

Memory representations guide targeting eye movements in a natural task

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The change blindness phenomenon suggests that visual representations retained across saccades are very limited. In this paper we sought to specify the kind of information that is in fact retained. We investigated targeting performance for saccadic eye movements, since one need for visual representations across eye and body positions may be to guide coordinated movements. We examined saccades in the context of an ongoing sensory motor task in order to make stronger generalizations about natural visual functioning and deployment of attention. Human subjects copied random patterns of coloured blocks on a computer display. Their eye movement pattern was consistent from block to block, including a precise saccade to a previously-placed, neighbouring block during each additional block placement. This natural, consistent eye movement allowed the previously-placed, neighbouring block to serve as an implicit *target* without instructions to the subject. On random trials, we removed the target object from the display during a preceding saccade, so that observers were required to make the targeting saccade without a currently visible target. Targeting performance was excellent, and appeared to be influenced by spatial information that was not visible during the preceding fixation. Subjects were generally unaware of the disappearance and reappearance of the target. We conclude that spatial information about visual targets is retained across eye movements and used to guide subsequent movements.

INTRODUCTION

Memory vs. real-time representations

A variety of recent findings demonstrate that observers are profoundly insensitive to changes in visual displays made in the presence of some kind of spatial

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or temporal masking stimulus, or during some kind of visual discontinuity, such as a change in gaze position or a film cut (Irwin, 1991; McConkie & Currie, 1996; O'Regan, Rensink, & Clark, 1996; Rensink, O'Regan, & Clark, 1996; Simons & Levin, 1997). There is general agreement that this implies that visual representations maintained across different views are of limited capacity or complexity (Simons & Levin, 1997). The challenge, however, is to understand exactly what is and is not represented. Our knowledge of the structure of visual representations maintained over periods greater than 200 ms is currently quite limited. This is a critical issue in understanding visual processes. How do we make the transition from computations within a fixation to those required to guide ongoing behaviour? To approach this question we consider what behavioural functions such visual representations subserve. Visual perception typically takes place in the context of ongoing, goal-directed movements of eyes, hands and body, so some continuity of visual representations seems necessary for coordinated actions. In this paper we ask whether coordinated movements are guided solely by the current image on the retina, or whether such movements are guided by a more enduring representation constructed from information captured in different gaze positions and across different moments in time.

In this paper we consider the case of saccadic eye movements. Saccadic targets are usually selected on the basis of the current image in the peripheral retina, but many orienting movements are to targets not currently visible. How are these movements targeted? A variety of evidence demonstrates that accurate eye movements to remembered locations are possible (Becker & Fuchs, 1969; Hayhoe, Lachter, & Møller, 1992; Karn, Møller, & Hayhoe, 1997; Gnadt, Bracewell, & Andersen, 1991), and considerable evidence shows a neural substrate for this in the activity of cells in posterior parietal cortex and prefrontal cortex (Andersen, Snyder, Bradley, & Xing, 1997, for a review; Funahashi, Bruce, & Goldman-Rakic, 1989, 1990; Funahashi, Chafee, & Goldman-Rakic, 1993). However, it is not clear how much we normally rely on these memory representations to guide our everyday actions. Most of what we know concerning the use of memory in guiding movement comes from highly structured, unnatural tasks in sparse visual environments. Under normal circumstances our memory of spatial information is not dissociated from current visual input. In this experiment we investigate memory use in saccadic targeting while observers perform a simple task that involves many of the kinds of actions we use in everyday tasks. What representations do people normally use when permitted to choose, and to shift between, representations in the context of natural, ongoing, goal-directed tasks in complex visual environments? The goal of this experiment is to investigate the contributions of real-time versus memory representations in specifying targets for eye movements in the context of a more natural task.

Studying targeting in a natural task also provides the advantage that attentional state is well defined. Momentary attentional state affects visual

representations in complex ways (Ballard, Hayhoe, & Pelz, 1994a, b; Hayhoe, Bensinger, & Ballard, 1998). Thus, attention is likely to have an important role in the kind of visual representations that span fixations. Judgements of visual direction, for example, appear to depend on the subject's task (Bridgeman, 1989). In many standard experimental paradigms it is not clear how attention is being distributed. For example, in many experiments on the nature of visual processing of putatively unattended information, subjects covertly distribute their attention across the visual field while performing the primary task (Mack & Rock, 1996; Rock, Linnett, Grant, & Mack, 1992). Experiments using the change detection paradigm also reveal the role of attention (McConkie & Currie, 1996; Rensink et al., 1996). In the context of an ongoing task, attention is deployed in a predictable manner, and the visual representations are those needed for natural performance. This allows us to manipulate the information used in saccadic targeting, at crucial points in task performance. If targeting is based solely on information in the currently visible scene (i.e., not on memory from prior fixations), then removal of that information at the point in the task where the target is being computed should disturb targeting performance.

Block copying task

In this experiment we use the block copying task developed by Ballard, Hayhoe, and colleagues (Ballard, Hayhoe, Li, & Whitehead, 1992). This provides a natural goal-directed task which maintains sufficient structure to provide experimental manipulation of many variables. The subject sees a display divided into three regions (see Figure 1). A set of eight coloured blocks forms a contiguous two-dimensional pattern in the *model* area. There are additional blocks randomly placed in a separate *resource* area. The subject builds a copy of the model pattern in a nearby *workspace* area as quickly and accurately as possible using the blocks from the resource area.

Eye and hand movements are monitored during the task. Earlier experiments with this task (Ballard et al., 1992; 1994a, b; Hayhoe, Ballard, & Pelz, 1994; Hayhoe et al., 1998) indicate that humans seem to rely surprisingly little on their memory of the model configuration and instead make repeated re-fixations of the model during a trial, typically fixating the model twice in the course of moving a single block. A reanalysis of a small sample of data from these previous experiments indicated that during the placement of blocks in the workspace area, the subjects' fixations cluster around the edge shared between a previously placed block and the intended location of the block currently being moved. Saccades into the workspace area appear precise and accurate, as indicated by the tight clustering of saccade landing points and the relatively low frequency (about 50%) and small size (less than about 1.5 degrees) of corrective saccades. Saccades to other areas of the display and during other parts of the task do not show such predictable patterns.

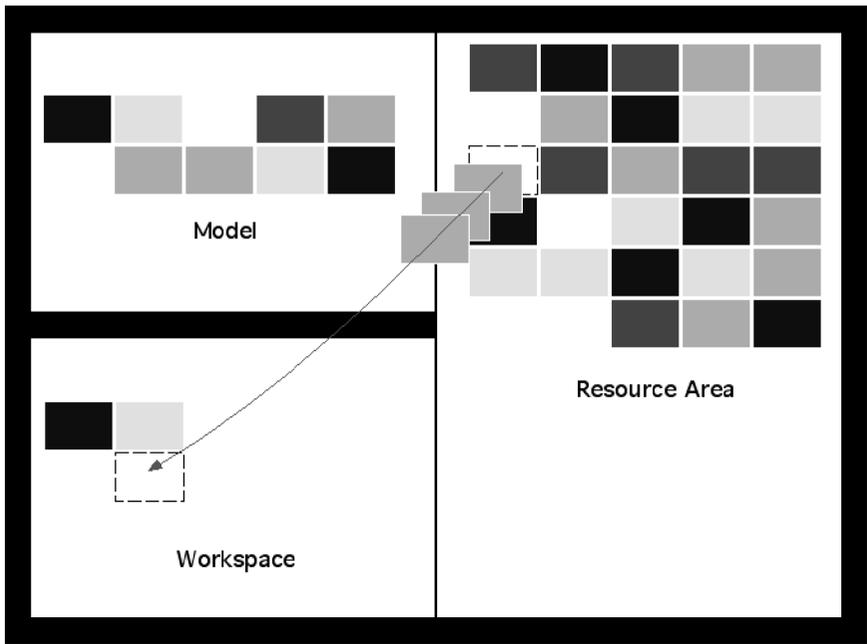


Figure 1. Schematic diagram of the display used in the block copying task. The subject builds a copy of the model in the workspace as quickly and accurately as possible using blocks from the resource area. The actual display is in colour (blocks, shown here in four shades of grey, are red, green, blue, and yellow). Movement of the blocks is accomplished by clicking and dragging with the computer mouse.

The saccade targeting performance into the workspace area indicates that a target or the targeting movement itself is well represented in the brain before the launching of the saccade. Unlike the much more constrained laboratory investigations of saccade targeting performance prevalent in the literature, in this paradigm the experimenters do *not* specify a target nor explicitly instruct subjects regarding any aspect of their eye movements. However, despite this lack of instruction, we are able to take advantage of the highly regularized pattern of saccades into the workspace just prior to block placement to infer a target of these saccades. The spatial and temporal predictability of the endpoints of these eye and hand movements into the workspace area, provides an opportunity to study the representations people use in planning and executing these natural, goal-directed movements.

Changing the display during a saccade

The experiment described here runs on a computer-generated version of the task because this allows display manipulations during a saccadic eye movement. Although saccade contingent updating has been used for some time with simple text displays (Rayner & Pollatsek, 1987), only recently has the

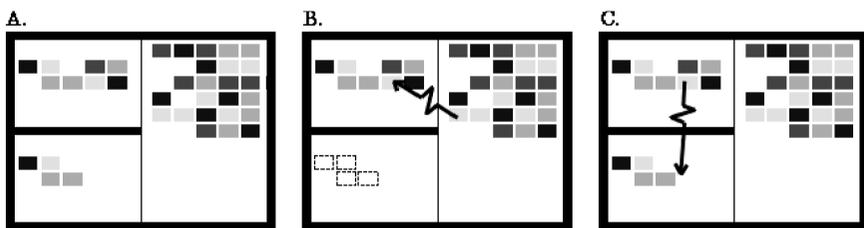


Figure 2. Sequence of events for the disappearing condition. The blocks disappear only for the period in which the subject fixates in the model area as described in the following sequence. A. The control software detects a situation in which one or more blocks have been placed in the workspace and another block is about to be moved from the resource area to the workspace copy. B. During a saccade from the resource area to the model area, the blocks that have been previously placed in the workspace disappear. C. During the next saccade from the model area, the blocks reappear in the workspace.

technique been applied to more complex displays. This technology allows us to investigate the nature of the internal representation of spatial information by manipulating the display during ongoing goal-directed movements and with the natural deployment of attention to accomplish these tasks. In the current experiment we test whether the normal planning of saccadic eye movements relies solely on current real-time sensory information (i.e., the peripheral retinal image of a target) or whether it might include other representations of the target's location. We hypothesized that if the subject relies critically on the current retinal image to guide eye movements, removing the target from the scene just prior to planning a saccade should disrupt performance by increasing endpoint variable error. With careful timing we removed all of the blocks which the subject had previously placed in the workspace so that they were not visible during the fixation immediately preceding the targeting saccade. The blocks reappeared during the saccade out of the model area. Figure 2 illustrates this sequence. An otherwise identical *non-disappearing* condition served as a control for comparison to study the effects of the presence or absence of blocks in the workspace when planning saccadic eye movements to this area of the display.

Movements guided by memory differ in some ways from movements guided by real-time visual input. Eye movements made to remembered targets have a lower peak velocity and are less accurate (Becker & Fuchs, 1969; Gnadt et al., 1991). Memory guided reaching movements have increased variability in velocity and grip aperture (Goodale & Servos, 1992). Wong and Mack (1981) provided additional evidence for a difference between spatial representations in real-time and in memory, reporting that saccadic eye movements to visible objects were not susceptible to perceptual illusions of target location caused by the surrounding reference frame as were memory guided saccades. These differences have caused some to theorize that real-time and memory representations of spatial information are largely independent (Goodale & Servos, 1992).

METHODS

Overview

Human subjects viewed a computer-driven display and manipulated blocks on the display with the computer mouse and screen cursor. The subject's task was to build an exact copy of an existing model of coloured blocks. The subject received instructions to copy the model as quickly and accurately as possible,¹ but no instructions concerning eye movements. The head was restrained and eye and hand positions were monitored. The software controlling the experiment presented the images on the display, kept track of appropriate times for modifying the image, and then triggered these changes when it detected an eye movement from the resource area to model area. Half of the time that these conditions were met, all blocks previously placed in the workspace disappeared with minimal delay. The other half of these events were flagged for the non-disappearing control condition. The disappearing blocks reappeared after fixation in the model area during the next eye movements out of this area.² We analysed the landing points of these saccadic eye movements into the workspace. The methods are described in more detail later and by Karn (1995).

Subjects

Five adults (four females and one male) ranging in age from 18 to 32 years (mean: 23 years) were paid for participating. Subjects were recruited from University of Rochester students and staff and selected based on trackability with the eyetracker. All had normal colour vision and acuity which allowed them to perform the task easily. Three of the subjects had uncorrected Snellen acuity of 20/30 or better in both eyes. One subject (number 3) had Snellen acuity of 20/40 and 20/50 in right and left eyes respectively, which did not interfere with task performance. One subject (subject 1) had a vague understanding of the nature of the experiment and was aware that the display might change at times during the task. The other four were completely naive to the methods and purpose of the experiment including the disappearing blocks. All had prior experience using a computer mouse, were right handed, and used this hand for controlling the mouse.

¹Accuracy was enforced by aborting a trial immediately upon incorrect placement of a block. No records were kept of frequency of errors, but they were generally very low.

²Note that subjects could, and often did, make more than one fixation within the model area before the blocks reappeared in the workspace. Past results indicate that under these conditions, the next saccade away from the model area typically lands in the workspace. On occasions when the next saccade out of the model area goes into the resource area, the workspace blocks reappeared and the event was discarded.

Display

The images for the block copying task appeared on a colour, raster, cathode ray tube refreshed at 66.7 Hz. The display had an active surface area 16.6 degrees of visual angle horizontally by 12.8 degrees vertically. Each block subtended approximately 1.5 degrees horizontally by 1 degree vertically. The model consisted of eight blocks in a contiguous random pattern. The resource area contained 28 blocks in the top six rows which was ample for the task. Both the luminance and the chromatic properties of the blocks changed quite dramatically during the disappearance and reappearance of the blocks. The maximum luminance change, associated with blocks changing from blue to the background colour (white), was 52.8 cd/m^2 and the minimum luminance change (yellow to white) was 5.0 cd/m^2 .

Eye and hand position monitoring

The position of either the subject's right or left eye was monitored with one of two SRI, Generation-V, dual-Purkinje-image eyetrackers (Crane & Steele, 1985). A bite bar and a forehead rest constrained the subject's head. The non-tracked eye was patched. Analogue signals from the eyetracker were sampled 500 times per second. The position of the subject's hand was digitally sampled at a rate of 60 Hz during the task by monitoring the computer mouse. The subject signalled the beginning and end of each trial by pressing a button on a keypad.

To compensate for non-linear response properties of the eyetracker and optimize accuracy of eye position readings, we calibrated eyetracker output to the subject's fixation of known target positions before every block of 10 trials. The subject fixated a calibration target as it jumped to 25 positions on the display. When fixating each position the subject triggered the collection of 500 samples from the eyetracker, of which the median was used. A 256×512 look-up table was constructed to associate the horizontal and vertical eyetracker voltages to points on the display (Karn, 1995). The look-up table was designed to optimize the speed and accuracy of assessing eye position in real time. During experiment run time, further interpolation between the look-up table values allowed on-line determination of the position of the eye relative to the screen with sub-pixel resolution and with an access time on the order of microseconds. Each calibration was checked immediately by simultaneously displaying an array of check-points and a small movable cursor, the position of which varied with eye position. If the subject's fixation of the check-points resulted in the eye-slaved cursor falling outside the 0.28 degree radius target on more than two points, or if fixation of any one point indicated an error of more than 0.5 degrees, the calibration procedure was repeated.

Computer-triggering of display changes

A computer program presented the stimuli to the subject, controlled the sampling of the eye and mouse positions, modified the display according to the subject's mouse manipulations, and flagged potential opportunities for the saccade-contingent display changes based on these criteria:

- The subject had placed at least one block (but not all) in the workspace.
- Only one of these previously placed blocks (the *preceding neighbour*) shared a single edge with all of the unplaced blocks (i.e., there was only one location in the workspace where a block was expected assuming contiguous building of the copy).

When these conditions were met, the next eye movement³ that caused the eye's point of regard on the display to cross from the resource area into the model area triggered the disappearance of all the blocks previously placed in the workspace 50% of the time (determined randomly). The other 50% of these eye movements under these identical conditions were flagged as the non-disappearing trials to serve as the control condition. The block disappearance was accomplished quickly (usually in the next refresh cycle of the CRT) by animation of the video colour look-up table which obviated redrawing the entire image in video memory. When the blocks disappeared, the next eye movement out of the model area triggered their reappearance.

Timing checks of display changes

Because this experiment critically depends on making changes to the display during a saccadic eye movement we performed tests to confirm that this occurred. A trained observer made saccades that caused the blocks in the workspace to change from their various colours to white (background) or black as the eye's point of regard crossed into the model area then to change back to their original colours as the point of regard crossed into the workspace. These changes were not visible to the observer, whereas they were always clearly visible to the experimenter, whose eye movements were not linked to the changes.

In a separate experiment we simultaneously measured eye position and the display luminance change during the task. We used a fast photodiode to gather light from a single block. Blocks turned black for maximum detectability by the photodiode and sampling rate was 800 Hz to capture rapid changes. Figure 3

³Changes were not contingent on a *saccadic* eye movement, but rather on any eye movement that caused the eye's point of regard to cross the triggering border when the triggering conditions were met. Any sort of eye movement could trigger the display change. However, due to the nature of the task, a non-saccadic eye movement triggered the disappearance only once in the course of the experiment when a subject fixated close to the triggering border and a slight drift in eye position triggered the display change.

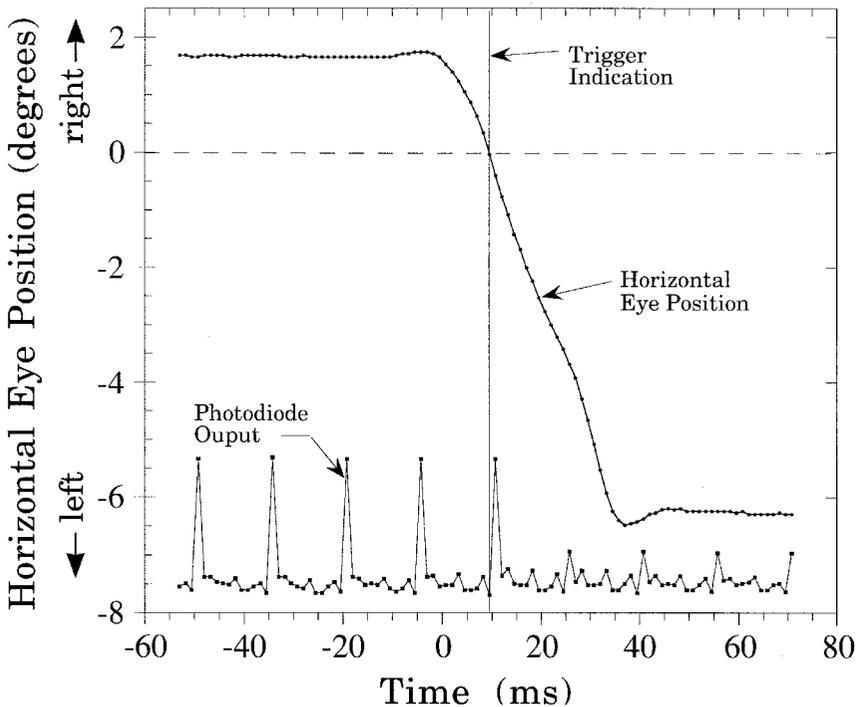


Figure 3. Photodiode test of the timing of display changes. Output from a photodiode held over a changing block at the surface of the CRT is shown at the bottom of the figure (arbitrary output units, but accurately timed). Refresh of the CRT every 15 ms caused regular pulses in the output of the photodiode. The horizontal eye position signal is shown above. Time zero is the approximate start of the saccade. When the eye position crossed the boundary between resource area and model area (the midpoint of the display, indicated by the dashed line at position zero), the software signalled the display change, which is apparent in the rapid suppression of the block's luminance as seen in the photodiode output. The vertical marker was captured in the data stream as the time at which the display change was triggered. Note that even in the off (black) state, the periodic sweep of the CRT refresh can be seen in the photodiode output, but greatly reduced.

shows both horizontal eye position from the eyetracker and the luminance of the workspace block from the photodiode plotted over time. The photodiode's response shows that the display luminance is changed to its new level well before the end of the saccade. This confirmed that the system response time was fast enough to produce the changes during a saccadic eye movement.

We performed an additional test with the experimental data, which include the time of the last video refresh. We computed the time from the video refresh following the eye position triggering time (plus 3 ms to allow for processing delays measured in the earlier test) to the end of the saccade as determined by our off-line analysis. All of these times were greater than zero, indicating that the screen changed before the end of the saccade in every instance.

We were also concerned about the effect the eyetracker's mechanical delays might have on timing of saccadic eye movements and display updating. We measured response time while tracking an artificial eye and concluded that the slight delays⁴ do not introduce significant error in saccade endpoint measurement.

Data analysis

An off-line analysis program computed the speed of the eye in each sample interval.⁵ The resulting eye speed data was passed through another routine which classified the start and end points of saccadic eye movements based on a threshold velocity of 15 degrees/second for a minimum duration of 40 ms.⁶

RESULTS

General observations

The overall pattern of behaviour in the block copying task was similar to what we have seen in previous experiments with this task (Ballard et al., 1992, 1994b). Subjects built copies of the models as instructed, quickly and with relatively few errors and made frequent fixations in the model area. They nearly always built contiguously—placing blocks that shared an edge with previously placed blocks—and they usually constructed the patterns from top down. Thus, the infrequent saccade-contingent changes to the display did not appear to affect the overall strategy of the subjects. Figure 4 shows an example of the most common pattern of eye and hand movements. After placing a block in the workspace, the stereotypic sequence of fixation locations is: Model area, resource area (during pickup of the selected block), model area again, and workspace (just prior to block placement).

Although some subjects do not regularly produce this pattern of eye and hand movements in their first few trials, nearly all subjects use this pattern as the modal response after several trials. Anticipating this strategy was important

⁴The mechanical delays cause it to behave as a low-pass filter with a bandwidth greater than 100 Hz. Pure delay is 1.0 ms. Rise time for simulated 2.5 degree saccades is 4.7 ms, and total response time (to 1 % of final position) is 10.9 ms.

⁵Horizontal and vertical eye position data were passed through a 29 point non-recursive, finite impulse response, digital filter (pass band: 0 to 45 Hz, transition band: 45 to 90 Hz, attenuating above 90 Hz) resulting in differentiation of the signals. The resulting horizontal and vertical components of eye velocity were combined with the Pythagorean theorem to determine the speed of the eye in each sample interval.

⁶These values were chosen in order to detect reasonably small saccades without inappropriately classifying as separate saccades the small overshoots in measured eye position (Deubel & Bridgeman, 1995).

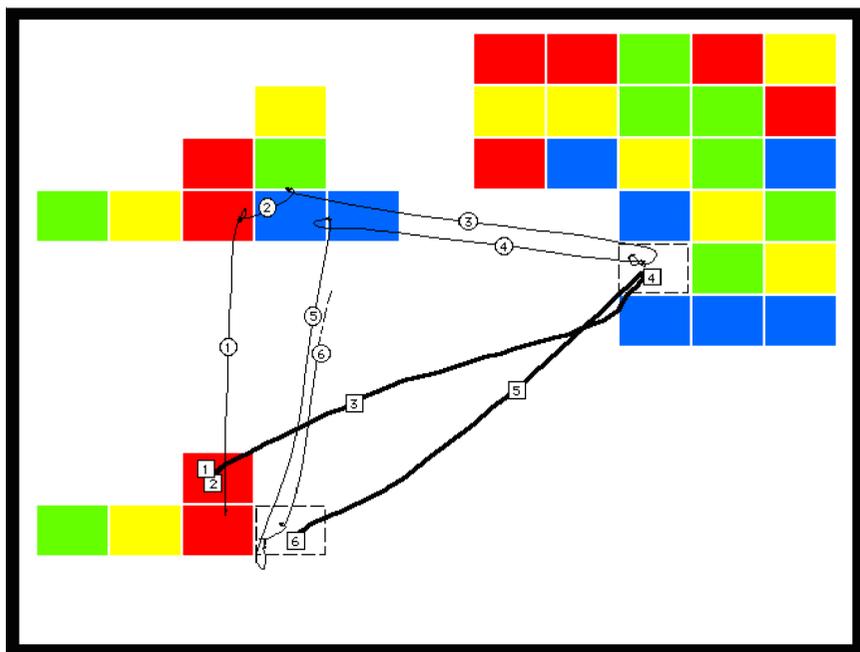


Figure 4. Typical pattern of eye and hand movements during the block copying task. Eye position trace is thin line; hand position is thick line. The circled numbers on eye position trace mark the approximate midpoints of saccades. The corresponding numbered squares represent hand position at time of each saccade. The traces begin just after the placement of a block (at hand position 1) and end just prior to placement of the next block (at hand position 6). Fixations prior to block pickup and placement are tightly linked to the location where the action will occur. However, the eye typically leaves the location just before block pickup or placement. Note: the border between the Workspace and Model areas of the display, which was visible to the subjects, is left off this figure to more clearly show the eye and hand movement traces.

in designing the saccade-contingent display changes. The saccade-contingent display changes occurred only when the previously placed blocks had a single open edge (i.e., there was only one location in the workspace where a block was expected assuming contiguous building of the copy), and when the subject made an eye movement from the resource area into the model area and then from the model area into the workspace. Thus, the display changes depended on the subject's sequence of eye and hand movements and occurred with slightly different frequencies for different subjects. The triggering pattern coupled with the 50% probability of flagging an event for a disappearing condition resulted in the workspace blocks disappearing in 8% of the individual block movements. This equates to an average of 6.5 occurrences of disappearing blocks in a batch of 10 trials. A total of 280 non-disappearing (control) and 328 disappearing events were recorded from the five subjects.

Subjects' awareness of display changes

All subjects reported the experiment to be fun and challenging and thus were attentive to the task. Although most subjects seemed unaware of the saccade-contingent changes until specifically informed, they varied in their ability to report the disappearance of the blocks. In order to have a broader sample of this idiosyncratic behaviour, the results for this section include the five subjects who participated in the full experiment as well as results from four additional naive subjects who participated in just one or two experimental sessions.

Method for probing awareness. In order to test the subject's awareness of the disappearances and reappearances of the workspace blocks without explicitly drawing attention to these occurrences, we asked after each batch of 10 trials if they noticed anything unusual during the task. This question was mentioned under the guise of potential problems with the hardware and software. Due to the complexity of the experimental systems used, there were a few bugs in the system at the beginning of the experiment which were corrected by the second or third session with each subject. These intermittent disruptions included:

- discontinuities in the updating of the block's position during block movement, causing the block to jump across the screen
- error messages indicating an overflow of the buffer on the A-to-D board, which caused the trial to end prematurely
- errors in the eye tracking signal during calibration.

These bugs served to provide some indication of the subject's sensitivity to, and willingness to report, unusual behaviour of the system. Subjects were warned that there were bugs in the system and told that the experimenters were aware of some, but probably not all, of the problems with the system and that they should report anything unusual at the end of each batch of 10 trials. They were prompted again at the end of each batch of trials to report any problems.

Most unaware of changes. All subjects reported annoyance with the bugs listed previously. However, of the total of eight naive subjects, only two (subjects 7 and 8) appeared to be immediately aware of the saccade contingent changes. Subject 8 could report the location accurately; subject 7 localized it to the left side of the screen. Neither correctly identified the event triggering the change.⁷ A third subject (subject 4) mentioned noticing the disappearing blocks after the third batch of ten trials. During the second trial in this batch, six previ-

⁷Subjects 7 and 8 did not participate in the full experiment due to poor eye tracking. These track loss problems may be related to the awareness of the changes as the erroneous eye position signals may have occasionally caused a display change to occur independently of the planned triggering events.

ously placed blocks in the workspace disappeared. The subject made several fixations in the model area over a period of 1482 ms and then looked back to the resource area causing the blocks to reappear. After this experience, the subject indicated for the first time that she had seen the blocks disappear. She also reported at this time that she had seen the blocks in the workspace blinking off prior to this. As this subject continued in the full experiment, we specifically asked about the disappearances in later batches of trials. She reported seeing the disappearances “a couple of times” in each of three batches of trials in which disappearances occurred 6, 16, and 9 times in three consecutive batches of ten trials each. In a final batch of trials we gave the subject the additional task of reporting each disappearance as it occurred. The subject reported all nine of the disappearances that occurred with no false alarms.

Most could detect changes once disclosed. The other five subjects made no report of the disappearing blocks after the first few batches of trials (which typically exposed them to about six disappearing conditions per batch of ten trials). Of these five subjects, three continued through the entire experiment. Towards the end of their visits to the laboratory, we gradually disclosed the disappearing blocks. One (subject 2) was unable to detect the disappearances or reappearances even after explicit disclosure regarding the conditions under which these events occurred. The two remaining subjects (subjects 3 and 5) were surprised when we disclosed the display changes, but seemed to become aware of these occurrences gradually. After being told of the display changes, both indicated that they had been vaguely aware of something like that, but had attributed it to their own blinking or “just my eyes”. Finally when we modified the subject’s task, asking them to report the disappearances as they detected them, these two subjects were able to perform with no errors. There were no obvious differences in strategy or saccadic performance between subjects who varied considerably in their notice of the saccade-contingent display changes. The disappearances of blocks from the display apparently went unnoticed most of the time and caused minimal task disruption.

Saccade accuracy

Observations in earlier studies with the block copying task revealed that subjects fixate close to the common edge between a previously placed block (the preceding neighbour) and the placement site for the selected block that is being moved. To quantify this, we looked at the landing points of saccades into the workspace from the model area in our non-disappearing condition. We normalized the saccade landing points in the workspace to the centre of the placement site for the selected block for each trial. The average normalized saccade landing points are plotted in Figure 5 separately for each of the four relative locations of the previously placed neighbouring block. Note the clear differences in

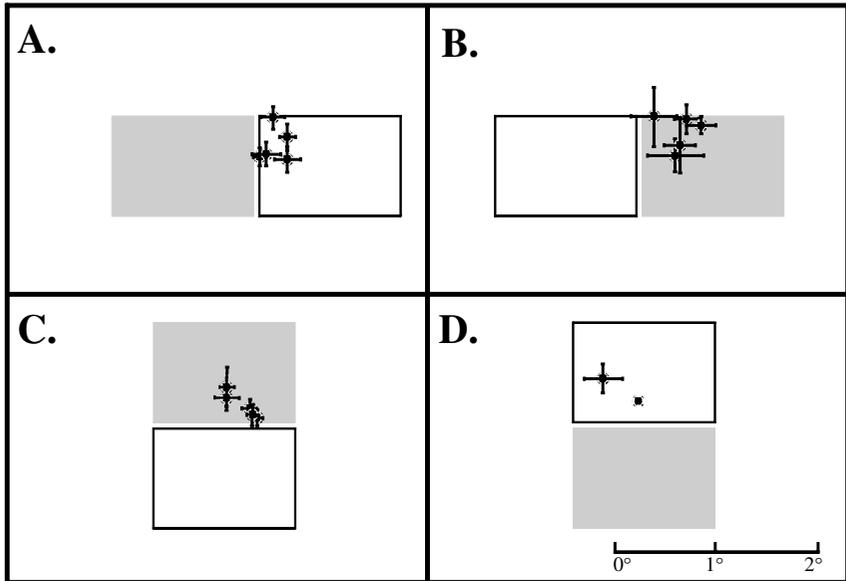


Figure 5. Normalized mean landing points for the non-disappearing (control) condition. Landing points of targeting saccades from the model area into the workspace were normalized to the placement site for the selected block. The individual mean landing point, for each of the five subjects is plotted separately for the four preceding neighbour locations (A. left, B. right, C. above, and D. below) relative to the placement site. Data are limited in the below condition (panel D) due to the natural tendency for subjects to build from top down. A scale appropriate for both horizontal and vertical dimensions is shown in panel D (note: a block is approximately $1^\circ \times 1.5^\circ$). Error bars represent ± 1 standard error of the mean.

mean landing point between the different preceding neighbour locations. These differences proved to be reliable in separate one-way analyses of variance for the distances in the horizontal, $F(2, 8) = 153.5$, $p = .001$, and vertical, $F(2, 8) = 17.8$, $p = .0011$, directions.

All subjects exhibited a strong tendency to copy the block patterns from top down resulting in few instances of placing a block with a previously placed neighbour below the placement site. Therefore, only the left, right, and above conditions for the previously placed neighbour location were used in these analyses. Planned contrasts revealed that the three mean landing points differ from each other in their horizontal positions ($p < .0001$). As expected, the mean landing points for the left and right preceding neighbour locations do not differ from each other in their vertical position, $F(1, 3) = 0.39$, $p = .551$, but both the left, $F(1, 3) = 23.4$, $p = .0013$, and the right, $F(1, 3) = 29.8$, $p = .0006$, locations differ in the vertical direction from the mean landing point for the upper location. These differences clearly indicate that the accuracy and precision of these targeting saccades are remarkably good. The subjects are reliably generating

saccades to locations that differ by half the height of a block (i.e., less than $\frac{1}{2}$ degree).

The results from the disappearing condition were surprisingly similar to the nondisappearing condition. Despite the absence of the previously placed blocks to serve as targets for the saccades into the workspace, subjects were able to direct their eyes with a single saccade close to the same location as when the blocks were present. Figure 6 shows the mean landing points for the disappearing condition for the five individual subjects plotted separately for the four possible relative locations of the preceding neighbour block (left, right, above, and below). We again see that the saccade landing points are clearly biased in the direction of the preceding, neighbouring block. Variability appears to be only slightly increased compared to the non-disappearing condition.

To test if the disappearance of the previously placed blocks from the workspace biased the mean landing points of the targeting saccades, we performed separate analyses for the vertical and horizontal deviations of the saccade landing points relative to their associated block placement sites. The

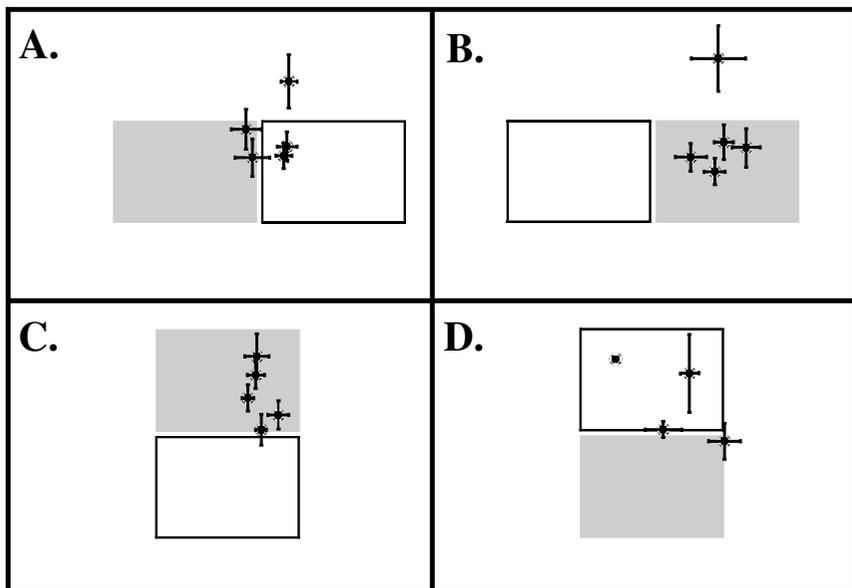


Figure 6. Normalized mean landing points for the disappearing condition. As in Figure 5, landing points of targeting saccades from the model area into the workspace were normalized to the placement site for the selected block. The individual mean landing point for each of the five subjects is plotted separately for the four preceding neighbour locations (A. left, B. right, C. above, and D. below) relative to the placement site. Data are limited in the below condition (panel D) due to the natural tendency for subjects to build from top down. A scale is shown in panel D (note: a block is approximately $1^\circ \times 1.5^\circ$). Error bars represent ± 1 standard error of the mean.

two-way ANOVAs included the three preceding neighbour locations and the two experimental conditions. The preceding neighbour location produced a significant main effect in the analyses of both the horizontal, $F(2, 8) = 185.5$, $p = .0001$, and vertical, $F(2, 8) = 60.2$, $p = .0001$, directions. All three preceding neighbour locations differed from each other ($p < .0001$) indicating that the saccades are targeted to horizontal position on the display with an accuracy of less than half the width of a block (i.e., less than 0.75 degrees) and to vertical positions within half the height of a block (less than 0.5 degrees).⁸ There was not a significant interaction between condition and preceding neighbour location in either of these ANOVAs indicating that the differences between the mean landing points related to preceding neighbour locations were consistent across both conditions. There was a small difference, however, in that the mean saccade landing points for the disappearing condition were biased slightly to the right. Some bias is also present in the control condition, but it is larger in the disappearing condition as indicated by a significant main effect of condition in the ANOVA for the horizontal direction, $F(1, 4) = 12.4$, $p = .024$.

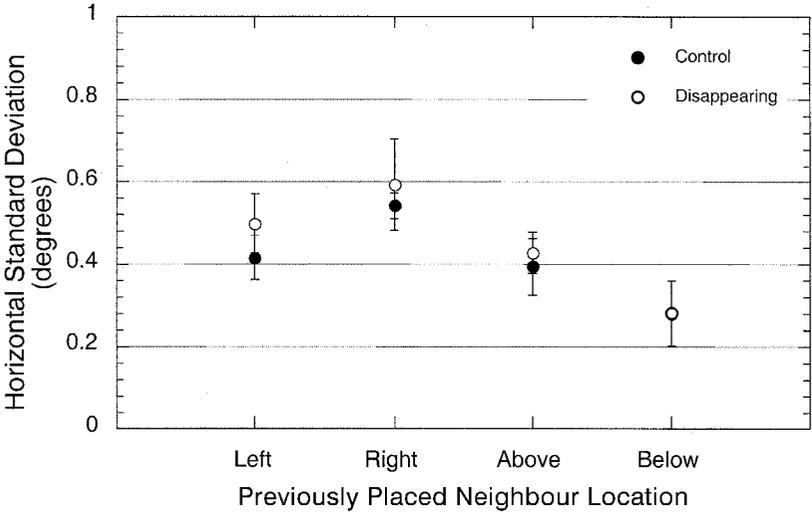
Saccade precision

Variability in the saccade landing points was computed as the standard deviation in the horizontal and vertical directions for each subject and for each relative location of the previously placed neighbouring block. The standard deviations in the non-disappearing condition were approximately 0.4° which is comparable to values previously reported (Van Opstal & Van Gisbergen, 1989).

The landing point variability for the disappearing condition, along with the data from the control condition, are plotted in Figure 7. To determine if the slight increases in variable error in the disappearing condition were significant in either the vertical or the horizontal directions, we conducted separate two-way ANOVAs on the standard deviations of the landing point scatter in the vertical and horizontal directions. These ANOVAs included three preceding neighbour locations (left, right, and above) and the two experimental conditions (disappearing and non-disappearing). The horizontal standard deviations did not differ significantly by condition, $F(1, 4) = 1.15$, $p = .34$, preceding neighbour location, $F(2, 8) = 2.50$, $p = .14$, or their interaction, $F(2, 8) = 0.06$, $p = .95$. The vertical standard deviations did not differ significantly between the three preceding neighbour locations, $F(2, 8) = 1.58$, $p = .26$. However, the condition (disappearing vs. not disappearing) did produce a significant main effect, $F(1, 4) = 24.73$, $p = .008$, with the standard deviation of landing points in the vertical dimension 0.22 degrees larger, on average, for the disappearing

⁸Remember that the saccade landing points into the workspace did not include corrective saccades.

A.



B.

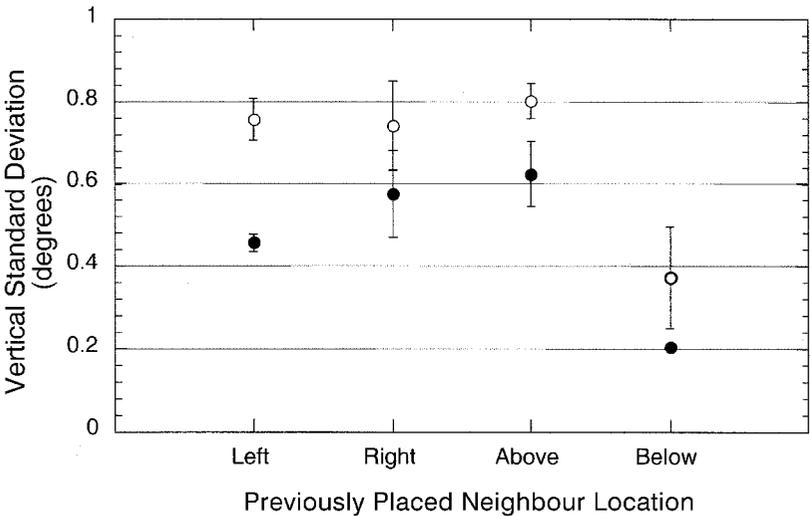


Figure 7. Comparison of variability of saccade landing points between the disappearing and control conditions. Panel A shows the standard deviation of saccade landing points in the horizontal direction and Panel B shows the standard deviation in the vertical direction for the four possible relative locations of the previously placed neighbouring block. Error bars represent the standard error between subjects. Filled symbols represent the control condition; open symbols, the disappearing condition.

condition (mean SD: 0.77°) than the non-disappearing condition (mean SD: 0.55°). The interaction between condition and location of the preceding neighbour was not significant, $F(2, 8) = 0.901$, $p = .44$.

Effects on timing

Another aspect of the targeting performance that might be affected by the disappearance is the time spent in the various components of the task. We tested for this by comparing the total amount of time looking at the model area prior to the targeting movement, duration of the fixations immediately preceding and following the targeting movement, and the total time spent on a block-from pickup to placement. A within-subjects, paired, two-tailed t -test was used for each. The total time that subjects spent fixating in the model area during the disappearance (mean: 327 ms) did not differ significantly ($T_4 = -0.0435$, $p = .686$) from that in the control condition (mean: 332 ms). Neither did the duration of the fixation in the model area just prior to the targeting saccade (disappearing mean: 233 ms, control mean: 228 ms; $T_4 = 0.717$, $p = .512$). The average duration of the post-saccadic fixation in the workspace was slightly greater in the non-disappearing condition (mean: 420 ms) than in the disappearing condition (mean: 377 ms) and this difference approached significance ($T_4 = -2.72$, $p = .053$). If this difference is real, it could be due to a greater probability of a corrective saccade in the disappearing condition. The total time spent on a block (from pickup with the mouse till placement) was longer ($T_4 = 3.12$, $p = .035$) by about 5% in the disappearing condition (mean: 1783 ms) compared to the non-disappearing condition (mean: 1692 ms).

Ruling out alternative explanations

How is it that saccades find their target locations so accurately even when no target is visible during the fixation immediately preceding these saccades? One interpretation is that the movements are based on a short-term visual memory of the target block's location. However, there are several alternative explanations to consider.

Visual guidance from hand. If the hand (represented on the screen by the moving mouse cursor and the selected block) arrived at the placement site in the workspace before the saccade from the model to the workspace was launched, this visible block could provide the goal for the targeting saccade. To test this hypothesis, we computed the distance between the moving block and its eventual workspace placement site at the time of the launch of the targeting saccade for all of the disappearing events. The mean distance between the block and its target placement site at the time of the saccade is 5.0 degrees (standard deviation = 2.3 degrees). It is clear that the hand rarely beats the eye to the target site. The block is within 1.5 degrees (one block width) of its final destination in less

than 6% of these records. This indicates that the moving block is not a source of useful information for planning the targeting saccade.

Real-time exocentric encoding. The block copying task required subjects to build the copy in the same position relative to the workspace area as the model was positioned within the model area. Subjects could use the borders surrounding the workspace and model areas for visual reference. We refer to the encoding of an object's location relative to another visible object as an exocentric representation. Subjects might rely on a *real-time* exocentric representation by gathering relational information in the model area just prior to the targeting saccade and transferring this relational information to the workspace area. The subject could fixate in the model area and encode the location of the model block (corresponding to the selected block to be placed) relative to the frame surrounding the model area. Then the corresponding frame around the workspace could be located on the peripheral retina, and an offset based on the exocentric encoding of the model block could be applied. The result would be the location of the saccade goal in the workspace area. This would eliminate the need for a more enduring representation. To test this we compared landing points of saccadic eye movements from the model area into the workspace prior to the placement of the first block to the eye movements in the disappearing condition. Note that these two conditions are similar in that no blocks are visible in the workspace at the time of launching the model to workspace saccade in either case. The only information available to guide the eye movement in the first-block condition is the exocentric encoding of the block in the model area relative to the surrounding visible frame. We would expect performance to suffer in the first-block condition relative to the disappearing condition, if a memory representation of previously placed blocks is important to the task. Although the variable error was slightly greater in the first block condition (mean standard deviation = 0.82°) compared to the disappearing condition (0.63°) these are not significantly different ($T_4 = 1.74, p = .16$). However, subjects reported that placement of the first block felt more difficult than subsequent blocks, and this difficulty was evident in the time required to place the blocks. Subjects took 809 ms longer on average to place the first block compared to all subsequent blocks in the control condition and the placement of the first block was usually accompanied by additional eye movements between model and workspace. Although somewhat inconclusive, these data seem to indicate that subjects did not rely solely on realtime exocentric information when a more enduring memory representation was available.

Long-term memory of target locations. It might be possible that subjects learn the 25 possible block placement sites over time as they gain experience with the task. If this were the case, subjects might learn to classify the target location into one of these screen positions. If so, we would expect to see a

decrease in absolute targeting error as experience increases. A plot of landing error over the course of the experiment revealed no decrease in error as subjects gained experience with the task. Thus, there is no evidence that performance benefits from long-term memory of the block placement sites.

Non-visual “motor” memory. Another possible explanation for the precision of the targeting saccades in the disappearing condition is the use of a memorized motor response, or *motor memory* (Fuster, 1994). The task might encourage this strategy since the model and the workspace are aligned vertically and the task required that the copy be built in the same position relative to the workspace boundaries as the model was positioned relative to the model area boundaries. The subject could fixate the point in the model that corresponds to the target workspace location and execute a saccade of fixed direction (down) and magnitude (6.3 degrees). To test this hypothesis, we examined the direction and amplitude of the targeting saccades, finding normal distributions of each that were similar in the disappearing and control condition.⁹ This indicates that the subjects’ strategy is not changing between conditions. If a fixed motor response were executed after the model area fixation, we would expect a strong correlation between the fixation locations in the two areas. Any unintended deviation of the fixation point in the model area would be expected to show up as a similar deviation in the saccade landing point in the workspace. A least squares linear fit produced r^2 values for these regressions of .18 for the horizontal and .11 for the vertical directions indicating that only a small amount of the variation in the saccade landing points is explained by the location of the pre-saccadic fixation in the model area. We conclude that subjects do not rely heavily on memory of a motor response to perform this task.

In summary, we conclude that it is unlikely that the targeting precision in the disappearing condition is attributable to visual guidance from the hand, real-time exocentric encoding, long-term memory of target locations, or non-visual “motor” memory. Although we cannot conclusively rule out the use of a real-time exocentric representation, a short-term visual memory for the target location of previously placed blocks seems to be the most plausible explanation for this targeting performance.

⁹Histogram plots of the amplitude and direction of the targeting saccades revealed approximately normal distributions for both the disappearing and control conditions (mean length: 5.63° control and 5.56° disappearing—on average 11% short of the required 6.3° magnitude). The saccade length did not differ significantly between these conditions ($T_{607} = 1.02, p > .3$). The mean direction of the targeting saccades is close to vertical (disappearing: -1.50° ; non-disappearing: -1.71°) but not significantly different between the two conditions ($T_{607} = 0.295, p > .5$). Negative direction values indicate an angle slightly clockwise from vertically down.

DISCUSSION

Subjects performed a visual-motor task that required constructing a copy of a random pattern of coloured blocks on a computer display. Eye and hand movements followed a regular pattern. Saccadic eye movements just prior to block placement accurately and precisely landed near the border between a previously placed block and the new block placement site. Differences in targeting location as small as half a degree are evident in these landing points. This allowed us to study saccade targeting performance in the context of a natural task in which we specified neither a target nor eye movement instructions. To investigate the use of memory in saccade planning, on a small percentage of trials we removed the partially built copy during the saccade which immediately preceded the targeting saccade to the copy. Display changes occurred entirely within the duration of a saccade. The partially built copy remained hidden during the fixation preceding the targeting saccade that accompanied block placement. The blocks reappeared during the targeting saccade. Thus, target blocks were not visible during the fixation preceding the targeting saccade when saccadic programming presumably takes place. Landing point variability of targeting saccades was surprisingly small and only slightly greater than the control condition with continuously visible targets. Naive subjects were usually unaware of the display changes despite the unexpected disappearance of the visual target.

Current image vs. memory representation

If the current retinal image is the only thing used to direct eye movements, we would expect targeting performance to fall apart when no retinal image is present. Overall, saccadic targeting performance is extraordinarily good even when the subject is forced to rely on memory of the target location. This does not preclude use of the current retinal image in programming movements when it is available. Indeed, performance is slightly less variable when the target blocks are available in peripheral vision. But, saccades are still surprisingly precise and accurate even when there is no image of the target blocks available during saccade programming. Models of visual search that rely solely on real-time retinal input cannot account for this result. Such models should be modified to incorporate other mechanisms such as a more enduring memory representation (in head-centred, motor, or exocentric reference frames), or a more complex use of real-time exocentric spatial information.

Lack of awareness of memory representations

Measures of conscious awareness are, of course, difficult to quantify, but the general finding was clear: Subjects were generally unaware of the sudden need to rely on a representation other than the current retinal image to guide their eye

movements. Conscious perceptual awareness of the saccade contingent display changes appears to be independent of the subject's performance on the task. This is compatible with similar findings in related tasks (Goodale, Pelisson, & Prablanc, 1986; Hayhoe et al., 1998; McConkie, 1991; McConkie & Currie, 1996). The new finding here is that a representation other than one generated from the current retinal image was used to guide a natural movement. The fact that subjects were generally unaware of these unusual display changes, is interpreted as evidence that strategies used to perform the task did not change dramatically when the target image disappeared. Subjects were able to program saccades to within less than a degree of the target despite being unaware that the target was not present. Thus, it appears that information about the target's location is retained across eye movements and used to guide subsequent movements without awareness.

The nature of memory representations across saccades

We have argued that spatial information about a target's location is retained across eye movements. The nature of this memory representation is not well understood, but some properties can be inferred from this experiment.

Persistence. Our results indicate that performance on this task is not based on the build-up of information across sessions spanning days or weeks; what we would refer to as long-term memory. So what is the time scale of the accumulation and retention of this memory information? Is this representation used to guide movement re-created for each block (i.e., every 1 to 2 seconds) or is it built up over the course of a trial? If an internal representation of the target blocks in the workspace is built up over the course of multiple fixations of the display during a trial, a richer representation and better targeting performance should be available later in the trial. To test this, we computed the variable error for these saccades at various times in the block copying task and found that this error did *not* decrease over the course of a trial, indicating no improvement in performance with greater time and experience with a particular block configuration. If there is some accrual of information over the time scale of the eight block trial, it does not appear to affect saccade targeting performance. Although the time scale of memory representations used in this task cannot be described in detail, it seems likely that the memory representation of target location is updated for each block placed (i.e., on a time scale of about a second).

Reference frames for visual spatial representations. Memory representations of spatial information could be created and maintained in a variety of reference frames. These can be coarsely classified into egocentric (relative to

some part of the observer such as eye, head, or shoulder) and exocentric (relative to some other visible structure). There has been much recent debate on the nature of egocentric reference frames (see reviews by Goldberg & Colby, 1992 and Andersen, Snyder, Li, & Stricanne, 1993).

The subject could encode the target in a retina-centred frame during the resource area fixation just prior to the disappearance when previously placed workspace blocks are visible in peripheral vision. Such a representation could then be maintained for the brief intervening memory period in a retinotopic frame which is updated after each eye movement. If this were true, we might expect to find increasing variable error in the targeting saccades when more intervening saccades occur between the resource area fixation and the targeting saccade (see Goldberg & Colby, 1989; Moschovakis, Karabelas, & Highstein, 1988). So to test this we compared the variable error for the targeting saccades when there was one versus two intervening saccades between the disappearance of the workspace blocks and the targeting saccade into the workspace. It turns out that the variable error in saccade targeting is actually less after two intervening saccades (average standard deviation = 0.51 degrees) than after one intervening saccade (0.67 degrees).¹⁰ This difference is not reliable ($T_4 = 1.20, p = .31$) so we have no evidence supporting an updated retina-centred representation. This result and previous results from our laboratory (Karn, et al., 1997) seem to indicate that we do not rely on a retina-centred representation, but more likely use a head or body-centred representation when an egocentric representation is needed.

Exocentric representations have received little attention in the literature addressing motor programming. However, there is growing evidence that such representations of a target's location with respect to other visible landmarks can be used to guide action (Dassonville, Schlag, & Schlag-Rey, 1995; Gordon, Forssberg, Johansson, & Westling, 1991a, b, c; Hayhoe et al., 1992; Levi & Klein, 1990; Mateeff & Hohnsbein, 1989; McNaughton, Chen, & Markus, 1991; Møller, Hayhoe, Ballard, & Albano, 1989; Smeets & Brenner, 1995; White, Levi, & Aitsebaomo, 1992;). The visual environment in this task provided considerable structure and therefore ample opportunity for encoding locations of target objects with respect to surrounding objects such as the border between model and workspace areas, and screen edges. For example, the subject could remember the target block's location as something like "two

¹⁰Note that there was no attempt to control for timing in the one versus two intervening saccade cases. Those with two intervening saccades typically had a longer duration between the disappearance and the targeting saccade. This might allow the subject to extract more exocentric spatial information for planning the targeting saccade leading to more precise targeting. Conversely, the longer delay could result in a greater decay in spatial memory for information gathered in the previous fixation, resulting in decreased precision. See Palmer and Ames (1992) for a related discussion.

degrees below the border and three degrees from the left edge of the screen". Such a strategy again might be encouraged by the task requirement for subjects to build the copy in the same location relative to the workspace area borders as the model is located relative to the model area borders. This sort of exocentric representation might be retained across saccades. In this experiment, we do not have any clear way to separate this representation from a memory representation in a head- or body-centred reference frame since the head was stationary.

Motor coordinates are another possible reference frame in which a memory of target location might be stored. It is difficult in the current experiment to study this factor in detail due to the fixed relationship between the model (saccade starting point) and target blocks in the workspace copy (saccade end-point). We speculate that this, along with the repetitive nature of the movements, might encourage saccades of a fixed magnitude and direction. In spite of this, motor memory does not dominate saccade programming as indicated by the rather weak correlation between the location of pre-saccadic fixations in the model area and the landing points in the workspace. It appears that in this task, a memory representation based on motor coordinates may make a small contribution to the programming of the targeting movements.

Saccade sequence planning. It is possible that the targeting saccades are planned in advance prior to the disappearance of the target blocks as part of sequence of saccades.¹¹ Zingale and Kowler (1987) have proposed such a strategy as a natural behaviour in realistic tasks. In our task, subjects typically fixate in the resource area as they pick up a block, then saccade to the model area about the same time that the hand begins to move toward the workspace. After a brief fixation in the model area the eye is typically directed to the workspace (the targeting saccade that we measure) just prior to the hand's arrival for block placement. The subject could plan a sequence of two saccades from resource to model, and from model to workspace. The planning could take place during the time that the subject is fixating in the resource area prior to the disappearance of the target blocks. We have no direct way to test this hypothesis. We can compare our results to those of Zingale and Kowler (1987), who found that variable error increased when the number of saccades in the sequence changed from one to two. Although it is not a strictly analogous comparison, our subjects did not show such a change when there was an extra saccade in the sequence. Although we cannot rule it out, we have no evidence that subjects plan the targeting saccade as part of a longer movement sequence.

¹¹The strategy shares some common elements with an updated retina-centred representation in that the execution of the targeting saccade (a later step in the sequence) relies on the success of the preceding step (the resource to model saccade). In the sequence planning strategy, the intervening steps must be anticipated, whereas according to the updating theory, the intervening steps must be accounted for.

Combining multiple representations

There is an interesting synergy between the combination of findings that (1) people make slightly more precise saccades when there is a visible target present and (2) people are often unaware of the sudden requirement to rely on a representation other than this image on their retina. Taken together, these two findings seem to indicate that we normally use both direct retinal stimulation *and* memory representations of target location to guide saccades. If memory representations were not part of our normal repertoire of saccadic programming inputs, we would expect the sudden requirement to switch to such representations extremely disruptive.¹² These results seem to indicate that we normally use multiple representations of target location. Furthermore, the results indicate that these multiple representations are either combined or are available in such a way as to allow rapid switching between representations. In either case, when one representation becomes suddenly unavailable, the other representations appear adequate to perform the task with a high degree of precision and accuracy. Of course we expect that different representations have differing levels of precision. Therefore, it is not surprising that targeting performance changes slightly when shifting from one representation to another or when removing one representation from the composite.

Memory representations and real-time retinal information might be combined as a weighted average or in more complex ways (Karn, Lachter, Møller, & Hayhoe, 1994). For example, in our block-copying task, memory might be used to help specify the general saccade goal relative to visible landmarks or relative to the head, or both. The targeting goal might then be fine-tuned with the use of real-time exocentric information gained during the pre-saccadic fixation in the model area. The fact that the hand is typically already moving directly from the resource area toward the workspace and the head (when free) is also typically rotating along a similar trajectory (Pelz, Hayhoe, Ballard, & Forsberg, 1994) is an indication of such a strategy. Thus, a sequence of two saccades may be planned while fixating in the resource area, with the second (targeting) saccade specified only coarsely at the start of the sequence. Then, the memory representation of the target could be combined with exocentric information gathered during the model area fixation.

Implications of current findings

In this experiment, we have addressed the question: How important is the retinal image of a target object in guiding saccades in the context of a goal-directed task? The findings from this study have several implications for current models of motor programming. First, we have shown that an explicit peripheral retinal

¹²In fact, two of eight naive subjects did find the disappearance of the previously placed blocks readily noticeable, perhaps indicating individual differences in this reliance on the retinal image.

image is not necessary for programming saccades with great precision and accuracy in the context of a natural visual-motor task. Second, it appears that there may be multiple representations available in various reference frames. Third, there appears to be great flexibility in either combining multiple representations or switching from one representation to another as evidenced by the lack of disruption caused by (even lack of awareness of) the sudden unavailability of the retinal image to guide the movement.

Our claim that retinal information is not the sole basis for saccade programming is not new. For example, well-accepted models of saccade programming (Robinson, 1973) have incorporated a head-centred representation of the saccade target. However, these models still implied that the target is solely represented by current sensory information and do not include exocentric representations or memory representations in any reference frame. The concept of an enduring internal representation to guide action is not a popular concept in the recent literature (Irwin, McConkie, Carlson-Radvansky, & Currie, 1994; McConkie, 1991; O'Regan, 1992; O'Regan & Lèvy-Schoen, 1983). Previous results from our laboratory and others indicate that memory representations have the required level of precision to guide these targeting eye movements. In the current experiment we showed that when the target's retinal image was suddenly unavailable to guide a saccade, alternative representations filled the void without major disruption to perception or performance. A memory representation, of some sort, appears to be at least partially responsible for the precise targeting performance when no visible target is present. The reference frames for memory representations cannot be specified in detail from the current results. We conclude that real-time retinal stimulation is not the sole determinant of the saccade target.

Real-world saccades

We know that a visual stimulus is not necessary to elicit a saccadic eye movement. Auditory, somatosensory, and even olfactory stimuli can and do (often in combination with visual cues) elicit orienting responses including eye, head, and locomotor movements. No apparent sensory stimulus is needed to trigger saccadic eye movements as demonstrated in spontaneous eye movements in the dark. Our memory of targets that are no longer present in our sensory input can also serve as a stimulus for these movements. Recently, there has been considerable study of saccades made to remembered target locations in an attempt to gain insight into mechanisms underlying saccade programming and short-term memory. We now know that saccades can be made to remembered targets with accuracy, precision, and dynamics slightly different, from visually-guided saccades. It is often assumed that visually-guided and memory-guided saccades are qualitatively different and rely on different mechanisms. However, there is evidence from several lines of research to suggest that real-time and

remembered spatial representations share at least some common pathways. Injury to the right parietal lobe of the brain which causes an inability to attend to things on the patient's left side seems to affect current visual sensory data and visual images recalled from memory in similar ways (Bisiach, Capitani, & Luzzatti, 1981). In addition, many brain areas involved in short-term spatial memory (e.g., hippocampus, posterior parietal cortex, dorsolateral prefrontal cortex, occipital cortex, premotor cortex, frontal eye fields, and supplementary eye fields), also appear to be active in real-time spatial information processing (Jonides, et al., 1993, Kesner, Bolland, & Dakis, 1993; McNaughton et al., 1991; McNaughton, Leonard, & Chen, 1989; Pierrot-Deseilligny, Israel, Berthoz, Rivaud, & Gaymard, 1993; Snyder, Batista, & Andersen, 1997; Quintana & Fuster, 1993; Wilson, O'Scalaidhe, & Goldman-Rakic, 1993). Stimulus attributes such as texture (Fikes, Klatzky, & Lederman, 1994) and size (Gordon et al., 1991a, b, c; Johansson & Edin, 1992) influence the forces used by subjects in grasping objects even before lifting, indicating that memory plays a role in our everyday actions. Although differences between memory-guided and visually-guided movements may be due to differences in the representations used to guide these movements, it is also possible that similar representations serve both types of movements. If common representations underlie both visually-guided and memory-guided movements, differences in these movements could be due to degradation of the representations during the memory delay period or to the open-loop nature of memory-guided movements caused by lack of visual feedback. The existence of separate systems for real-time and short-term memory representations remains an open issue.

Many also assume that saccades to visible objects rely solely on the peripheral retinal image to guide the movement. Although it seems likely that this retinal image is of primary importance when an observer's task is to make a saccade to a simple target that suddenly appears in the dark, it may not be the case in the context of more natural tasks and environments. We know very little about the nature of representations used to guide our everyday movements in natural environments in the context of ongoing goal-directed tasks. We should not be surprised if findings regarding the saccadic system from simple situations do not transfer readily to more complex environments and tasks as suggested by McConkie and Currie (1996). In most natural tasks, we have multiple opportunities to acquire visual information about potential target objects as we look around our environment. We often manipulate objects, thereby establishing their location. Repeated patterns of eye movements are common in many tasks and learning such patterns may further aid movement control. Other nearby objects may serve as prominent landmarks, providing the context in which we perceive the locations of target objects. Thus, the location of one object relative to others may be a salient feature of the scene. This study indicates the use of multiple representations of target location in guiding our action.

In conclusion, we performed this experiment to understand better the nature of visual representations preserved across different eye positions. The experiment provides evidence that memory representations are used to guide movement during ongoing behaviour. Even when unavailable for conscious report, representation of the visual environment created from information acquired across saccades appears to be used to guide subsequent movements in natural tasks. A representation of spatial information that endures across saccadic eye movements may be necessary for coordinated action.

REFERENCES

- Andersen, R.A., Snyder, L.H., Bradley, D.C., & Xing, J. (1997). Multimodal representation of space in the posterior parietal cortex and its use in planning movements. *Annual Review of Neuroscience*, 20, 303–330.
- Andersen, R.A., Snyder, L.H., Li, C., & Stricanne, B. (1993). Coordinate transformations in the representation of spatial information. *Current Opinion in Neurobiology*, 3, 171–176.
- Ballard, D.H., Hayhoe, M.M., Li, F., & Whitehead, S. D. (1992). Hand-eye coordination during sequential tasks. *Philosophical Transactions of the Royal Society of London*, 337, 331–339.
- Ballard, D.H., Hayhoe, M.M., & Pelz, J. (1994a). Memory limits in sensory-motor tasks. In J.C. Houk, J.L. Davis, & D.G. Beiser (Eds.), *Models of information processing in the basal ganglia*. Cambridge, MA: MIT Press.
- Ballard, D.H., Hayhoe, M.M., & Pelz, J.B. (1994b). Memory representations in natural tasks. *Journal of Cognitive Neuroscience*, 7(1), 66–80.
- Becker, W., & Fuchs, A.F. (1969). Further properties of the human saccadic system: Eye movements and correction saccades with and without visual fixation points. *Vision Research*, 9, 1248–1258.
- Bisiach, E., Capitani, E., & Luzzatti, C. (1981). Brain and conscious representation of outside reality. *Neuropsychologica*, 19(4), 543–551.
- Bridgeman, B. (1989). Separate visual representations for perception and for visually guided behaviour. In S.R. Ellis, M.K. Kaiser, & A. Grunwald (Eds.), *Spatial displays and spatial instruments* (NASA Conference Publication No. 10032, pp. 14.1–14.9). National Aeronautics and Space Administration, Ames Research Center, Moffett Field, Asilomar, CA.
- Crane, H.D., & Steele, C.M. (1985). Generation-V dual-Purkinje-image eyetracker. *Applied Optics*, 24, 527–537.
- Dassonville, P., Schlag, J., & Schlag-Rey, M. (1995). The use of egocentric and exocentric location cues in saccadic programming. *Vision Research*, 35(15), 2191–2199.
- Deubel, H., & Bridgeman, B. (1995). Fourth Purkinje image signals reveal eye-lens deviations and retinal image distortions during saccades. *Vision Research*, 35(4), 529–538.
- Fikes, T.G., Klatzky, R.L., & Lederman, S.J. (1994). Effects of object texture on pre-contact movement time in human prehension. *Journal of Motor Behaviour*, 26, 325–332.
- Funahashi, S., Bruce, C.J., & Goldman-Rakic, P.S. (1989). Mnemonic coding of visual space in the monkey's dorsolateral prefrontal cortex. *Journal of Neurophysiology*, 61(2), 331–349.
- Funahashi, S., Bruce, C.J., & Goldman-Rakic, P.S. (1990). Visuospatial coding in primate prefrontal neurons revealed by oculomotor paradigms. *Journal of Neurophysiology*, 63(4), 814–831.
- Funahashi, S., Chafee, M., & Goldman-Rakic, P.S. (1993). Prefrontal neuronal activity in rhesus monkeys performing a delayed anti-saccade task. *Nature*, 365, 753–756.
- Fuster, J.M. (1994). Call it what it is: Motor memory. *Behavioural and Brain Sciences*, 17(2), 208.

- Gnadt, J.W., Bracewell, R.M., & Andersen, R. A. (1991). Sensorimotor transformation during eye movements to remembered visual targets. *Vision Research*, 31(4), 693–715.
- Goldberg, M. E., & Colby, C.L. (1989). The neurophysiology of spatial vision. In F. Boller & J. Grafman (Eds.), *Handbook of neuropsychology* (pp. 301–315). Amsterdam: Elsevier Science Publishers.
- Goldberg, M.E., & Colby, C.L. (1992). Oculomotor control and spatial processing. *Current Opinion in Neurobiology*, 2, 198–202.
- Goodale, M.A., Pelisson, D., & Prablanc, C. (1986). Large adjustments in visually guided reaching do not depend on vision of the hand or perception of target displacement. *Nature*, 320, 748–740.
- Goodale, M.A., & Servos, P. (1992). Now you see it, now you don't: How delaying an action system can transform a theory. *Behavioural and Brain Sciences*, 15(2), 335–336.
- Gordon, A.M., Forssberg, H., Johansson, R.S., & Westling, G. (1991a). Integration of sensory information during the programming of precision grip: Comments on the contributions of size cues. *Experimental Brain Research*, 85, 226–229.
- Gordon, A.M., Forssberg, H., Johansson, R.S., & Westling, G. (1991b). The integration of haptically acquired size information in the programming of precision grip. *Experimental Brain Research*, 83, 483–488.
- Gordon, A.M., Forssberg, H., Johansson, R.S., & Westling, G. (1991c). Visual size cues in the programming of manipulative forces during precision grip. *Experimental Brain Research*, 83, 477–482.
- Hayhoe, M.M., Ballard, D.H., & Pelz, J.B. (1994). Visual representations in natural tasks. In *Proceedings of the workshop on visual behaviors* (pp. 1–9). Los Alamitos, CA: IEEE Computer Society Press.
- Hayhoe, M., Bensinger, D., & Ballard, D.H. (1998). Task constraints in visual working memory. *Vision Research*, 38, 125–137.
- Hayhoe, M.M., Lachter, J., & Møller, P. (1992). Spatial memory and integration across saccadic eye movement. In K. Rayner (Ed.), *Eye movements and visual cognition: Scene perception and reading* (pp. 130–145). Springer-Verlag: New York.
- Irwin, D.E. (1991). Information integration across saccadic eye movements. *Cognitive Psychology*, 23, 420–456.
- Irwin, D.E., McConkie, G.W., Carlson-Radvansky, L.A., & Currie, C. (1994). A localist evaluation solution for visual stability across saccades. *Behavioural and Brain Sciences*, 17(2), 265.
- Johansson, R.S., & Edin, B.B. (1992). Mechanisms for grasp control. In A. Pedotti & M. Ferrarin (Eds.), *Restoration of walking for paraplegics: Recent advancements and trends* (pp. 57–63). Amsterdam: IOS Press.
- Jonides, J., Smith, E.E., Koeppe, J.A., Awh, E., Minoshima, S., & Mintun, M.A. (1993). Spatial working memory in humans as revealed by PET. *Nature*, 363, 623–625.
- Karn, K.S. (1995). Spatial representations for programming saccadic eye movements. *Dissertation Abstracts International V57-P2B* (pp. 1478–1632). Ann Arbor, MI: University of Rochester, New York.
- Karn, K.S., Lachter, J., Møller, P., & Hayhoe, M.M. (1994). Task dependent spatial memory across saccades. *Behavioural and Brain Sciences*, 17(2), 267–268.
- Karn, K.S., Møller, P., & Hayhoe, M.M. (1997). Reference frames in saccadic targeting. *Experimental Brain Research*, 115, 267–282.
- Kesner, R.P., Bolland, B.L., & Dakis, M. (1993). Memory for spatial locations, motor responses, and objects: Triple dissociation among the hippocampus, caudate nucleus, and extrastriate visual cortex. *Experimental Brain Research*, 93, 462–470.
- Levi, D.M., & Klein, S.A. (1990). The role of separation and eccentricity in encoding position. *Vision Research*, 30(4), 557–585.
- Mack, A., & Rock, I. (1996). *Inattention blindness*. Cambridge, MA: MIT Press.

- Mateeff, S., & Holmsbein, J. (1989). The role of the adjacency between background cues and objects in visual localization during ocular pursuit. *Perception, 18*, 93–104.
- McConkie, G.W. (1991). Perceiving a stable visual world. In J. Van Rensbergen, M. Devijver, & G. d'Ydewalle (Eds.), *Proceedings of the sixth European conference on eye movements* (pp. 5–7). Leuven, Belgium: Laboratorium voor Experimentale Psychologie, Katholieke Universiteit Leuven.
- McConkie, G.W., & Currie, C.B. (1996). Visual stability across saccades while viewing complex pictures. *Journal of Experimental Psychology: Human Perception and Performance, 22*(3), 563–581.
- McNaughton, B.L., Chen, L.L., & Markus, E.J. (1991). “Dead reckoning,” landmark learning, and the sense of direction: A neurophysiological and computational hypothesis. *Journal of Cognitive Neuroscience, 3*(2), 190–202.
- McNaughton, B.L., Leonard, B., & Chen, L. (1989). Cortical-hippocampal interactions and cognitive mapping: A hypothesis based on reintegration of the parietal and inferotemporal pathways for visual processing. *Psychobiology, 17*(3), 230–235.
- Møller, R., Hayhoe, M.M., Ballard, D., & Albano, J. (1989). Spatial memory and the accuracy of saccades to remembered visual targets. *Investigative Ophthalmology and Visual Science, 30*, S456
- Moschovakis, A.K., Karabelas, A.B., & Highstein, S.M. (1988) Structure-function relationships in the primate superior colliculus: II. Morphological identity of presaccadic neurons. *Journal of Neurophysiology, 60*, 263–302.
- O'Regan, J.K. (1992). Solving the “real” mysteries of visual perception: The world as an outside memory. *Canadian Journal of Psychology, 46*, 461–488.
- O'Regan, J.K., Rensink, R., & Clark, J.J. (1996). Mud splashes render picture changes invisible. *Investigative Ophthalmology and Visual Science, 37*, S213.
- O'Regan, J.K., & Lévy-Schoen, A. (1983). Integrating visual information from successive fixations: Does trans-saccadic fusion exist? *Vision Research, 23*(8), 765–768.
- Palmer, J., & Ames, C.T. (1992). Measuring the effect of multiple eye fixations on memory for visual attributes. *Perception and Psychophysics, 52*(3), 295–306.
- Pelz, P., Hayhoe, M.M., Ballard, D., & Forsberg, A. (1994). Separate motor commands for eye and head. *Investigative Ophthalmology and Visual Science, 35*(4), S1550.
- Pierrot-Deseilligny, C., Israel, L., Berthoz, A., Rivaud, S., & Gaymard, B. (1993). Role of the different frontal lobe areas in the control of the horizontal component of memory-guided saccades in man. *Experimental Brain Research, 95*, 166–171.
- Quintana, J., & Fuster, J.M. (1993). Spatial and temporal factors in the role of prefrontal and parietal cortex in visuomotor integration. *Cerebral Cortex, 3*, 122–132.
- Rayner, K., & Pollatsek, A. (1987). Eye movements in reading: A tutorial review. In M. Coltheart (Ed.), *Attention and performance XII: The psychology of reading* (pp. 327–362). Hove, UK: Lawrence Erlbaum Associates Ltd.
- Rensink, R., O'Regan, J.K., & Clark, J.J. (1996). To see or not to see: The need for attention to perceive changes in scenes. *Psychological Sciences, 8*, 368–373.
- Robinson, D.A. (1973). Models of saccadic eye movement control system. *Kybernetik, 14*, 71–83.
- Rock, I., Linnett, E., Grant, P., & Mack, A. (1992). Perception without attention: Results of a new method. *Cognitive Psychology, 24*, 502–534.
- Simons, D.J., & Levin, D.T. (1997). Change blindness. *Trends in Cognitive Sciences, 1*(7), 261–267.
- Smeets, J.B.J., & Brenner, E. (1995). Perception and action based on the same visual information: Distinction between position and velocity. *Journal of Experimental Psychology: Human Perception and Performance, 21*(1), 19–31.
- Snyder, L.H., Batista, A.P., & Andersen, R.A. (1997). Coding of intention in the posterior parietal cortex. *Nature, 386*, 167–169.

- Van Opstal, A.J., & Van Gisbergen, J.A.M. (1989). Scatter in the metrics of saccades and properties of the collicular motor map. *Vision Research*, 29(9), 1183–1196.
- White, J.M., Levi, D.M., & Aitsebaomo, P. (1992). Spatial localization without visual references. *Vision Research*, 32(3), 513–526.
- Wilson, F.A., O'Scalaidhe, S.P., & Goldman-Rakic, P.S. (1993). Dissociation of object and spatial processing domains in primate prefrontal cortex. *Science*, 260, 1955–1958.
- Wong, E., & Mack, A. (1981). Saccadic programming and perceived location. *Acta Psychologica*, 48, 123–131.
- Zingale, C.M., & Kowler, E. (1987). Planning sequences of saccades. *Vision Research*, 27(8), 1327–1341.

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