (Robinson 1973), but none makes use of an exocentric reference frame. Similarly, physiologically motivated models of the saccadic system such as that proposed by Pierrot-Deseilligny (1991) have grown increasingly complex, indicating the involvement of such structures as the posterior parietal cortex, prefrontal cortex (see Funahashi et al. 1990, 1993; Jonides et al. 1993), thalamus (see Gaymard et al. 1994), and frontal eye fields in memory guided saccade tasks. None of these models has yet focused on structures thought to process exocentric information.¹⁵ Models that do not include the involvement of exocentric representations seem incomplete in light of our findings. We have proposed a system that combines multiple representations in different reference frames where the weighting of the

¹³ In addition, there is evidence for target representation in the brain using body- (Brotchie and Andersen 1991; Fogassi, et al. 1992; Snyder et al. 1993; Brotchie et al. 1995), shoulder- (Flanders et al. 1992), and world-centered reference frames (McNaughton et al. 1991)

¹⁴ The current experiments used a task very similar to the one used by Møller et al. (1989b) and Hayhoe et al. (1990). In one of their experiments, the landmark was shifted between its initial presentation and its later presentation within the same trial. In this way the egocentric representation and exocentric representation of the memory targets location were put into conflict. Observers consistently made saccades to a location, which indicated an averaging of the egocentric and exocentric representations. Dassonville et al. (1995) came to a similar conclusion after studying saccades to targets presented in a way known to impair egocentric localization (i.e., presented around the time of a preceding saccade). The presence of a landmark reduced, but did not eliminate, targeting errors caused by the egocentric impairment

¹⁵ The hippocampus might be one such structure (McNaughton et al. 1983; Baylis and Moore 1994)

information from various sources could vary with task demands (Karn et al. 1994).

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