

Visual memory capacity in transsaccadic integration

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Abstract How we perceive the visual world as stable and unified suggests the existence of transsaccadic integration that retains and integrates visual information from one eye fixation to another eye fixation across saccadic eye movements. However, the capacity of transsaccadic integration is still a subject of controversy. We tested our subjects' memory capacity of two basic visual features, i.e. luminance (Experiment 1) and orientation (Experiment 2), both within a single fixation (i.e. visual working memory) and between separate fixations (i.e. transsaccadic memory). Experiment 2 was repeated, but attention allocation was manipulated using attentional cues at either the target or distracter (Experiment 3). Subjects were able to retain 3–4 objects in transsaccadic memory for luminance and orientation; errors generally increased as saccade size increased; and, subjects were more accurate when attention was allocated to the same location as the impending target. These results were modelled

by inputting a noisy extra-retinal signal into an eye-centered feature map. Our results suggest that transsaccadic memory has a similar capacity for storing simple visual features as basic visual memory, but this capacity is dependent both on the metrics of the saccade and allocation of attention.

Keywords Visual perception · Saccades · Visual working memory

Introduction

A central question in cognitive neuroscience is how we perceive a unified and continuous visual world despite viewing it in a disjointed and discontinuous manner. The typical observer makes 2–5 eye movements, called saccades, per second (Rayner 1978, 1998). This means that a visual scene is processed in what is often perceived as discrete 'snapshots' during eye fixations of approximately 300 ms between saccades (Henderson and Hollingworth 1998). In some way, the brain retains and integrates visual input from each eye fixation to form a unified mental percept of the visual scene—often this leaves observers with the impression that their perception of the visual world is much like putting together a jigsaw puzzle. This process is called transsaccadic integration (e.g. Irwin 1991; Prime et al. 2006).

A related, but separate, process that is necessary for transsaccadic integration is transsaccadic memory: the ability to retain information from previous fixations. However, the capacity of such memory is a much-debated topic. Some early studies assumed that detailed visual information is retained across saccades

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in an internal ‘spatial buffer’ (Jonides et al. 1982; McConkie and Rayner 1976). Evidence of the existence of such a highly detailed spatial buffer has been questioned by several studies (Bridgeman and Mayer 1983; Irwin et al. 1983; McConkie and Zola 1979; O’Regan and Levy-Schoen 1983; Rayner and Pollatsek 1983). In particular, it has been noted that observers are largely insensitive to unexpected changes in the visual scene that occur during saccades and other visual disruptions (Grimes 1996; Simons 1996; Simons and Levin 1997; O’Regan et al. 2000; Rensink et al. 1997). These ‘change blindness’ experiments have questioned the very existence of transsaccadic memory and prompted some researchers to propose that visual memory is essentially wiped clean with the acquisition of a new fixation after an eye movement (Bridgeman et al. 1994; O’Regan 1992; Tatler 2001).

However, there are other explanations for transsaccadic change blindness that do not rely on the assumption that memory is wiped clean (Niemeier et al. 2003). Moreover, a “no memory” theory of visual search is inconsistent with evidence that scene perception is more accurate when observers are free to make eye movements (Schillingensiepen et al. 1986) requiring an accumulation of visual information across saccades during visual search (McCarley et al. 2003; Peterson et al. 2001) even for more complex natural scenes (Melcher 2001; Tatler et al. 2003, 2005).

Most recent studies propose an intermediate view of transsaccadic memory, where some, but not all information is retained across saccades to influence processing of visual information in subsequent fixations (e.g. Pollatsek et al. 1984; Rayner and Pollatsek 1983; Rayner et al. 1980). It is well known that visual working memory can maintain about four objects each as units of integrated feature conjunctions (Luck and Vogel 1997; Vogel et al. 2001), depending on the complexity of the object’s features (Alvarez and Cavanagh 2004). These studies, however, did not take into account eye movements during the memory delay interval. If transsaccadic memory does not exist as suggested by some of the studies mentioned earlier (e.g. O’Regan 1992), subjects in the study by Luck and Vogel (1997), for example, should have difficulty in maintaining objects in memory when a saccade is added to the task. This does not seem to be the case. Irwin and colleagues have found that subjects can retain up to 3–4 objects when cued to remember several visual stimuli across saccades (Irwin 1992; Irwin and Andrews 1996; Irwin and Gordon 1998).

Moreover, these studies by Irwin and colleagues (Irwin 1992; Irwin and Andrews 1996; Irwin and Gordon 1998) have found that subjects were most accurate

when reporting on the object closest to the next to-be-fixated target (i.e. saccade-target). This finding has since been replicated and expanded in several other studies (Currie et al. 2000; Henderson and Hollingworth 1999; McConkie and Currie 1996). This has led to the suggestion that the allocation of attention to intended saccade-targets plays a crucial role in transsaccadic integration—the ‘saccade-target’ theory (see Deubel and Schneider 1996; Kowler et al. 1995).

Several important questions remain. First, in most previous studies of transsaccadic memory, the remembered objects, such as letters and toys, had semantic meaning for human subjects (e.g. Irwin and Zelinsky 2002; cf. Carlson et al. 2001; Deubel et al. 2002). It is possible that these stimuli engaged memory systems or top-down processes that are not available to early vision. Moreover, while this may show that meaningful objects can be retained across saccades (e.g., for the purpose of complex scene analysis), little is still known how many pre-semantic visual features can be stored, for example to recognize larger objects that are not visible in a single fixation. Second, a few studies have shown evidence of transsaccadic memory in the absence of allocentric cues (De Graef et al. 2001; Hayhoe et al. 1991; Verfaillie 1997). However, in these studies allocentric spatial cues were not entirely eliminated and remained visible across saccades (e.g. the edges of the computer monitor), which likely aided in solving the problem of spatial correspondence between pre- and post-saccadic stimuli. Moreover, accuracy in the transsaccadic integration study by Hayhoe et al. (1991) still depended on a reference point remaining present during the saccade trials for performance to be on par with a similar fixation condition. Thus, it is still unknown if transsaccadic memory has the same capacity when forced to rely on the egocentric sense of eye movement. It is also not known how saccade metrics might influence this process. If signals from the oculomotor system are used to ‘update’ visual memory, then one would expect performance to degrade with saccade size, because larger saccades are underrepresented compared to smaller saccades in oculomotor topography (Gandhi and Keller 1999; Robinson 1972; Sparks and Hartwich-Young 1989).

Finally, in previous studies, the attended location usually coincided with the target of the next saccade; thus, little is still known how the dissociation of attention from the saccade-target modulates transsaccadic memory. One exception is a study by Irwin and Gordon (1998). They manipulated their subjects’ attention by instructing subjects to pay attention to a particular location of a stimulus array about to be presented. In the present study, however, we used a

more rigorous method of manipulating attention by using exogenous cues intended to draw the subjects' attention to a specific stimulus—either the critical to-be-remembered target or a distracter—rather than a general location as in Irwin and Gordon (1998).

In a recent paper we showed that humans can spatially retain and integrate a single pre-saccadic feature with a single post-saccadic feature in the absence of any allocentric visual cues, although small errors occurred that depended in part on saccade metrics (Prime et al. 2006). We also found that the psychophysical thresholds for comparing the luminance, orientation, or shape of two sequentially presented features are not influenced by an intervening saccade (Prime et al. 2007).

In the present study we use a modified version of this paradigm to investigate the numerical capacity of transsaccadic memory. Our goal was to estimate how many objects and their details can be stored across saccades in transsaccadic memory. Subjects viewed a spatially randomized group of 1–15 feature objects, followed after a memory interval by a single probe with the same location as one of these objects. Subjects were required to judge (forced choice) how a visual feature of that object location had changed. We compared their performance when they maintained eye fixation throughout the trial (*Fixation task*) or made a saccade of randomized size and direction during the memory interval (*Saccade Task*). This task required subjects to remember both the features and locations of several objects, based on an egocentric sense of eye position.

This paradigm allowed for the rigorous control of stimuli and quantification of psychophysical responses and eye movements required to answer the following questions: first, what is the numerical capacity of transsaccadic memory when subjects are required to retain the visual features of multiple objects across a randomly directed saccade in complete darkness, and in the absence of visual cues for pre-/post-saccadic spatial correspondence? Second, does the capacity depend on the type of visual feature (e.g. orientation or luminance)? Third, is there an effect of saccade size? Fourth, how is subjects' performance influenced when they are cued in advance about which object will be tested? Lastly, how well are the details of the uncued objects in this task retained across saccadic eye movements? The answers to these questions will allow us to distinguish between three possibilities. First, transsaccadic memory and visual working memory may be separate and distinct memory systems, and thus, have different capacities. As mentioned earlier, Irwin and colleagues (1992, 1996, 1998) have shown this is

not the case. Another possibility may be that the two memory systems are identical except transsaccadic memory preferentially retains items related to the saccade due to attention (e.g. Kowler et al. 1995). If this were the case we would expect judgement accuracy of unattended items (e.g. unrelated to the saccade) to be at chance. However, this did not occur in our study; non-saccade targets were remembered above chance for at least 3–4 objects. Lastly, transsaccadic memory and visual working memory are identical but transsaccadic memory may be susceptible to noisy extra-retinal signals related to the saccade's metrics leading to the likelihood that the wrong item is used in comparing items across saccades. Saccade magnitude-dependent performance would offer support for this last scenario.

Methods

Subjects

A total of nine subjects (5 males and 4 females; mean age was 27.5) participated in this study, six subjects in each experiment. All subjects had normal or corrected-to-normal visual acuity. Two subjects were aware of the purpose of the experiments but their data followed the same trends as the naïve subjects.

Apparatus

A customized computer network system of three microprocessor personal computers was used for both stimulus presentation and data recording. A projector back-projected stimuli onto a 1.9 m by 1.4 m display screen spanning 100° visual angle horizontally by 90° visual angle vertically. The screen was unlit (black) with a luminance level of 0.015 cd/m². Eye position was monitored using the scleral search coil technique (Robinson 1963) at a sampling frequency of 1,000 Hz. Saccades were detected using a velocity criterion of 36° per second and eye position criterion of 1.5° visual angle around the fixation-cross. In both the *Saccade* and *Fixation Tasks*, eye position was monitored on-line by a personal computer which was programmed to accept only trials with no errors in eye movements and eye fixation. A trial was successful if eye fixations were maintained within a 1.5° window around the fixation-cross, and in the case of the *Saccade Task*, the saccade was initiated within 1 s after the onset of the second fixation-cross and the saccade was executed to the correct location. If any of these criteria were not met, then the trial was aborted, automatically removed from

the data, and repeated. Auditory tones were presented as feedback to indicate whether the trial was successful or aborted. It is well known that during eye fixation small fixational eye movements, such as microsaccades, still occur. It is likely that these fixational eye movements occurred within the eye position criterion's threshold without being detected by the computer. We address this possibility in "Results" by performing an off-line analysis of the subjects' number of microsaccades and variance of total fixational eye movements. The subject's head was stabilized using a bite-plate made by dental compound.

General experiment design

Figure 1 illustrates the general experimental design for our study. We tested our subjects' capacity to

remember multiple items in transsaccadic memory. Subjects were required to compare a specific feature of the probe (presented after the saccade) relative to the same feature of the same spatially located target (presented before the saccade) sometimes among similar looking distracters. In a typical *Saccade Task* trial (Fig. 1a), subjects fixated on a cross (subtended 1.5°) presented randomly at one of 29 possible spatial locations within a display area spanning $18^\circ \times 18^\circ$. Upon fixation, subjects were briefly presented (100 ms) with a target-display. Subjects were required to maintain eye fixation during target-display presentation.

The target-display consisted of either a solitary target or a target accompanied by a random number of distracters ranging from 1 to 5, 7, 9, or 14. In other words, the total set-size of the target-display ranged from 1 to 6, 8, 10, or 15 items (target + distracters).

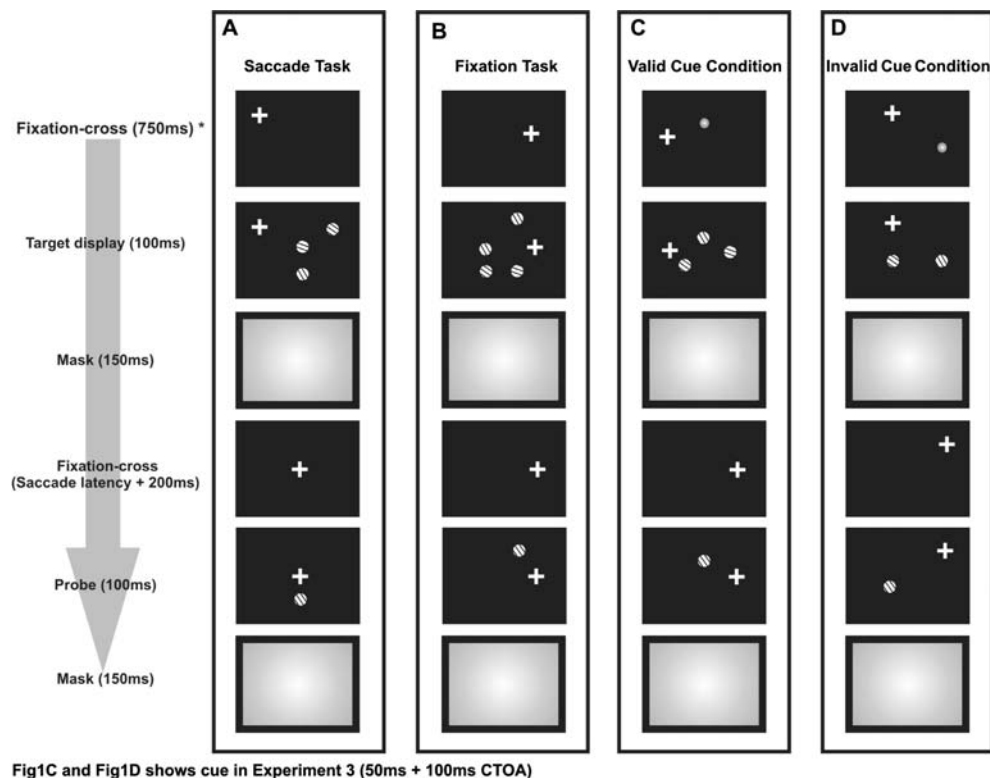


Fig. 1 General experimental paradigm for our study. The rectangles of each panel show that the temporal order for presentation of fixation-crosses (plus) and the visual stimuli (filled circle). **a** shows the *Saccade Task*. Subjects fixate on the fixation-cross while the target display is briefly presented (100 ms) containing either a lone target or a target accompanied by a random number of distracters (i.e. total set-size of target + distracters 1 to 6, 8, 10, or 15). Following the mask (150 ms), subjects move their eyes to the fixation-cross's new location. After the saccade a probe is presented (100 ms) at the same location as the target. Subjects' task was to indicate how the probe's features differed relative to the features of the target. The *Fixation Task* is illustrated in **b**. This task is the same as the

Saccade Task except that subjects are required to maintain eye fixation through target display and probe presentations, as the fixation point remains fixed in the same position throughout the trial. **c, d** are examples of typical *Saccade* trials in Experiment 3. This experiment is similar to Experiment 2 except with the addition of a cue flashed 100 ms before the target display. **c** shows the valid cue condition for the *Saccade Task*. The cue is flashed (50 ms) at the same spatial location as the target. In the invalid cue condition (**d**), the cue appears at the same spatial location in advance of a randomly determined distracter. The *Fixation Task* of Experiment 3 was identical to the *Saccade Task* except subjects maintained eye fixation throughout *Fixation* trials

When distracters were included in the target-display, subjects did not know which pre-saccadic item was the target and which items were distracters; thus, they were forced to remember the details of as many of the pre-saccadic items of the target-display as possible. Spatial locations for all items in the target-display (i.e. target and distracters) were randomly generated within the display area except at the fixation-cross. The visual stimuli of the target-display were either varying luminance patches (Experiment 1) or gabor-like patches of varying orientation lines (Experiments 2 and 3). The details of the target and distracters are described below in the sections specifying each experiment.

The target-display was followed immediately with a mask: a white uniform field (i.e. 33.61 cd/m^2) covering the entire screen—briefly flashed (150 ms) to reduce any chance of visual persistence. In previous control experiments we have shown that this mask has no effect on spatial performance in transsaccadic perception (Prime et al. 2006). Following the mask, the fixation-cross reappeared in a new randomly determined spatial location within the display area. Subjects followed the fixation-cross by making a saccadic eye movement to its new location. After subjects re-fixated the fixation-cross and a brief delay (200 ms), a probe was flashed (100 ms) in the same location as the pre-saccadic target followed by a second mask. The purpose of the brief delay before presenting the probe was to avoid the common visual distortions that occur around the time of a saccade such as saccadic compression (e.g. Lappe et al. 2000). One may argue that including a delay may artificially enhance *Saccade Task* performance by creating a “blinking effect” (Deubel et al. 1996), i.e. higher accuracy in reporting the details of a visual stimulus that temporally disappeared during a saccade and its post-saccadic image was not available immediately after the saccade. However, there are important differences between the experimental design in Deubel et al. (1996) and the one here. For example, the stimulus subjects had to judge was always the saccade target whereas in our study the target is never the saccade target. This is an important difference because it is not clear if the blinking effect occurs for an object that is other than the saccade target particularly when there are multiple objects.

The probe resembled the target except that the probe’s luminance (Experiment 1) or line orientation (Experiments 2 and 3) differed by a pre-determined amount. This probe–target difference was equivalent to the average discrimination threshold across a population of subjects at 80% of correct responses when

comparing the luminance or orientation of only a pair of targets separated by a saccade as obtained in an earlier study (Prime et al. 2007).

In this study, the subjects’ task was to compare the probe and target with respect to a specific visual feature. In Experiment 1, subjects judged whether the probe was brighter or darker than the target. In Experiments 2 and 3, subjects judged whether the probe’s lines clockwise or counter-clockwise to the target’s lines. Subjects responded by a two alternative forced-choice task manually by pressing one of two computer mouse buttons—response instructions were specific to each experiment and are described below. Subjects were instructed to make their best guess if they were not sure.

An important aspect of our study was comparing the *Saccade Task* to a *Fixation Task* (Fig. 1b). The *Fixation Task* was identical to the *Saccade Task* except that the fixation-cross did not change location after the target-display’s presentation, and thus, subjects maintained eye fixation throughout the trial. This means that the targets and probes are presented within a single fixation. Comparing these tasks allowed us to determine whether—and to what extent—saccadic eye movements interfere with the subjects’ capacity to retain and spatially update visual information. To ensure the stimulus onset asynchrony (SOA) of the target-display and the probe were the same between the two tasks by taking into account the time required for subjects to make a saccade, saccade latencies of Saccade trials were recorded online and used as the SOA of subsequent Fixation trials. For this reason, the tasks were presented in a block design, always beginning with the *Saccade Task*. The order of the blocks was counter-balanced between subjects (A–B–B–A or A–B–A–B). Each block consisted of 135 trials for a total of 540 trials—30 trials for each set-size of the target-display (i.e. 1, 2, 3, 4, 5, 6, 8, 10, and 15) in both tasks.

Experiment 1: luminance

Subjects judged whether the probe was brighter or darker than the target in Experiment 1. Targets, distracters, and probes were circles subtending 2° in diameter. Targets and distracters in the target-display varied randomly amongst six luminance levels (cd/m^2): 4.3, 6.4, 8.4, 10.3, 13.5, and 16. Probe luminance was either 3 cd/m^2 brighter or darker than the target’s luminance. Subjects responded by pressing the left computer mouse button if the probe was darker than the target’s luminance or the right button if the probe was brighter.

Experiment 2: orientation

In Experiment 2, we tested our subjects' ability to compare line orientations of the target and probe. All targets, distracters, and probes were gabor-like patches (2° in diameter) of alternating black and white bars. The gratings' mean luminance was 17 cd/m^2 and the spatial frequency was two cycles per degree of visual angle. The orientation of the target and each distracter in the target-display was randomly selected from six possible orientations— 35° , 45° , or 55° clockwise or counter-clockwise from vertical. Probe orientation was either 9.9° clockwise or counter-clockwise to the target's orientation. Subjects responded by pressing the left mouse button if the probe's orientation was counter-clockwise of the target's orientation or the right mouse button if the orientation was clockwise.

Experiment 3: attentional factors

In Experiment 3 we examined the effects of attention and controlled for any low-level visual factors like peripheral acuity in our main task. More specifically, we wished to determine how cuing attention to either the target or a distracter would influence performance—particularly for the *Saccade Task*. We used the same stimuli and task as Experiment 2 (comparing target and probe orientations) with one important difference (Fig. 1). Preceding the target-display, a visual cue appearing as a 1.5° white dot was flashed (50 ms) either at the target location (valid cue condition, Fig. 1c) or one of the distracters (invalid cue condition, Fig. 1d). The valid cue condition was presented on half of all trials in this experiment and subjects were instructed to ignore the cue. Cue–target onset asynchrony (CTOA) was set at 100 ms for all trials. Because it was not possible to have an invalid cue in trials with only a solitary target and no distracter, we only used trials with at least one distracter (i.e. set-sizes of 2, 3, 4, 5, 6, 8, 10, or 15 target + distracters).

Simple predictive statistical model

As illustrated in Fig. 2, we constructed a simple statistical model showing what performance we can expect from our subjects for different potential retention capacities of transsaccadic memory. This model accounted for correct guesses of non-remembered targets, and assumed that the items retained across the saccade are a random subset of the target display and that there are no non-linear interactions between the items. We used the model to determine

which curve predicting transsaccadic memory for a specific capacity best fits our data, as shown in the results, and to judge if other non-linear factors are required to explain the data. Proportion of correct responses were given a ceiling of 0.80 to match the pre-determined average discrimination threshold of 80% correct responses when comparing the luminance or orientation of targets separated by a saccade as obtained in an earlier study (Prime et al. 2007). The parameters were the expected proportion of correct responses (z), capacity of transsaccadic memory (y), and number of items presented in target display (x). This is expressed as:

$$z = \begin{cases} \frac{y \times 0.8}{x} + \frac{x-y}{2x}, & \text{if } x \geq y, \\ 0.8, & \text{if } x < y. \end{cases}$$

According to this model, if transsaccadic memory had a capacity of only one object, as depicted in Fig. 2 by the solid curve under the number 1, we would expect that subjects would respond at 80% correct but rapidly decline with two objects reaching 50% correct for 15 objects. On the other hand, the curve for ten items predicts that our subjects' performance should remain at 80% correct for set-sizes up to ten objects but drop to 70% for 15 objects. Note that for the purpose of data fitting, we inputted the actual performance on the single-target trial (approximately 0.8 from Prime et al. 2007) into the equation to generate the expected curves.

Results

Fixation performance

Before proceeding to our comparison of data from the *Saccade Tasks* and the *Fixation Tasks*, here we confirm our subjects' ability to fixate during the latter set of tasks. As mentioned earlier in "Methods", eye position was monitored on-line by a personal computer which was programmed to accept only trials with no errors in eye movements and eye fixation. If the subjects erred in their eye movements or eye fixation, the trial was immediately aborted, automatically removed from the data, and repeated. To ensure that there were no fixational eye movements, in particular microsaccades, large enough to escape detection and confound the results, we computed the subjects' average number of microsaccades and their average standard deviation of fixational eye position in every trial. Of particular interest were fixational eye movements during the critical interval from the onset of ocular fixation on the

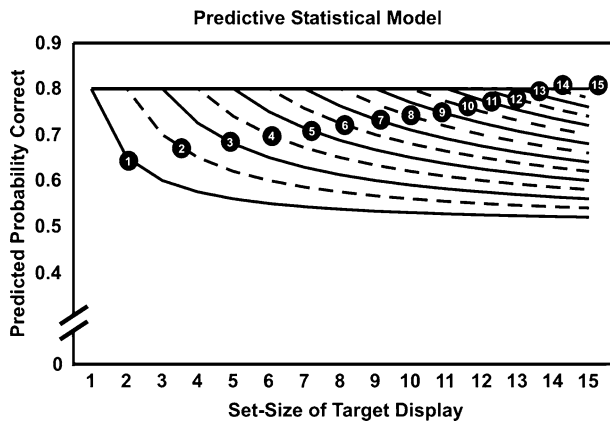


Fig. 2 Simple predictive statistical model. Each *curve* predicts the probability of correct response as a function of set-size for each possible capacity of transsaccadic memory. Theoretical capacities are indicated by the *numbers* above each *curve*. We alternated the *curves solid and dash* only to make reading the figure easier. The maximum probability correct is set at 80% because the difference between the target and the probe was fixed at magnitude corresponding to 80% threshold for comparing differences in orientation and luminance as determined in a previous study (Prime et al. 2007). For example, a capacity of two items would predict 80% correct for set-sizes of one and two items in the target display but decline to 70% correct for three items and 60% correct for six items. On the other hand, a larger capacity of six items would predict 80% for set-sizes up to six items before steadily declining as the number of items in the target display are increased

first fixation-cross to the offset of the probe in *Fixation Task* trials. In accordance with the conventional definition of a microsaccade, we assumed a size criterion for detecting microsaccades as a saccade, detected by the earlier mentioned velocity criterion in “*Methods*”, that was less than 0.17° (Ditchburn 1973; Ratliff and Riggs 1950).

During the critical interval, we found subjects had a microsaccade rate of 1.1 per trial in the *Fixation Task* and 0.9 per trial in the *Saccade Task* across all subjects close to the expected range of the usual rate of microsaccades of about 1–2 per second found in pervious studies (i.e. Ditchburn 1973). Moreover, the average standard deviation of fixational eye position in the *Fixation Task* across all subjects was 0.07° horizontal and 0.08° vertical. In the *Saccade Task*, average deviation of fixational eye position across all subjects was 0.05° horizontal and 0.07° vertical. These average standard deviations include the slight changes in fixational eye position due to microsaccades. Thus, we concluded that the subjects’ fixational eye movements were too small and microsaccades too infrequent to have any significant impact on our general findings and likely do not play any more of a role in this transsaccadic memory task as they do in other visual tasks.

For most of the subsequent analyses we used the Kolmogorov–Smirnov (K–S) goodness-of-fit test to determine whether two distributions differed significantly. For all analyses, a *P* value of 0.05 was adopted for significance.

Exp1: luminance

In Experiment 1 subjects compared the luminance between target and probe. Figure 3a shows the mean proportion of correct responses across all subjects for both tasks as a function of the target display’s set-size. In general, subjects’ mean proportion of correct responses was near 0.80 for set-sizes 1–4. Correct responses steadily decreased as set-sizes increased from 5–15 items in both tasks but more rapidly in the *Saccade Task*. Based on visual inspection, it appears that the data from both tasks best resemble the curves in Fig. 2 for a capacity of three or four items with set-sizes from 1 to 8 items. Set-sizes of more than eight items in the *Fixation Task* still follow these curves fairly well but the data of the *Saccade Task* was slightly poorer than what this curve would predict. These qualitative observations were evaluated quantitatively by the following statistical analysis.

First, the curve representing the data of the *Fixation Task* in Fig. 3a was statistically the same as the curve of the *Saccade Task* as determined by a Kolmogorov–Smirnov (K–S) goodness-of-fit test: $K-S = 0.471$, $P = 0.98$. This is consistent with an analysis of proportion of shared variance between the *Saccade* and *Fixation* tasks showing a nearly perfect result ($r^2 = 0.91$). This confirms our observations of Fig. 3a—*Saccade Task* performance was statistically the same as *Fixation Task* performance.

To quantitatively determine the best parameter set for our predictive model shown in Fig. 2 that provides the best fit for the data in each task, and thus estimate our subjects’ capacity of maintaining items across saccades, we calculated the mean squared residual errors (MSR errors) for each subject between their actual data at every specific set-size to the corresponding point on each curve. The bar graphs of Fig. 4 show the average MSR errors across subjects against set-size in the *Fixation Task* (Fig. 4a) and the *Saccade Task* (Fig. 4b). The solid strip in each bar indicates the MSR error obtained when the data were first averaged across subjects and then compared to the theoretical curves. As Fig. 4a shows, the least MSR error in the *Fixation Task* indicates the best fit to the model from Fig. 2 is the curve predicting a capacity of four items. On the other hand, the least MSR error in the *Saccade Task* best fits the model for three items. A comparison

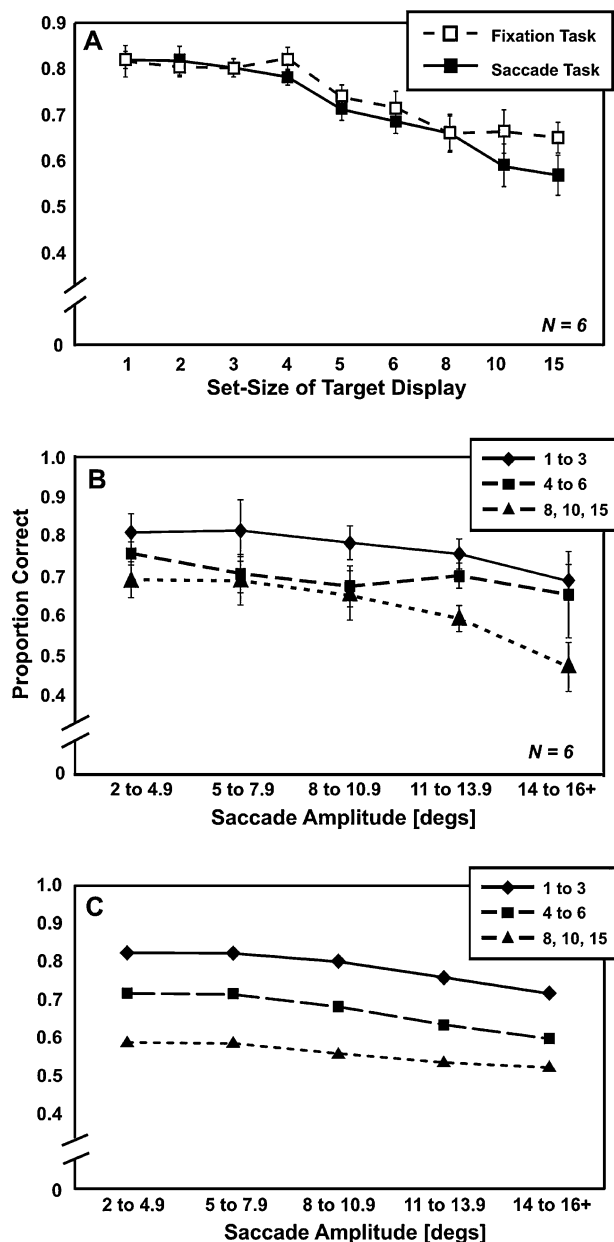


Fig. 3 Main results of Experiment 1. **a** Mean proportion of correct responses across all subjects in each task for each set-size. Using goodness-of-fit analysis we found performance in the *Saccade Task* (closed squares) was statistical the same *Fixation Task* performance (open squares): $P = 0.98$. **b** Effect of saccade amplitude on accuracy in Experiment 1. In general, mean proportion of correct responses decreased as saccade size increased. Statistically, this was only significant for set-sizes of 8–10–15 items (closed triangles) and saccades of 11°–13.9° and 14°–16.9° ($P = 0.03$). All error bars represent standard error. **c** Model best-fit of *Saccade Task* from Experiment 1 accounting for saccade amplitude. We assumed noisy remapping error took on a 2D Gaussian distribution whose width was proportional to saccade size. Using this model we found the best-fit to our data from the *Saccade Tasks* of Exp1 and Exp2 when the Gaussian width of remapping error was 14 and 15% of saccade size, respectively. This model explained 76 and 85% of the variability from the *Saccade Tasks* of Exp1 and Exp2, respectively

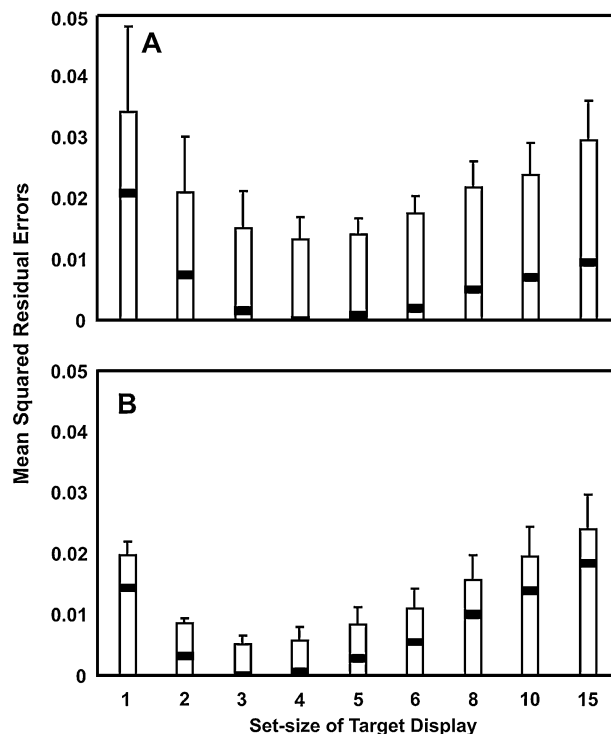


Fig. 4 Mean squared residual errors (MSR errors) in Experiment 1 between actual data curves from Fig. 3 and the curves of the predictive model in Fig. 2. Bars represent the average MSR errors across all subjects after calculating the MSR errors for each subject individually. The MSR errors on the averaged data pooled from all subjects are indicated by the solid strip within each bar. The least average MSR error is an indication of the best fit to the analogous predictive model from Fig. 2. We found the average MSR errors of the *Fixation Task's* data (a) best fit the curve predicting a capacity of four items from our model. *Saccade Task's* average MSR errors (b) showed the best fit for the curve predicting a capacity of three items. These average MSR errors between the two tasks were not significantly different (K–S 0.707; $P = 0.69$). All error bars represent standard error

between the tasks' MSR data found they were statistically the same: K–S = 0.802; $P = 0.54$. Thus, our findings from Exp1 suggest transsaccadic memory has a capacity for comparing luminance features of about three or four items. The fits to the overall average data (indicated by the solid strips in Fig. 4) showed the same trends, but lower MSR errors, presumably because these data were less noisy.

Effect of saccade size in Experiment 1

Although we found no significant differences between the *Saccade Task* and *Fixation Task* it should be noted that *Saccade* trials consisted of different sizes of saccades. To determine if saccade size influenced performance in the *Saccade Task*, we plotted the average

data across all subjects according to set-size and saccade amplitude (Fig. 3b). For the sake of simplicity, saccade amplitude was segregated into five groups (2.0°–4.9°, 5.0°–7.9°, 8.0°–10.9°, 11.0°–13.9°, and 14.0°–16.9°) and set-sizes were segregated into three groups of 1–3 items, 4–6, and 8–15. We grouped the data this way to keep the size of the groups equal so the results would be clearer and easier to interpret. As Fig. 3b shows, larger saccade amplitudes yielded more errors overall: $F_{(4,75)} = 2.74$; $P = 0.03$. In particular, separate pairwise comparisons among the different groups of saccade amplitudes collapsing set-size yielded only significant differences when comparing the largest saccades (i.e. 14.0°–16.9°) with all other saccade amplitudes with the exception of the 11.0°–13.9° saccades (e.g. 2.0°–4.9° vs. 14.0°–16.9°: $t_{(23)} = 2.69$, $P = 0.01$). In addition, we conducted separate trend analyses for each data curve representing the group of set-sizes in Fig. 3b. We found only significant linear trends for the data curve of 1–3 set-sizes ($P < 0.001$) and set-sizes with 8, 10, and 15 items ($P < 0.001$). The curve representing set-sizes 4–6 items was not significant ($P = 0.66$). To be sure this saccade size effect was not due to or confounded by varying target retinal eccentricities, we analysed our subjects' accuracy when the target was at all possible pre-saccadic and post-saccadic retinal distances from the fixation-cross. We found accuracy did not vary as a function of the target retinal eccentricity either before the saccade ($F_{(4,20)} = 0.36$; $P = 0.83$) or after the saccade ($F_{(4,20)} = 1.72$; $P = 0.19$), thus, eliminating retinal eccentricity as an alternative explanation for this saccade size effect.

Exp2: orientation

In Experiment 2 we examined the number of objects retained across saccades when subjects are required to maintain the objects' orientations. Figure 5a shows the mean proportion of correct responses across all subjects in both tasks. In general, accuracy was about the same for 1–4 set-sizes and then gradually decreased as set-size increased in both tasks. Also, the *Saccade Task* data were nearly identical to the *Fixation Task* data up to six items, but then took an even sharper decline. In the *Saccade Task* performance for set-size 10 and 15 items were even below chance (50%) suggesting some constraints unique to this orientation memory task.

The Kolmogorov–Smirnov test performed on the data between the *Fixation Task* and the *Saccade Task* shown in Fig. 5a yielded no significance difference: $K-S = 0.707$, $P = 0.69$. Again, this is consistent with

the proportion of shared variation between the tasks ($r^2 = 0.94$).

As in Experiment 1, we calculated the average MSR errors across subjects in each task (Fig. 6) and the MSR errors on the average data pooled together (indicated by the solid strip within each bar in Fig. 6) to estimate our subjects' capacity of transsaccadic memory for comparing orientations. The average MSR errors show that the curves from our model that best fit our data was the one predicting three items in the *Fixation Task* (Fig. 6a) and four items in the *Saccade Task* (Fig. 6b). The tasks MSR data were statistically the same: $K-S = 1.18$, $P = 0.12$. That is, our subjects' capacity of comparing orientation features is 3–4 items regardless of a saccade. Again, the MSR errors for the overall average data were lower but showed the same trends.

Effect of saccade size in Experiment 2

Again, we found a significant inverse relationship between proportion of correct responses and the size of the saccade. Figure 5b shows the results when we group the data according to saccade amplitude and set-size across all subjects. Saccade amplitude was segregated into five groups (2°–4.9°, 5°–7.9°, 8°–10.9°, 11°–13.9°, and 14°–16.9°) and set-size was segregated into three groups (1–3, 4–6, and 8–15 items). Recall that we grouped the data this way purposely to keep the size of the groups equal for statistical comparison. As in Experiment 1, the subjects' mean correct responses decreased as the size of the saccade increases in each group of set-size: $F_{(4,85)} = 5.645$; $P < 0.001$. In general, pairwise comparisons yielded significance only when comparing the largest saccade sizes (i.e. 11°–13.9° or 14°–16.9°) with the smallest saccades (e.g. 2°–4.9° or 5°–7.9°) after collapsing set-size: for example, 2°–4.9° saccades were significantly more accurate than both 11°–13.9° ($t_{(23)} = 4.34$; $P < 0.001$) and 14°–16.9° saccades ($t_{(23)} = 6.04$; $P < 0.001$). Trend analyses on each data curve representing the groups of set-sizes in Fig. 5b yielded only significance for the grouped set-sizes of 8, 10, and 15 items ($P = 0.02$). Both data curves representing 1–3 set-sizes grouped together and 4–6 set-sizes grouped together were not significant ($P = 0.07$ and 0.28 , respectively). Again, we analysed our subjects' accuracy when the target was at all possible pre-saccadic and post-saccadic retinal distances from the fixation-cross, and as before, we found accuracy did not vary as a function of the target retinal eccentricity either before the saccade ($F_{(4,20)} = 0.93$; $P = 0.46$) or after the saccade ($F_{(4,20)} = 0.83$; $P = 0.52$). We conclude that the saccade size effect we observed

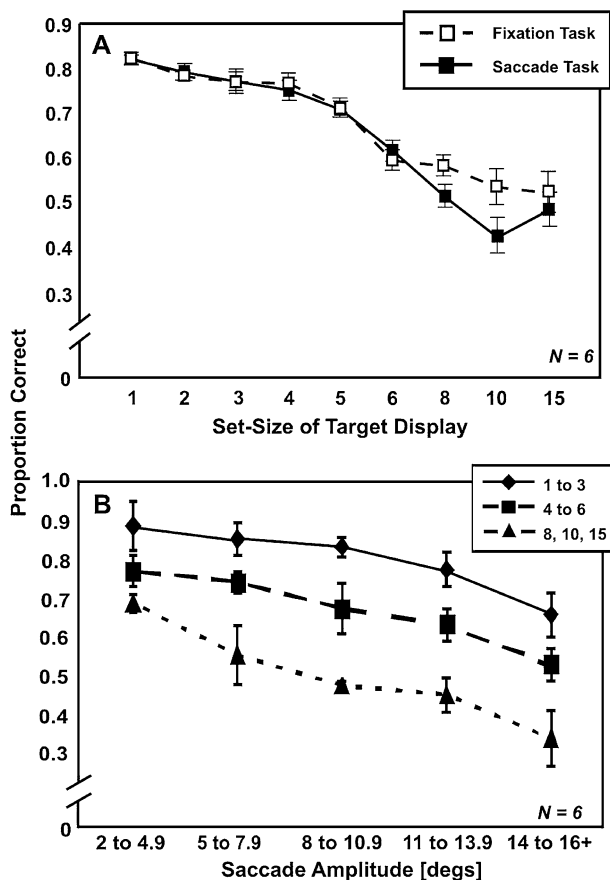


Fig. 5 Experiment 2 main results. **a** Goodness-of-fit analysis of performance between the *Saccade Task* (closed squares) and the *Fixation Task* (open squares) yielded no significant differences ($P = 0.69$). **b** Effect of saccade amplitude in the *Saccade Task* of Experiment 2 show a similar trend as Experiment 1. The average data for all subjects was grouped by set-size and plotted by mean proportion of correct responses against saccade amplitude. In general, subjects were most accurate for set-sizes of 1–3 items (closed diamonds) and least accurate for set-sizes of 8, 10, or 15 items (closed triangles). Mean correct responses decreased as saccade size increased ($P < 0.001$). All error bars represent standard error

was not due to or confounded by varying target retinal eccentricities.

Comparing Exp1 and Exp2

Thus far, the results from Experiments 1 and 2 suggest similar memory capacities regardless of the visual feature subjects were required to retain in memory showing a best fit of three or four targets for both *Fixation* and *Saccade* tasks. To test this observation statistically we compared the average proportion of correct responses from Experiment 1 as shown in Fig. 3a with that of Experiment 2 as shown in Fig. 5a within the same tasks. Our results show the data of

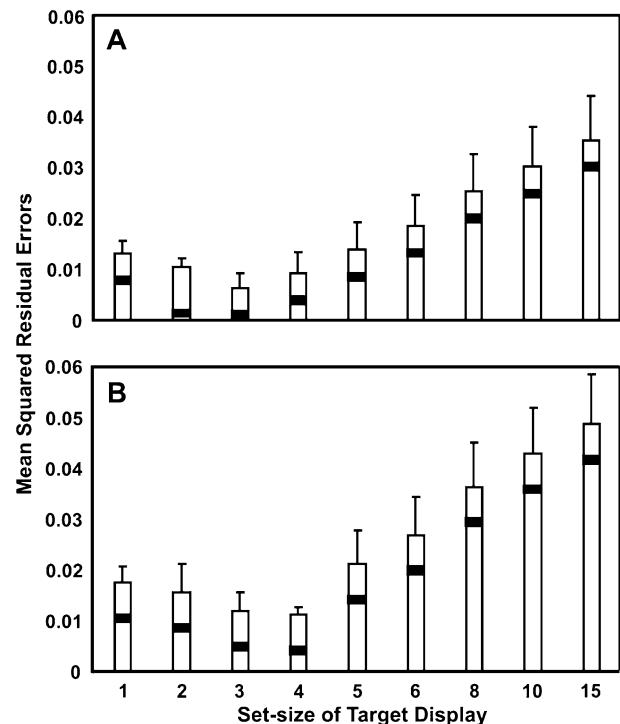


Fig. 6 Mean squared residual errors (MSR errors) in Experiment 2 between actual data curves from Fig. 5 and the curves of the predictive model in Fig. 2. Bars represent the average MSR errors across all subjects after calculating the MSR errors for each subject individually. The MSR errors on the averaged data pooled from all subjects are indicated by the solid strip within each bar. The least average MSR error is an indication of the best fit to the analogous predictive model from Fig. 2. Average MSR errors of the *Fixation Task*'s data (a) show the best fit for the curve predicting a capacity of three items from our model. The *Saccade Task*'s data (b) best fits the curve predicting a capacity of four items. These MSR errors between the tasks were not significantly different (K-S = 1.18, $P = 0.12$). All error bars represent standard error

Experiment 1's *Fixation Task* was the same as Experiment 2's *Fixation Task* (K-S = 0.943, $P = 0.34$). Likewise, the *Saccade Task* between Experiment 1 and Experiment 2 were the same (K-S = 0.707, $P = 0.70$). Moreover, the mean squared residual errors of the *Fixation Tasks* from each experiment (Fig. 4a vs. 6a) were statistically the same (K-S = 0.76; $P = 0.6$) as were the mean squared residual errors of the *Saccade Tasks* (Fig. 4b vs. 6b) from each experiment (K-S = 0.87; $P = 0.44$).

Thus, to summarize the main results so far, our subjects were able to retain up to about three to four luminance or orientation features across saccades. This capacity is the same when performing a similar task without eye movements. Beyond four objects, however, subjects' accuracy decreased as set-sizes increased. Lastly, large saccades in the *Saccade Task* were related to poorer performance (i.e. more errors).

Exp3: attentional factors

In Experiment 3, we examined the effect of an attentional cue presented in advance of the target display. On half the trials the cue correctly informed the subjects about which item in the target display was the target (valid cue condition) and on other trials the cue mislead subjects by directing them to a distracter (invalid cue condition). Figure 7a shows the mean proportion of correct responses across all subjects in the *Fixation Task* for both cue conditions. The first observation from these data show lower proportion of correct responses for invalid cues, as depicted by the open squares, compared to valid cues (closed squares). The same seems to be true in the *Saccade Task* (Fig. 7b). This was confirmed when we compared the cue conditions within each task: the *Fixation Task*'s cue conditions were significantly different from each other ($K-S = 1.5, P = 0.002$) as were the *Saccade Task*'s ($K-S = 1.75, P = 0.008$). Thus, an attentional cue significantly influenced performance in our task most likely by directing our subjects' attention to the potential target. Such results suggest that performance in this task is not mediated solely by some low-level or sensory mechanism, and attention plays a role in what

information is encoded and preserved across saccadic eye movements.

To compare the two tasks more directly we replotted the data from Fig. 7a, b according to each cue condition. Figure 7c shows that valid cue performance in the *Saccade Task* was the same as the *Fixation Task* ($K-S = 0.75, P = 0.63$). Similarly, Fig. 7d shows the invalid cue condition yields the same results in both tasks ($K-S = 0.5, P = 0.96$).

In addition, it can be seen in each of the four panels of Fig. 7 that subjects committed more errors with larger set-sizes despite receiving a valid cue (although these errors were not as pronounced as those in the invalid cue condition), suggesting that even when the subjects knew which object to remember, additional objects acted as distracters or used up memory resources. This effect of set-size in valid cue trials was confirmed by running separate one-way ANOVAs for each task: *Saccade Task* ($F_{(7,40)} = 5.447; P < 0.001$) and *Fixation Task* ($F_{(7,40)} = 3.421; P = 0.006$).

Interestingly, accuracy in the invalid cue condition also declined with set-size but still remained well above chance. One possibility is that the spatial extent of the subjects' attention, while directed at the cued distracter, was spread far enough to include the target.

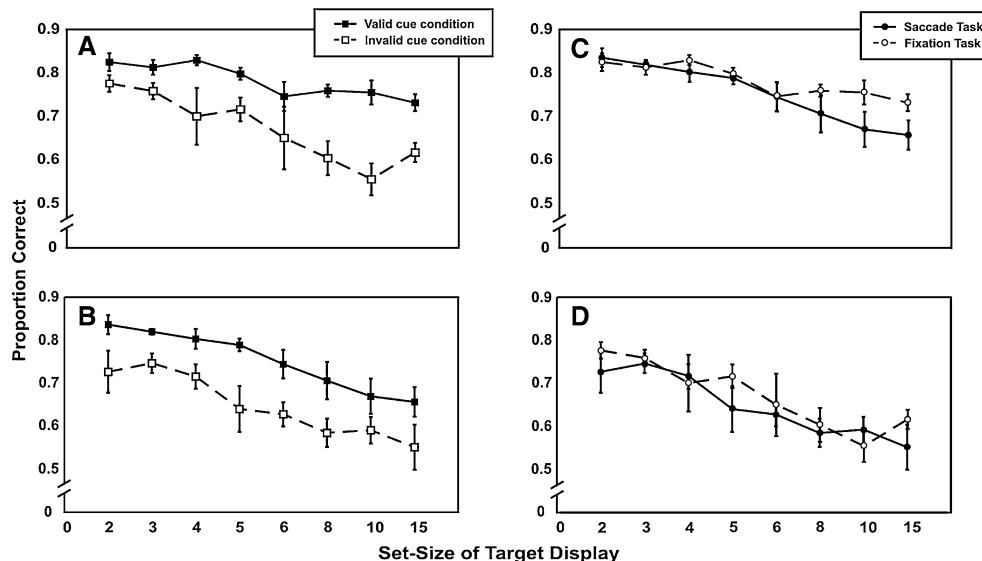


Fig. 7 The effect of an attentional cue in Experiment 3 shown as mean proportion of correct responses across all subjects against set-size. **a** Results for the *Fixation Task* show that mean correct responses were higher in the valid cue condition (closed squares) than invalid cue condition (open squares). Errors were more pronounced for both conditions at larger set-sizes. **b** Similar results were found for the *Saccade Task*. Subjects were most accurate in the valid cue condition (closed squares) though this accuracy declined as a function of set-size more rapidly than in the *Fixation Task*. Comparing these results with the data from

Exp2, we found that cuing the target facilitated subject performance even for larger set-sizes but invalid cues more errors. The data from **a, b** are replotted by comparing the tasks in each cue condition. **c** shows the data of each task according to the valid cue condition. Valid cues elicited equal accuracy between the tasks for set-sizes of up to eight items. *Fixation Task* performance (open squares) was better than the *Saccade Task* (closed squares) for only the highest set-sizes (i.e. 10 or 15 items). The tasks were identical during the invalid cue condition (**d**). All error bars represent standard error

If this was the case the proportion of correct responses should be higher for targets nearer to the cued distracter. Figure 8 shows this by plotting mean proportion of correct responses of the invalid cue trials against both set-size and target–cue distance for the *Fixation Task* (Fig. 8a) and the *Saccade Task* (Fig. 8b). The cued targets (valid cue condition) are included in this data-set as the zero-target distance points. In both tasks, subjects were most accurate among *invalid cue* trials consisting of set-sizes two or three and target–cue distances of 1°–3°. Increasing either set-size or distance between the target and cue corresponded to a reduction in accuracy.

We confirmed these observations of Fig. 8 with separate twoway (set-size \times target–cue distance) ANOVAs for repeated measures for each task. For the *Fixation Task* (Fig. 8a), we found significant differences for both set-size ($F_{(3,15)} = 9.49$; $P = 0.001$) and Target–cue distance ($F_{(4,20)} = 4.84$; $P = 0.007$) but no significant effect for the interaction ($F_{(2,60)} = 1.25$; $P = 0.27$). Similar results were found for the *Saccade Task* (Fig. 8b): set-size ($F_{(3,15)} = 5.23$; $P = 0.011$), Target–cue distance ($F_{(4,20)} = 4.23$; $P = 0.012$), interaction ($F_{(2,60)} = 1.13$; $P = 0.35$). Altogether, these results show performance in invalid cue trials depended on the distance of the target from the cued distracter, and thus, the spatial extent of the subjects' attention.

Modelling the data

From the preceding, it should be clear that the simple statistical model used as a predictor in Fig. 2 describes some of the basic aspects of this behaviour, but does not describe several of the important details, most particularly the saccade magnitude-dependent and attention-dependent effects described above. In order to characterize these findings from a deeper mechanistic perspective, we required a more sophisticated model, developed here. More mathematical details of this model are provided in the “Appendix”, and the physiological correlates for this model will be described in “Discussion”.

For the purposes of this model, it was assumed that all targets were encoded in eye-centered coordinates (Colby et al. 1995; Baker et al. 2003). In brief, the encoded target feature, either luminance or orientation, was assumed to take a Gaussian distribution about the actual target feature value and having a sigma of σ_{ENC} . We also assumed that there were S items that can be stored in working memory of object feature information. If the set-size of the target-display presented initially, N , was less than or equal to the numerical capacity of working memory (i.e. S),

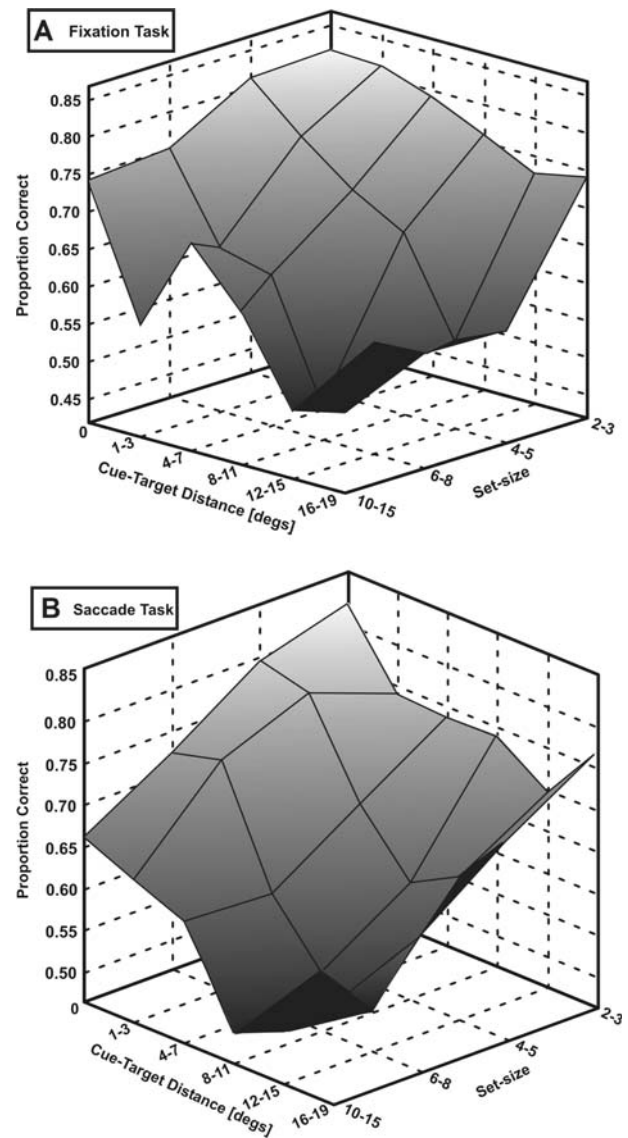


Fig. 8 The effect of target–cue distance and set-size in Experiment 3. Mean proportion of correct responses of the invalid cue condition is plotted as a function of target–cue distance and set-size. We also plotted the data of the valid cue condition (as indicated by zero target–cue distance) as a comparison. In general, accuracy in the *Fixation Task* (a) was highest for set-sizes of two or three items and the shortest distance between the cue and target ($P < 0.001$). Increasing either set-size or target–cue distance led to a corresponding drop in accuracy with the lowest performance at 12°–15° target–cue distance for 6–8 items. Results from the *Saccade Task* (b) show a similar trend ($P = 0.012$). Altogether these results confirm that the closer the target is to the cued distracter in invalid cue trials the more likely subjects made a correct response. This may be in part due to a gradient of attention spatially extending beyond the cued distracter to include the target

the features of all items would be encoded. In this case the probability of making a correct comparison of target and probe feature values, PO_{CORR} , depended on

the width of the encoding distribution. This calculation is given in “[Appendix](#)”. The value of $P_{0\text{corr}}$ was matched to the performance when there were no distracters.

If the set-size was larger than the hypothesized storage capacity ($N > S$), however, then each item of the target-display had a non-zero probability of having its feature encoded. In this condition, the

$$P_{\text{corr}}(N; S) = \frac{P_{0\text{corr}}S + 0.5(N - S)}{N}$$

where the 0.5 is chance probability of a correct comparison when the target’s feature was not encoded. We found that the fit to the *Fixation Task* data to the model was best when the number of items of the target-display was four, and that in this case the model accounted for 95% of the data variance for the *Fixation Tasks* in both the luminance and orientation experiments (i.e. Experiments 1 and 2, respectively). This storage capacity is consistent with other studies on the limitations of spatial or comparison “channels” in visual processing (Bundesen 1998; Fisher 1984).

We then assumed that the *Saccade Task* employed the same computations, except that during the saccade an internal vector representing the eye movement direction and magnitude was used to remap the pre-saccadic representations in retinal coordinates, i.e., by an equal and opposite amount to the saccade metrics (Duhamel et al. 1992; Medendorp et al. 2003; and see “[Possible neurophysiological mechanisms of trans-saccadic memory](#)” for a detailed physiological discussion of this process). We modeled the data from the *Saccade Task* by incorporating a noisy remapping error that had a 2D Gaussian probability distribution about the correct remapping value (the negative of the saccade vector) and whose width was proportional to saccade size. This error in remapping meant that the remapped target position may be different than that of the probe so that larger saccades would be more likely to result in a distracter being interpreted as the target and thus to produce incorrect comparisons. Since the feature, luminance or orientation, of the distracters was random and bore no relation to the probe feature value, such an interpretation would lead to a success rate of chance, 0.5, in comparing target and probe feature values.

This is physiologically reasonable, because peripheral targets involving larger saccades are represented by relatively fewer neurons in oculor-motor areas like the superior colliculus (Robinson 1972; Sparks and Hartwich-Young 1989) and therefore are more

susceptible to biological noise. Since these same areas are thought to provide the internal estimate of saccade metrics for remapping (Sommer and Wurtz 2002), one should expect larger errors for tasks that involved remapping with larger saccades.

In the presence of this noise, there was a non-zero probability that one of the distracters would be inferred to be the target stimulus, as opposed to the actual target. We assumed that the stimulus item whose remapped location was closest to the probe location would be interpreted as the target, whether it was the target or not. If the actual remapped target was closer to this position than any of the distracters, then the probability of making a correct comparison of feature value between target and probe was the same as in the *Fixation Task*. If one of the distracters was closer to the probe position than the target, then the probability of making a correct comparison was reduced to chance (0.5), since the feature values of the distracters bore no systematic relation to that of the target. Thus, the total probability of making a correct comparison would be:

$$P_{\text{corr}}(N; S) = \frac{[P_{T_{\text{is_closest}}}P_{0\text{corr}} + (1 - P_{T_{\text{is_closest}}})0.5]S + 0.5(N - S)}{N}$$

where $P_{T_{\text{is_closest}}}$ is the probability that the remapped target is closer to the probe’s retinal location than any of the distracters.

The best-fit to the data occurred for the *Saccade Task* in the luminance and orientation experiments when the Gaussian width of the remapping error was 14 and 15% of saccade size, respectively, for the two experiments, the model in each case explaining 76 and 85% of the variability of the data, respectively. The model predictions for the data from the *Saccade Task* of the luminance experiment (Fig. 3b) are plotted in Fig. 3c.

This model was also useful in fitting the data in our attentional cue task (see “[Appendix](#)” for details). To model this task, we assumed that an attentional spotlight centered at the cue location, and whose effect was to suppress the likelihood of encoding the features of items that were distant from the cue location. With these additions the model explained 68 and 74% of the variability of the data from Experiment 1 (luminance feature) and Experiment 2 (orientation feature) when the sigma of the spotlight Gaussian was 4° and 9°, respectively. Allowing the spotlight width to vary with set-size did not increase the model’s performance, so it would appear that these factors are independent.

Discussion

Our study tested the capacity of memory both within a single fixation—i.e. visual working memory—and across separate fixations—i.e. transsaccadic memory. The basic findings of our *Fixation Task* confirm the well-known result that visual working memory can maintain about 3–4 objects of simple features (Luck and Vogel 1997; Vogel et al. 2001). More to the point, we found that in general memory capacity was not significantly reduced by an intervening saccade of random size and direction in the *Saccade Task* and subjects were also able to maintain 3–4 objects in transsaccadic memory. Again, these findings are consistent with previous studies of transsaccadic memory capacity (Irwin 1992; Irwin and Andrews 1996; Irwin and Gordon 1998). In addition, we show that adding a brief delay before presenting the post-saccadic probe had no effect on *Saccade Task* performance relative to the *Fixation Task*.

However, the novel methodologies in our study led to several new findings. First, unlike most previous studies, we measured the capacity of transsaccadic memory for simple, pre-semantic visual features (cf. Carlson et al. 2001; Deubel et al. 2002). The results show that subjects can perform just as well (in both the orientation and luminance task) in the absence of meaningful memory cues. Moreover, the *Saccade Task* was designed so that subjects could not use allocentric cues to aid performance (e.g. edges of a computer monitor or reference points). Clearly, our subjects were able to rely on egocentric cues (i.e., an internal sense of saccade direction and magnitude) to make spatially correct comparisons between pre- and post-saccadic stimuli, and this did not significantly degrade memory capacity in either of the stimulus tasks. An exception to this rule—detectable because we used a variety of saccade sizes and directions measured using scleral search coils—was that within the *Saccade Task* performance degraded with saccade magnitude. Finally, we probed the role of directed (or misdirected) attention in these processes. Each of these factors, and their neural/computational mechanisms, will be considered in more detail in the following sections.

Other similarities between visual working memory and transsaccadic memory have been reported (for review see Irwin 1996). This leaves open the question whether these are separate and distinct memory stores or whether we are referring to a single memory store. While this question has not yet been answered conclusively, nor was it the purpose of this study, it would seem reasonable that transsaccadic memory is synonymous with visual working memory since it would be

more economical for the brain to utilize an existing multi-purpose memory system rather than having a separate memory for only storing visual information across eye movements. The crucial difference of transsaccadic memory, as in the case of the *Saccade Task*, is the introduction of an additional problem for the brain to solve—the change in the target’s location relative to the eye due to a saccade. The view that transsaccadic memory is essentially visual working memory with additional computations is discussed latter in more detail when we consider some of the neurophysiological mechanism that may govern *Saccade Task* performance.

Fitting data to predictive curves: why were the fits not perfect?

In some instances our overall average data provided a nearly perfect fit to one of the simple statistical models shown in Fig. 2 (i.e. the MSR errors approached zero), but clearly the data from individual subjects did not. One factor was the magnitude-dependence that we described, but this was also the case even in the *Fixation Task*. There are several possible reasons for this. First, performance was likely degraded in the impoverished visual environment, in particular the lack of allocentric cues (Lemay et al. 2004; Schoumense et al. 2000). Without these cues, the system may be more noisy and susceptible to independent sources of error like the “cognitive gravity” (Hubbard 1995; Kerzel 2002) or a bias toward the fovea (Mateeff and Gourevich 1983; Musseler et al. 1999; Sheth and Shimojo 2001; van der Heijden et al. 1999).

Second, the simple statistical model assumes items stored in memory were done in parallel and independent from each other, whereas in reality internal representations of remembered stimuli may interact in different ways. For example, memory of multiple objects may be better captured by a shared resource model, in which memory of one object may reduce the storage capacity for another object (Alvarez and Cavanagh 2004). Moreover, the system may have used global heuristics to encode the multiple stimuli. Though visual analysis can occur at either global level or local level (Coren et al. 1999), some evidence suggests the visual system’s default may be at a global analysis (Hughes et al. 1984; Kimchi 1992; Nakayama 1990; Navon 1977), especially at large visual field eccentricities (Amirkhiabani and Lovegrove 1996; Austen and Enns 2000; Navon and Norman 1983). Finally, Experiments 1 and 2 did not explicitly control the subjects’ allocation of attention—which, as we showed in our third experiment, has a major impact on

performance. This will be considered in more depth below.

Role of extra-retinal signals in transsaccadic integration

We designed our experiments so that subjects would have to rely on an egocentric sense of eye movement size and magnitude to solve the *Saccade Task*. The results show that subjects can solve this problem using egocentric information, but also suggests that subjects relied on an imperfect internal measure of saccade metrics. Simply introducing an amplitude-dependent noise to our model explained most of this data (Fig. 3c). This agrees with the results of our previous study where larger saccades introduced additional, albeit small, errors in mental integration of separate visual inputs (Prime et al. 2006). These data are also consistent with previous studies which attributed errors in memory guided saccades and arm movements to a noisy extra-retinal eye movement signals (Abrams et al. 1989; Honda 1991, 1993; Li and Matin 1990, 1997). However, this does not mean that the visual system only uses extra-retinal signals to solve the transsaccadic integration problem. Indeed, we believe that an optimal visual system would use all available information, both retinal and extra-retinal signals, in natural conditions (Niemeier et al. 2003; Prime et al. 2006). So again, normal performance is probably much better in a visually enriched environment.

Attentional direction and misdirection

Another finding in this study is the effect that attentional cues have on accuracy. Classical cueing studies that resemble the *Fixation Task* have consistently shown greater accuracy when a cue directs attention to the location of the impending target (Posner et al. 1978, 1980). Moreover, information of attentional cued visual stimuli is more likely to be stored in visual working memory than uncued visual stimuli (Schmidt et al. 2002). Consistent with Irwin and Gordon (1998), we show that this effect persists despite an intervening saccade. This is evidence that transsaccadic memory is not exclusively a low-level, sensory process but also depends on top-down cognitive processes such as the allocation of attention.

It has been suggested that normally attention is directed to the saccade-target immediately preceding a saccade like an “advance scout” (Deubel and Schneider 1996; Kowler et al. 1995) possibly for encoding the saccade-target in transsaccadic memory along with the saccade-source for the purpose of

maintaining visual stability across eye movements (Currie et al. 2000; Henderson and Hollingworth 1999; McConkie and Currie 1996). According to this model of transsaccadic memory, one might expect that information from other regions of the visual scene—that is, unattended objects—is not remembered across saccades (Henderson and Hollingworth 1999; Irwin and Gordon 1998).

Studies by Verfaillie and colleagues provide some evidence that is inconsistent with this ‘exclusive’ version of the saccade-target theory by showing that spatial information, object identity, and in-depth orientation of bystander objects—objects in the visual display other than the saccade-source or the saccade-target—are retained across saccades (De Graef and Verfaillie 2002; Germeys et al. 2002, 2004). Using a significantly different task in the present study, we show how many bystanders and their visual details are preserved across saccades. Our results add to the findings from Verfaillie and colleagues by showing that subjects can retain the details of multiple objects beyond the saccade-source and saccade-target in a limited capacity store (i.e. 3–4 simple object features). Moreover, our attention experiment showed that when attention is explicitly directed to a distracter, accuracy of the target still remained well above chance. However, our data are consistent with a ‘non-exclusive’ saccade-target theory: normally the saccade-target is the most attended stimulus, and memory of this target would be enhanced.

Our model suggests that most of the cued affects that we observed could be explained by a simple Gaussian distribution of attentional resources with a half width of 4°–9°, depending on the task. This is consistent with other models of attention that propose attention can change in its spatial extent (Eriksen and Yeh 1985; Eriksen and St James 1986) and the spread of attention is a gradient of processing efficiency that either decreases uniformly from the centre (Castiello and Umilt 1990; LaBerge et al. 1997). It is possible that a more complex “Mexican-hat” pattern—where efficiency decreases in the immediate region around the centre and then increases slightly at farther distances (Cutzu and Tsotsos 2003; Hopf et al. 2006)—would have provided an even better fit, but we did not model this. Finally, we did not attempt to model the physiological details of attention, but the differences between performance in our valid and invalid cue conditions appear to fit well with the biased competition model of attention (Desimone and Duncan 1995; Duncan and Humphreys 1989), which simulates inter-neuronal competition at the level of visual areas V2 and V4 (Liu et al. 2003; Reynolds et al. 1999).

Possible neurophysiological mechanisms of transsaccadic memory

For convenience, the neural mechanisms for transsaccadic integration and memory task in this experiment can be broken down to a series of computational stages: initial encoding, analysis, synthesis, storage, and transformations for action. We have dealt with the latter in detail elsewhere (e.g. Crawford et al. 2004) so will focus on the initial stages here. Both our basic tasks, luminance and orientation memory, involve both object feature memory and spatial memory (Klauer and Zhao 2004). The initial sources of feature information in our *Fixation Task* would depend on the version of the task: the orientation task would presumably engage the orientation channels of the early visual system (Movshon and Blakemore 1973; Thomas and Gille 1979) whereas the luminance task could be solved using contrast information channels alone (e.g., Cheng et al. 2004). Clearly, at early levels of the visual system features and locations of multiple objects would be coded topographically, i.e., multiplexed within different points in the retinotopic maps of V1 and V2 (Fox et al. 1987; DeYoe et al. 1996).

It is widely accepted that at higher stages of visual analysis there is a relative specialization for spatial and object vision in the ‘dorsal’ (occipital–parietal) and ‘ventral’ (occipital–temporal) streams, respectively (Mishkin and Ungerleider 1982; Goodale and Milner 1992). It has also been suggested that the object–spatial dissociation persists at higher levels of parieto-frontal working memory system (Ventre-Dominay et al. 2005; Courtney et al. 1996, 1998a, b; Wilson et al. 1993; Belger et al. 1998; Smith and Jonides 1997). If so, then our task would require additional binding mechanisms to re-combine spatial and feature information before or within the mechanisms for visual memory.

Moreover, as shown in this study, this binding mechanism must be able to account for changes in eye position within some egocentric frame. We have recently proposed a neural mechanism (Prime et al. 2006) that is consistent with the data and model simulations described above (Fig. 3c). No one knows the physiology of how this is done for perceptual integration, but it is fairly well established that representations for saccade and reaching targets are stored and remapped within an eye-centered frame in occipital, parietal, and frontal cortex. (Andersen 1987; Duhamel et al. 1992; Medendorp et al. 2003; Nakamura and Colby 2000; Tian et al. 2000; Umeno and Goldberg 1997; Zhang and Barash 2004). It is thought that this is accomplished by using an internal copy of the saccade vector that arises either from the cortex (Colby et al.

1995; Heide et al. 1995) or the brainstem (Sommer and Wurtz 2002; Medendorp et al. 2002). As noted above, noise in this system, particularly for under-represented larger saccades, should contribute to saccade-dependent errors in any system that uses these signals. We and others have proposed that these visuomotor mechanisms are also used in object memory tasks like that employed here (Niemeier et al. 2003; Kaiser and Lappe 2004; Prime et al. 2006). If so, then where do these eye-centered spatial signals converge with the object feature information required for transsaccadic integration?

One possibility is that this only happens at the latest stages, like prefrontal cortex, an area directly implicated in spatial working memory (Vogel et al. 2001; Curtis and D’Esposito 2003). But in some ways, the simplest way to combine this information is not forward, but backward: by ‘borrowing’ from the eye-centered remapping signal and using recurrent projections from both the dorsal and ventral streams to combine them in earlier retinotopic visual maps like V2 and V3 (Nakamura and Colby 2000) before the complete divergence of egocentric and allocentric signals for the analysis of “what” and “where”. Since these early and intermediate mechanisms clearly project forward to frontal cortex, and frontal cortex oculomotor signals are now known to influence early areas of visual processing like V4 (Moore et al. 1998), this occipital–parieto-frontal remapping network either overlaps or closely interconnects with the major neural mechanisms for all aspects of short term visual memory, including prefrontal and infero-temporal cortex (Funahashi et al. 1993a, b; Fuster and Jervey 1981; Fuster 2000; Gnadt and Andersen 1988), Super et al. 2002).

Indeed, oculomotor signals have been identified throughout the cortical circuits for visual working memory (Fukushima et al. 2004; Funahashi et al. 1989, 1993b; Hasegawa et al. 1998; Niki and Watanabe 1976; Rainer et al. 1998; Takeda and Funahashi 2002). It is not our conjecture that the eye-centered remapping mechanism is the only mechanism used by this network, but rather that this forms the egocentric foundation for a network that is somehow able to from egocentric, allocentric, and feature-based linkages through the kind of recurrent loops described above. It is apparent from this and similar studies that the number of these linkages is limited—probably by the attention system—to retain only 3–4 objects at a time, but our results show that the system is set up so that an intervening saccade produces only a minimal impact on the capacity of this system—an important feature considering that in real life humans make 2–5 saccades per second (Rayner 1978, 1998).

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Appendix

Modeling the *Fixation Task*

We assumed that each stored object's feature value, whether it was disk luminance or Gabor patch orientation, had a Gaussian probability distribution centered on the actual feature value and having a width, σ_{ENC} . Thus, a disk of luminance L_0 will have a probability density of being encoded as having luminance L of:

$$L(L_0) = \left(\frac{1}{\sigma_{\text{ENC}} \sqrt{2\pi}} \right) e^{-(x-L_0)^2/2\sigma_{\text{ENC}}^2}$$

A correct comparison of target and probe feature values requires that both target and probe encoded feature values be compared. Thus, for luminance, if the probe's luminance, L_{OP} , were greater than that of the target's luminance, L_{OT} , a correct comparison would reflect the total probability that the encoded probe luminance, L_{P} , is greater than that of the target, L_{T} :

$$P_{\text{corr}} = \left(\frac{1}{\sigma_{\text{T}} \sqrt{2\pi}} \right) \left(\frac{1}{\sigma_{\text{P}} \sqrt{2\pi}} \right) \int_{-\infty}^{\infty} \int_{-\infty}^{L_{\text{P}}} e^{-(L_{\text{T}}-L_{\text{OT}})^2/2\sigma_{\text{T}}^2} dL_{\text{T}} e^{-(L_{\text{P}}-L_{\text{OP}})^2/2\sigma_{\text{P}}^2} dL_{\text{P}}$$

Modelling the remapping error in *Saccade Task*

Since the target was defined as the item presented at the same spatial location as the probe and there was a saccade between target and probe presentations, the target was identified as being the item of the target-display whose remapped location in eye coordinates was the same as that of the probe. We assumed that the remapping had an element of noise in it, and that the noise had a 2D Gaussian distribution whose width was proportional to the size of the saccade. This error in remapping meant that one of the distracters presented along with the target may be closer to the probe position and thus be incorrectly interpreted as the target. Such a probability distribution, written in terms of error magnitude, r , must account for variability of space with this magnitude:

$$P(r) = \left(\frac{r}{\sigma_{\text{REM}}^2} \right) e^{-r^2/2\sigma_{\text{REM}}^2}$$

where σ_{REM} is the remapping error magnitude width. We used Monte Carlo techniques to determine how the remapping error would affect performance in the *Saccade Task*, repeatedly generating the remapping of target position that included this remapping error, and measuring the distance to the target and randomly-assigned distracter positions.

Modeling the *Fixation* and *Saccade tasks* in the cue experiment

In modeling the cue experiment (Experiment 3), we assumed that the flashing of the cue before the target-display presentation centered an attentional spotlight at the cue location. This spotlight was assumed to modulate the saliency of items presented in the subsequent target-display by the distance, r , between each item and the cue location, this modulation having a Gaussian dependence on r . The half-width of the attentional spotlight was the constant associated with this Gaussian function, σ_{A} . The probability of an item at a distance r from the cue location registering followed this modulation. The effect was to reduce the number of items the subject actually registered, preferentially eliminating those items distant from the cue location, and creating a 'virtual' number of items. These virtual items were used in place of the actual N items in our modeling of the *Fixation* and *Saccade tasks*, whose treatment otherwise followed that outlined in the non-cue experiments above.

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