10. Transsaccadic Memory of Visual Features

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Abstract

In order to integrate perceptions across saccades, some visual information must be retained, but the quality and quantity of this retention has been the subject of controversy. We tested transsaccadic memory of three basic features, luminance, orientation, and shape, either within a single fixation or between separate fixations. Subjects obtained lower discrimination thresholds for orientation and shape when the probes were retinally, rather than spatially fixed. However, discrimination thresholds did not differ significantly for any feature between the saccade and fixation tasks. This shows that the visual system retains the basic feature information necessary for perceptual integration across saccades.

10.1 Introduction

The visual world is rich with information distributed over a wide area. The fovea, however, only provides detailed information for a small portion of the visual world at one time. Consequently, to fully encode and process the surroundings humans make many fast, or "saccadic", eye movements (Yarbus, 1967; Stark and Ellis, 1981). Since vision is poor during a saccade (e.g. Matin, 1974) the brain must somehow encode discrete "snapshots" of the visual scene during fixations between saccades if it is to integrate these into a perceptual whole. However, at this time it is not known how and to what extent the brain pieces together these spatially and temporally separated snapshots.

Intuitively, it might seem that the brain would retain a highly detailed representation of the visual world in a spatiotopic "integrative visual buffer" (McConkie and Rayner, 1976). However, several studies suggest that relatively little information is stored across saccades (Bridgeman, Hendry, and Stark, 1975; Bridgeman and Mayer, 1983; Irwin, Yantis, and Jonides, 1983; O'Regan and Levy-Schoen, 1983; Rayner and Pollatsek, 1983; McConkie and Zola, 1979; Rayner, McConkie, and Zola, 1980; Irwin, Brown, and Sun, 1988; Henderson, Pollatsek, and Rayner, 1987). Moreover, humans show "change blindness", an inability to detect even significant changes in the visual scene when these changes occur during saccades and other brief visual interruptions (Grimes, 1996; Simons, 1996; Simons and Levin, 1997; O'Regan, Deubel, Clark, and Rensink, 2000; Rensink, O'Regan, and Clark, 1997).

It may be erroneous to assume that transsaccadic change blindness is proof that we retain nothing across saccades. Change blindness may occur for different reasons besides limitations in visual short-term memory (Irwin, 1991, 1992; Irwin and Andrews, 1996) or insufficient encoding of objects that are poorly attended (Scholl, 2000; Henderson and Hollingworth, 1999; Hollingworth, Schrock, and Henderson, 2001). In particular, a recent study shows that some forms of change blindness can be due to a probabilistic process the brain employs to make optimal inferences about events such as sudden changes in the visual scene (Niemeier, Crawford, and Tweed, 2003). In brief, these authors argue that transsaccadic change blindness can occur because outside a vision lab sudden external events are unlikely to happen in perfect sync with a saccade, and thus, apparent changes in stimuli that coincide with a saccade are more likely to arise from unreliable sensorimotor signals. The brain is, therefore, inclined to ignore sensory information about visual changes that occur during saccades or to underestimate them.

These developments suggest that the question of what information is retained across saccades needs to be re-examined. Recently, most investigators have considered intermediate views between the extreme beliefs that visual information is either completely retained or not retained at all. So to understand how transsaccadic memory operates we first need to understand the basic "building blocks" of this process, like what and how much visual feature information is retained across saccades. For example, some models of transsaccadic integration assume that basic visual features are retained in transsaccadic memory (Irwin, 1992; Currie, McConkie, Carlson-Radvansky, and Irwin, 2000; McConkie and Currie, 1996). In support of this, several studies have found evidence of transsaccadic retention of the visual features of shape (Pollatsek, Rayner, and Collins, 1984; Palmer and Ames, 1992; Schlingensiepen, Campell, Legge, and Walker, 1986; Carlson-Radvansky, 1999; Deubel, Schneider, and Bridgeman, 2002), colour (Hayhoe, Bensinger, and Ballard, 1998; Irwin and Gordon, 1998; Irwin and Andrews, 1996), and orientation (Henderson and Hollingworth, 1999; Landman, Spekreijse, and Lamme, 2003; Verfaillie, De Troy, and Rensbergen, 1994; Henderson and Siefert, 1999; Moore, Tolias, and Schiller, 1998).

While the preceding studies suggest that features information is retained across saccades, they do not provide detailed psychometric functions for feature discrimination necessary to build a quantitative model of transsaccadic memory. The aim of the present study was to provide these building blocks by measuring to what degree subjects are able to retain visual features across saccades. Specifically, we studied our subjects performance in comparing probes both within and between fixations for changes in luminance, orientation, and shape in three experiments. To test the effect of spatial context on retention of these features, we had subjects make these comparisons in two separate spatial tasks. For the first task, same-retinal task, both probes shared the same retinal position. In contrast, the probes in the second task, same-spatial task, were presented at the same spatial position.

10.2 Methods

10.2.1 Subjects

A total of eight subjects (4 males and 4 females; mean age 28.5) participated in this study, six subjects in each experiment. All subjects had normal or corrected-to-normal visual acuity. Informed consent was obtained from each subject. Two subjects were aware of the purpose of the experiments but followed the same trends as the naïve subjects.

10.2.2 General procedure and apparatus

We determined to what extent saccades affect transsaccadic memory for visual features in three experiments. Figure 10.1 illustrates the general experimental design for all 3 experiments. The four staggered rectangles of each panel illustrate the temporal order for presentation of ocular fixation targets (+) and the stimulus probes (∘), and their relative spatial locations. Most studies on transsaccadic perception use some form of a *same-spatial task* (Fig. 10.1C). This task involves subjects comparing stimuli that share one spatial location. So, typically the first stimulus appears in the retinal periphery, then the subject makes a saccade towards that location and after the saccade a second stimulus appears in the same spatial location. That is, this task looks at how we integrate visual information from a presaccadic peripheral preview and to a postsaccadic foveal view. Yet, transsaccadic perception may also serve to integrate the snapshots we obtain by discrete foveal views. Therefore, a second aim of this study was to examine how we integrate visual information that shares the same retinal location on the fovea by including a "*same-retinal task*" (Fig. 10.1A). We were interested in seeing how transsaccadic memory may differ when stimuli at different fixation locations are compared, so when they share the same retinal positions rather than the same spatial position. As control conditions we simulated the same retinal stimulation patterns from these two saccade conditions but within a single fixation (Fig. 10.1B, D).

The temporal sequence for an experimental trial was the same for all four conditions. Figure 10.2 shows horizontal eye position plotted as a function of time from one typical trial onto the respective stimulus events. Each trial began with a fixation cross, subtending $0.4°$ by $0.4°$ of visual angle, presented randomly at either $4°$ left or $4°$ right from subjects' head-centre. Once fixation was detected the first probe was presented. Probe duration from onset to offset was 40 milliseconds. In Experiments 2 and 3 this was followed immediately by a mask at the same spatial location to prevent confounds due to afterimages. Following the mask was the second fixation cross. Upon fixation on the second fixation cross the second probe was presented after a short delay. For saccade trials this delay would depend on the subject's saccade response latency. The

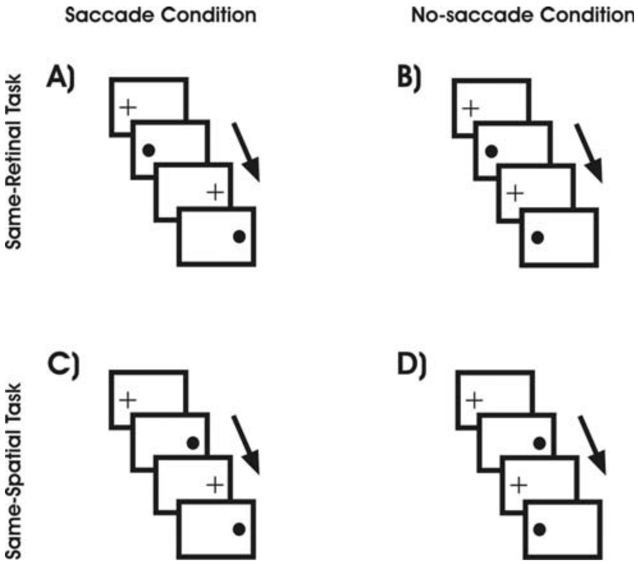

Figure 10.1: General experimental paradigm. Subjects were required to make two alternative forced choice comparisons between two probes (●). **A**) Saccade condition of the same-retinal task. Subjects looked at a fixation-cross (+), which was replaced with the first probe, and then, the second fixation-cross on the opposite side of the display. Subjects made a saccadic eye movement to the second fixation-cross and were presented with the second probe. **B**) No-saccade condition of the same-retinal task. Subjects maintained eye fixation as the two probes were presented at the same, foveal location as in (A). **C**) Saccade condition of the same-spatial task. The first probe was presented in the retinal periphery (position opposite to where the subject was fixating). After the subjects saccaded to the same location as the first probe, as shown by the second fixation-cross, the second probe was presented. **D**) No-saccade condition of the same-spatial task. This condition simulated the retinal stimulation of (C) as the subjects maintained eye fixation on the fixation cross.

delay during control trials was matched to the subject's saccade latency from saccade trials.

At the end of each trial subjects were required to compare the two probes by way of a two alternative forced-choice task. Subjects responded manually by pressing mouse buttons. Subjects were instructed to make their best guess if they were not sure. The second probe varied according to an adaptive test procedure that took the subjects'

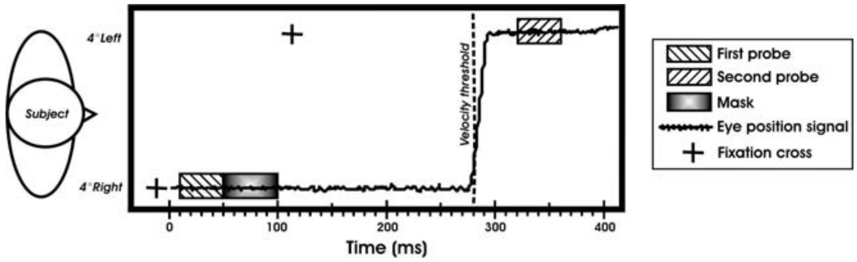

Figure 10.2: Time course for an experimental trial. The fixation cross is first presented to the right target location. Upon eye fixation the first probe (40msec) and mask (50msec) is presented. Following the mask is the presentation of the second fixation cross. After the subject saccades to the second fixation cross there is a short delay and the second probe (40msec) is presented.

performance on a trial-by-trial basis into account (Kontsevich and Tyler, 1999).

Each experimental session began with a calibration and a block of 50 practice trials. The practice block consisted of trials from each condition. Each condition consisted of 100 trials for a total of 400 trials. A customized computer network system of 3 microprocessor personal computers was used for both stimulus presentation and data recording. A projector back-projected stimuli onto a 1.9m by 1.4m display screen spanning 100° of visual angle horizontally by 90° of 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) with a sampling rate of 1000 Hz. Saccades were detected using a velocity criterion of 36° per second and eye position criterion of 1.5° of visual angle from the fixation point. The subject's head was stabilized using a bite-plate made by dental compound.

10.2.3 Experiment 1: Luminance

For experiment 1 subjects were required to determine whether the second probe was brighter or darker than the first probe. The probes subtended 2° of visual angle in diameter. The first probe (standard) was always the same luminance value (13 cd/m^2). Luminance levels for the second probe ranged from a luminance of 32cd/m^2 (white) to 3cd/m^2 (dark gray). The order of presentation for all 4 conditions was randomized and the discrimination threshold was determined concurrently for all 4 conditions.

10.2.4 Experiment 2: Orientation

Subjects were required to discriminate whether the second probe was oriented clockwise or counter-clockwise relative to the first probe. The probes were circles 2° of visual angle in diameter and displayed as sinusoidal gratings of varying luminance. The gratings' mean luminance was 17 cd/m^2 and the spatial frequency was 2 cycles per degree of visual angle. The orientation of the first probe's (standard) grating was randomly selected from 6 possible orientations, 40°, 45°, or 50° clockwise or counterclockwise relative to the straight-up direction. The second probes orientation varied by a step-size of 0.1° randomly presented on either side of the first probe. We deliberately did not test cardinal orientations as it has been shown that discrimination sensitivity for these angles are very high (Orban, Van den Bussche, and Vogels, 1984; Regan and Price, 1986).

The mask was a white circle subtending 2° of visual angle in diameter, presented for 50msec, and had a luminance of 33.61 cd/m^2. Conditions were blocked. Block A consisted of 50 trials from the same-retinal task with both the saccade and control conditions. Block B consisted of 50 trials from the same-spatial task with both the saccade and control conditions. Trials from each condition were randomized in both blocks. The order of blocks was either A-B-B-A or B-A-A-B and was counterbalanced between subjects.

10.2.5 Experiment 3: Shape

In this experiment, the probes were ellipses varying in size along the horizontal axis. Subjects discriminated whether the second probe was longer or shorter than the first probe. The first probe (standard) subtended 2° of visual angle vertically and 5.5°, 5°, or 4.5° of visual angle horizontally. The second probe changed by a step-size as small as 0.12° of visual angle either shorter or longer than the first probe. All ellipses were white (luminance: 33.61 cd/m^2). A mask was presented during the inter-probe interval. This mask was a white rectangle subtending 8° of visual angle horizontally and 2° of visual angle vertically, presented for 50msec, and had a luminance of 33.61 cd/m^2. Again, conditions were blocked for the same-retinal task and the same-spatial task.

10.3 Results

Trials that contained errors in eye movements were removed from the data before analysis. Using Matlab's nlinfit procedure we fitted Weibull functions to the subjects' data to estimate the subjects' discrimination thresholds defined at 75% probability correct. Figure 10.3 provides the psychometric functions for each condition of experiment 1 for one typical subject. A 2-way analysis of variance (ANOVA) for repeated measures was performed on the thresholds for each condition. The within-subject factors were Saccade (saccade condition versus control condition) and Task (same-retinal task versus same-spatial task). For these and all subsequent analyses, a p-value of 0.05 was adopted for significance. To examine transsaccadic memory directly we performed t-tests by comparing the saccade conditions with their respective control conditions within each task, that is, condition 1 (Fig. 10.1A) with condition 2 (Fig. 10.1B) and condition 3 (Fig. 10.1C) with condition 4 (Fig. 10.1D).

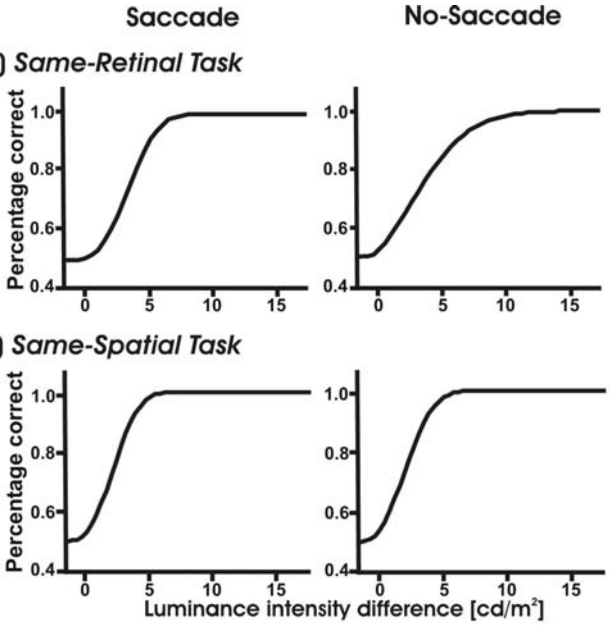

Figure 10.3: Psychometric functions of a typical subject for each condition in both the same-retinal task (**A**) and same-spatial task (**B**). Saccade conditions are shown in the left panels and no-saccade conditions are shown in the right panels. Absolute difference in stimulus intensity is plotted on the abscissa and percentage correct on the ordinate. Thresholds were determined at 75% percent correct.

10.3.1 Experiment 1: Luminance

Fig. 10.4 shows the average thresholds across all subjects for each condition derived from psychometric functions as in Fig. 10.3. Subjects showed slightly lower thresholds when comparing probes within a single fixation rather than across saccades and lower thresholds for the same-spatial task than the same-retinal task. However, the ANOVA did not yield any significant effects. The main effect for the saccade factor was $F_{(1,5)} = 3.965$; $p = 0.103$ and the main effect for Task was $F_{(1,5)} = 2.120$; $p = 0.205$. Likewise, the interaction was not significant, $F_{(1,5)} = 0.020$; $p = 0.894$. Even without Bonferroni correction we found no significant difference for either of the two comparisons between the saccade conditions and control conditions for both tasks, $t_{(5)} = 1.338$; $p = 0.238$ and $t_{(5)} = 1.261$; $p = 0.263$ respectively. Based on these results we concluded that subjects were as accurate comparing the luminance levels between the two probes during the saccade conditions as they were during the control

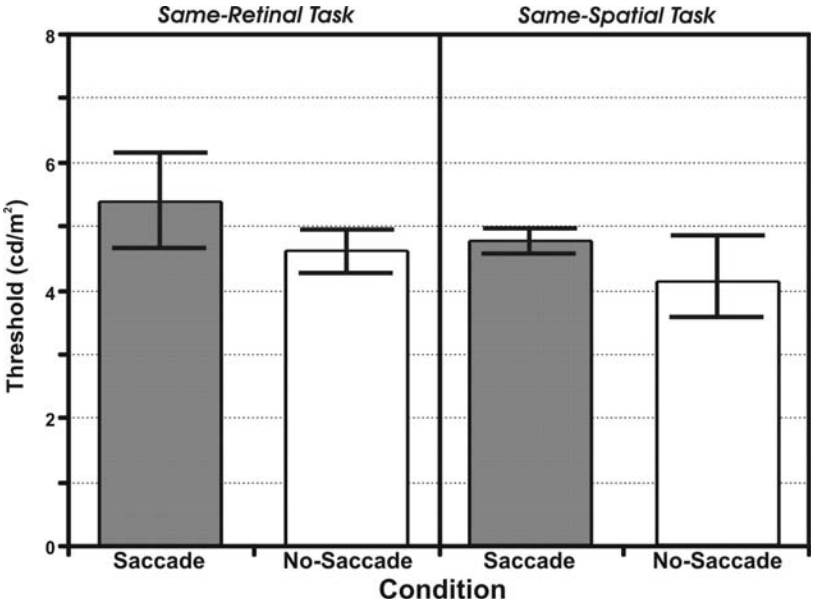

Figure 10.4: Results from experiment 1. The bars show the average thresholds across all subjects for each condition in both tasks. The results for the same-retinal task are shown in the left panel and the same-spatial task in the right panel. Within each task, the saccade condition (dark bar) was compared to the no-saccade condition (white bar). Subjects' discrimination thresholds were the same between saccade and no-saccade conditions in both tasks. Moreover, no significant difference of discrimination threshold was found between the two tasks.

conditions. Moreover, we found no significant difference for accuracy in comparing probes between the two tasks.

10.3.2 Experiment 2: Orientation

Figure 10.5B shows the results of Experiment 2 represented by the average thresholds for each condition derived from psychometric functions like those shown in Fig. 10.5A from one typical subject. Subjects had significantly higher thresholds when performing the same-spatial task than the same-retinal task; $F_{(1,5)} = 11.502$; $p = 0.019$. Thus, it was more difficult to compare the probes when one of them was presented in the retinal periphery than when they both appeared on the fovea. However, the interaction and the main effect for Saccade were non-significant; $F_{(1,5)} = 0.406$; $p = 0.552$ and

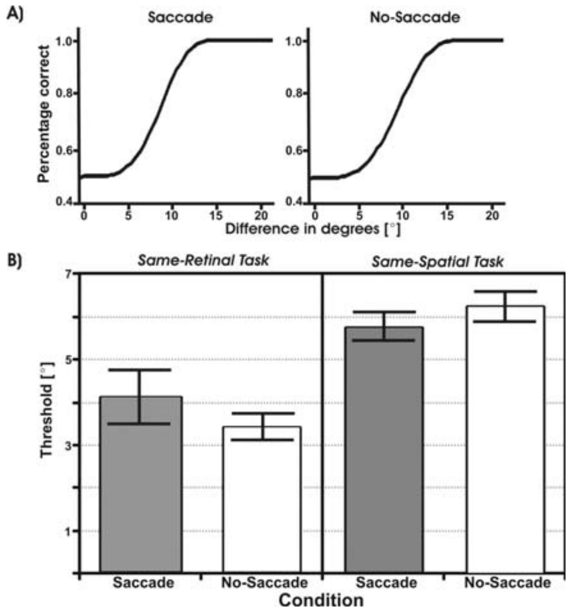

Figure 10.5: Experiment 2 results. **A**) psychometric functions from a typical subject for both conditions in the *same-spatial task*. Absolute difference in stimulus intensity is plotted on the abscissa and percentage correct on the ordinate. Thresholds were determined at 75% percent correct. **B**) The bars show the average thresholds across all subjects for each condition in both tasks. No difference was found between the saccade condition (dark bar) and the no-saccade condition (white bar) in either task. Subjects' comparisons were more accurate in the *same-retinal task* than in the *same-spatial task*.

$F_{(1,5)} = 0.103$; $p = 0.762$ respectively. No difference was found between saccade conditions and control conditions within both tasks; same-retinal task ($t_{(5)} = 0.742$; $p = 0.491$) and saccade-target task ($t_{(5)} = -0.317$; $p = 0.764$). These results suggest that subjects were able to compare the probes' orientation with the same accuracy during saccade conditions as non-saccade conditions. Moreover, these data are consistent with previous studies that show fine orientation discrimination in humans during fixation (Andrews, Butcher, and Buckley, 1973; Westheimer, Shimamura, and McKee, 1976).

10.3.3 Experiment 3: Shape

Figure 10.6A shows an example of one subject's psychometric functions for the same-retinal task and Fig. 10.6B shows the average thresholds obtained for each condition of experiment 3. As with experiment 2 the same-spatial task yielded significantly higher thresholds than the same-retinal task; $F_{(1,5)} = 6.585$; $p = 0.05$. In contrast, again the main effect for Saccade failed to be significant; $F_{(1,5)} = 0.038$; $p = 0.854$. And there was no evidence for a disrupting effect from saccades when we preformed individual t-tests (same-retinal task $t_{(5)} = -0.361$; $p = 0.733$ and same-spatial task $t_{(5)} = 0.31$; $p = 0.976$). Lastly, the interaction was non-significant; $F_{(1,5)} = 0.083$; $p = 0.785$. The relative low thresholds obtained by our subjects are consistent with previous studies that show that humans are very accurate at discriminating ellipses during fixation (e.g., Laursen and Rasmussen, 1975). Our data show that subjects were able to compare probes for differences in shape across saccades with the same accuracy as within a single fixation. As found in experiment 2, the subjects' comparisons were more accurate when both probes were presented on the fovea rather comparing one probe presented on the periphery and the other on the fovea.

10.4 Discussion

In this study, we investigated if the visual features of luminance, orientation, and shape are retained in transsaccadic memory and available for comparisons across saccades. We measured the extent to which subjects can retain these features across saccades by means of psychometric functions. For each of these three features tested in this study, we found that subjects were able to compare stimulus probes across saccades with statistically the same accuracy as when the probes appeared within a single fixation.

In addition, we used two tasks to study the effect of transsaccadic memory of these visual features at either same spatial or same retinal positions. For the *same-retinal task* both probes shared the same retinal position. In contrast, the probes in the second task, *same-spatial task*, were presented at the same spatial position. We found that for each experiment the discrimination thresholds were the same for the saccade and control conditions in both tasks. That is, our results suggest that transsaccadic memory works for both tasks and that visual information can be integrated regardless whether the stimuli were spatially or retinally fixed.

Our results from experiments 2 and 3 show that subjects had higher discrimination thresholds for the *same-spatial task* than the *same-retinal task*. One interpretation of this finding is that the visual system is better tuned for discriminating feature changes within local regions of the retina than it is for discriminating changes that occur within spatially, but not retinally, fixed regions. However, a simpler explanation could be that subjects were less accurate for orientation and shape comparisons when one probe was presented in the peripheral regions of the retina. These findings are consistent with previous studies that show that discrimination thresholds for orientation and shape are sensitive to retinal eccentricity (Paradiso and Carney, 1988; Whitaker, Latham, Makela, and Rovamo, 1993).

One possible solution to resolve this issue is to increase the size of the probes as a

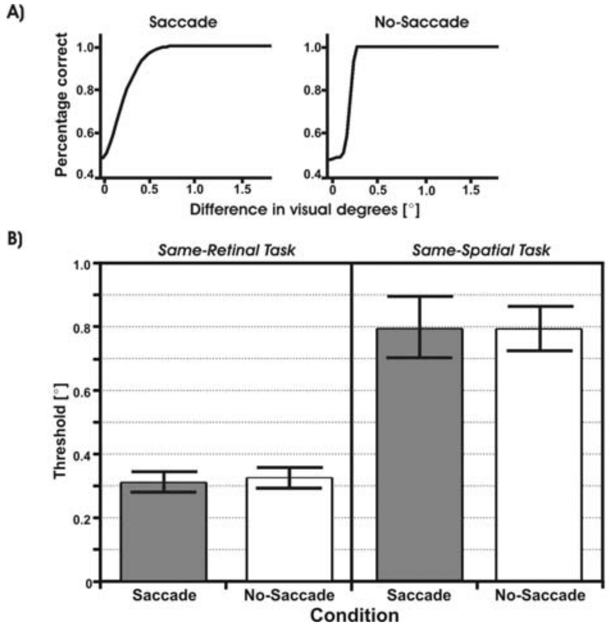

Figure 10.6: Experiment 3 results. **A**) Psychometric functions from a typical subject for both conditions in the same-retinal task. Absolute difference in stimulus intensity is plotted on the abscissa and percentage correct on the ordinate. Thresholds were determined at 75% percent correct. **B**) The bars show the average thresholds across all subjects for each condition in both tasks. No difference was found between the saccade condition (dark bar) and the no-saccade condition (white bar) in either task. Subjects' comparisons were more accurate in the *same-retinal task* than in the *same-spatial task*.

function of retinal eccentricity in the *same-spatial task*. Previous studies of orientation discrimination have found that discrimination thresholds are lowered (i.e. subjects are more sensitive) when stimulus-size is increased in scale as retinal eccentricity is increased (Makela, Whitaker, and Rovamo, 1993; Paradiso and Carney, 1988). If retinal eccentricity is the reason for the differences between the tasks in experiments 2 and 3, we should then expect lower discrimination thresholds in the *same-spatial task* by scaling the size of the probes. Theoretically thresholds of the *same-spatial task* may be able to equal thresholds of the *same-retinal task*.

Based on our findings we conclude that certain visual features are retained in transsaccadic memory and are available for comparisons across saccades. This is consistent with previous studies (Pollatsek et al., 1984; Palmer and Ames, 1992; Schlingensiepen, et al., 1986; Verfaillie, et al., 1994; Henderson and Siefert, 1999; Moore et al., 1998).

Our study, however, provides quantitative data to show to what extent these visual features are retained transsaccadically.

Regarding more complex tasks, it has been suggested that transsaccadic memory is poor with limited capacities of storage (Irwin and Andrews, 1996) and of encoding of information across saccades (Scholl, 2000; Henderson and Hollingworth, 1999; Hollingworth, Schrock, and Henderson, 2001). This has been interpreted to mean that our subjective impression of perceiving a highly detailed representation of the visual world is an illusion. For example, O'Regan (1992) has proposed that there is no need to retain information across saccades because the world can be used as an "external memory store".

We agree in that it does make sense to use the physical visual scenery as a form of memory – at least to some extent. However, one limitation of a purely external storage of information is that the visual input has to be processed. This is a time and energy consuming procedure (Salthouse, Ellis, Diener, and Somberg, 1981, Henderson, 1992). It would be surprising if the brain discarded all processed information with each saccade. But it is rather likely that the brain's transsaccadic memory takes into account the costs and gains of storing visual information and integrating it with new information. Indeed, this is likely the reason why we scan the features of complex objects with multiple saccades (Yarbus, 1967; Stark and Ellis, 1981) rather than fixating some central point within the object.

Further evidence for transsaccadic memory comes from neurophysiological studies showing that the brain retains visual representations during eye movements. For instance, certain brain areas are involved in keeping track of spatial locations of objects in the world with corresponding changes in eye position. That is, spatial information is updated as the head or eyes move. This so called "remapping" has been found to take place on many levels of the primate's visual system including the lateral intraparietal area (Duhamel, Colby, and Goldberg, 1992), the frontal eye field (Umeno and Goldberg, 1997), the superior colliculuss intermediate layer (Walker, Fitzgibbon, and Goldberg, 1995), and the striate and extrastriate cortex (Nakamura and Colby, 2000; 2002). Moreover, an objects orientation may be another form of visual information that is retained across saccades (Moore, Tolias, and Schiller, 1998). These researchers found that neurons from area V4 in the primate brain retain orientation information by a resurgent response in neurons selectively tuned to that orientation of a saccade target immediately prior to the saccade. Our current study suggests that similar studies should test the neural retention of luminance and shape information across saccades.

In conclusion, the mechanisms that govern transaccadic memory are only beginning to be understood. This study investigated the quantitative effect of saccades on the storage of visual features of luminance, orientation, and shape. We found that subjects were able to compare these visual features across saccades with the same accuracy as when comparing them within a single fixation. This is an essential condition for transsaccadic integration to occur. We suggest that further research is necessary to construct a quantitative model of transsaccadic memory. The data from the present study may serve as building blocks for such a model.

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