Vision Research 49 (2009) 1256–1266

Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

Attention during sequences of saccades along marked and memorized paths

Timothy M. Gersch [a,*], Eileen Kowler [a], Brian S. Schnitzer [a], Barbara Anne Dosher [b]

[a] Department of Psychology, Rutgers University, 152 Frelinghuysen Road, Piscataway, NJ 08854, USA
[b] Department of Cognitive Sciences, University of California, Irvine, 3151 SSP Irvine, CA 92697, USA

ARTICLE INFO

Article history:
Received 5 June 2007
Received in revised form 22 October 2007

Keywords:
Saccades
Attention
Eye movements
Sequences
Motor control
Orientation discrimination

ABSTRACT

Natural scenes are explored by combinations of saccadic eye movements and shifts of attention. The mechanisms that coordinate attention and saccades during ordinary viewing are not well understood because studies linking saccades and attention have focused mainly on single saccades made in isolation. This study used an orientation discrimination task to examine attention during sequences of saccades made through an array of targets and distractors. Perceptual measures showed that attention was distributed along saccadic paths when the paths were marked by color cues. When paths were followed from memory, attention rarely spread beyond the goal of the upcoming saccade. These different distributions of attention suggest the involvement of separate processes of attentional control during saccadic planning, one triggered by top-down selection of the saccadic target, and the other by activation linked to visual mechanisms not tied directly to saccadic planning. The concurrent activity of both processes extends the effective attentional field without compromising the accuracy, precision, or timing of saccades.

© 2007 Elsevier Ltd. All rights reserved.

1. Introduction

Selective attention plays a crucial role in the control of saccadic eye movements. Attention determines which visual objects or details are used to compute the location of the saccadic endpoint (Cohen, Schnitzer, Gersch, Singh, & Kowler, 2007; Vishwanath & Kowler, 2003; Melcher & Kowler, 1999). Attending to the chosen target ensures that the saccade will be accurate, and the line of sight will not be drawn to irrelevant, unwanted objects or locations nearby.

The central role of attention in the control of saccades is consistent with the longstanding practice of equating shifts of attention with shifts of the line of sight during visual or cognitive tasks. This is represented by the attempts to use patterns of saccades to infer the locus of attention in tasks such as reading, search, visual problem solving, or picture perception (e.g., Epelboim & Suppes, 2001; Itti & Koch, 2001; Legge, Klitz, & Tjan, 1997; Rao, Zelinsky, Hayhoe, & Ballard, 2002). The belief in unbreakable links between eye movements and attention is so well entrenched that it affects the interpretation of seemingly unrelated attentional phenomenon. For example, attention can be distributed across space to regions sharing common features—a pattern at variance with the sequential nature of eye movements. Nevertheless, such broad distributions of attention have been thought to provide the perceptual landmarks that guide saccades to (presumably) useful or important regions (Bichot, Rossi, & Desimone, 2005; Sàenz, Buraĉas, & Boynton, 2003). This is an interesting idea, but it is not known whether, or how, such distributed patterns of attention are converted to sequences of saccades, or even whether broad distributions of attention can be maintained during the intervals between successive saccades when saccadic planning places additional, and perhaps conflicting, demands on attention.

Thus, while there is little doubt that attention plays an important role in saccadic guidance, significant questions remain about how closely eye movements and attention are linked to each other during the performance of active visual tasks. One major reason for such limited knowledge is that virtually all the prior "dual-task" studies of the connections between saccades and attention (i.e., studies that assessed both eye movements and perceptual attention concurrently) have been restricted to events that occur during the latency interval between a target-cue and a single saccadic response. By contrast, naturally occurring saccades are made as part of ongoing saccadic sequences, and the important attentional and perceptual events occur during the intersaccadic pauses. Planning and executing saccadic sequences calls upon mechanisms of visual analysis and saccadic preparation that are never needed during single-saccade tasks. As a result, attention may be distributed differently, and perhaps more broadly, during the performance of saccadic sequences than during the interval preceding single saccades performed in isolation.

* Corresponding author. Present address: Mahoney Center for Brain and Behavior, Center for Neurobiology and Behavior, Columbia University College of Physicians and Surgeons, 1051 Riverside Drive, Kolb Research Annex, New York, NY 10032, USA.
E-mail addresses: tgersch@rci.rutgers.edu, tmg2121@columbia.edu (T.M. Gersch).

0042-6989/$ - see front matter © 2007 Elsevier Ltd. All rights reserved.
doi:10.1016/j.visres.2007.10.030

The goal of the present study was to examine the distribution of attention during the performance of saccadic sequences. A detailed outline and rationale of the experiments will be presented after a brief summary of relevant prior dual-task work on pre-saccadic shifts of attention.

1.1. Pre-saccadic shifts of attention

Prior studies using dual-task methods (perceptual and saccadic performance measured concurrently) have shown that it is not possible to fully dissociate the locus of attention from the selected saccadic goal. For example, Kowler, Anderson, Dosher, and Blaser (1995) found that perceptual recognition of targets located at the goal of a saccade is better than recognition of targets at other locations. Shifting some attention away from the saccadic goal could improve perceptual performance, but at a cost of prolonged saccadic latency and diminished saccadic accuracy. Other studies have obtained similar perceptual results for either the latency interval preceding a single saccade (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; McPeek, Maljkovic, & Nakayama, 1999), or a pair of saccades (Godijn & Theeuwes, 2003), or for the pauses between successive saccades made as part of repetitive sequences (Gersch, Kowler, & Dosher, 2004). In the case of the repetitive sequences, Gersch et al. (2004) found that when saccades were made in a simple triangular path, attention (assessed by an orientation discrimination task) was limited to the goal of the next saccade, and did not spread to the subsequent saccadic targets. Recent neurophysiological findings that low-level microstimulation within FEF increases V4 activity at the presumed saccadic landing site point to a neural pathway that may mediate the pre-saccadic perceptual changes (Moore & Armstrong, 2003; also, Müller, Philiastides, & Newsome, 2005, for a related finding).

Some neurophysiological studies have reported that ties between saccades and attention may be weaker than the behavioral studies have suggested. Neurons in FEF or LIP that typically fire before saccades also respond to attention-grabbing visual targets far from the saccadic goal (Bisley & Goldberg, 2003; Murthy, Thompson, & Schall, 2001). Whether such neural activity implies a general ability to dissociate saccades and perceptual attention during scanning tasks remains to be determined.

1.2. The present study

The present study investigates attention during the performance of non-repetitive sequences of saccades to find out how closely attention is connected to the planning of saccades. Non-repetitive saccadic sequences are more characteristic of natural viewing than either the single saccades, saccadic pairs, or repetitive sequences studied in the prior work reviewed above. For reasons outlined in the following section, the distribution of attention during non-repetitive saccadic sequences may be different from that observed so far in studies of single saccades.

In this study, attention will be assessed by an orientation discrimination task in which perceptual probe targets are flashed during randomly selected intersaccadic pauses. Thus, our study of pre-saccadic attention shifts can be viewed as analogous to psychophysical studies of attention during steady fixation that manipulate attention by means of location cues (e.g., Dosher & Lu, 2000a,b). The crucial difference is that the variable that manipulates the allocation of attention is not a location cue, but the location of the saccadic targets.

1.2.1. Dissociating saccades and attention with non-repetitive sequences

We studied two kinds of saccadic sequences: (1) sequences in which targets were marked by a visual cue (specifically, a color difference), and (2) sequences followed from memory. We specified the location of the targets making up the sequence, rather than allowing the subjects to scan freely, in order to remove ambiguity about the saccadic path and make it possible to relate the observed distribution of attention to the locations of multiple saccadic targets.

With the first type of sequence we studied, sequences marked by a color cue, the color cue itself could provide a basis for allocating attention to locations beyond the immediate target of the saccade (i.e., "feature-based" attention: e.g., Melcher, Papathomas, & Vidnyanszky, 2005; Motter, 1994; Motter & Belky, 1998; Shih & Sperling, 1996; Sàenz et al., 2003), either ahead or behind the current locus of fixation. Psychophysical evidence for such a distribution of attention across space has been obtained for periods of steady fixation, but not for the pauses between saccades. If attention is allocated across space to locations other than the immediate saccadic goal, and, importantly, if such a distribution of attention does not draw saccades along with it, we would have evidence for a useful dissociation between attention and saccadic planning, a dissociation that improves the perceptibility of portions of a scene without interfering with the ongoing pattern of saccades. Such a dissociation would also show that "feature-based" attention is not related directly to saccadic planning.

With the second type of saccadic sequence we studied, sequences executed from memory, it is also possible that attention can be allocated to locations beyond the immediate saccadic target, but for a different reason than suggested above for color-cued paths. With memorized sequences of saccades, attention could be controlled by processes involved in planning the sequence or representing the plans. Sternberg, Wright, Knoll, and Monsell (1978), in a classical study of sequential motor planning, studied the performance of memorized sequences of button presses or spoken syllables and found that both the time to initiate a sequence, and the time interval between successive responses, increased with the number of required elements in the sequence. The same pattern of results has been found for sequences of saccades (Inhoff, 1986; Zingale & Kowler, 1987). Sternberg et al. (1978) proposed a model in which the plans for the motor responses making up the sequence are stored in advance, and then retrieved as needed while the sequence is in progress. More recent neurophysiological work has provided evidence that plans for memorized sequences of movements may be represented in neural areas such as premotor cortex (PMC) and prefrontal cortex (PFC) (Fujii & Graybiel, 2003; Ohbayashi, Ohki, & Miyashita, 2003). Performance with the non-repetitive memorized sequences can show whether perceptual attention, in contrast to purely memory-based processes, is involved in the representation of the stored saccadic plan. Godijn and Theeuwes' (2003) finding that attention is allocated to both saccadic targets prior to a 2-saccade sequence is consistent with a role for attention in representing multiple saccadic plans.

1.2.2. Outline of the study

Part 1 of this paper will study attention during the performance of saccadic sequences in which the path is marked by a color cue. Part 2 will study attention during the performance of sequences performed from memory. Analyses will verify that the sequences are performed accurately, and then will evaluate the distribution of attention during the intersaccadic pauses.

Perceptual attention will be assessed by reports of the orientation of a perceptual probe (a medium-contrast Gabor tilted 22.5° to the left or right of vertical) presented during randomly selected intersaccadic pauses. Probed Gabor locations will include those on and off the designated saccadic path, and locations ahead and behind the current locus of fixation. The comparison of performance ahead and behind the current locus of fixation is important. Any effects on attention that could be attributed solely to the color

difference between on and off-path locations (in Part 1) would be expected to affect perceptual performance equivalently for locations ahead and behind the current locus of fixation. By contrast, effects on attention due solely to saccadic planning would be expected to apply to perceptual performance at the locations ahead of (not behind) current fixation, and lead to better perceptual performance at saccadic targets than non-targets.

Analysis of perceptual performance in Part 2 (memorized path) will also show the extent to which attention is involved in long-range saccadic plans. Any allocation of attention along the saccadic path ahead of current fixation and extending beyond the next saccadic target will implicate a role for attention in the representation or retrieval of the saccadic plans for the sequence.

Finding evidence for an allocation of perceptual attention to locations other than the immediate saccadic goal, without cost to saccadic performance, in either Part 1 (marked path) or Part 2 (memorized path), will show that there is not a 1:1 relationship between the locus of extrafoveal attention and the selected saccadic goal. Maintenance of accurate saccades in the face of a broader spatial distribution of attention will require either a process for converting a broad distribution of attention into a single goal location, or a separate executive designation of the goal region independently of the distribution of perceptual attention.

2. Methods

2.1. Eye movement recording

Movements of the right eye with head stabilized by a bitebar were recorded by a Generation IV SRI Double Purkinje Image Eyetracker (sensitivity < 1 arcmin) (Crane & Steele, 1978). Tracker output was filtered (100 Hz) and sampled every 5 ms (see Gersch et al., 2004, for details).

2.2. Observers

Three paid volunteers were tested (EC, GT and SK), each with normal, uncorrected vision. Each was unaware of the purpose of the experiment.

2.3. Stimulus display

Stimuli were displayed on a Dell P793 CRT monitor (13° × 12°; viewing distance 115 cm; resolution 1.46 pixels/minarc; refresh rate 75 Hz). Background luminance was 54.4 cd/m^2 and maximum luminance was 108 cd/m^2 at the refresh rate used. The display was a 5 × 5 array of 1° diameter outline circles separated by 1.5° (center-to-center). Circles were green (x = .280, y = .602, luminance = 81.6 cd/m^2) or red (x = .628, y = .338, luminance = 22.2 cd/m^2) as measured with a UDT SLS 9400 Colorimeter. The 5 × 5 array was bordered by four rectangular areas that each held three crosses.

In Part 1 (marked path), five of the circles were green and the rest red (see Fig. 1). Saccades were made in sequence across either columns or rows to look from one green circle to the next. Scanning began at the green cross on one of the four sides (chosen randomly) and ended at the central red cross on the opposite side. In Part 2 (memorized path), all circles were either red or green (randomly selected), a line diagram presented before each trial showed the saccade path, and an arrow in place of the starting green cross showed the direction of the first saccade (Fig. 7).

Perceptual performance was assessed by the ability to identify the orientation of a Gabor test stimulus that was flashed briefly in one of the central nine circles during a randomly selected intersaccadic pause (Fig. 1b) (Carrasco, Penpeci-Talgar, & Eckstein, 2000; Dosher & Lu, 2000a,b; Gersch et al., 2004). The Gabor was generated according to the following:

$$l(x,y) = l_0(1.0 + a\sin(2\pi f(x\cos(\theta) \pm y\sin(\theta))\exp(-(x^2+y^2)/(2\sigma^2)))), \quad (1)$$

where f is the spatial frequency (2.24 cycles/deg), l_0 the mean luminance (54.4 cd/m^2), θ the orientation (±22.5° from vertical), σ the standard deviation of the Gaussian window (0.89°), (x, y) the spatial coordinates in the display, and a the amplitude. Amplitude was determined from the contrast (the difference between maximum and minimum luminance divided by twice the mean), and contrast was chosen to obtain, on average, about 70–90% correct reports on the orientation discrimination task. Testing multiple contrasts was impractical because of the large number of conditions in the experiment (see below).

Three frames of Gabor were interleaved with four frames of visual noise (total duration 91 ms). The Gabor with superimposed noise is depicted in Fig. 1b, second panel from top. The noise was a matrix of 20 × 20 dots (dot size = 3 × 3 pixels)

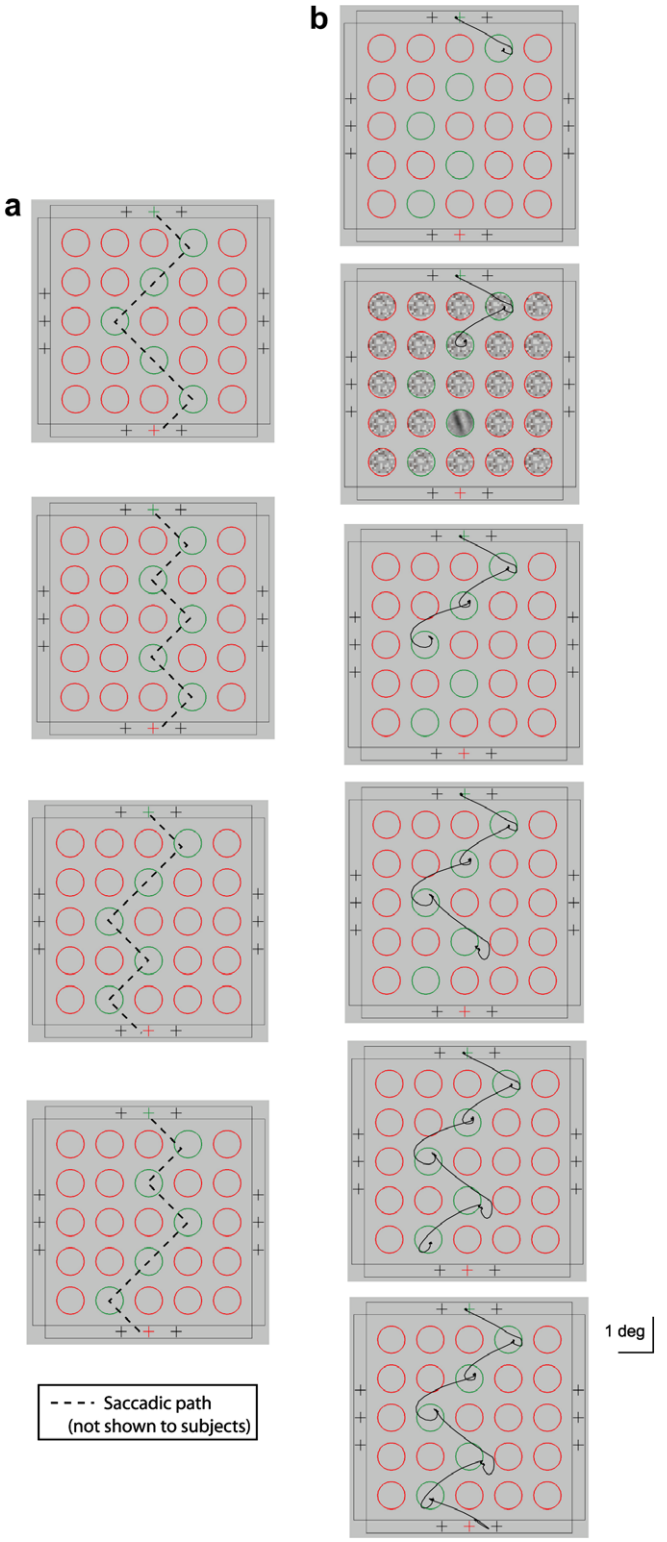

Fig. 1. (a) Examples of experimental displays. Each contains 25 circles (diam = 1°, center-to-center separation = 1.5°). The dashed line (not shown to subjects) designates the saccadic path. In the actual experiment, five green circles designated the saccadic path with the eye starting at the green cross and ending at the red cross. Eight different saccadic paths were tested (the four shown plus their left/right mirror images). Display orientation varied so that start position (green cross) was either top, bottom, right, or left. The Gabor appeared in one of the central nine circles. (b) Sequence of events during a typical trial. Time runs from top to bottom The superimposed black line is a representative eye trace showing the path of saccades made from the starting cross (top panel), along the path (middle panels), to the ending cross at the bottom. The Gabor and superimposed noise fields appeared briefly (91 ms; second panel) while the eye was fixating near the middle of the path.

whose luminance levels were Gaussian distributed (*SD* = 33% maximum display contrast). The Gabor and noise frames could appear in one of the central nine circles of the display, thus avoiding testing near the edges. The noise was presented in all circles so that transients would not call attention to the location of the Gabor. To avoid testing near the onset or termination of the saccadic sequence, the Gabor and noise appeared during a randomly chosen time when the eye was likely to be fixated on one of the three on-path locations within the central nine of the display. Thus, the full mapping of attention during the saccadic sequence required testing at each of the nine different central locations when fixation was at each of the three central on-path locations, for a total of 27 different conditions.

2.4. Gabor location cue

Part 1 included sessions in which the location of the Gabor either was or was not cued in advance of the trial. The Gabor location cue, when used, was a yellow circle for locations on the saccadic path, or a purple circle for locations off the path. Analysis of both the saccadic and perceptual data showed that the pattern of the results was the same regardless of the presence of the Gabor location cue. Thus, both saccadic and perceptual results will be combined across the pre-cue and no pre-cue sessions.

2.5. Procedure

The sequence of events is shown in Fig. 1b (time is running from top to bottom). The subjects fixated a green cross and started the trial when ready by pressing a button. After 100 ms a beep sounded for 50 ms, which was the signal to begin making the sequence of saccades. Eight different saccadic paths were tested (the 4 in Fig. 1a plus their mirror images). Subjects were instructed to make a saccade to each circle along the path, and to maintain a steady, brisk pace, not altering the rate of saccades in anticipation of or in response to the Gabor (the same instructions as used in Gersch et al., 2004) for each of the four possible starting locations (one for each side of the display).

After a random delay (300–1500 ms after the signal to begin making saccades) an on-line algorithm began monitoring the eye movement data for the occurrence of the next saccade using a velocity criterion determined for each subject and verified empirically by inspection of individual eye traces. At 30–160 ms after this saccade was detected, the seven critical frames (three Gabor and four noise) were presented. Subjects continued to scan the display even after the Gabor appeared until they reached the red cross on the other side of the screen. A post-cue (same color as the pre-cue described above), was displayed after the saccadic sequence was completed to indicate the location of the Gabor. The post-cue appeared in all trials and was needed to avoid errors expected solely on statistical grounds when the location of a signal is unknown (Sperling & Dosher, 1986). The report of Gabor orientation (right or left) was given by a button press. Feedback was presented after the response.

Sessions were also run using identical stimuli on the same days in which (1) perceptual performance was tested during steady fixation on one of the on-path location (randomly selected on each trial) within the central nine circles, and (2) saccades were made but without a report of the Gabor orientation taken at the end of the trial.

Experimental sessions contained 60–100 trials each. Trial length was 2 s for GT, 2.2 s for EC, and 2.5 s for SK. These lengths were chosen for each observer in preliminary sessions to ensure that each would be able to complete the sequence. Data collection and calibration required laboratory visits of about 2 h on any given day. Data were collected in 120–150 laboratory visits per subject, distributed over a period of 10 months.

2.6. Analyses of eye movement data

The beginning and end positions of saccades were detected off-line by means of a computer algorithm employing an acceleration criterion. The "critical saccade" was defined as the first saccade that occurred after the appearance of the Gabor and noise frames. Eye position at the onset of the critical saccade determined which circle was fixated at the time of the presentation of the critical frames.

To establish that the saccadic sequences were followed correctly, each saccade was categorized as either following the prescribed path ("good") or according to the type of error. The majority of errors fell into two categories: saccades that landed off the path, or saccades that skipped over a location on the path. A saccade was deemed to be off the path if the eye fixated a circle that was not one of the five circles in the prescribed saccadic path. Saccades directed back to an on-path location originating from a location off the path, and saccades that were directed from one off-path location to another, were grouped as "other" in the presentation of the data. Corrective saccades (secondary saccades that followed a primary saccade to the target) were not included in the analysis. Note that only trials in which the critical saccade was on the path were included in the analysis of the perceptual data.

Other saccadic characteristics that were analyzed were: (1) offset error (distance between fixation position and the center of the fixated circle) of the "good" saccades; (2) the average number of targets hit per trial; (3) the average time interval preceding saccades.

Trials were omitted from the perceptual results if off-line analyses showed that the Gabor appeared during a saccade (1–13%). Occasional trials (~1%) were eliminated because saccades were initiated before the start signal. Data were based on a total of 8522 trials for EC (7209 dual-task, 744 steady fixation and 569 saccades-only), 11,678 trials for GT (9152 dual-task, 1558 steady fixation and 968 saccades-only), and 6877 for SK (5796 dual-task, 775 steady fixation and 306 saccades-only). Trials eliminated from the analyses of the perceptual results were included in the overall analyses of saccadic performance.

2.7. Statistical analysis: Generalized estimating equations

Analyses of the perceptual results determined the magnitude and significance of the influence of path status (on the path of saccades vs. off the path) and the location of the Gabor probe relative to current fixation (ahead vs. behind). As noted earlier, an effect of saccadic planning on orientation identification would be expected to improve performance on the path for locations ahead of current fixation. An effect of other variables (e.g., color) would be expected to improve performance on the path for locations both ahead and behind current fixation. Since the dependent perceptual variable in this case is binary (correct or incorrect report of Gabor orientation), logistic regression was used to predict perceptual performance (Hosmer & Lemeshow, 2000). Logistic regression determines the percentage of variance in the dependent variable (the orientation report) that is explained by the independent variables, namely, path status (on vs. off) and location (ahead vs. behind). The influence of these two independent variables can also interact such that path status (on/off) could have a significantly greater effect at locations ahead of current fixation than at locations behind current fixation.

Logistic regression applies maximum likelihood estimation after transforming the dependent variable into a logit variable (where logit refers to the natural log of the odds of a correct orientation report). The coefficients of the fitted model for the separate independent variables (path status and location), therefore, represent the log-odds ratio, which is the natural log of the odds ratio. (The odds ratio is the ratio of number of correct orientation reports to the number of incorrect reports.) Significant main effects of the independent variables (path status and location) are shown by significant coefficients in the fitted model (and their corresponding odds ratios). In addition, the interaction coefficients of the fitted model represent the significance of the interaction between these two independent variables on orientation discrimination.

To include the data from our three subjects in the analysis, the method of Generalized Estimating Equations (GEE) was used to fit the logistic regression model (Liang & Zeger, 1986). The GEE method takes into account possible within-subject correlations, thus allowing one model to be fit to the data set that consists of multiple observations from three subjects.

3. Results

3.1. Marked saccadic paths (Part 1)

3.1.1. Saccadic performance

The vast majority of saccades followed the path, as shown by the high proportion of "good" saccades in Fig. 2a and Table 1. Table 1 also shows that these on-path saccades landed well within the target circles (average error of 20′–24′ from the center of the 1° diameter circle). Pauses between saccades were on average about 200–300 ms, allowing 4.6–5.7 of the six targets (five on-path circles and the ending cross) to be scanned during the trials.

Table 1 shows that saccadic performance in the control trials in which no concurrent Gabor judgments were made (see Section 2) was essentially the same as it was for trials with the concurrent judgments. This result shows that the perceptual task did not impair saccadic planning, and the effects of attention (discussed below) were not due to a strategy of either delaying or redirecting saccades.

3.1.2. Perceptual performance

To evaluate the distribution of attention across space, perceptual performance was analyzed separately for each of the nine central locations of the display where the Gabor could appear. Analyses were restricted to trials in which the Gabor appeared while the eye was fixating one of the three on-path locations within the central nine locations of the display. These constituted the vast majority (95%) of the trials, which was expected, given that the range of possible times of the Gabor was selected so that it would appear when the eye was in the central portion of the path.

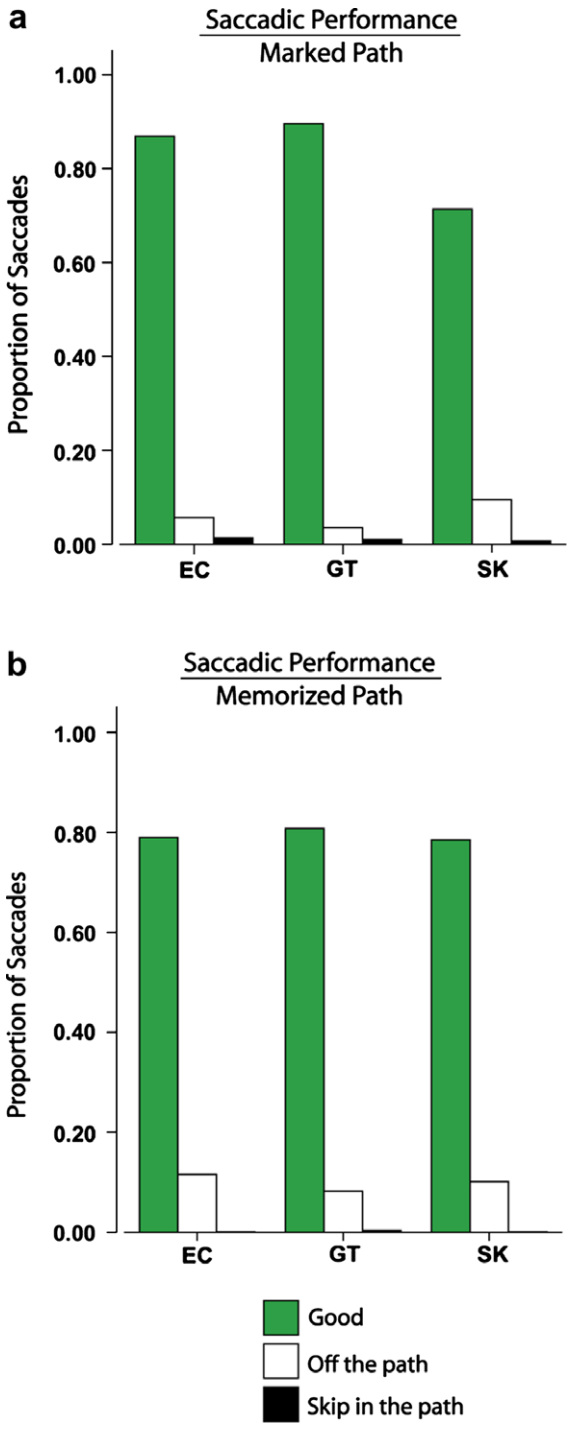

Fig. 2. Proportion of saccades in three categories: "Good" saccades that remained on the path, saccades that strayed off the path, and saccades that skipped over a location on the path. Results are shown separately for (a) Part 1 (marked paths) and (b) Part 2 (memorized paths). Proportions are based on 16,000–26,000 saccades/subject.

To illustrate the comparisons that will be made across locations, Fig. 3 shows performance (proportion correct) for each Gabor location for subject EC when the eye was fixating the first (Fig. 3, Ahead) and the last (Fig. 3, Behind) of the on-path locations within the central nine. If the color difference between on and off-path locations were solely responsible for the distribution of attention, the perceptual performance ahead of current fixation, when the eye was at the first of the three on-path locations (Fig. 3, Ahead), and behind current fixation, when the eye was at the last on-path location (Fig. 3, Behind), would be equivalent because the perceptual features and retinal eccentricities of the display were identical in these two cases. On the other hand, if saccadic planning were solely responsible for the allocation of attention, perceptual performance would be different for locations that are ahead and behind current fixation. In particular, for on-path locations ahead of current fixation (i.e., saccadic targets), we would expect better perceptual performance than for the surrounding off-path locations. For on-path locations behind current fixation (i.e., previously examined locations), we would not expect any on-path advantage.

Analyses (below) show that both saccadic planning and color differences contributed to the perceptual results. Specifically, there was an on-path advantage both ahead and behind, with the on-path advantage stronger in the first case, when the eye was at the first location and the on-path locations were saccadic targets.

These effects are shown for all three observers in Fig. 4. The figure shows the proportion of correct identifications for on-path locations that were either ahead or behind the current locus of fixation. Performance for the surrounding off-path locations is also shown. Thus, the "ahead" data corresponds to performance when the eye was at the first of the three central on-path locations (e.g., in Fig. 3) and the "behind" data corresponds to performance when the eye was at the last of the three central on-path locations (Fig. 3). For both "ahead" and "behind", data obtained for off-path locations with the same retinal eccentricity were combined.

Fig. 4 shows that there was an on-path advantage for both "ahead" and "behind" data. That is, perceptual performance at on-path locations was better than at off-path locations of equivalent eccentricities whether on-path locations were ahead or behind the current fixation. Thus, at least some of the on-path advantage was not due to saccadic planning, because saccadic planning would have come into play only for the "ahead" data. Saccadic planning did, however, play a role because Fig. 4 also shows that the on-path advantage was greater for the "ahead" locations than the "behind" locations. Note that the main reason for the greater on-path advantage in the "ahead" data was a suppression of off-path performance relative to that obtained for locations behind current fixation.

The on-off path differences are further summarized in Fig. 5, which compares the magnitude of the on-path advantage for locations "ahead" and "behind" current fixation, and for equivalent locations during the steady fixation trials. The on-path advantage was greater ahead than behind fixation, shown by a significant interaction between path status and location (GEE (see Section 2) Interaction coefficient = 0.365, $p = 0.0386$). The on-path advantage during steady fixation was not statistically different from that in the "behind" locations during saccadic scanning (Interaction coefficient = 0.1108, $p = 0.5694$), but was significantly different from that found in the "ahead" locations (Interaction coefficient = 0.4875, $p = <0.0001$, also see Fig. 5).

Performance ahead of current fixation, on the path, also had another interesting feature. Fig. 4 shows that performance for the first saccadic target on the path (eccentricity = 2.12°) was better than performance at the same eccentricity off the path (Odds ratio, OR = 2.71, $p = <0.0001$). In addition, performance for the second saccadic target on the path (eccentricity = 3°) was also better than performance at an off-path eccentricity of 2.12° (OR = 1.67, $p = .0012$). These results show that when performing non-repetitive sequences of saccades along a marked path, attention is allocated to locations beyond the target of the immediate saccade. This allocation of attention to a target not related to the immediate saccadic plan occurred without causing frequent skips or inaccurate saccades. (Note that these results show that attention is allocated to multiple locations on the saccadic path. This pattern could result either from the simultaneous distribution of attention in

Table 1
Marked path[a] (Part 1)

Characteristics of saccades							
Subject	Proportion of total saccades[b]				Good saccades[f]		
	Good[f]	Skips[g]	Off the path[h]	Other[i]	Error at saccade offset[c] (minarc) Mean (*SD*) *N*	Average number of targets hit per trial[d]	ISP[e] (ms) Mean (*SD*) *N*
With concurrent Gabor judgments							
EC	0.88	0.01	0.06	0.05	24 (12) 14,257	4.6	291 (90) 14,257
GT	0.90	0.01	0.03	0.06	20 (11) 19,222	5.7	209 (56) 19,222
SK	0.75	0.01	0.10	0.14	24 (12) 13,460	5.5	261 (94) 13,460
Without concurrent Gabor judgments							
EC	0.94	0.01	0.03	0.02	23 (10) 648	4.6	299 (76) 648
GT	0.91	0.004	0.03	0.06	20 (11) 1809	5.5	220 (57) 1809
SK	0.79	0.01	0.08	0.12	23 (12) 2877	5.6	254 (89) 2877

[a] "Marked path" refers to trials in which the saccadic path was marked by a color cue.
[b] "Total saccades" refers to all saccades except secondary, corrective saccades that followed a primary saccade to a target.
[c] "Error at saccadic offset" refers to vector distance between eye position at the time of saccadic offset and the center of the nearest circle.
[d] "Average number of targets hit per trial" refers to number of saccadic targets on the path that were successively fixated during a trial.
[e] "ISP" refers to intersaccadic pause duration, the interval preceding each good saccade.
[f] "Good" refers to saccades that followed the prescribed saccadic path.
[g] "Skips" refers to saccades that skipped the next location on the path and brought the line of sight to a subsequent on-path location.
[h] "Off the path" refers to saccades that brought the line of sight to a location off the prescribed path.
[i] "Other" refers to the remaining types of erroneous saccades (off-path to on-path locations, off-path to off-path locations, backward saccades).

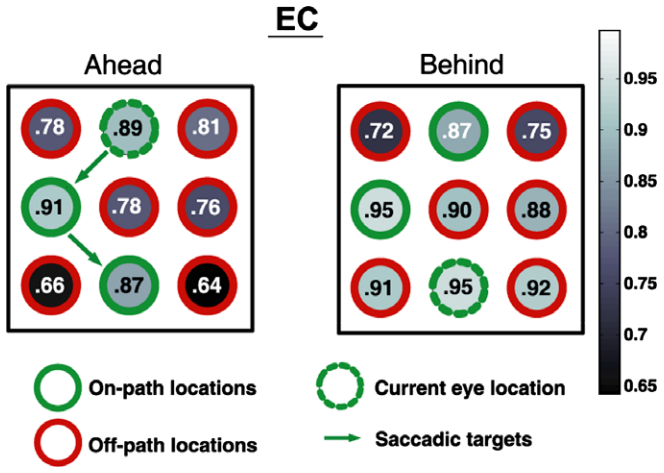

Fig. 3. Orientation discrimination during pauses between saccades for different locations of the eye when the Gabor appeared. Data are shown for one observer. Ahead (left panel): Current eye position (dashed circle) was the first location in the central nine. Two other locations in the central nine (shown by the green arrows) are targets of saccades. The dashed circles and the green arrows are for illustration purposes only and were not shown to the subjects. Behind (right panel): The eye reached the final location in the central nine. Numbers inside and intensity levels of the circles represent proportion correct reports. Green outlined circles are on the saccadic path, and red outlined circles are off the saccadic path. For each of the three locations along the path, data were pooled across the four starting locations and eight different saccadic paths (see Fig. 1), and across trials in which Gabor location was cued or not cued. Each proportion was based on 100–200 observations.

parallel to multiple locations or, alternatively, from a strategy of attending to a different selected on-path location, or a different subset of locations, on each trial (Sperling & Melchner, 1978). To distinguish these possibilities, it will be necessary to collect perceptual reports from multiple display locations during the same intersaccadic pause.)

To summarize, there was an on-path advantage during saccadic sequences, both ahead and behind current fixation. The on-path advantage was greater for saccadic target locations ahead of current fixation than for previously examined locations behind current fixation. This means that perceptual characteristics of the display (e.g., color differences), as well as saccadic planning, contributed to the observed pattern of the allocation of attention.

3.1.3. Influence of time within the trial

The "ahead" and "behind" data in Figs. 3 and 4 came from trials in which the Gabor appeared at different temporal epochs of the trial. Analyses of the data obtained during the steady fixation condition, where the set of Gabor appearance times was the same as during the saccadic condition, showed that performance did not change systematically over time within a trial (Fig. 6). Thus, the greater on-path advantage for the saccadic target locations ahead of current fixation during the saccadic condition was due to saccadic planning, and not to the passage of time.

3.1.4. Summary

The results of Part 1 show that while sequences of saccades are in progress, attention can be distributed to locations other than the target of the next saccade without disrupting the saccadic sequence. This distribution of attention can be attributed both to the perceptual features marking the path, and to the planning of saccades.

3.2. Memorized saccadic paths (Part 2)

If the distribution of attention to locations along the marked saccadic path was aided by the perceptual features of the path, as noted above, then removing the color cues marking the path should alter the distribution of attention. Part 2 tested this hypothesis.

Stimuli and procedures were the same as in Part 1, except that the path was not marked by a color difference. All circles were the same color (either red or green) and the subjects followed the designated saccadic path from memory. A line diagram off to the side of the display, available only until the trial was started, indicated the saccadic path to be followed during the trial (Fig. 7). In order to reduce memory load, only the two simpler saccadic paths used in the marked path experiment (where results did not differ across the different types of paths) were tested (Fig. 7, and their mirror rotations).

3.2.1. Saccadic performance

All subjects were able to follow the paths from memory. The vast majority of saccades followed the specified path (Fig. 2b). In addition, Table 2 shows that the average saccadic landing error, the number of targets hit/trial, and the intersaccadic pause

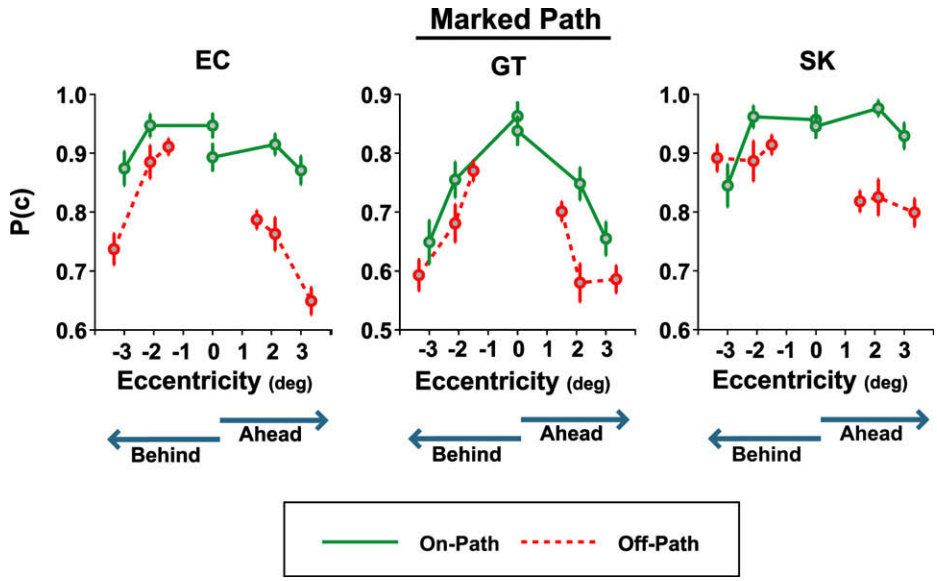

Fig. 4. On-path vs. off-path performance. Proportion correct reports of Gabor orientation as a function of retinal eccentricity for Gabors presented on (green solid) or off (red dashed) the saccadic path. Data in each function were obtained by pooling across the four starting locations, eight different saccadic paths (see Fig. 1), and trials in which Gabor location was cued or not cued. "Ahead" refers to data obtained when the eye was at the first on-path location in the central nine (Fig. 3, Ahead), and "Behind" refers to data obtained when the eye was at the last on-path location in the central nine (Fig. 3, Behind). Each proportion is based on approximately 150–300 observations. Error bars show ± 1 standard error. (For interpretation of the references in color in this figure legend, the reader is referred to the web version of this article.)

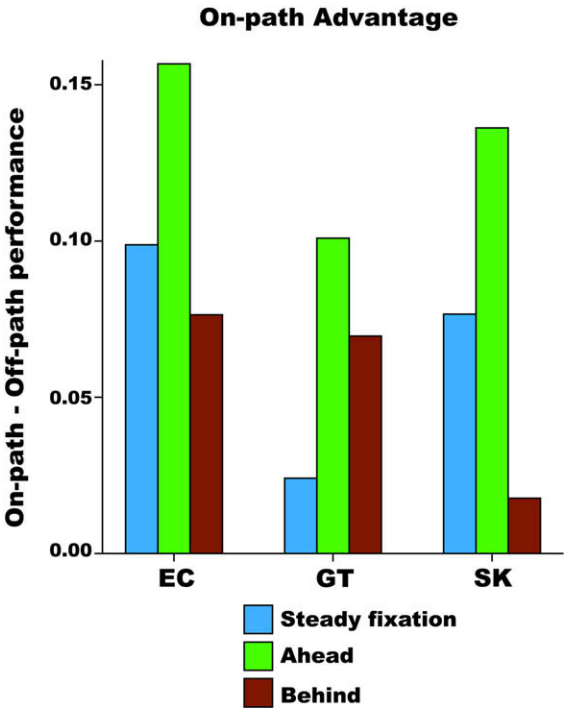

Fig. 5. On-path advantage. Each bar represents the difference between the average on-path performance (proportion correct) and the average off-path performance (proportion correct) for the three subjects. The blue bars show the on-path advantage for the steady fixation control trials. The green and red bars show the on-path advantage during intersaccadic pauses for Gabor locations that were Ahead (green) and Behind (red) current fixation position. Within each condition, data were collapsed across eccentricity. Thus, a portion of the on-path advantage in all conditions is due to the smaller average eccentricity of the on-path locations. Since eccentricities were the same across all conditions, the portion of the on-path advantage due to eccentricity was the same in all three cases shown (Ahead, Behind, Steady fixation). The greater size of the on-path advantage for the "Ahead" condition relative to both "Behind" and "Steady fixation" represents the effects of saccadic planning.

durations were comparable to those found with the marked paths in Part 1. Memorized paths were harder than marked paths in that there were more "off-path" errors for subjects EC and GT, and longer intersaccadic pauses for SK. The variance of the intersaccadic pauses was about the same in marked and memorized paths. Skipping errors, rare to begin with (1%), were even less frequent with the memorized paths. Memorized path performance was about the same in trials in which the Gabor judgments were not made, except for a larger proportion of off-path errors for SK. The accuracy and timing of saccades with the memorized paths were well within bounds of expected performance of saccadic sequences (e.g., Zingale & Kowler, 1987; Vishwanath & Kowler, 2003; Gersch et al., 2004) and shows that subjects could successfully follow the path.

3.2.2. Perceptual performance

The distribution of attention with the memorized paths shows a different pattern than that found with the marked paths. With memorized paths, and no color cue: (1) overall performance was poorer, (2) the attentional advantage for on-path locations both ahead and behind current fixation was diminished, and (3) the advantage for locations ahead of current fixation was apparent only for the target of the upcoming saccade.

Figs. 8 and 9 show that the on-path advantage was reduced for locations behind current fixation. The on-path advantage for saccadic targets ahead of current fixation was still present (OR = 1.58, $p < 0.001$) and significantly greater than the on-path advantage behind current fixation (Interaction coefficient = 0.1328, $p = 0.035$). Fig. 8 also shows that the on-path advantage observed ahead of current fixation was due primarily to effects at the immediate saccadic target rather than the target further along the path. Specifically, performance at the immediate target was better than at off-path locations at the same eccentricity, while performance two targets ahead of current fixation (eccentricity = 3°) was not better than performance at off-path locations of equivalent or smaller eccentricity (eccentricity = 2.12°) (OR = 1.25, $p = 0.171$).

To summarize Part 2: with the memorized paths, in contrast to marked paths, the effects of attention were largely restricted to

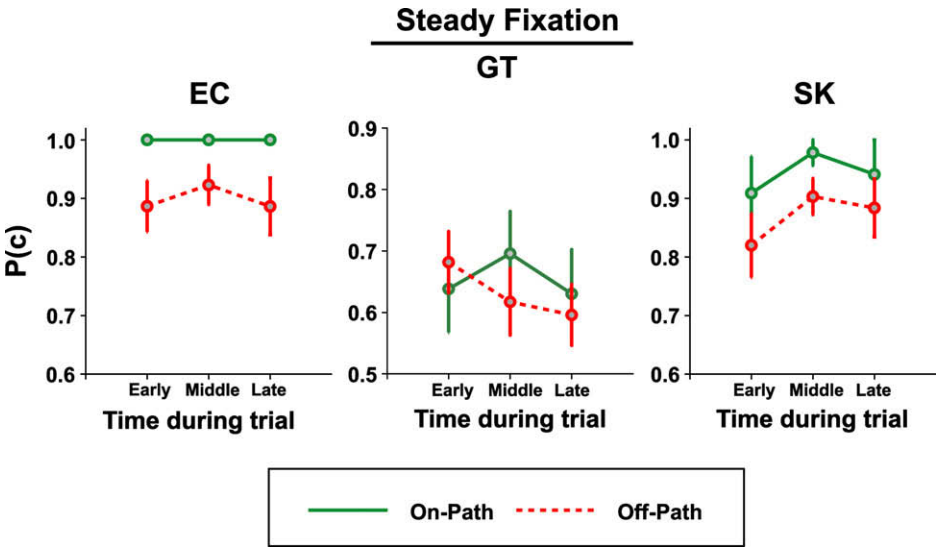

Fig. 6. Orientation discrimination performance during steady fixation control trials as a function of when during the trial the Gabor appeared. Data are shown for three subjects during "no pre-cue" sessions. Means were averaged over all possible Gabor eccentricities ($n = 5$). The Gabor could have appeared early (~300 ms), in the middle (~550 ms), or late (~900 ms) in trials. Error bars show ±1 standard error.

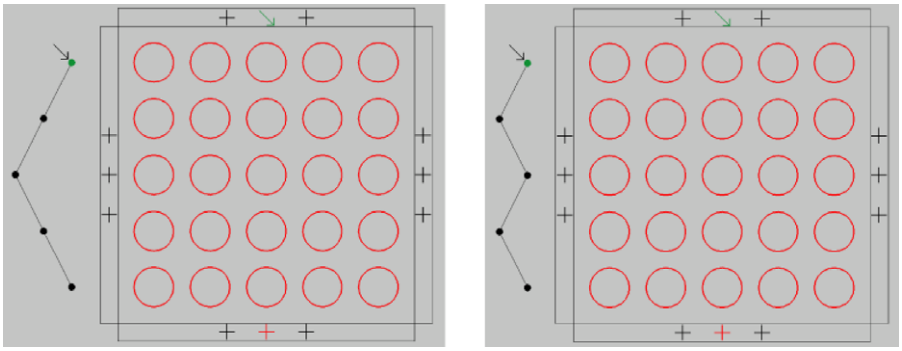

Fig. 7. Memorized path. Sample displays used in the memorized path experiment. Displays are the same as in Fig. 1, except that all the circles were the same color (either red or green, chosen randomly). The line diagram on the left (visible only before the start of each trial) showed the saccadic path to be followed in any given trial. Four different saccadic paths were used (the two shown plus their mirror images), starting from any of the 4 sides of the display.

Table 2
Memorized path[a] (Part 2)

Characteristics of saccades							
Subject	Proportion of total saccades[b]				Good saccades[f]		
	Good[f]	Skips[g]	Off the path[h]	Other[i]	Error at saccade offset[c] (minarc) Mean (*SD*) *N*	Average number of targets hit per trial[d]	ISP[e] (ms) Mean (*SD*) *N*
With concurrent Gabor judgments							
EC	0.80	0.001	0.12	0.08	27 (12) 14,201	4.4	299 (119) 14,201
GT	0.81	0.004	0.08	0.11	22 (11) 20,741	5.7	209 (63) 20,741
SK	0.77	0.001	0.11	0.12	25 (12) 11,093	5.1	299 (96) 11,093
Without concurrent Gabor judgments							
EC	0.79	0.01	0.12	0.08	27 (12) 2920	4.4	302 (101) 2920
GT	0.89	0.004	0.05	0.06	22 (12) 5041	5.7	208 (59) 5041
SK	0.59	0.001	0.20	0.21	28 (12) 640	4.7	299 (98) 640

[a] "Memorized path" refers to trials in which the saccadic path was executed from memory.
[b] "Total saccades" refers to all saccades except secondary, corrective saccades that followed a primary saccade to a target.
[c] "Error" at saccadic offset" refers to vector distance between eye position at the time of saccadic offset and the center of the nearest circle.
[d] "Average number of targets hit per trial" refers to number of saccadic targets on the path that were successively fixated during a trial.
[e] "ISP" refers to intersaccadic pause duration, the interval preceding each good saccade.
[f] "Good" refers to saccades that followed the prescribed saccadic path.
[g] "Skips" refers to saccades that skipped the next location on the path and brought the line of sight to a subsequent on-path location.
[h] "Off the path" refers to saccades that brought the line of sight to a location off the prescribed path.
[i] "Other" refers to the remaining types of erroneous saccades (off-path to on-path locations, off-path to off-path locations, backward saccades).

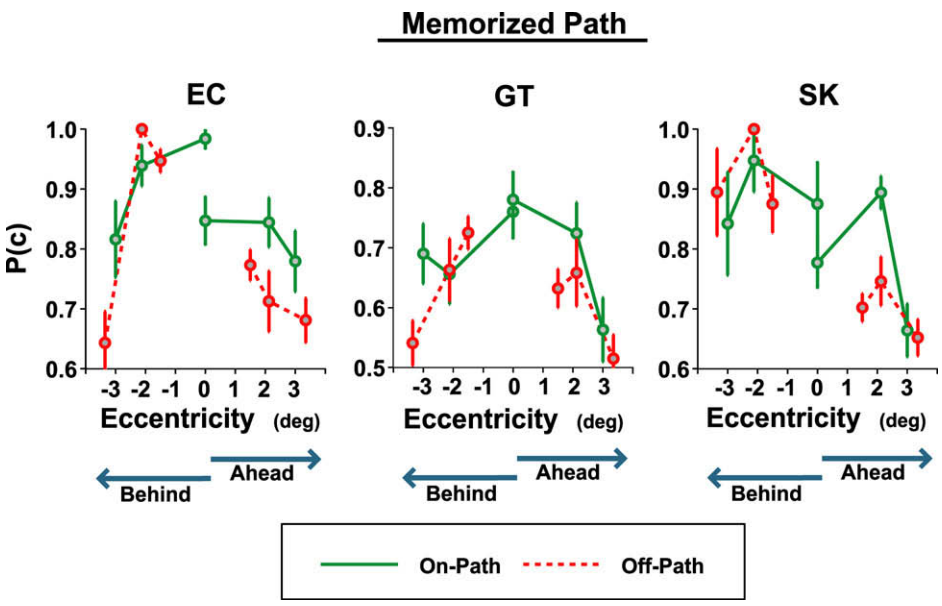

Fig. 8. On-path vs. off-path performance when the path was memorized. Proportion correct reports of Gabor orientation as a function of retinal eccentricity for Gabor locations on (green) or off (red dashed) the saccadic path. Data in each function were obtained by pooling across the four starting locations. "Ahead" refers to data obtained when the eye was at the first on-path location in the central nine, and "Behind" refers to data obtained when the eye was at the last on-path location in the central nine. Each proportion is based on approximately 100–150 observations. Error bars show ±1 standard error.

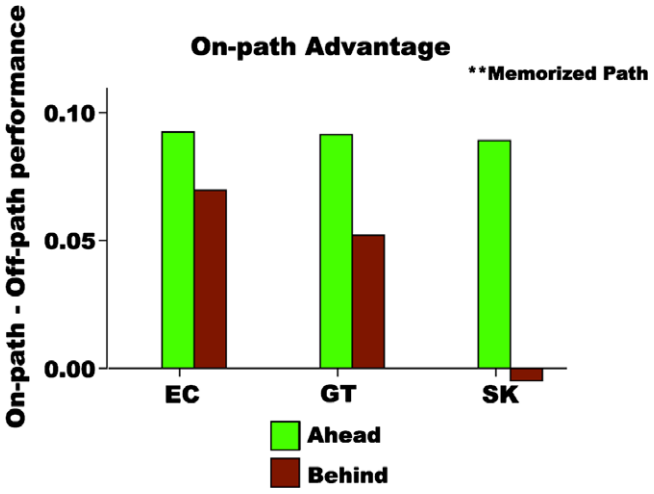

Fig. 9. On-path advantage when the path was memorized. Each bar represents the difference between the average on-path performance (proportion correct) and the average off-path performance (proportion correct) for three subjects. The green bars show the on-path advantage for Gabor locations that were "Ahead" of current fixation position, and the red bars show the advantage for locations "Behind" current fixation. Within each condition, data were collapsed across eccentricity. Thus, a portion of the on-path advantage in both conditions is due to the smaller average eccentricity of the on-path locations. Since eccentricities were the same for both conditions, the portion of the on-path advantage due to eccentricity was the same. The greater size of the on-path advantage for the "Ahead" condition relative to that "Behind" represents the effects of saccadic planning.

producing better performance at the immediate saccadic target than at the surrounding off-path locations. There was little, if any, attention to multiple locations ahead or behind current fixation along the saccadic path. This is consistent with the conclusion drawn in Part 1 that the distribution of attention was due both to effects of saccadic planning and to perceptual characteristics of the display. With no perceptual markers distinguishing the saccadic path, extrafoveal attention was largely confined to the saccadic target.

4. Discussion

A perceptual task (orientation identification) was used to map the distribution of attention over space and time during the performance of sequences of saccades. Saccadic sequences resemble natural scanning more closely than the single saccades that have dominated prior work on saccades and attention. We found that attention could be allocated beyond the target of the upcoming saccade to other locations along the saccadic path provided that the path was marked by a perceptual cue. The distribution of attention along the path, beyond the target of the next saccade, was reduced or eliminated when the path was not marked. These results are significant for the following reasons:

First, the absence of broad attentional enhancement with the unmarked paths shows that attention is not an obligatory "marker" that highlights the saccadic path or stores the locations of a set of saccadic targets. Our results show that it is possible to perform a memorized sequence well without such attentional highlighting. Attention, in principle, could have played such a role by activating regions within proposed top-down "salience maps" believed to be present in areas such as FEF, SC or LIP, which are connected to both attention and to the generation of saccades (Awh, Armstrong, & Moore, 2006; Bisley & Goldberg, 2006; Thompson, Bichot, & Sato, 2005). Our results suggest that any such top-down salience map in neural areas related to attention and saccades may not be complete in that task-relevant locations—namely, targets of future saccades—are not included. Top-down salience maps may be limited to representing information with consequences for immediate, pre-saccadic behavior. Longer term representations of information related to planning of saccadic sequences would be separate from these maps, for example, in premotor or prefrontal cortex (Fujii & Graybiel, 2003; Ohbayashi et al., 2003) or in other locations within FEF, SC, or LIP. Our results also suggest that representations of long-term saccadic plans, in these or other areas, have no necessary consequences for perceptual attention.

Second, the broader distribution of attention observed with the marked paths shows that under some circumstances it is possible to dissociate saccades and attention enough to pay attention to

locations other than the immediate saccadic target without disrupting the saccadic sequence. This is significant because other studies (using different stimuli and tasks) found that ties between saccades and attention were so close that drawing attention away from the target of a saccade would either delay the saccade (Kowler et al., 1995) or create large saccadic errors (McPeek, Skavenski, & Nakayama, 2000; Theeuwes, Kramer, Hahn, Irwin, & Zelinsky, 1999). We found that distributing attention over the feature-marked saccadic paths was able to benefit perceptual performance without disturbing the pattern of saccades. Saccades rarely skipped over a target (1%), and the perceptual enhancement along the saccadic path was found when saccades were accurate. Thus, the distribution of attention along the marked path resulted in better perceptual performance without increasing saccadic errors.

It is important to be clear about the scope and novelty of these findings. We found two different patterns of perceptual attention during the performance of saccadic sequences. In one pattern, obtained with the memorized paths, attention was largely confined to the saccadic target (similar to the pattern observed in Gersch et al., 2004, for repetitive sequences). In the other, obtained with the marked paths, attention was distributed more broadly (similar to the pattern observed by Godijn & Theeuwes, 2003, prior to sequence initiation). Thus, these results address issues about the links between saccades and attention that were raised, but not resolved, in prior studies that used either single saccades or sequences (see Section 1). Namely, our results show that: (1) is it possible to distribute attention to locations other than the immediate saccadic target without interfering with the accuracy or timing of the saccades, and (2) it is also possible to confine attention (as assessed by perceptual measures) to the saccadic target and still perform the remembered saccadic sequences. Thus, extending the distribution of attention beyond the target of the next saccade is not necessary to perform the sequence, nor does it interfere. Taken together, the results show no obligatory connection between perceptual attention and the long-term planning of sequences, and some ability to distribute perceptual attention to regions other than the immediate saccadic target.

A separate, and more difficult, issue is the question of what aspects of the stimuli or tasks encouraged different distributions of attention with the marked and the memorized paths. As was noted in the description of the results, perceptual processes are implicated in the distribution of attention with the marked path, not only because of the difference in performance between marked and memorized paths, but also because the on-path advantage was found (albeit reduced) for previously examined locations, and not just for the saccadic targets. It could still be argued, however, that the differences between performance with the marked and memorized paths was due to the use of different top-down attentional strategies in each task, or were due to the color markers providing a more effective way of guiding attention. Thus, there may be other display or task characteristics that will also prove to be able to facilitate the allocation of attention to locations beyond the immediate target of the saccade. While we are not ruling out these suggestions, consideration of our results in the context of prior work on attention reveals a plausible role of feature-based processes in producing the distribution of attention that we observed.

Specifically, the finding that attention could be allocated along the marked path without drawing saccades along with it implies that the distribution of attention along the marked path was mediated by visual areas not tied closely to saccadic planning. Area V4, an area not directly linked to saccadic programming, is one plausible candidate area because it receives signals indicating the location of the next saccadic target from FEF (Moore & Armstrong, 2003), and then generates enhanced signals in sets of neurons tuned to the same feature (Bichot et al., 2005; Motter, 1994). Given that the strongest focus of attention in our task would be the immediate saccadic target, a symmetrical distribution of activation around the target location would favor future saccadic targets over locations recently fixated. This agrees with the spatial pattern of attentional enhancement we found, where saccadic targets showed a greater on- vs. off-path advantage than recently viewed locations. Thus, activity in V4 (or other visual areas), could benefit perception without triggering saccades when the saccadic path is marked by a feature cue.

Our finding of a broader distribution of attention during sequences of saccades along marked paths supports a capacity to dissociate attention from saccadic planning. Neurophysiological studies have also found dissociations, but these were linked to stimuli appearing or changing abruptly during pre-saccadic intervals (Bisley & Goldberg, 2003; Murthy et al., 2001). The dissociations we found did not require abrupt onsets, but instead were linked to visual characteristics of the saccadic path. It will be interesting to find out what other conditions, perhaps connected either to task or visual variables, might also promote a broad distribution of attention without disrupting ongoing saccades.

4.1. The links between attention and saccades

We found that attention was involved at two distinct levels during saccadic scanning: attention to the immediate saccadic goal was connected to saccadic planning, and the allocation of attention along the marked path was connected mainly to perceptual or visual mechanisms, and not to saccades. This dual role for attention during saccadic scanning can be a valuable asset during natural task performance. It allows attention to set the spatial endpoint of the saccade, while at the same time extending perceptual processing over a wider region to benefit global scene perception. These different roles for attention may be mediated by separate processes: an executive or top-down process connected to saccadic planning, and a visual process connected to attention, independently of saccades.

Acknowledgments

This research was supported by NIH EY 15522. We thank Doug DeCarlo, Jacob Feldman, Thomas Papathomas, Manish Singh for valuable comments and suggestions. We are also very thankful to Marco daCosta DiBonaventura for help with the statistical analyses.

References

Awh, E., Armstrong, K. M., & Moore, T. (2006). Visual and oculomotor selection: Links, causes and implications for spatial attention. *Trends in Cognitive Sciences, 3*(10), 124–130.

Bichot, N. P., Rossi, A. F., & Desimone, R. (2005). Parallel and serial neural mechanisms for visual search in macaque area V4. *Science, 308*, 529–534.

Bisley, J. W., & Goldberg, M. E. (2003). Neuronal activity in the lateral intraparietal area and spatial attention. *Science, 299*, 81–86.

Bisley, J. W., & Goldberg, M. E. (2006). Neural correlates of attention and distractibility in the lateral intraparietal area. *Journal of Neurophysiology, 95*, 1696–1717.

Carrasco, M., Penpeci-Talgar, C., & Eckstein, M. (2000). Spatial covert attention increases contrast sensitivity across the CSF: Support for signal enhancement. *Vision Research, 40*, 1203–1215.

Cohen, E. H., Schnitzer, B. S., Gersch, T. M., Singh, M., & Kowler, E. (2007). The relationship between spatial pooling and attention in saccadic and perceptual tasks. *Vision Research, 47*, 1907–1923.

Crane, H. D., & Steele, C. S. (1978). Accurate three-dimensional eyetracker. *Applied Optics, 17*, 691–705.

Deubel, H., & Schneider, W. X. (1996). Saccade target selection and object recognition: Evidence for a common attentional mechanism. *Vision Research, 36*, 1827–1837.

Dosher, B. A., & Lu, Z. L. (2000a). Mechanisms of perceptual attention in precuing of location. *Vision Research, 40*, 1269–1292.

Dosher, B., & Lu, Z. L. (2000b). Noise exclusion in spatial cuing of attention. *Psychological Science, 11*, 139–146.

Epelboim, J., & Suppes, P. (2001). A model of eye movements and working memory during problem solving in geometry. *Vision Research, 41*(12), 1561–1574.
Fujii, N., & Graybiel, A. M. (2003). Representation of action sequence boundaries by macaque prefrontal cortical neurons. *Science, 301*, 1246–1249.
Gersch, T. M., Kowler, E., & Dosher, B. (2004). Dynamic allocation of visual attention during the execution of sequences of saccades. *Vision Research, 44*(12), 1469–1483.
Godijn, R., & Theeuwes, J. (2003). Parallel allocation of attention prior to the execution of saccade sequences. *Journal of Experimental Psychology: Human Perception and Performance, 29*, 882–896.
Hoffman, J. E., & Subramaniam, B. (1995). The role of visual attention in saccadic eye movements. *Perception and Psychophysics, 57*, 787–795.
Hosmer, D. W., & Lemeshow, S. (2000). Applied logistic regression (2nd ed.). New York: Wiley Inc.
Inhoff, A. W. (1986). Preparing sequences of saccades under choice reaction conditions. Effects of sequence length and context. *Acta Psychologica, 61*, 211–218.
Itti, L., & Koch, C. (2001). Computational modelling of visual attention. *Nature Reviews Neuroscience, 2*(3), 194–203.
Kowler, E., Anderson, E., Dosher, B. A., & Blaser, E. (1995). The role of attention in the programming of saccades. *Vision Research, 35*, 1897–1916. 1995.
Legge, G. E., Klitz, T. S., & Tjan, B. S. (1997). Mr. Chips: An ideal-observer model of reading. *Psychological Review, 104*(3), 524–553.
Liang, K. Y., & Zeger, S. L. (1986). Longitudinal data analysis using generalized linear models. *Biometrika, 73*, 13–22.
McPeek, R. M., Maljkovic, V., & Nakayama, K. (1999). Saccades require focal attention and are facilitated by a short-term visual visual memory system. *Vision Research, 39*(8), 1555–1556.
McPeek, R. M., Skavenski, A. A., & Nakayama, K. (2000). Concurrent processing of saccades in visual search. *Vision Research, 40*(18), 2499–2516.
Melcher, D., & Kowler, E. (1999). Shape, surfaces and saccades. *Vision Research, 39*, 2929–2946.
Melcher, D., Papathomas, T. V., & Vidnyanszky, Z. (2005). Implicit attentional selection of bound visual features. *Neuron, 46*, 723–729.
Moore, T., & Armstrong, K. M. (2003). Selective gating of visual signals by microstimulation of frontal cortex. *Nature, 421*, 370–373.
Motter, B. C. (1994). Neural correlates of attentive selection for color or luminance in extrastriate area V4. *Journal of Neuroscience, 14*, 2178–2189.
Motter, B., & Belky, E. (1998). The guidance of eye movements during active visual search. *Vision Research, 38*, 1805–1815.
Müller, J. R., Philiastides, M. G., & Newsome, W. T. (2005). Microstimulation of the superior colliculus focuses attention without moving the eyes. *PNAS, 102*, 524–529.
Murthy, A., Thompson, K. G., & Schall, J. D. (2001). Dynamic dissociation of visual selection from saccade programming in frontal eye field. *Journal of Neurophysiology, 86*, 2634–2637.
Ohbayashi, M., Ohki, K., & Miyashita, Y. (2003). Conversion of working memory to motor sequence in the monkey premotor cortex. *Science, 301*, 233–236.
Rao, R. P., Zelinsky, G. J., Hayhoe, M. M., & Ballard, D. H. (2002). Eye movements in iconic visual search. *Vision Research, 42*(11), 1447–1463.
Sàenz, M., Buraĉas, G. T., & Boynton, G. M. (2003). Global feature-based attention for motion and color. *Vision Research, 43*, 629–637.
Shih, S. I., & Sperling, G. (1996). Is there feature-based attentional selection in visual search. *Journal of Experimental Psychology: Human Perception and Performance, 22*(3), 758–779.
Sperling, G., & Dosher, B. A. (1986). Strategy and optimization in human information processing. In K. R. Boff, L. Kaufman, & J. P. Thomas (Eds.), Handbook of perception and human performance I. Sensory processes and perception (pp. 1–65). NY: Wiley.
Sperling, G., & Melchner, M. J. (1978). The attention operating characteristic: Some examples from visual search. *Science, 202*, 315–318.
Sternberg, S., Wright, C., Knoll, R., & Monsell, S. (1978). The latency and duration of rapid movement sequences: Comparisons of speech and typewriting. In G. E. Stelmach (Ed.), *Information processing in motor control and learning* (pp. 117–152). NY: Academic Press.
Theeuwes, J., Kramer, A. F., Hahn, S., Irwin, D. E., & Zelinsky, G. J. (1999). Influence of attentional capture on oculomotor control. *Journal of Experimental Psychology: Human Perception and Performance, 25*, 1595–1608.
Thompson, K. G., Bichot, N. P., & Sato, T. R. (2005). Frontal eye field activity before visual search errors reveals the integration of bottom-up and top-down salience. *Journal of Neurophysiology, 93*, 337–351.
Vishwanath, D., & Kowler, E. (2003). Localization of shapes: Eye movements and perception compared. *Vision Research, 43*(15), 1637–1653.
Zingale, C. M., & Kowler, E. (1987). Planning sequences of saccades. *Vision Research, 27*, 1327–1341.