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Dynamic allocation of visual attention during the execution of sequences of saccades

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Abstract

Laboratory tasks used to study vision and attention usually require steady fixation, while natural visual processing occurs during the brief pauses between successive saccades. We studied vision and attentional allocation during intersaccadic pauses as subjects made repetitive sequences of saccades. Displays contained six outline squares located along the perimeter of an imaginary circle (diam 4°). Saccades were made in sequence to every other square. The visual task was to identify the orientation (2AFC) of a Gabor test stimulus that appeared briefly (91 ms) along with superimposed noise in one of the squares during a randomly selected intersaccadic pause. Gabor location was cued in advance and noise frames were presented in all squares. Contrast thresholds during intersaccadic pauses were as much as 2–3 times higher than during steady fixation with comparable cueing. Thresholds improved over time during the intersaccadic pause, and the lowest extrafoveal thresholds (statistically indistinguishable from those at the same locations during steady fixation) were found for the location that was to be the target of the next saccade in the sequence. These results show that vision during intersaccadic pauses varies over space and time due to changes in the distribution of attention, as well as to visual suppression that may be related to the execution of the saccades themselves. Generation of sequences of accurate saccades encouraged a strategy of attentional allocation in which resources were dedicated primarily to the goal of the next saccade, leaving little attention for processing objects at other locations.

Keywords: Saccades; Eye movements; Attention; Contrast thresholds; Contrast sensitivity; Intersaccadic pause; Saccadic sequences; Allocation of attention; Saccadic suppression

1. Introduction

Selective visual attention controls the allocation of limited cognitive processing capacities, affecting our ability to perceive, distinguish, and remember the objects or features in the visual field. In addition to its influences on perception, selective attention is also a significant contributor to motor control. For example, a selective attentional filter is necessary to direct saccades to chosen objects within crowded visual environments. The selective filter designates which object or region serves as the effective input to saccadic programming mechanisms (He & Kowler, 1991; Vishwanth & Kowler, 2003), thus ensuring that the saccade is directed accurately to the chosen target without being diverted to surrounding irrelevant objects. Understanding the contribution of attention to the generation of accurate saccades is important both for explaining the normal operation of saccades, and, for characterizing the quality of vision during the intervals between successive saccades.

One of the central issues about the role of attention in saccadic control is the relationship between the selective filter that determines the effective target of a saccade and the attentional filter that serves perception. Does the same selective attentional filter that enhances perceptual processing also provide analogous signals to the saccade programming system, so that only information from the attended target determines the spatial parameters of the upcoming saccadic command? Or, alternatively, do saccades use a dedicated and independent filtering mechanism, one that has no links to perception?

Several recent studies have used dual-task methods to address this issue. These experiments were based on the

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rationale that if a single attentional filter is used by both saccadic and perceptual systems, then perceptual performance at the location that contains the target of the saccade should be better than at non-target locations. If, on the other hand, separate and independent attentional mechanisms are at work, perceptual performance will not vary with the status of a location as a saccadic target. Previous results have not supported separate, independent attentional filters for saccades and perception. For example, Hoffman and Subramaniam (1995), Kowler, Anderson, Dosher, and Blaser (1995) and Deubel and Schneider (1996) all found that identification of a target letter was more accurate at the intended goal of the saccade than elsewhere, implying that perceptual attention is allocated to the saccadic goal. To determine whether shifts of attention to the saccadic goal were compulsory, Kowler et al. (1995) studied the "attention operating characteristic" (AOC) describing the trade-off between saccadic and perceptual performance. They found that when saccadic and perceptual targets were in different places, improvement in perceptual performance required a sacrifice of saccadic performance (i.e., longer latency and diminished accuracy), an indication that saccades and perception share a common attention resource pool. The AOCs reported by Kowler et al. (1995) also showed that it was possible to divert a small amount of attention away from the saccadic goal, enough to produce some perceptual improvements, with little or no cost to either saccadic latency or accuracy.

In contrast to this psychophysical evidence for a single attentional filter, recent neurophysiological research has emphasized the separation between spatial attention and saccadic planning, at least at the level of single neurons. For example, Bisley and Goldberg (2003) had monkeys either saccade, or not saccade, to a remembered location based on the interpretation of an eccentric cue. The cue was positioned so that it appeared in the receptive fields of neurons in area LIP. Activity in LIP has been argued to reflect the saccadic plan (Andersen, Snyder, Bradley, & Xing, 1997), but Bisley and Goldberg (2003) found that activity evoked by the cue was greater when it instructed the monkey to withhold the saccade than when it instructed the monkey to make the saccade. They concluded that the LIP activity was related to attention, and not to the preparation of saccades.

Using a different approach, Murthy, Thompson, and Schall (2001) also found evidence for a dissociation between spatial attention and the saccadic plan in visual neurons in frontal eye field. In their task monkeys made a saccade to a color "oddball" target (i.e., a red target among green distractors) that sometimes unexpectedly swapped positions with a distractor. They found that in the critical trials, when the target moved to a new position, but the monkey made an erroneous saccade to its former location, FEF activity did not correlate with the locus of the saccadic endpoint. Instead, neurons fired when the target was in the receptive field, even if the monkey failed to look at it. This dissociation demonstrated that the frontal eye field may reflect the perceptual processing of the image, and not an obligatory saccade command. Thus, neurons in areas such as LIP and FEF that were candidates for encoding pre-saccadic attention shifts instead may be representing attended locations independently of saccades. The links between saccades and attention at a neural level may rest, not on having a neural area dedicated to representing "pre-saccadic attention shifts," but rather on more complex spatial and temporal relationships between the allocation of attention and the intentions to make saccades.

1.1. Saccadic sequences

Given the evidence presented above for partial dissociations between attention and saccades, seen both neurally (Bisley & Goldberg, 2003; Murthy et al., 2001) and behaviorally (AOCs in Kowler et al., 1995), it may be valuable to begin to re-examine the links between attention and saccades in tasks that are more complex, and incorporate more of the demands characteristic of natural tasks. In the present study, we examined the links between attention and saccades executed as part of sequences of several eye movements, rather than as single eye movements programmed in isolation.

Saccades executed as part of sequences may have different attentional requirements than saccades executed in isolation. Previous studies have shown that the latency of saccades in a sequence depends on both the number of targets in the sequence and on the ordinal position of the saccade within the sequence (Inhoff, 1986; Zingale & Kowler, 1987). These findings imply that programs for the entire sequence can largely be prepared and stored in advance of sequence execution (Sternberg, Wright, Knoll, & Monsell, 1978). Such advance preparation may mean that allocating visual attention to the targets is important only before the execution of the entire sequence begins, when saccadic plans are prepared. Attention could become less relevant once the sequence is underway, when stored representations of the saccadic plans may contribute to the generation of each eye movement command. Alternatively, if the spatial parameters of saccades are not fully determined before the sequence begins, then attention may continue to be important while the sequence is in progress to ensure that the spatial parameters of each saccadic command are based exclusively on selected (attended) information and are not influenced by surrounding visual details. The experiments in the present paper were designed to distinguish these possibilities and determine the attentional demands of saccades executed as part of sequences.

Few studies have tried to look at the allocation of attention during saccadic sequences. Recently, Godijn and Theeuwes (2003) measured the accuracy of letter identification in the time interval preceding the execution of a sequence of two saccades. Identification was better for letters presented at the saccadic goals than for non-goal locations. These results show that attention was allocated to both targets, but given that attention was evaluated before the first saccade was made, it is possible that the results reflected processes related to the initial determination of the saccadic path, rather than the execution of saccades.

1.2. Outline of the present study

In the present experiments a visual task, contrast sensitivity for orientation discrimination, was used to infer patterns of the allocation of attention during the execution of a sequence of saccades. Gabor patches with superimposed visual noise were presented briefly (91 ms) at various locations during randomly selected inter-saccadic pauses while subject scanned in a triangular path around a display. Using relative contrast sensitivity as a measure of perceptual attention (e.g., Carrasco, Penpeci-Talgar, & Eckstein, 2000; Lu, Lesmes, & Dosher, 2002), it was possible to evaluate visual performance at: (1) the location that was target of the upcoming saccade, (2) locations that were targets of saccades subsequent to the very next one, and (3) locations that were non-targets. Comparison of performance at these locations with performance at equivalent locations during steady fixation will be used to evaluate the modulation in attention over space and time that accompanies the execution of sequences of saccades.

2. Methods

2.1. Subjects

Two subjects were tested, Jason and Sara. Both were naïve as to the purpose of the present experiment. They have normal vision, and need no spectacle correction.

2.2. Eye movement recording

Two-dimensional movements of the right eye were recorded by a Generation IV SRI Double Purkinje Image Tracker (Crane & Steele, 1978). The subject's left eye was covered and the head was stabilized on a dental biteboard.

The voltage output of the Tracker was fed online through a low pass 100 Hz filter to a 12 bit analog to digital converter (ADC). The ADC, controlled by a PC, sampled eye position every 2 ms. The digitized voltages were stored for later analysis. The PC controlled the timing of the stimulus display via a serial link to the SGI computer. Voltage from a photocell that recorded stimulus onset and offset directly from the display monitor was fed into a channel of the ADC and recorded along with the eye position samples to ensure accurate temporal synchronization between stimulus display and eye movement recording.

Tracker noise level was measured with an artificial eye after the tracker had been adjusted so as to have the same first and fourth image reflections as the average subject's eye. Filtering and sampling rate were the same as those used in the experiment. Noise level, expressed as a standard deviation of position samples, was $0.4'$ for horizontal and $0.7'$ for vertical position.

Recordings were made with the tracker's automatically movable optical stage (autostage) and focusservo disabled. These procedures are necessary with Generation IV Trackers because motion of either the autostage or the focusservo introduces larger artifactual deviations of Tracker output. The focusservo was used, as needed, only during inter-trial intervals to maintain subject alignment. This can be done without introducing artifacts into the recordings or changing the eye position/voltage analog calibration. The autostage was permanently disabled because its operation, even during inter-trial intervals, changed the eye position/voltage analog calibration.

2.3. Stimulus display

Stimuli were displayed on an SGI GDM 17-E21 17″ color monitor controlled by an SGI Iris O2 workstation. The display was located directly in front of the subject's right eye at a distance of 119 cm. The display area subtended 11.3° horizontally by 9° vertically with a resolution of 1.9 pixels/′ at a refresh rate of 72 Hz.

Stimuli consisted of six outline boxes (1° on a side), located at equal intervals along the perimeter of an imaginary circle with a radius (measured from the center of the display to the center of each box) of 2°. The array of six boxes was either oriented as shown in Fig. 1 or rotated by 90°. The boxes were drawn on a background whose mean luminance was 19 cd/m^2 at the refresh rate used. Maximum display luminance was 41 cd/m^2.

Fig. 1 shows the sequence of frames in each trial. Before the trial a cue frame was presented. The small white square inside one of the boxes in the cue frame indicated the location that would contain the stimulus to be identified during the trial, namely, an oriented Gabor patch. The black cross in the cue frame indicated which box the subject was to fixate before the start of the trial. (The white cross in the center, which remained on throughout the experimental session, was a spatial reference used occasionally to check eyetracker alignment between trials and was not related to the experimental task.) The locations of the Gabor and the starting

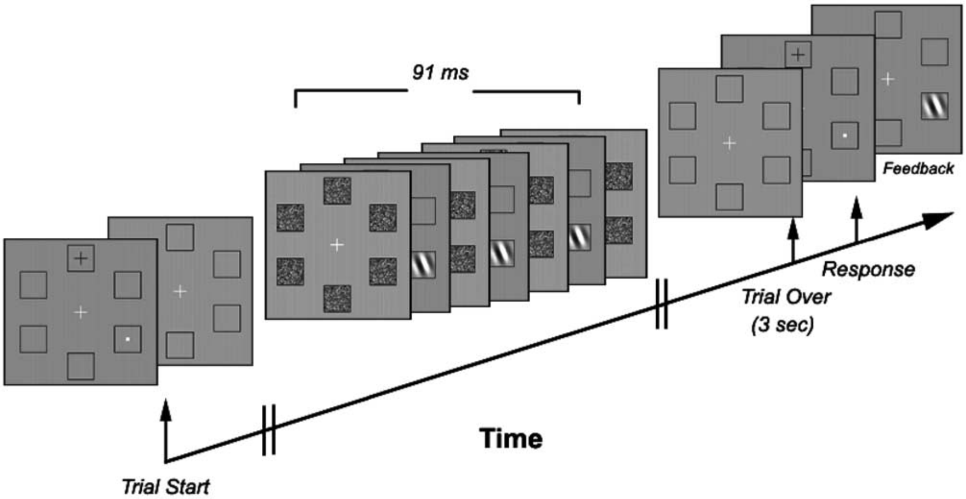

Fig. 1. The sequence of frames. The first is the cue frame indicating starting fixation position (black cross, inside one of the boxes) and location of Gabor (small white square). Saccades to every other box began 100 ms after trial start. The Gabor + noise frames were presented during a randomly selected saccadic pause. The Gabor appeared superimposed on noise during the trial. The starting fixation position and Gabor location varied randomly on each trial. The boxes were 1° on a side.

fixation position were chosen randomly and independently on each trial.

Following the start of the trial, the white square and the black cross in the cue frame were removed, and in response to an auditory signal, the subject began to make saccades around the display, looking in sequence at every other box (distance = 3.46°) (see Section 2.4 for additional details). After a randomly selected saccade, a sequence of seven critical frames were presented. The first, third, fifth and seventh frames contained visual noise in each of the six boxes. The noise was a matrix of 20×20 dots (dot size = 3×3 pixels) whose luminance was Gaussian distributed (SD = 33% maximum display contrast). The second, fourth, and sixth frames contained a Gabor patch in the box that was cued before the start of the trial. The Gabor was generated according to the following:

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

where f is the spatial frequency (2.2 cycles/°), l_0 the mean luminance (19 cd/m^2), θ the orientation (±23° from vertical), σ the standard deviation of the Gaussian window (0.7°), (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 luminance), and contrast was selected at random from seven equally spaced values ranging from 0% to 36%. Orientation was also selected randomly on each trial from two values (23° right or left of vertical). The seven frames of Gabor and noise were presented at a rate fast enough (13 ms/frame) so that the individual frames were not distinguished and the Gabor and noise appeared superimposed.

The perceptual task was to indicate the orientation (right or left of vertical) of the Gabor. Contrast sensitivity for orientation discrimination was determined with the method of constant stimuli, with psychometric functions fit by Weibull functions.

2.4. Procedure: dual-task (saccades and perception)

The subjects fixated the black cross (see Fig. 1) before the trial 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 saccades in sequence to every other box. The direction of scanning was chosen by the subject and adhered to throughout the experiment (both subjects scanned counterclockwise). Subjects were instructed to make saccades accurately, and maintain a steady, brisk pace throughout the trial. They were told not to try to slow or otherwise alter the rate of saccades in anticipation of the appearance of the Gabor.

The time of presentation of the Gabor was determined in the following way. After a random delay (0, 150, 500, 1000 or 1500 ms relative to the signal to begin making saccades), a computer algorithm operating on incoming eye position data detected the occurrence of the next saccade by means of a velocity criterion. Then, the sequence of seven critical frames (duration 91 ms) containing the interleaved noise and Gabor frames were presented at a randomly selected time, either about 10–20 ms after saccade offset ("early") or 150 ms later ("late"). Subjects continued to scan the boxes until the end of the 3 s trial, when the cue frame reappeared. The orientation report (right or left) was given by a button press. Feedback was presented after the response. The criterion for detecting the saccade on-line was determined empirically and verified by inspection and analysis of the recorded eye and stimulus traces.

2.5. Single tasks

The basic experiment, described above, used a dual-task design in which both a saccadic task (scanning in a triangular path) and a perceptual task (discriminating the orientation of the Gabor) were performed in each trial. In addition, two different types of single-task conditions were tested in separate experimental sessions:

Steady fixation. The line of sight remained at the initial fixation location designated by the cross. Trial duration was reduced to 2 s. In some sessions the location of the Gabor was cued before the trial while in others no pre-trial cue was given. The presentation time of the Gabor was randomly selected from the same set of delays used during the saccadic scanning trials, thus ensuring that temporal uncertainty associated with the presentation of the Gabor was the same in the steady fixation and in the scanning trials. The location of the Gabor was always disclosed at the end of the trial, when the cue frame reappeared, before the subject reported orientation. This was done to reduce errors expected solely on statistical grounds when the location of signals is uncertain (see Sperling & Dosher, 1986, for discussion).

Saccades only. The displays and cues were the same as in the sessions requiring both saccades and a perceptual report, except that no report of the Gabor orientation was taken at the end of the trial.

2.6. Detection and measurement of saccades

The beginning and end positions of saccades were detected by means of a computer algorithm employing an acceleration criterion. Specifically, eye velocity was calculated for two overlapping 10 ms intervals. The onset of the second interval was 2 ms later than the onset of the first. The criterion for detecting the beginning of a saccade was a velocity difference between the samples of 800′/s or more. The criterion for saccade termination was more stringent in that 12 consecutive velocity differences had to be less than 800′/s. This more stringent criterion was used to ensure that the overshoot at the end of the saccade would be bypassed. The values of the criteria were determined empirically by examining a large sample of analog records of eye position. Saccades as small as the microsaccades that may be observed during maintained fixation (Steinman, Haddad, Skavenski, & Wyman, 1973) could be reliably detected by the algorithm.

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 was used to determine which box was fixated at the time of the presentation of the critical frames. Vector error (distance between eye position and the center of the fixated box), as well as the duration of the intersaccadic pause during which the critical frames were presented, were calculated. The rare trials in which a saccade occurred before the sequence of critical frames was completed were eliminated.

2.7. Experimental sessions

Experimental sessions consisted of either 50 or 100 trials for Jason and either 25 or 50 trials for Sara. Subjects usually were tested in 200–300 trials/day (about 150–200 trials/day of the dual-task sessions, 50–100 trials/day of each single task session). Before testing began each subject ran several hundred trials of a preliminary experiment under slightly different conditions. By the time the present data were collected, performance on both saccadic and perceptual tasks had reached asymptotic levels.

A few trials were eliminated. Trials in which the subject made a saccade before the beep (1.0% for Jason, 0.4% for Sara) and trials in which one or more Gabor or noise frames occurred during any part of a saccade (1.6% for Jason, 1.6% for Sara) were discarded. Data were based on a total of 5222 trials for Jason (1591 dual-task, 3300 steady fixation and 331 saccades-only) and 7739 for Sara (2147 dual-task, 5000 steady fixation, and 592 saccades-only).

3. Results

3.1. Perceptual performance during steady fixation

To verify that the orientation discrimination task was sensitive to attention, contrast thresholds during steady fixation were obtained when the location of the Gabor was either cued or not cued before the start of the trial. In all cases a "post-cue" presented after the trial indicated the Gabor location, thus avoiding performance errors that would be expected due solely to uncertainty about which location should constitute the basis of the report (see Sperling & Dosher, 1986).

Thresholds are shown in Fig. 2 for different locations of the Gabor relative to the position of the line of sight during steady fixation. The top box represents the current fixation position, a convention that will be followed in all subsequent graphs. During the actual experiment, both the position of fixation and the location of the Gabor could have been any of the six outline boxes in the display. The thresholds shown in the figure were determined by first categorizing the data obtained for each fixation position into 6 groups according to the

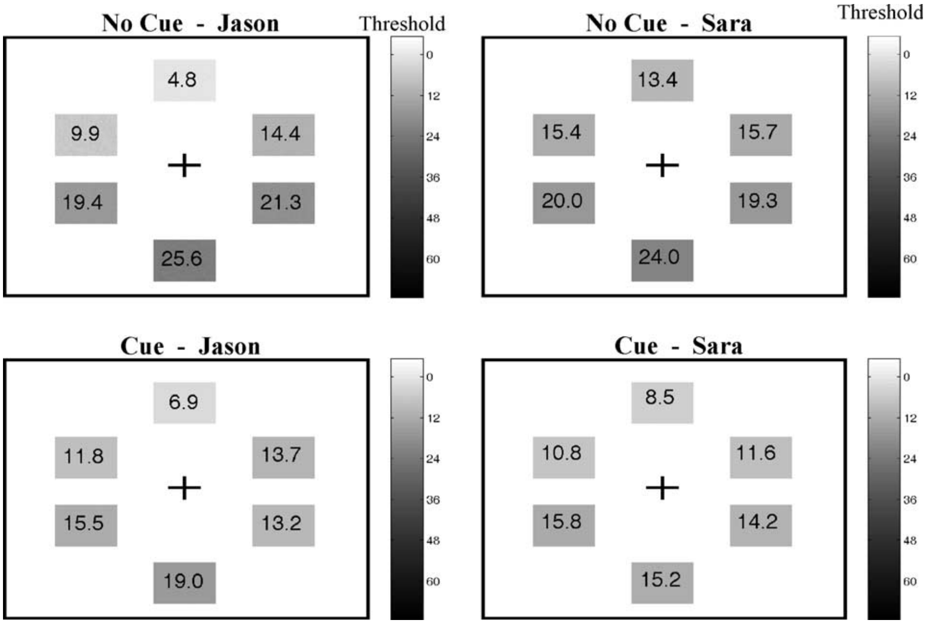

Fig. 2. Contrast thresholds for orientation discrimination of the Gabor for two subjects during steady fixation in the presence and absence of cues indicating the location of the Gabor (SDs were about 20% of threshold). The gray level in each square corresponds to its threshold. The uppermost square represents the location of current fixation. In the experiment, fixation could have been at any of the six outline boxes when the Gabor was presented. Prior to any analysis, data were pooled across the different outline boxes and categorized according to the location of the Gabor relative to the location of current fixation. This categorization was based on both the distance (measured in number of boxes) and the direction (clockwise or counterclockwise) of the Gabor relative to the current fixation position.

location of the Gabor relative to fixation. This categorization was based on both the distance (measured in number of boxes) and the direction (clockwise or counterclockwise) of the Gabor relative to the current fixation position. Thresholds were then determined for each of the six possible relative locations based on the best fitting Weibull function. Thresholds were defined as the contrast corresponding to 75% correct reports of orientation.

Fig. 2 shows that thresholds were reduced (average reduction = 16% for Jason, 29% for Sara) when the pretrial cue allowed attention to be allocated to the appropriate location. The size of these cueing effects is about the same as those reported previously for orientation discrimination (Dosher & Lu, 2000). Thresholds also increased with eccentricity for both subjects, showing that directing attention to the cued location improved performance, but did not overcome the effect of eccentricity. These data will serve as a baseline against which the effects of attentional allocation during saccadic scanning will be assessed.

3.2. Saccadic performance

Subjects had no difficulty following the instructions to scan the sequence of boxes. Fig. 3 shows representative traces of horizontal and vertical eye movements in which the event marker indicates the presentation of the sequence of critical frames containing the Gabor and noise.

Table 1 summarizes the details of saccadic performance. On average intersaccadic pauses were about 310 ms, and were approximately the same as during the single task sessions (see Section 2) when only saccades were required and no orientation judgments were made. At this rate of scanning, about 2.5 loops around the display could be completed in a trial. The duration of the intersaccadic pauses for the interval in which the Gabor was flashed were about 20 ms longer than other intervals, presumably reflecting the effect of the highly visible presentation of the visual noise. Average vector errors of the line of sight from the center of the boxes were about 30′. Average error measured at the offset of a saccade was slightly greater than at the onset of the next saccade. This may be due to small post-saccadic drift in which eye position moves closer to the target after saccade offset (Kapoula, Robinson, & Hain, 1986).

3.3. Perceptual performance during pauses between saccades

Fig. 4 shows thresholds during intersaccadic pauses in which the Gabor and noise occurred either early in the pause (right after saccade offset) or 150 ms later. As in Fig. 2, the data were pooled across the six different possible fixation positions at the time of the presentation

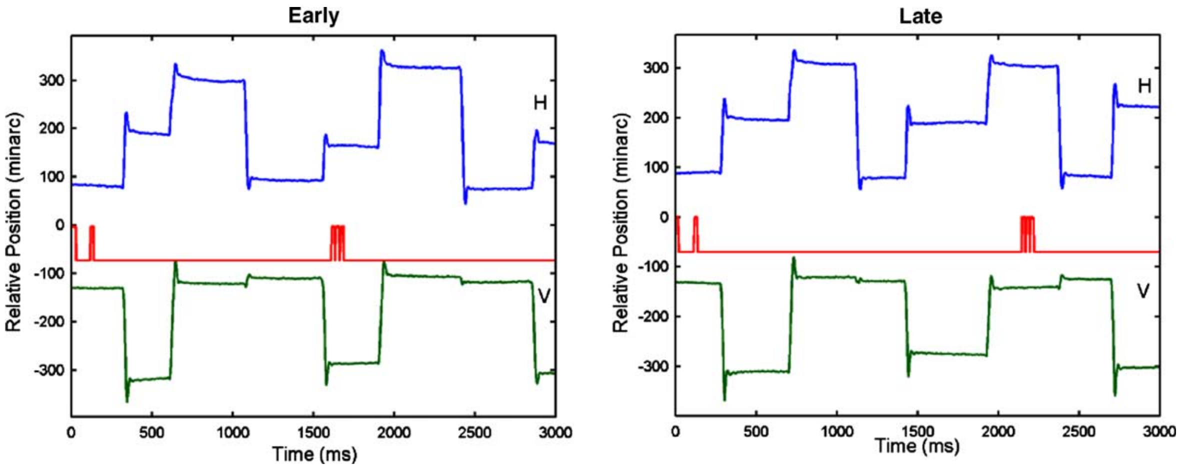

Fig. 3. Sample eye traces (top: horizontal; bottom: vertical) during a trial. The series of Gabor/noise frames appeared either right after a saccade (Early) or after a 150 ms delay following saccade offset (Late). The middle trace is the event marker recording the start of the trial (at time = 0), the signal to begin scanning, and finally, the appearance of the frames containing the Gabor.

Table 1
Saccadic performance during scanning: triangular pattern

	Subject	Saccades only[a]		Saccades and perceptual judgments[b]	
		Early: Mean (SD) *N*	Late: Mean (SD) *N*	Early: Mean (SD) *N*	Late: Mean (SD) *N*
Critical saccade[c]					
Error at saccade onset[d]	Jason	27 (13) 150	26 (14) 159	26 (13) 762	26 (14) 671
(′)	Sara	25 (15) 323	25 (14) 269	25 (14) 990	24 (12) 1040
Error at saccade offset[e]	Jason	32 (17) 150	28 (14) 159	32 (17) 762	30 (17) 671
(′)	Sara	26 (15) 323	26 (15) 269	26 (15) 990	27 (16) 1040
Intersaccadic interval[f]	Jason	320 (145) 150	328 (110) 159	300 (38) 762	319 (70) 671
(ms)	Sara	308 (65) 323	337 (53) 269	332 (64) 990	356 (68) 1040
All saccades[g]					
Error at saccade onset[d]	Jason	24 (15) 1051	23 (15) 1114	23 (15) 5390	23 (16) 4726
(′)	Sara	24 (17) 2208	23 (16) 1815	23 (16) 6411	23 (16) 6623
Error at saccade offset[e]	Jason	33 (18) 1051	32 (17) 1114	33 (17) 5390	32 (18) 4726
(′)	Sara	28 (18) 2208	27 (16) 1815	27 (16) 6411	27 (16) 6623
Intersaccadic interval[f]	Jason	309 (74) 1051	309 (71) 1114	302 (53) 5390	304 (54) 4726
(ms)	Sara	304 (64) 2208	308 (64) 1815	319 (69) 6411	325 (69) 6623

[a] "Saccades only" refers to trials in which subjects were required to make saccades among the outline squares only, without the accompanying perceptual judgments.

[b] "Saccades and perceptual judgments" refers to trials in which subjects made saccades and identified the orientation of the Gabor stimulus.

[c] "Critical saccade" is the saccade that occurred after the appearance of the Gabor and noise frames.

[d] "Error at saccade onset" refers to the vector distance between eye position at the time of saccadic onset and the center of nearest outline square from which the saccade is about to depart.

[e] "Error at saccadic offset" refers to vector distance between eye position at the time of saccadic offset and the center of nearest outline square, where the saccade just landed.

[f] "Intersaccadic interval" refers to the interval between the onset of the saccade and the offset of the immediately preceding saccade.

[g] "All Saccades" refers to all saccades observed in any given trial, including those before and after the Gabor and noise frames.

of the Gabor, and the locus of current fixation is represented by the top box in the graphs.

The thresholds in Fig. 4 were in general higher than those during steady fixation (Fig. 2). In addition, thresholds late in the intersaccadic pause were lower than those early in the pause at all locations other than those neighboring the current fixation position.

A better depiction of the differences among thresholds across locations is given by the ratios of thresholds during the intersaccadic pauses to thresholds obtained during steady fixation (pre-cue condition), shown in Fig. 5. Plotting ratios takes into account the effect of eccentricity, and thus can show more clearly the contribution of saccadic planning to the modulation of thresholds over space and time.

The ratios in Fig. 5 show that early in the pause thresholds were as much as three times higher than during fixation. Performance improved later in the

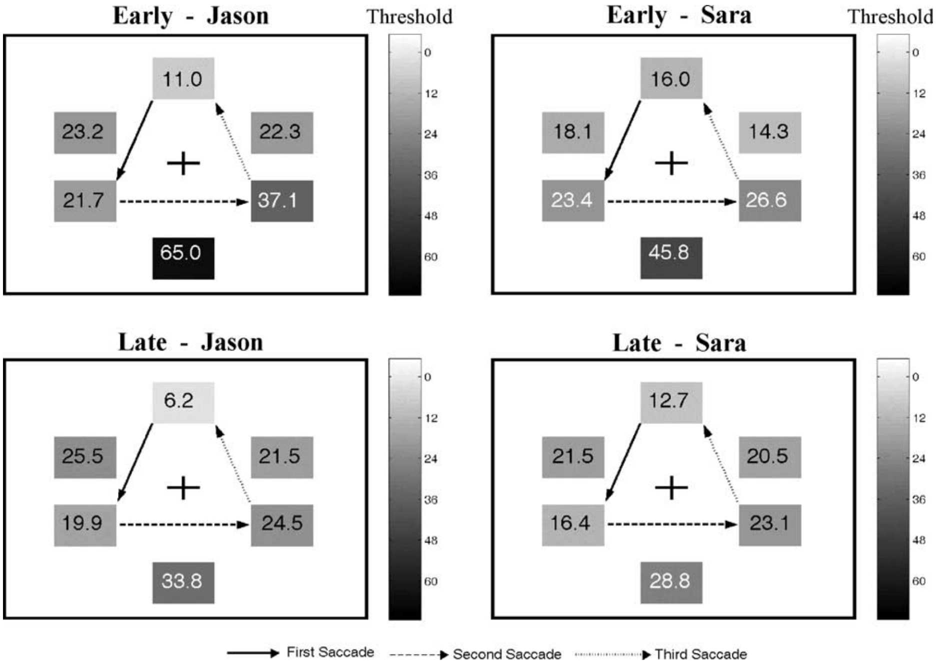

Fig. 4. Contrast thresholds for orientation discrimination of the Gabor for two subjects during intersaccadic pauses (SDs were approximately 20% of threshold). Gabors appeared during a randomly selected intersaccadic pause. The gray level in each square corresponds to its threshold. The uppermost square represents the location of current fixation and the arrows show the directions of the next three saccades (counterclockwise). In the experiment, fixation could have been at any of the six outline boxes when the Gabor was presented. Prior to any analysis, data were pooled across the different outline boxes and categorized according to the location of the Gabor relative to the location of current fixation. This categorization was based on both the distance (measured in number of boxes) and the direction (clockwise or counterclockwise) of the Gabor relative to the current fixation position.

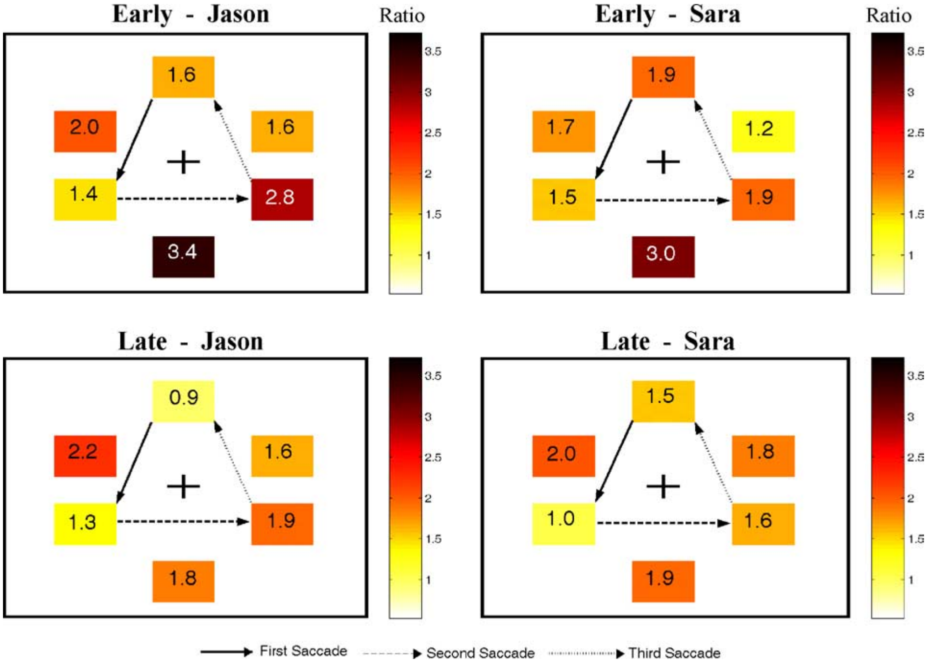

Fig. 5. The ratio of thresholds obtained during intersaccadic pauses (Fig. 4) to thresholds obtained during steady fixation (Fig. 2). The redder the boxes the higher the ratio. The uppermost square represents the location of current fixation and the arrows show the directions of the next three saccades (counterclockwise). In the experiment, fixation could have been at any of the six outline boxes when the Gabor was presented. Prior to any analysis, data were pooled across the different outline boxes and categorized according to the location of the Gabor relative to the location of current fixation. This categorization was based on both the distance (measured in number of boxes) and the direction (clockwise or counterclockwise) of the Gabor relative to the current fixation position.

pause when the lowest ratios were found for the current locus of fixation and for the target of the next saccade.

The ratios in Fig. 5 show that late in the intersaccadic pause, close to the time of the saccade, visual performance at only one of the extrafoveal locations, namely, the target of the next saccade, was comparable to that observed during steady fixation when the location of the Gabor was cued in advance. These low thresholds reflected the shift of attention to the saccadic target. Visual performance at the other extrafoveal locations suffered, presumably due either to insufficient attention, or to sensory or motor factors connected to the planning and programming of the saccades.

3.4. Statistical evaluation

Statistical tests were performed to evaluate the significance of the differences between performance late in the intersaccadic pause and performance during steady fixation at each of the six locations in the display (the location of current fixation and the five extrafoveal locations). The statistical procedure used was the same as that employed by Lu et al. (2002) to compare psychometric functions obtained under different attentional conditions. In the present experiment, the statistical comparisons allow us to find out whether a given ratio shown in Fig. 5 was reliably different from one.

To perform the statistical comparisons, parameters of each of the best fitting Weibull functions were determined under two different models. In the *constrained* model the assumption was made that there is no reliable difference between performance at a given location during an intersaccadic pause and performance at the same location during steady fixation. In the constrained model the slope and threshold parameters of the best-fitting Weibull functions were constrained to be the same for the pair of psychometric functions obtained at each location during the intersaccadic pause and during steady fixation. The quality of the fits obtained under this constrained model was compared to an *unconstrained* model. In the unconstrained model, each psychometric function was fit with its own parameters. The thresholds obtained under the unconstrained model are thus the same as those shown previously in Figs. 2 and 4. If the quality of the fit obtained for a given location under the unconstrained model is significantly better than that obtained under the constrained model for the same location, we would conclude that perceptual performance at this location during intersaccadic pauses is reliably different from that obtained during steady fixation.

To compare the fits of the constrained and unconstrained models, a likelihood value for each psychometric function at each location under each model was computed. The likelihood value was defined as

$$\text{likelihood} = \prod_{i=1}^{7} \frac{N_i!}{K_i!(N_i - K_i)!} P_i^{K_i}(1 - P_i)^{N_i - K_i} \tag{2}$$

where N_i refers to the number of trials for each contrast level i, K_i refers to the number of correct trials, and P_i refers to the percent correct predicted by the following Weibull equation:

$$P_i = \max - (\max - 0.25)2^{-(c/\rho)^{\eta}} \tag{3}$$

P_i refers to the probability of correct orientation discrimination at contrast c, and ρ and η are the free parameters: ρ is the threshold of the psychometric function at $p = 0.75$ and η is the slope.

The likelihoods obtained for both the constrained and unconstrained models for each location were then compared using a chi-square statistic:

$$\chi^2(\text{df}) = 2.0 \times \log\left(\frac{\text{maxlikelihood}_{\text{unconstrained}}}{\text{maxlikelihood}_{\text{constrained}}}\right)$$
$$\text{where df} = k_{\text{unconstrained}} - k_{\text{constrained}} \tag{4}$$

Application of these tests to the data obtained at each location confirmed the basic features that were observed in the ratios shown in Fig. 5. Specifically, performance during intersaccadic pauses at all locations other than: (1) the target of the next saccade, and (2) the location of current fixation, were reliably different from performance during steady fixation. Performance at the target of the next saccade and at the locus of current fixation achieved levels characteristic of what was obtained during steady fixation. Fig. 6 shows the chi-square (Eq. (4)) and p-values for each of the locations. These results show that the benefit from attention at both the location of current fixation and the target of the next saccade was comparable to that produced by cues delivered during steady fixation. Visual performance at the remaining locations was suppressed during intersaccadic pauses relative to that during fixation, presumably due to reduced attentional levels or to factors connected to the programming of the saccades themselves.

In summary, the pattern of contrast thresholds for orientation discrimination showed that during pauses between saccades, extrafoveal attention was preferentially allocated to the saccadic goal. Thresholds at the saccadic goal were comparable to those during steady fixation, given comparable cues. Thresholds at other extrafoveal locations, including the target of the second saccade in the sequence, were significantly higher.

3.5. Changing the saccadic pattern: back-and-forth saccades

The results thus far showed a clear attentional advantage for the target of the upcoming saccade and little advantage for the target of the second saccade of the sequence. To examine the status of this second target

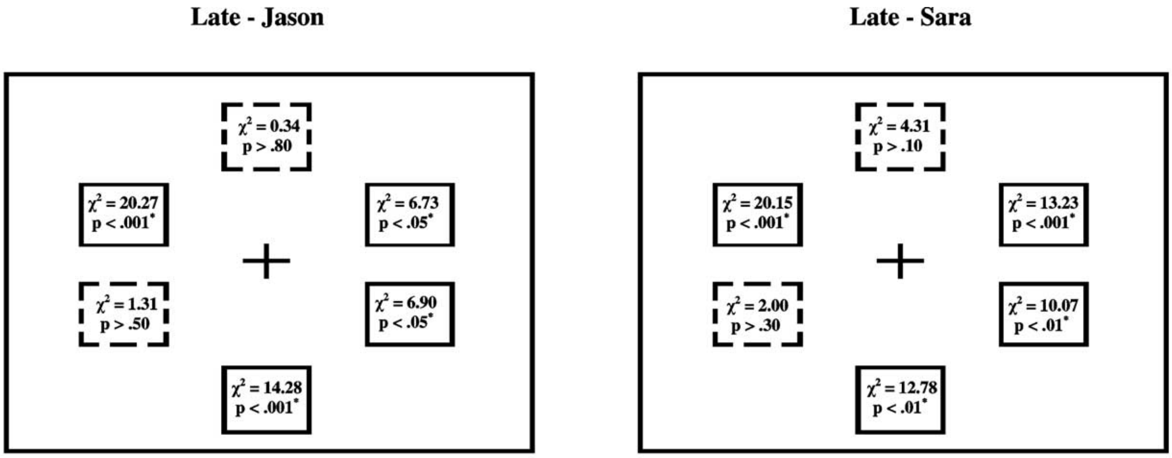

Fig. 6. Chi-square statistics and *p*-values computed for each location based on a comparison of performance during intersaccadic pauses and during steady fixation (see text for details). Thresholds were significantly higher during intersaccadic pauses at all but two locations (shown by dashed outline squares), the location of current fixation (top box) and the target of the next saccade (lower left-hand box).

more closely, a different saccadic pattern was tested with the same displays. Specifically, subjects made saccades back-and-forth between two locations, the starting fixation position and a location two boxes away in the counterclockwise direction. This back-and-forth pattern changed the status of the target of the second saccade in the original, triangular saccadic pattern (Figs. 4 and 5, lower right-hand location) to that of a non-target.

Except for the new saccadic pattern, the stimulus and procedures were the same in this experiment as they were in the basic triangular scanning pattern experiment. Trials in which the subject made a saccade before the start signal (2.0% for Jason, 3.7% for Sara) and trials in which one or more Gabor or noise frames occurred during a saccade (9.5% for Jason, 22.5% for Sara) were discarded. Data were based on a total of 1821 trials for Jason (1753 dual task and 68 saccade only) and 2245 for Sara (2163 dual task and 82 saccade only).

Saccadic performance for the back-and-forth saccadic pattern was similar to that observed for the triangular scanning pattern except that intersaccadic intervals were slightly shorter (average duration was about 290 ms). Table 2 summarizes the details of saccadic performance.

Fig. 7 shows ratios of thresholds for the back-and-forth saccadic pattern relative to thresholds during steady fixation. Early in the intersaccadic pause, ratios tended to be higher during back-and-forth scanning than during triangular scanning (Fig. 5), particularly at the location depicted below and to the right of the current fixation position. This location was the target of the second saccade in the sequence during triangular scanning, but was never looked at during back-and-forth scanning. Differences between the two different scanning patterns did not persist throughout the intersaccadic pause. Later in the pause, performance at all locations was nearly identical for both types of saccadic patterns. The similarity in thresholds for different scanning patterns late in the pause, closer to the time of executing the next saccade, shows that there was no attentional advantage for the target of the second saccade.

4. Discussion

In natural scanning saccades are made as sequences, taking the line of sight from one chosen location to the next. Understanding how attention is deployed during the execution of saccadic sequences is crucial for describing vision during the momentary periods of fixation, for determining the contribution of attention to the accurate targeting of saccades, and for assessing how much attention is available to survey the scene and identify useful places to look.

To address these issues we used a visual task to assess the pattern of allocation of attention over space and time during the execution of some simple saccadic sequences. Contrast thresholds for identifying the orientation of a Gabor patch presented during a randomly selected pause between saccades were compared to thresholds obtained while the eye remained fixated at a single location within the display. The results showed that visual thresholds during intersaccadic pauses depended on when and where the visual target (Gabor) appeared relative to the ongoing pattern of saccades. The main findings were: (1) visual performance during intersaccadic pauses, relative to that obtained at comparable retinal eccentricities during steady fixation, was better at the goal of the upcoming saccade than at other extrafoveal locations, reflecting the beneficial effect of the shift of attention to the target of the saccade; (2)

Table 2
Saccadic performance during scanning: back-and-forth pattern

	Subject	Saccades only[a]		Saccades and perceptual judgments[b]	
		Early: Mean (SD) *N*	Late: Mean (SD) *N*	Early: Mean (SD) *N*	Late: Mean (SD) *N*
Critical saccade[c]					
Error at saccade onset[d]	Jason	27 (17) 35	26 (15) 31	25 (14) 757	25 (12) 799
(′)	Sara	23 (15) 58	29 (17) 24	33 (20) 929	35 (20) 679
Error at saccade offset[e]	Jason	29 (16) 35	23 (13) 31	31 (17) 757	29 (16) 799
(′)	Sara	23 (13) 58	24 (13) 24	34 (21) 929	35 (20) 679
Intersaccadic interval[f]	Jason	267 (41) 35	291 (41) 31	297 (44) 757	317 (52) 799
(ms)	Sara	275 (71) 58	331 (60) 24	302 (106) 929	387 (144) 679
All saccades[g]					
Error at saccade onset[d]	Jason	25 (16) 288	23 (16) 252	24 (16) 5560	23 (15) 5729
(′)	Sara	25 (16) 458	30 (19) 175	30 (20) 7053	32 (20) 4392
Error at saccade offset[e]	Jason	33 (18) 288	31 (16) 252	34 (18) 5560	33 (18) 5729
(′)	Sara	29 (17) 458	32 (19) 175	33 (20) 7053	33 (19) 4392
Intersaccadic interval[f]	Jason	258 (53) 288	257 (54) 252	288 (59) 5560	294 (61) 5729
(ms)	Sara	265 (80) 458	291 (87) 175	274 (106) 7053	323 (126) 4392

[a] "Saccades only" refers to trials in which subjects were required to make saccades among the outline squares only, without the accompanying perceptual judgments.

[b] "Saccades and perceptual judgments" refers to trials in which subjects made saccades and identified the orientation of the Gabor stimulus.

[c] "Critical saccade" is the saccade that occurred after the appearance of the Gabor and noise frames.

[d] "Error at saccade onset" refers to the vector distance between eye position at the time of saccadic onset and the center of nearest outline square from which the saccade is about to depart.

[e] "Error at saccadic offset" refers to vector distance between eye position at the time of saccadic offset and the center of nearest outline square, where the saccade just landed.

[f] "Intersaccadic interval" refers to the interval between the onset of the saccade and the offset of the immediately preceding saccade.

[g] "All saccades" refers to all saccades observed in any given trial, including those before and after the Gabor and noise frames.

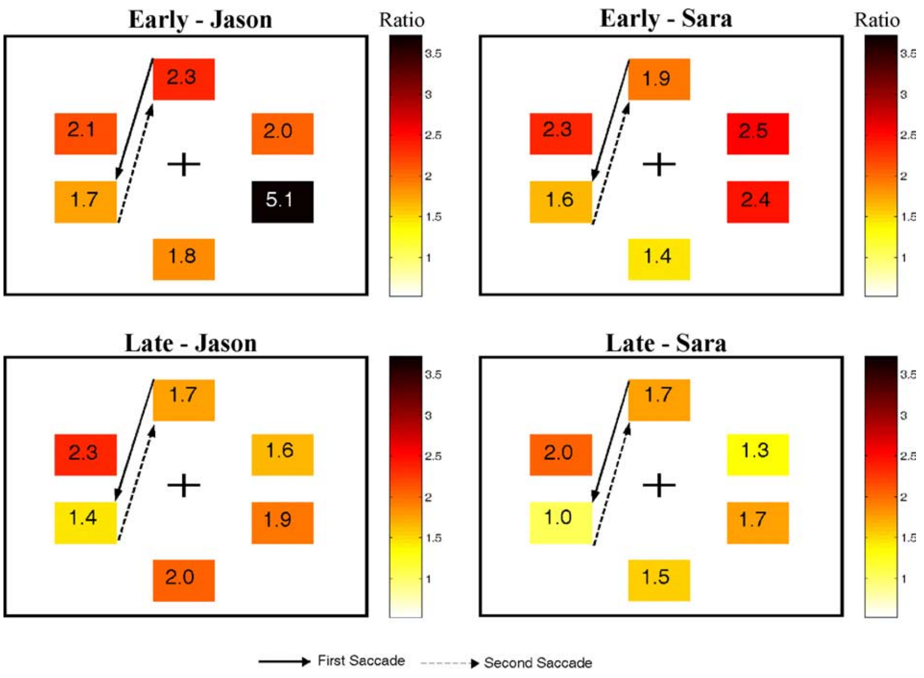

Fig. 7. Ratio of thresholds obtained during back-and-forth scanning to those obtained during steady fixation (Fig. 2). The redder the box the higher the ratio. The uppermost square represents the location of current fixation and the arrows show the directions of the next two saccades. In the experiment, fixation could have been at any of the six outline boxes when the Gabor was presented. Prior to any analysis, data were pooled across the different outline boxes and categorized according to the location of the Gabor relative to the location of current fixation. This categorization was based on both the distance (measured in number of boxes) and the direction (clockwise or counterclockwise) of the Gabor relative to the current fixation position.

thresholds at extrafoveal locations other than the target of the upcoming saccade were significantly higher during intersaccadic pauses than during fixation; (3) there was no evidence for any visual or attentional benefit at the target of subsequent saccades, beyond the very next one in the sequence.

The pattern of visual enhancement and suppression during intersaccadic pauses reflects the shifts in attention associated with the planning and programming of saccades, along with sensory or motor factors related to the programming of the saccades themselves. These are considered below.

4.1. Visual performance at the saccadic goal vs. visual performance elsewhere

Visual performance during intersaccadic pauses was better at the goal of the upcoming saccade than at other extrafoveal locations. The visual enhancements at the saccadic goal, which were particularly clear late in the intersaccadic pause, 150 ms after the offset of the previous saccade, were most likely due to a shift of attention to the target of the saccade. These pre-saccadic shifts of attention are similar to the pre-saccadic attention shifts reported previously for single saccades programmed in isolation (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler et al., 1995). This result gives further support to the idea that saccadic and perceptual mechanisms do not use separate and independent selective attentional filters to designate objects or locations for enhanced processing. Any differences between the programming and execution of saccadic sequences and single saccades, such as the contribution of memory to the execution of the saccadic sequences (Zingale & Kowler, 1987), does not obviate a role for selective attention in directing each saccade to its target.

In addition to the relatively good visual performance at the saccadic target, there were other ways in which location influenced visual performance. For example, visual thresholds at the current locus of fixation during intersaccadic pauses were the same as those measured during longer periods of steady fixation. The high level of performance at fixation could mean either that attention was unimportant for accurate processing of foveal material (at least for the orientation discrimination task), or, alternatively, that the fovea always received some attention during saccadic scanning. Our results do not allow us to eliminate either possibility.

Visual performance at the pair of locations surrounding the current locus of fixation differed from that at other locations in that thresholds increased over time during the intersaccadic pause. It is possible that the tendency toward poorer performance at the locations surrounding fixation may have resulted from local competition for limited processing resources. The importance of local competition has been demonstrated in previous experiments done with briefly flashed, dense arrays of letters, which showed that the ability to report a cued pair of letters depended on their separation, with accuracy of reports declining the closer the attended letters were to each other (Bahcall & Kowler, 1999). These previous results could be accounted for by a model in which the attentional enhancement of a target produces a surrounding region of relative attentional inhibition, where processing accuracy suffers (see also Cutzu & Tsotsos, 2003; Mounts, 2000). A zone of "attentional inhibition" around fixation, and perhaps around the saccadic target as well, would contribute to the poor visual performance observed surrounding fixation.

4.2. Intersaccadic pauses vs. steady fixation

Thresholds at extrafoveal locations, other than the target of the next saccade, were about 1.5–3 times higher during intersaccadic pauses than during steady fixation. Performance at these non-target locations undoubtedly suffered because attention was preferentially allocated to the saccadic target. But comparable changes in the pattern of attentional allocation had more modest effects during steady fixation, where removal of the pre-cue signaling the location of the Gabor produced thresholds elevations of less that 30% (Fig. 2, compare cue vs. no cue thresholds). Why were threshold elevations at extrafoveal, unattended locations so much larger during saccadic scanning?

One reason for the elevation in thresholds at non-target locations during saccadic scanning could have been a sub-optimal strategy of attentional allocation, in which more attention than needed was devoted to the target of the upcoming saccade. A strategy of allocating all or most of available attention to the saccadic goal may have been helpful for making accurate and timely saccades, but is not necessarily optimal for perceptual performance. Assuming that the performance benefits derived from increases in attentional allocation show a pattern of diminishing returns (Shaw & Shaw, 1977), then a broader distribution of attention among the locations might have improved perceptual performance at the non-targets without a substantial sacrifice either in visual performance at the saccadic target or in the accuracy or timing of the saccades. Addressing the consequences of various attentional strategies will require experiments that encourage different distributions of attention and determine the resulting effects of these distributions on both saccadic and perceptual performance (i.e., AOC analysis; Kowler et al., 1995).

Another factor that could have contributed to the relatively high thresholds at non-targets is any attentional demands imposed by the saccadic task itself. This seems unlikely given the good perceptual performance observed at both the saccadic goal and at the locus of current fixation. A similar conclusion was drawn for single saccades (Kowler et al., 1995). But we cannot completely dismiss the possibility that the saccadic task drew attention from perception. Perceptual performance may have reached asymptotic levels at the saccadic goal and at the locus of current fixation, so that removing some attention from these locations would not necessarily have been harmful.

Finally, visual performance during saccadic scanning could have been elevated due to saccadic suppression (Volkmann, 1986). It seems plausible that saccadic suppression affected performance early in the intersaccadic pause, when thresholds were found to be elevated at some locations by as much as three times that observed during steady fixation. Prior studies of saccadic suppression reported that threshold elevations continue until about 40 ms after a saccade has been completed (Beeler, 1967; Burr, Morrone, & Ross, 1994; Volkmann, Schick, & Riggs, 1968), an interval that would include the first half of our early Gabor stimulus. The time needed to recover from saccadic suppression has been found to increase with eccentricity (Mitrani, Mateeff, & Yakimoff, 1970), which might account for why we found the highest thresholds early in the intersaccadic pause at the most eccentric locations (Fig. 5). However, any increase in saccadic suppression with eccentricity cannot account fully for the pattern of thresholds we observed early in the intersaccadic pause because early performance was different for the two saccadic patterns studied (Figs. 5 and 7) even though the retinal eccentricities of the Gabor were the same in each case.

In summary, we proposed three processes that could have contributed to the relatively high thresholds observed at non-target locations during saccadic scanning: (1) non-optimal attentional strategies, (2) siphoning off of attentional resources to saccadic planning, and (3) saccadic suppression. These processes could have independently contributed to the observed location-specific elevations in thresholds.

4.3. Comparison of triangular vs. back-and-forth scanning: implications for the representation of saccadic plans

Additional experiments examined attentional allocation during a different spatial pattern of saccades in which sequences of saccades were made back-and-forth between two locations within the display instead of in a triangular pattern. A comparison of thresholds across these two scanning pattern showed that performance at the goal of the second saccade in the sequence during triangular scanning was the same as performance at the same spatial location during back-and-forth scanning, despite the fact that this location was never looked at during back-and-forth scanning. To the extent that these thresholds reflect attention, this pattern of results suggests that attention was not directed beyond the goal of the upcoming saccade and does not reflect longer range saccadic plans.

A different conclusion was drawn by Godijn and Theeuwes (2003), who studied attentional allocation preceding the execution of a pair of saccades. In their experiment the appearance of a pair of visual cues was the signal to begin making saccades to the two cued locations in sequence. Godijn and Theeuwes found that visual identification of letters presented briefly, before execution of the first saccade, was better for letters displayed at the saccadic goals than for letters at non-goal locations. This result indicated that attention was allocated to the goals of both upcoming saccades. It is possible that the attentional enhancements they observed reflected processes involved in the initial stages of saccadic planning, including the segregation of visual locations into saccadic goals and non-goals, and the initial preparation of saccadic programs. Our experiments were intended to assess allocation of attention during sequence execution, when any events connected solely to the initial preparation of the sequence were no longer relevant. We found no evidence that executing the sequence was associated with allocation of attention to locations beyond the goal of the upcoming saccade.

Attention to the goals of a pair of upcoming saccades may also come into play when two saccades occur in rapid sequence, separated by unusually brief (<100 ms) pauses. Observations of such rapid sequences have suggested that under some circumstances a pair of saccades can be programmed in parallel, so that the visual information acquired before the first saccade determines the spatial parameters of the second (e.g., Araujo, Kowler, & Pavel, 2001; Becker & Jurgens, 1979; McPeek, Nakayama, & Skavenski, 2000; Theeuwes, Kramer, Hahn, Irwin, & Zelinsky, 1999; Viviani & Swensson, 1982). In our experiments, very brief intersaccadic pauses were rare. The average duration of intersaccadic pauses was about 300 ms (Tables 1 and 2), typical of the average duration of pauses in tasks such as search or reading (Viviani, 1990). The absence of evidence for allocation of attention to locations beyond the target of the upcoming saccade in our experiments suggests that parallel programming may result in the preparation of rapid sequences and is not necessarily typical of saccadic sequences with more conventional intersaccadic pause durations.

If attention was not responsible for flagging the path of the saccadic sequence in our experiments, then some other mechanism had to be involved because the saccadic targets were not marked by visual cues. A neural mechanism capable of representing the spatial memory for sequences of saccadic targets was recently described by Ohbayashi, Ohki, and Miyashita (2003), who discovered neurons in monkey premotor cortex that represent memory for planned sequences of saccades. They trained monkeys to memorize the locations of a set of targets which were to be scanned in one of two possible orders. A class of neurons, "transient neurons", responded briefly when a color cue was given that indicated which of the two scanning orders was to be used in a given trial. These transient neurons stopped responding soon after this cue was presented, and long before the signal to initiate the sequence was given. Thus, their activity appeared to represent memory for the ordered sequence of required saccades, independently of saccade execution.

Interestingly, even though we found that attention enhanced the representation of only the very next saccadic target, and not subsequent targets, there was some perceptual advantage for the saccadic target early (during the first 100 ms) in the intersaccadic pause (Fig. 5). Finding that some attention is allocated to the saccadic target so early suggests that the critical neural events leading to the attention shift began during the previous intersaccadic interval. This result may indicate a link between memory and attention, in which imminent execution of one saccade triggers a retrieval process that brings attention to the next saccadic target and initiates preparation of the corresponding saccadic command.

4.4. Conclusions and implications

We found that during intersaccadic intervals, attentional resources were allocated primarily to the current fixation position and to the target of the next saccade. Relatively little attention was allocated to other locations, producing an elevation in visual thresholds at the unattended locations. One advantage to focusing so much attention on the saccadic target at the expense of other locations is that it increases the "attentional contrast" between the saccadic target and its neighboring locations, thus attenuating potential distractors and facilitating the programming of an accurate saccade. The obvious disadvantage of attending to only two places (the current fixation position and the saccadic target) is that less attention remains for broad attentional surveys of the visual scene to find potentially useful places to look.

Perhaps broad attentional surveys are not important for finding promising places to look. Alternative and less demanding strategies are available. Analysis of the saccadic patterns used in visual memory (Melcher & Kowler, 2001) or search tasks (Araujo et al., 2001) has shown a clear preference for low demand strategies, such as preferentially looking at objects at close eccentricities, or looking from one object to the next randomly, without regard for whether an object was fixated before. Although such strategies are not necessarily optimal for bringing the line of sight to the most important locations promptly, they are low cost, requiring little attention for assessing the content and significance of the extrafoveal visual field. Attention can thus be devoted to more pressing tasks, such as visual analysis of foveal details, and ensuring that the next saccade is accurate.

It will be necessary to explore other tasks requiring saccadic sequences to determine whether it is possible to induce more flexible attentional strategies without significant costs to either the accuracy or timing of the saccades, or, alternatively, whether the primary role of extrafoveal visual attention is to control the spatial parameters of saccades.

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