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Vision Research 45 (2005) 2685–2703

Vision Research

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Spatial deployment of attention influences both saccadic and pursuit tracking ☆

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Received 25 November 2004; received in revised form 17 May 2005

Abstract

We examined the effects of changing spatial aspects of attention during oculomotor tracking. Human subjects were instructed to make a discrimination on either the small (0.8°) central or the large (8°) peripheral part of a compound stimulus (two counter-rotating concentric rings) while the stimulus either translated across the screen or was stationary. During this period, a transient perturbation with either step or ramp movement profile occurred. For perturbations leading to a change in position larger than the small ring, saccades occurred more frequently and had much shorter latencies (by 135 ms) when attention was directed to the small ring than when attention was directed to the large ring. These latency differences were sufficiently great that from a single saccade one can identify the attentional instruction with 94% accuracy. However, with target steps as small as the small ring, saccade latencies differed less. For pursuit, ramp perturbations caused larger changes in eye velocity with little change in latency when attention was directed to the small ring. Finally, when only the motion of the non-attended ring was perturbed, most subjects showed stronger saccadic responses to perturbations of the small than the large ring, and stronger pursuit responses to perturbations of the large than the small ring. By fitting the saccade latency distributions with the Reddi and Carpenter LATER model, we found that our subjects apparently employed at least two distinct strategies for changing latency when attending large vs. small. We propose that the timing of the saccade decision process depends on both the size of the attended object and the magnitude of the perturbation.

Keywords: Eye movements; Attention; Saccade; Pursuit; Latency; Motor control; Human

1. Introduction

Saccades and pursuit are the voluntary eye movements used to acquire and stabilize the retinal image of a target on the fovea, the high-acuity region of the retina. Attention is important, perhaps even necessary, for the execution of both saccades and pursuit by allowing for the selection of relevant stimuli.

In the case of saccades, generating the movement appears to require a prior shift of attention to the target location. First, studies using single-unit recording, fMRI, and microstimulation suggest that the same brain areas are involved in both saccades and shifts of attention (frontal eye fields: Corbetta et al., 1998; Moore & Fallah, 2004; Schall, 2004; superior colliculus: Carello & Krauzlis, 2004; Cavanaugh & Wurtz, 2004; Ignashchenkova, Dicke, Haarmeier, & Thier, 2004; Kustov & Robinson, 1996). Second, subjects are poor at making visual discriminations just before a saccade except at the target location (Deubel & Schneider, 1996; Kowler,

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☆ This research was supported by National Eye Institute Grant EY-12212 (R.J.K.) and NIH Grant RR03060 (J.W.).

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doi:10.1016/j.visres.2005.05.009

Anderson, Dosher, & Blaser, 1995; Posner, Snyder, & Davidson, 1980; Shepherd, Findlay, & Hockey, 1986), and the same is true for auditory discriminations (Rorden & Driver, 1999). Third, saccades are triggered sooner if attention is first drawn to the target location and are delayed if attention is directed elsewhere (Crawford & Muller, 1992; Hoffman & Subramaniam, 1995; Kowler et al., 1995; Shepherd et al., 1986). Taken together, these results argue that a shift of the location of attention necessarily precedes saccadic eye movements.

In the case of smooth pursuit, the ability to selectively attend to the moving target while ignoring stationary stimuli is required to produce pursuit eye movements; without attention, the self-induced visual motion of the background would cancel pursuit (Kowler, van der Steen, Tamminga, & Collewijn, 1984; Lindner, Schwarz, & Ilg, 2001; Schwarz & Ilg, 1999; Suehiro et al., 1999). Because of the continuous nature of the pursuit response, it has been postulated that attention moves smoothly with the eyes during tracking (Kowler, 1990). As with saccades, discrimination performance is better at (Khurana & Kowler, 1987) or near (van Donkelaar & Drew, 2002) the location of the pursuit target than at other locations, suggesting that pursuit and perception share the same attentional mechanism. The amount of attention allocated to pursuit is not constant: adding attentional load impairs the quality of pursuit more at the start of pursuit than later (Chen, Holzman, & Nakayama, 2002), and other evidence also suggests that pursuit uses more attentional resources at the start and end of pursuit than during pursuit maintenance (van Donkelaar, 1999; van Donkelaar & Drew, 2002).

In everyday life, visual targets are usually complex and offer a variety of spatial scales at which they can be attended. That is, attention has a spatial extent as well as a spatial location, and these two aspects are somewhat independent in that one can attend either to a whole visual stimulus or to a single part of it, both at the same spatial location. This spatial feature of attention is not shared by saccadic or pursuit eye movements in any obvious way, in that the eye movements can be adequately described as a change in eye position; spatial extent is not relevant. In this paper, we investigate the effects of a spatial aspect of attention on both pursuit and saccadic eye movements by recording the response to position and velocity errors (i.e., the mismatches between the motion of the eye and the target) while a subject tracks a compound stimulus, consisting of two concentric, segmented rings rotating in opposite directions, with instructions to attend to and make a discrimination on one of the rings.

2. Methods

Four human subjects (26–38 years of age, one female and three males) participated in the experiment. Two of the subjects (R and L) were authors of the study; the other two (J and C) were naïve as to the experimental conditions and hypotheses. Subjects gave their written informed consent.

The probe and mask stimuli each consisted of two concentric rings (0.8° and 8° in diameter, 42% contrast) made up of several segments (Fig. 1A). The thickness of each ring and the size of the gaps between the segments were scaled according to the cortical magnification factor (Rovamo & Virsu, 1979). The two rings spun in opposite directions at different velocities. In each condition, the number of trials in which each ring spun clockwise and counterclockwise were equal. In all three experiments, the mask stimulus (nine segments in each ring) was briefly (166 ms) replaced by a probe stimulus and then reverted to a mask stimulus for 600 ms. In the probe stimulus, the small ring contained either four or five segments and the large ring either five or seven segments. At the beginning of each trial, subjects were instructed by a high or low frequency auditory tone to attend either to the small ring ("attend small" condition) or the large ring ("attend large" condition) and were asked to report the number of segments in the corresponding ring of the probe stimulus in a two-alternative forced-choice design. After each trial, subjects indicated the number of segments by a key-press; auditory feedback indicated whether the report was correct. In practice, to perform the task in the experiments in which the ring was moving across the screen, it was necessary to track the translational movement of the stimulus, but no specific instruction was given to track the stimulus. Thus, although the emphasis was on the discrimination, not the tracking, subjects generally kept the stimulus well centered on their foveas.

The size of the gaps between the segments was kept constant between mask and probe stimuli, so that the discrimination task could not be performed by analysis of just a segment of the ring, but instead required attention to the entire ring. Prior to the experimental sessions, we obtained psychometric functions for each subject to determine the spinning speed of each ring that yielded approximately 85% correct reports. The spinning speeds were 40–80 rpm, and were adjusted during the experiments to maintain this level of discrimination. The success of these procedures is demonstrated by the similar levels of performance when attending to the large and small rings; overall the percent correct was 79% for the attend small condition and 82% for the attend large condition (Table 1).

2.1. Assessment of attentional task

To confirm that the task required subjects to deploy their attention differently in the attend small and attend large conditions, we performed a control experiment to evaluate the effect of the instructions. This experiment

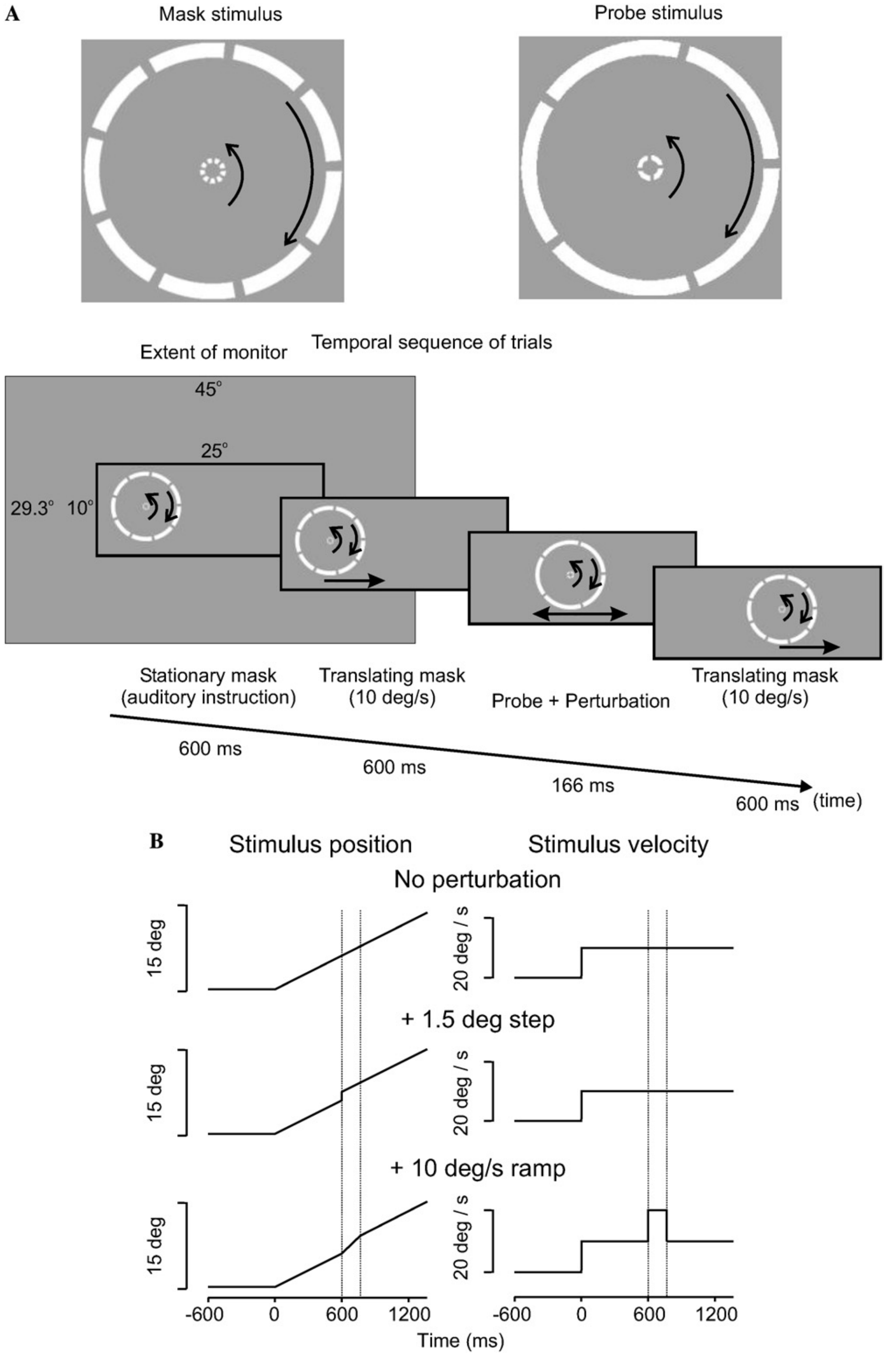

Fig. 1. Methods. (A) Top panels: mask and probe stimuli. The arrows indicate that the rings are rotating in opposite directions. The mask and probe stimuli both had the same thickness of each ring (0.50° and 0.17° of visual angle) and size of the breaks (0.35° and 0.12° of visual angle). Bottom panel: temporal sequence of a trial for experiments 2 and 3. In experiment 1, the temporal sequence is identical except that the rings do not translate. (B) Stimulus position (left panels) and corresponding velocity (right panels) in experiment 2. (We have omitted the spike in the velocity trace corresponding to the step.) Vertical dotted lines indicate the probe stimulus duration.

was similar to the 1.5° step condition in experiment 2 (see below) in that subjects were instructed by an auditory signal to attend to either the large or small ring, but after each trial a second auditory signal instructed them whether to report the number of segments in the large or small ring. In most trials (75%), this second

Table 1
Proportion of correct responses in each experiment for each attentional task

Subject	Ring	Attend-large % correct	Attend-small % correct
Assessment of attentional task			
L	Attended	77	71
	Unattended	50	46
H	Attended	87	86
	Unattended	51	50
A	Attended	83	80
	Unattended	57	49
M	Attended	83	72
	Unattended	51	54
Subject	Experiment	Attend-large % correct	Attend-small % correct
Eye movement experiments			
R	One	87	80
	Two	83	81
	Three	88	80
J	One	81	79
	Two	81	78
	Three	83	82
C	One	88	87
	Two	78	74
	Three	89	83
L	One	81	76
	Two	77	74
	Three	75	77

instruction confirmed that given at the start of the trial, but on the remainder (25%) it indicated that the subject should report the number of segments in the unattended ring. Four subjects (including one of the subjects in the principal experiments, L) participated in the experiment (800 trials). Results indicate that subjects performed at chance (51% of correct responses on average) in the unattended condition and well above chance (80%) in the attended condition (Table 1). Because the subjects had even more motivation here to allocate some attention to the non-designated ring than in the principal experiments of this paper (during which the subjects were never asked about the non-designated ring), the fact that they could not discriminate the non-designated ring makes us confident both that our instructions summoned the subjects' attention and that attention is required to carry out the discrimination task.

2.2. Experiment one: target steps during fixation

The first experiment compared the effects of attending to the small or large ring on saccades made to a small step during fixation. Each trial started with a fixation period of 1200 ms during which the mask stimulus was displayed spinning at the center of the screen. The mask was then replaced by the probe stimulus, which stepped 1.5° to the right or left in a balanced pseudorandom sequence. After 166 ms the probe stimulus was replaced by the mask stimulus in its new location for 600 ms. Experimental sessions consisted of 224 trials divided into four blocks alternating between the attend small condition (56 trials) and the attend large condition (56 trials); each subject performed two sessions on the same day.

2.3. Experiment two: target steps and ramps during pursuit

The second experiment studied the effects of attending to the small or large ring on responses to perturbations of the target trajectory during pursuit. Each trial started with a fixation period of 600 ms during which the mask stimulus was displayed at 7.2° left of the center of the screen. The mask stimulus then translated to the right at 10 deg/s for 600 ms, after which the probe stimulus was displayed for 166 ms followed again by the mask stimulus (see Fig. 1A).

At the onset of the probe stimulus, the stimulus trajectory was altered by either a step or ramp perturbation. Step perturbations were forward or backward steps of 0.75° or 1.5°, so that the resulting position errors would be either smaller or greater than the diameter of the small ring (0.8°). Ramp perturbations, which permitted us to study the effects of spatial scale of attention on changes in smooth eye velocity during pursuit, involved an increase or decrease in stimulus velocity by 5 or 10 deg/s (leading to velocities ranging from 0 to 20 deg/s) for the duration of the probe stimulus (166 ms), such that at the end of the ramp perturbation position errors were similar to those resulting from the step perturbations. We also included a condition (occurring in 8% of the trials) in which the target motion was not perturbed, to assess eye movements related to the expectation of a perturbation.

Perturbations of the two sizes, types (step or ramp), and directions (onward or backward) were interleaved and occurred in a balanced, pseudorandom order. Fig. 1B shows the target position and corresponding target velocity when the target trajectory was not perturbed (top panels), when a step of +1.5° was applied (middle panels), and when a ramp of +10 deg/s was applied (bottom panels).

Experimental sessions consisted of 208 trials divided into four alternating blocks of 26 trials in the attend small condition followed by 26 trials in the attend large condition. Each subject performed two daily sessions, for a total of 14 sessions (2912 trials). We also carried out a control experiment in which subjects were asked simply to track (without performing any attentional task) a 0.3° non-segmented ring moving with trajectories and perturbations identical to those of the compound stimulus.

2.4. Experiment three: perturbations of motion of a single ring

In the third experiment, the motion of the rings was similar to the one previously described in the second experiment, but the perturbation affected only the small ring or the large one. The unperturbed ring continued translating to the right at 10 deg/s at the time of the perturbation. We used both step (+ or −1.5°) and ramp (+ or −10 deg/s) perturbations. Perturbations of the two types and directions were interleaved and occurred in a balanced, pseudorandom order. Experimental sessions consisted of 208 trials divided into alternating blocks of 26 trials in the attend small condition followed by 26 trials in the attend large condition. Each subject performed two daily sessions, for a total of four sessions (832 trials).

2.5. Data acquisition and analysis

Stimuli were generated using VisionWorks® software (Swift, Panish, & Hippensteel, 1997) and displayed via a specialized graphics card (Cambridge Research System® VSG2/3) on a video monitor (Eizo FX-E7, 60 Hz, 800 × 600 pixels) at a viewing distance of 41 cm, such that each pixel subtended 3 arc min. Presentation of stimuli and acquisition, display, and storage of responses were controlled by a second computer using the Tempo software package (Reflective Computing®). Trigger signals from the visual display computer to the Tempo computer allowed us to synchronize data collection to stimulus presentation with 1 ms resolution. Eye movements were measured continuously with an infrared video-based eye tracking system (ISCAN Inc., RK-726) at 240 Hz. Head movements were minimized by use of a bite bar. The accuracy of the eye tracker measurements was ~0.10°. Before each session, we calibrated the eye tracker by having subjects repeatedly fixate for 500 ms a set of horizontal locations to generate a smooth function (using cubic spline interpolation) for converting raw eye tracker values to horizontal eye position.

For off-line analysis, an interactive analysis program was used to filter, display, and analyze the data. Horizontal eye velocities were obtained by differentiating the eye position signal using a finite impulse response (FIR) filter (−3 dB at 54 Hz). Eye acceleration was then obtained by differentiating the velocity signal using the same FIR filter. Saccades were detected by applying a set of velocity and acceleration criteria (Krauzlis & Miles, 1996). This algorithm permitted us to detect saccades with amplitudes as small as ~0.3°. In measurements of smooth eye movements, we excluded data from 5 ms before and after each detected saccade.

We measured the saccade latency as the time from the perturbation to the first saccade. We omitted trials in which the saccade was opposite in direction to the stimulus perturbation or had a latency shorter than 50 ms. If no saccade was detected within 500 ms after the perturbation, that trial was classified as containing no perturbation-induced saccades. If saccades occurred in fewer than 30% of trials for a particular condition and subject, we did not do statistical analyses of those saccades. To measure the pursuit response to the stimulus perturbations, we compared the average velocities during a 20 ms interval starting 110 ms after the perturbations (the latency of pursuit) and before any saccade occurred.

3. Results

In general, our results indicate that when the stimulus perturbation was a change in position greater than the diameter of the small ring but smaller than that of the large one, saccades had dramatically shorter latencies if the task involved attending to the small ring than to the large one, even though the visual stimulus was identical in both situations. Moreover, the smooth eye velocity response, both at the initiation of pursuit and when the target velocity was perturbed, was greater if the subjects attended to the small ring. Finally, when only one of the two rings transiently changed its motion, most subjects made saccades to perturbations of the unattended small ring and made pursuit to perturbations of the unattended large ring.

3.1. Saccadic latency to target perturbations

When subjects attended to the large ring, the latencies of the resulting saccades were much longer than when they attended to the small one. As illustrated by the examples of single trials (Fig. 2) subjects were always looking at the center of the stimulus before the perturbation occurred. However, if attention was directed to the large ring, the retinal error created by the perturbation persisted for a much longer time before it was corrected by a saccade, both for targets that had been previously stationary (Fig. 2A) or moving (Figs. 2B and C). In particular, when the perturbation was large—larger than the small ring but smaller than the large ring—the latency of the resulting saccades was approximately twice as long when subjects were instructed to attend to the large, rather than small, ring, as shown by the medians and standard deviations for each subject and condition (Fig. 3). These differences in median latency were significant in each case (Wilcoxon rank-sum test, $p < 0.001$), whether the stimulus had been stationary (158 ms vs. 314 ms, experiment1), or had stepped while moving and was being pursued (165 ms vs. 304 ms, experiment 2) or had made a transient 10 deg/s increase or decrease in speed (215 ms vs. 325 ms, experiment 2). Of these conditions, the effect of attention was greatest for the stationary target (156 ms), intermediate for the step perturbations (139 ms) and least for the ramp perturbations (110 ms).

Furthermore, the latency distributions were significantly broader in the attend large condition for the

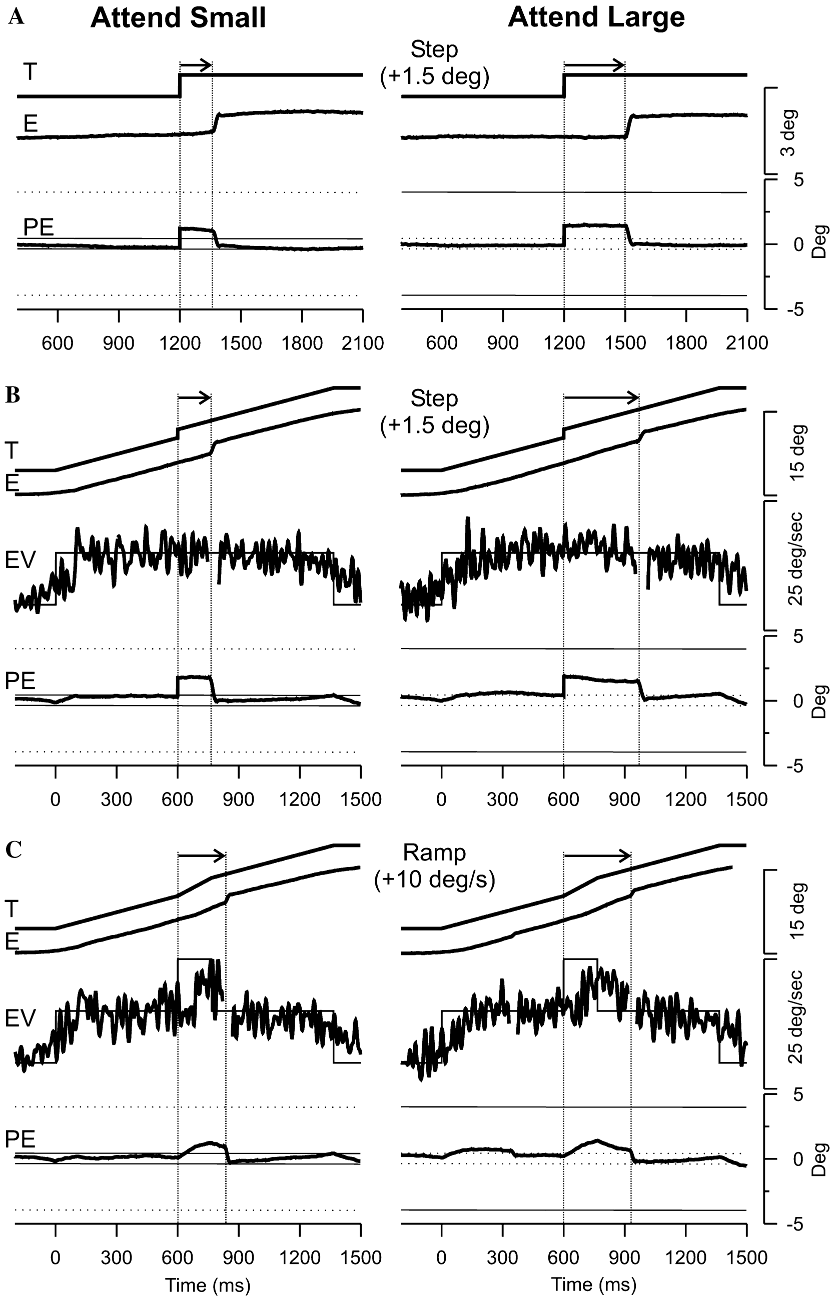

Fig. 2. Single trials in experiments 1 and 2. (A) +1.5° step condition in experiment 1, (B) +1.5° step condition in experiment 2, (C) +10 deg/s ramp condition in experiment 2 (subject J). Each panel, from top to bottom: T, target position; E, eye position; EV, eye velocity (thick line) superimposed on target velocity (thin line, velocity is zero at start and end of trial; 10 deg/s in between, except during perturbation); PE, retinal position error, the difference between the target position and the eye position. The gap in the eye velocity trace corresponds to the saccade shown in the eye position trace. The horizontal lines indicate the extent of the rings, the solid lines indicate the extent of the attended ring. The horizontal arrows show the saccade latencies.

two of our four subjects with enough data (subject R, $p = 0.003$; subject J, $p = 0.039$, tested by a paired t test on the standard deviations of latencies), across all step and ramp conditions, both when the target was stationary (experiment 1) and moving (experiment 2).

The distributions of latencies during attention to the small and large rings have little overlap when the perturbation was large, as shown by the example in Fig. 4A. To illustrate the distinctness of the distributions, we show cumulative distributions during attention to large and small rings (Figs. 4B, C and E; these cumulative distributions have a y-axis of total number of saccades, rather than percentage of all saccades, thereby showing the number of trials in which no saccades occurred). To quantify this lack of overlap for each subject and condition, we computed the Kolmogorov–Smirnov statistic

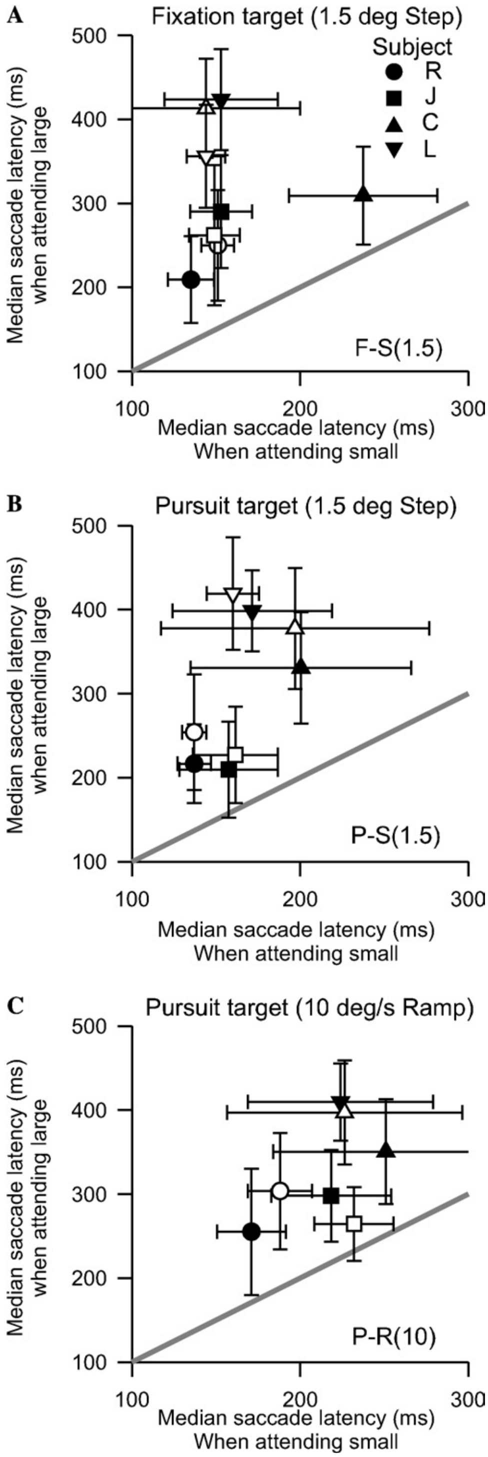

Fig. 3. Median latency of saccades (with standard deviations) following the perturbation for each subject: attend-large condition vs. attend-small condition. Filled symbols are perturbations to the right; unfilled symbols are perturbations to the left. (A) 1.5° steps during fixation. (B) 1.5° steps during pursuit. (C) 10 deg/s ramps during pursuit.

by measuring the maximum separation between the attend large and attend small cumulative distributions. In the example shown in Fig. 4F, by 156 ms (the vertical line marked D) 94% of the saccades in the attend small distribution had occurred, but only 3% of those in the attend large distribution had, giving a K–S value of 0.91. The results of this analysis (Fig. 4F) show that the average value of this measure of non-overlap was 0.79 for the large perturbations. Because the distributions were so different in the attend-small and attend-large conditions, we asked how well could one infer whether a subject was attending large or small by simply measuring the saccade latency. To address this issue, we calculated the receiver operating characteristic (ROC) for each subject by plotting for each latency the cumulative probability of that latency for attending small against the cumulative probability of that latency for attending large (Fig. 4G and H), and then calculating the area under the resulting curve. (If the distributions were identical, the area would be 0.5; if the distributions did not overlap at all, the area would be 1.0.) This analysis showed that by knowing the latency of a single saccade, an ideal observer would correctly identify whether the subject was attending small or large 94% of the time.

In contrast, when the target step was smaller (0.75°), approximately the diameter of the small ring, saccade latencies were longer and less dependent on which ring was attended (256 ms vs. 344 ms), although they were still significantly shorter in the attend small conditions than in the attend large conditions in every subject ($p < 0.01$, Wilcoxon rank-sum test). This weaker dependence on the attentional task is evident in the greater overlap in the cumulative distributions (Fig. 4D), summarized by a Kolmogorov–Smirnov distance of 0.54 and an ROC result indicating that an ideal observer would correctly classify the attentional task only 81% of the time. The longer latencies in this condition were not a consequence of the step size per se because when we tested the same subjects with the same 0.75° steps, but with an even smaller target (a single 0.3° non-rotating ring), the latencies were short, with the cumulative distributions resembling those of larger steps in the two-ring situation with attention on the smaller ring (compare broken lines in Fig. 4D with attend small in Fig. 4C).

In general, large perturbations caused shorter latencies (251 ms vs. 300 ms) and greater attentional differences (125 ms vs. 97 ms) than small perturbations. Saccade latencies were shortest for the stationary target condition (236 ms), intermediate for the step perturbation of the moving target (267 ms), and longest for the ramp perturbation of the moving target (286 ms).

3.2. Probability of saccades

When attention was directed to the large ring, not only were the saccade latencies longer, but subjects more often did not make a saccade in response to a target step or a change in target speed (48% vs. 22%; significant for each of the four subjects, $p < 0.03$ by paired t test). This

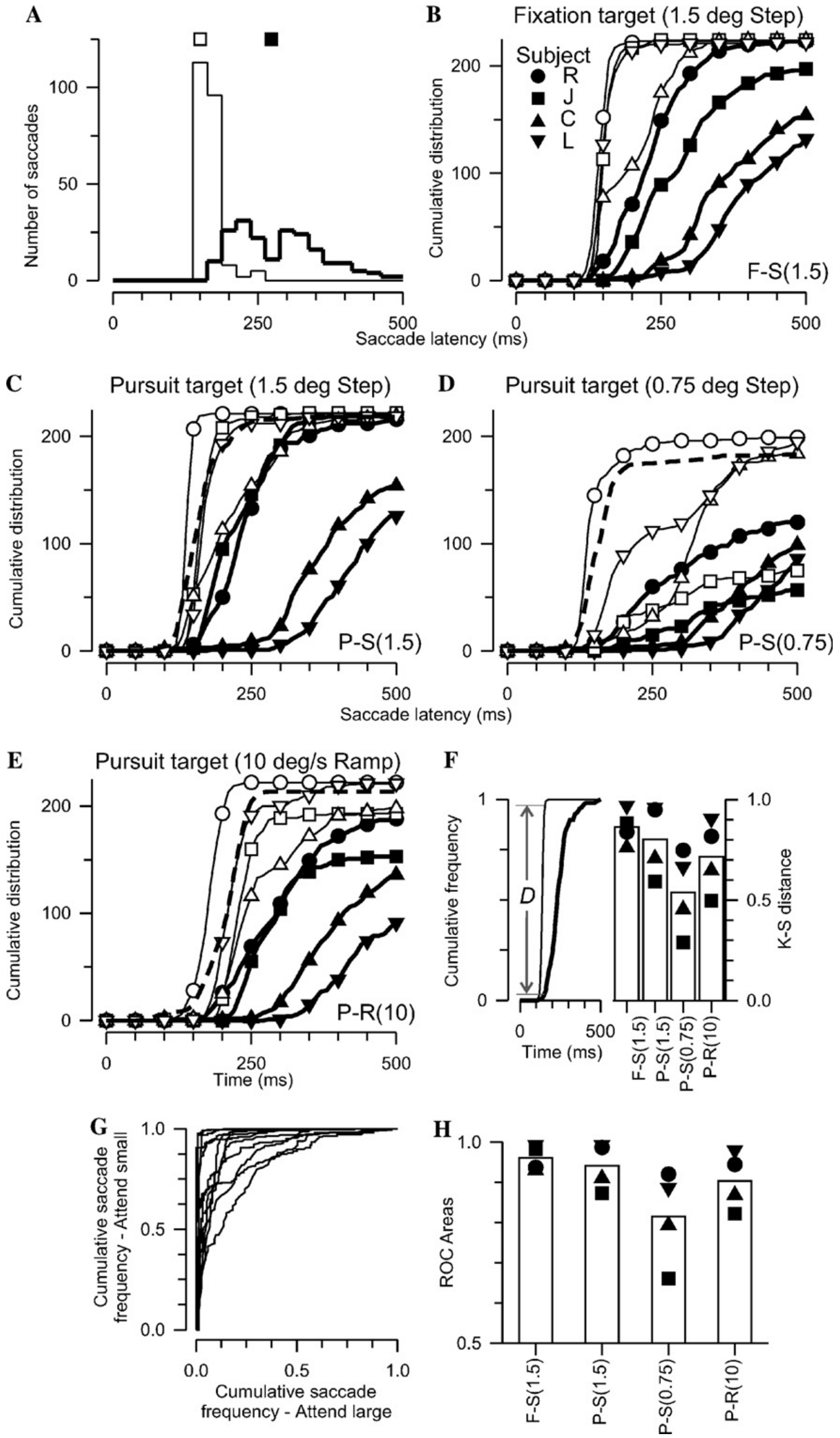

Fig. 4. Saccadic latencies in the attend-small (thin line, unfilled symbols) and attend-large (bold line, filled symbols) conditions combining both directions of perturbation for each subject (224 trials). In (C)–(E), the dashed line indicates the median distribution (across all subjects) for the single non-segmented 0.3° ring. (A) Histogram of latencies to perturbations during fixation. The squares indicate the respective median latency (subject J). (B) Cumulative distributions of latencies for 1.5° step during fixation. (C) Cumulative distributions of latencies for 1.5° step during pursuit. (D) Cumulative distributions of latencies for the 0.75° step during pursuit. (E) Cumulative distributions of latencies for the 10 deg/s ramp during pursuit. (F) (left) Graphic example of computation of K–S distance between two cumulative distributions. Arrows point to greatest separation between the distributions (156 ms). (right) Bar graph of average Kolmogorov–Smirnov (K–S) distance for conditions in (B)–(E) (symbols are individual subjects, identified in (B)). (G) ROC plot of cumulative distributions of saccade latencies with attend-large plotted against attend-small for conditions in (B), (C), and (E). (H) Bar graph of average ROC areas for conditions in (B)–(E).

is shown by the cumulative distributions reaching asymptotic values below 100% for the attend large condition (Figs. 4B, C and E). The effect of attention on saccade probability is especially evident with small perturbations: fewer saccades occurred in the attend large than attend small condition with small steps (40% vs. 73%; fewer in every subject and step-direction) and with small ramp perturbations (26% vs. 51%), as compared to large steps (80% vs. 98%) and large ramps (63% vs. 93%). It is clear from the cumulative distributions that this effect is correlated to the saccade latency, with those subjects with longer latencies making fewer saccades (compare the number of saccades at the right-hand end of the cumulative distribution with the median latency of each subject); this is especially evident in the case of target steps during fixation (Fig. 4B).

3.3. Amplitude of saccades

In contrast to the saccade latency distributions, the amplitude distributions across all step and ramp conditions were only slightly affected by the spatial scale of attention (Table 2). Although the saccade amplitudes differed significantly with attentional instruction in nineteen out of twenty-four cases (i.e., four subjects × six stimulus conditions), there were no systematic effects; in thirteen cases saccades were larger in the attend large condition and in six cases saccades were larger in the attend small condition (Wilcoxon rank-sum test on conditions with saccades on more than 30% of trials). The differences in the median amplitude between the attend large and attend small conditions were small, averaging 0.2° (range, −0.18 to +0.71°, attend large minus attend small). We obtained similar results when the target was stationary; saccades were larger in the attend small condition in two cases and larger in the attend large condition in five cases (average difference 0.02°). Therefore, the systematic differences in latencies between attend large and attend small conditions cannot be attributed to differences in the amplitudes of the saccades.

Not unexpectedly, the saccade amplitudes were principally determined by the position error, that is, the average distance of the stimulus from the fovea immediately after the perturbation, so that the slope of the linear regression of saccade amplitude vs. position error (i.e., the difference between the position of the fovea and the center of the stimulus at the time of the saccade), is 1.08 ($r^2 = 0.93$). The size of the attended ring did not systematically affect this relationship. During pursuit the position error at the time of the saccade was usually greater for perturbations in the onward direction, because the eye tended to lag behind the target, but was not influenced by the attentional condition (Table 3). As a consequence, the saccade amplitudes were larger in the case of onward perturbations in every subject with both types and sizes of perturbation.

Table 2
Amplitude of saccades for the steps and ramp perturbations

Subject	Step (°)	Attend-large			Attend-small			Diff	Test	Ramp (deg/s)	Attend-large			Attend-small			Diff	Test
		Median	(SD)	*N*	Median	(SD)	*N*				Median	(SD)	*N*	Median	(SD)	*N*		
R	1.5	2.14	0.36	112	2.07	0.27	112	0.07	NS	10	1.49	0.34	102	1.67	0.25	111	−0.18	*
	0.75	1.34	0.33	96	1.44	0.26	108	−0.1	*	5	0.99	0.2	48	1.11	0.26	85	−0.12	*
	−0.75	−0.11	0.21	24	−0.19	0.14	91	0.08	NT	−5	−0.1	0.13	20	−0.27	0.14	92	0.17	NT
	−1.5	−0.91	0.41	104	−0.75	0.18	109	−0.16	*	−10	−0.48	0.27	86	−0.69	0.2	111	0.21	*
J	1.5	1.93	0.23	112	1.94	0.23	110	−0.01	NS	10	1.49	0.22	67	1.65	0.29	90	−0.16	*
	0.75	1.32	0.15	53	1.27	0.12	59	0.05	*	5	1.18	0.12	13	1.13	0.17	21	0.05	NT
	−0.75	−0.08	0.1	4	−0.14	0.11	16	0.06	NT	−5	−0.17	0.14	9	−0.25	0.15	7	0.08	NT
	−1.5	−0.5	0.17	108	−0.68	0.18	112	0.18	*	−10	−0.32	0.16	86	−0.46	0.2	105	0.14	*
C	1.5	2.81	0.82	94	2.35	0.52	110	0.46	*	10	2.19	0.7	90	2.09	0.52	106	0.1	NS
	0.75	2.02	0.78	81	1.66	0.32	100	0.36	*	5	1.89	0.71	71	1.59	0.47	55	0.3	*
	−0.75	−0.44	0.29	18	−0.42	0.29	84	−0.02	NT	−5	−0.16	0.27	26	−0.4	0.23	51	0.24	NT
	−1.5	−0.65	0.56	60	−1	0.37	109	0.35	*	−10	−0.56	0.68	46	−0.94	0.3	92	0.38	*
L	1.5	2.77	0.66	86	2.06	0.29	112	0.71	*	10	2.44	0.74	62	2.04	0.4	109	0.4	*
	0.75	2.17	0.68	72	1.47	0.3	103	0.7	*	5	1.97	0.95	37	1.39	0.23	60	0.58	*
	−0.75	−0.59	1.12	14	−0.27	0.2	92	−0.32	NT	−5	−0.96	1.37	11	−0.41	0.41	82	−0.55	NT
	−1.5	−1.09	0.96	40	−0.92	0.34	107	−0.17	*	−10	−1.08	1.03	29	−1.07	0.31	112	−0.01	NT

Median, Standard deviation (SD), number of trials with saccades (*N*), and difference of medians (Diff). NT: not tested; NS: not significant.

* $p < 0.01$.

Table 3
Position errors for the steps and ramp perturbations

Subject	Step (°)	Attend-large			Attend-small			Diff	Test	Ramp (deg/s)	Attend-large			Attend-small			Diff	Test
		Median	(SD)	N	Median	(SD)	N				Median	(SD)	N	Median	(SD)	N		
R	1.5	1.62	0.28	112	1.73	0.29	112	−0.11	*	10	1.28	0.35	102	1.56	0.25	111	−0.28	*
	0.75	0.95	0.29	96	1.02	0.24	108	−0.07	NS	5	0.84	0.23	48	0.88	0.33	85	−0.04	NS
	−0.75	−0.29	0.21	24	−0.26	0.24	91	−0.03	NT	−5	−0.27	0.2	20	−0.25	0.24	92	−0.02	NT
	−1.5	−0.89	0.32	104	−1.05	0.29	109	0.16	*	−10	−0.73	0.34	86	−1.05	0.29	111	0.32	*
J	1.5	1.62	0.44	112	1.64	0.4	110	−0.02	NS	10	1.11	0.47	67	1.3	0.42	90	−0.19	NS
	0.75	0.94	0.5	53	0.89	0.33	59	0.05	NS	5	0.94	0.6	13	0.87	0.25	21	0.07	NT
	−0.75	−0.23	0.43	4	−0.28	0.39	16	0.05	NT	−5	−0.29	0.49	9	−0.31	0.48	7	0.02	NT
	−1.5	−0.91	0.42	108	−1.03	0.42	112	0.12	*	−10	−0.67	0.45	86	−0.77	0.46	105	0.1	*
C	1.5	1.56	0.37	94	1.53	0.29	110	0.03	NS	10	1.43	0.47	90	1.25	0.32	106	0.18	NS
	0.75	0.83	0.34	81	0.8	0.3	100	0.03	NS	5	0.71	0.41	71	0.64	0.39	55	0.07	NS
	−0.75	−0.75	0.32	18	−0.86	0.3	84	0.11	NT	−5	−0.61	0.3	26	−0.74	0.31	51	0.13	NT
	−1.5	−1.37	0.35	60	−1.52	0.29	109	0.15	*	−10	−1.28	0.31	46	−1.46	0.3	92	0.18	*
L	1.5	2.15	0.65	86	1.76	0.52	112	0.39	*	10	1.97	0.69	62	1.66	0.52	109	0.31	*
	0.75	1.67	0.62	72	1.18	0.5	103	0.49	*	5	1.61	0.57	37	1.08	0.44	60	0.53	*
	−0.75	−0.25	0.57	14	−0.46	0.45	92	0.21	NT	−5	−0.3	0.93	11	−0.59	0.49	82	0.29	NT
	−1.5	−0.86	0.72	40	−1.17	0.57	107	0.31	*	−10	−1.01	0.51	29	−1.25	0.5	112	0.24	NT

Median, Standard deviation (SD), number of trials with saccades (N), and difference of medians (Diff). NT: not tested; NS: not significant.

[*] $p < 0.01$.

3.4. Assessing changes in latency using the LATER model

Can the shapes of the latency distributions illuminate the changes in saccade programming that occurred with different attentional instructions? To examine this, we used an analysis procedure based on the LATER model (Reddi & Carpenter, 2000), which assumes that saccades are triggered when a monotonically rising decision signal reaches a threshold value. This simple model can account for the typical shape of latency distributions—skewed with a long tail toward longer latencies. When the distribution of latencies is plotted on a reciprobit graph (i.e., plotting the cumulative probability on a probit scale as a function of the reciprocal of latency), a straight line results (Figs. 5A and C).

From the viewpoint of this model, changes to the saccade trigger mechanism alter the reciprobit plots in distinctive ways. Changes in the rate of rise (r) of the decision signal with no change in the threshold result in a parallel shift of the line. Changes in the threshold (S) with no change in the rate of rise alter the slope of the line, such that the line pivots about the infinite-time intercept. An additional factor, not usually included in discussions of the LATER model is that increasing the variability (in this case, the standard deviation of the rate variable) decreases the slope and intercept of a cumulative distribution without changing its median. Thus the swivels of the reciprobit lines in Fig. 5 could have been caused by various combinations of changes in these three parameters. We applied the LATER model to our latency distributions following the fitting methods described by Reddi and Carpenter (2000). Because small perturbations often elicited few saccades, we limited our analysis to the large step (1.5°) data obtained in the first and second experiments and to the large ramp (10 deg/s) data obtained in the second experiment.

The effects on saccade latency in our task were associated with changes in both rate and threshold, and probably with changes in the variance of the rate as well. Figs. 5A and C provide examples from two subjects that illustrate the range of outcomes we found. For each data set, we computed the slope and the infinite-time intercept of the best linear fit for the attend small and attend large conditions ($r^2 > 0.9$). For the data in Fig. 5A (subject C), the distribution of shorter latencies in the attend small condition (unfilled symbols) fell on a line with a lower slope, suggesting mostly a decrease in the decision threshold ($S_L \rightarrow S_S$ in Fig. 5B). However, because the regression lines do not intersect at the infinite-time axis, the conventional LATER interpretation would require that the rate of the decision signal ($r_L \rightarrow r_S$) must also have slowed considerably to shift the line from where it would have intersected the attend large line at the infinite-time axis (Fig. 5B). The alternative interpretation would be that the threshold change was accompanied

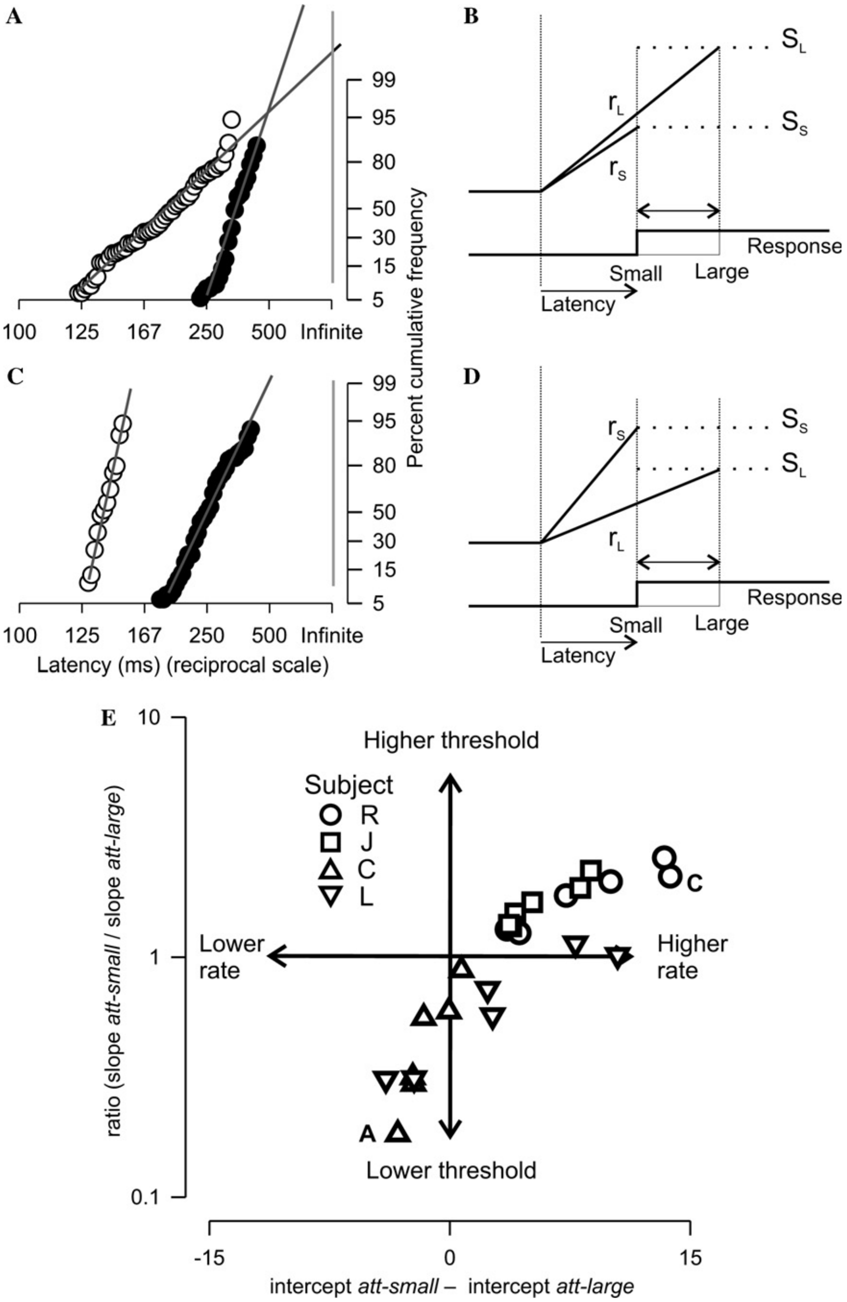

Fig. 5. The LATER model. (A) and (C): Illustration of the reciprobit plots for the two subjects identified by letters in the bottom panel (unfilled symbols, attend-small; filled symbols, attend-large, (A) subject C, pursuit target, +1.5° step, (C) subject R, fixation target, −1.5° step). (B) and (D): Schematic illustration of the changes in the LATER model, ignoring the likely changes in the variability of the rates: for each attentional condition, the rates of rise (r_S and r_L) and thresholds (S_S and S_L) were adjusted to account for the changes in latencies as predicted by the model. (E) Ratio of the slopes (attend-small/attend-large) plotted on a log scale as a function of the differences in the intercepts in SD units for all subjects.

by an increase in the variability of the rate of rise of the decision variable, which rotated the line in the clockwise direction.

Conversely, for the data in Fig. 5C (subject R), the distribution of latencies in the attend-small condition (unfilled symbols) mostly involved the distribution shifting leftward away from the distribution in the attend-large condition (filled symbols), suggesting that the shorter latencies were mostly a consequence of increasing the rate of rise of the decision signal. However, in this case as well, there were changes in slope as well as intercept, suggestive of simultaneous changes in the threshold as well. The alternative explanation would be that the increase in rate was accompanied by a small decrease in rate variability, which caused the line to rotate counterclockwise.

To summarize the data from all of our subjects and conditions, we plotted the difference between the infinite-time intercepts against the ratio of the slopes (on a logarithmic axis). We found that the change in latency from attending-large to attending-small involved two different strategies. Two subjects (R and J) mostly increased the rate of rise of the decision variable, with a (smaller) change in threshold or rate-variability (Fig. 5E, upper right quadrant), whereas the other two subjects (C and L) mostly decreased their threshold, with a smaller change in rate or rate-variability (lower left quadrant). Because the LATER model has three parameters (threshold, rate, and rate SD) but the reciprobit analysis fits only two (slope and intercept), this method results in ambiguity about what causes the secondary changes in each case. Nonetheless, the analysis identifies two primary explanations for the shorter latencies observed in the attend-small condition: (1) a higher rate of change for the decision signal, and (2) a lower threshold for triggering saccades.

3.5. Change in pursuit velocity in response to ramp perturbations

Pursuit velocity increased more during onward ramp perturbations when attending to the small ring (thin lines in Fig. 6A) than when attending to the large one (thick lines), with no evident effect on pursuit latency. In all but one case (subject L, +10 deg/s), the onward ramp perturbations caused a statistically significantly greater increase in pursuit velocity when attention was directed to the small ring compared to when it was directed to the large ring (Fig. 6; $p < 0.025$, one-tailed t test). No significant differences were found for the backward ramps. Subjects also tended to make stereotyped anticipatory changes in pursuit speed, beginning 200 ms before the motion onset, even when no perturbation occurred, as can be seen on Fig. 6B. These anticipatory changes probably occurred because the perturbations occurred at the same point in every trial.

3.6. Initiation of pursuit

Although our intent in these experiments was to study only the effect of perturbations of the stimulus motion, we noticed that the initiation of pursuit was also affected by which ring was attended. Although our intent in these experiments was to study only the effect of perturbations of the stimulus motion, we noticed that the initiation of pursuit was also affected by which ring was attended. If attention was directed to the small, rather than to the large, ring, eye velocity became higher only approximately 110 ms after the onset of target motion even though the time, direction, and speed of the target motion had been predictable, and the eye had been moving anticipatorily at the onset of target motion. The eye velocities remained distinct for 100 ms, with statistically significantly higher velocities (8% higher for subject R, 6% for J and L, 5% for C) in the attend-small condition than in the attend-large conditions during this interval in every subject ($p < 0.001$, one-tailed t test). These differences disappeared after pursuit velocity stabilized about 210 ms after the onset of stimulus motion.

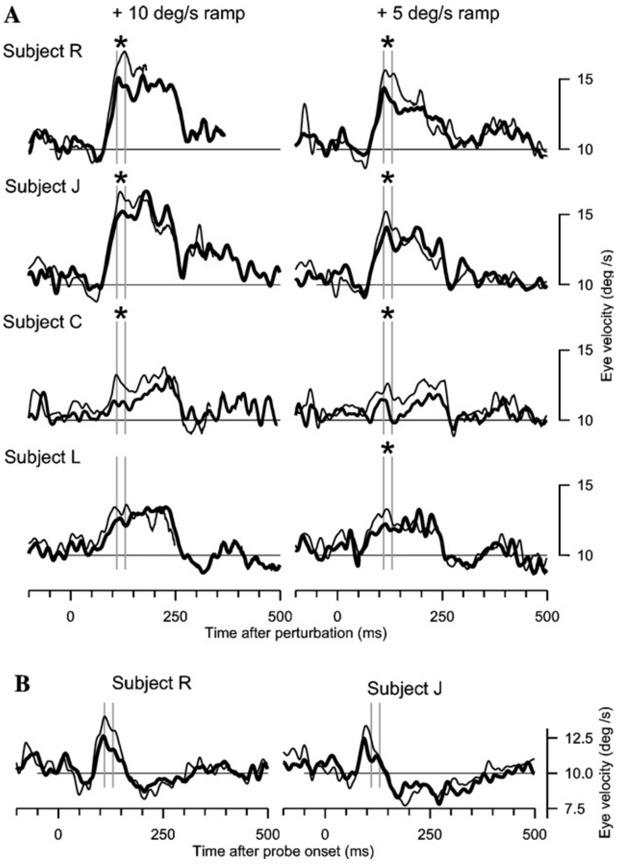

Fig. 6. (A) Average eye velocity with respect to time following the perturbation onset (experiment 2) for the attend-small (thin lines) and attend-large (bold lines) conditions for the onward ramps (10 and 5 deg/s) for each subject. The vertical gray lines indicate the interval 110–130 ms after the perturbation. *Significant differences between average velocities for that interval. All traces start as an average of 112 trials, but this number decreases over the course of the trace because each velocity trace was averaged only until the first saccade following the perturbation. (B) Example of average eye velocity around the time of probe onset in the no perturbation condition for subjects R and J.

3.7. Experiment three: perturbations of motion of a single ring

In this experiment, we perturbed the motion of either the attended or the unattended ring. This procedure tested the ability to respond selectivity to the motion of the attended ring while ignoring perturbations in the motion of the unattended ring.

When instructed to attend to the small ring, subjects almost always (99%) made saccades in response to perturbations in the motion of the small ring and rarely

(8%) made saccades in response to perturbations in the motion of the large ring (Fig. 7). However when instructed to attend to the large ring, strong individual differences emerged. One subject (subject R) almost always made saccades when the motion of the large ring alone was perturbed by a step or ramp (85% on average) while ignoring the perturbation in the motion of the small ring (saccades on 4% of trials). The other three subjects made more saccades when the motion of the small ring was perturbed (35, 36, and 26% for subjects J, C, and L, respectively) than when the large ring was perturbed (1, 24, and 8%, respectively). These differences could not be attributed to differences in the task difficulty because the percent correct was quite similar (attend-small, 81%; attend-large, 84%). Thus, most subjects were not totally able to suppress saccades to perturbations occurring in the motion of the small ring when attending the large one.

The results for pursuit were the opposite of those for saccades. When the motion of only the unattended ring was perturbed, subjects could more easily suppress responses to the small than the large ring (Fig. 8). By considering the difference between the two superimposed traces in each panel (onward vs. backward perturbation) to disentangle the responses to the perturbation from the anticipatory responses common to both traces, one can see that all subjects responded to perturbations of the motion of both the attended and unattended rings. Comparison of the average velocities evoked by onward and backward perturbations in the interval 110–130 ms after the perturbation onset, as we did in experiment 2, revealed statistically significant effects of attention on velocity in each subject and each combination of attentional instruction and which ring was perturbed (Wilcoxon rank-sum test, $p < 0.001$). Interestingly, all subjects tended to respond to perturbations in the unattended ring. Even subject R, who made no saccades to steps or ramps of the unattended stimulus, made pursuit responses to the large stimulus when attending small and to the small stimulus when attend-

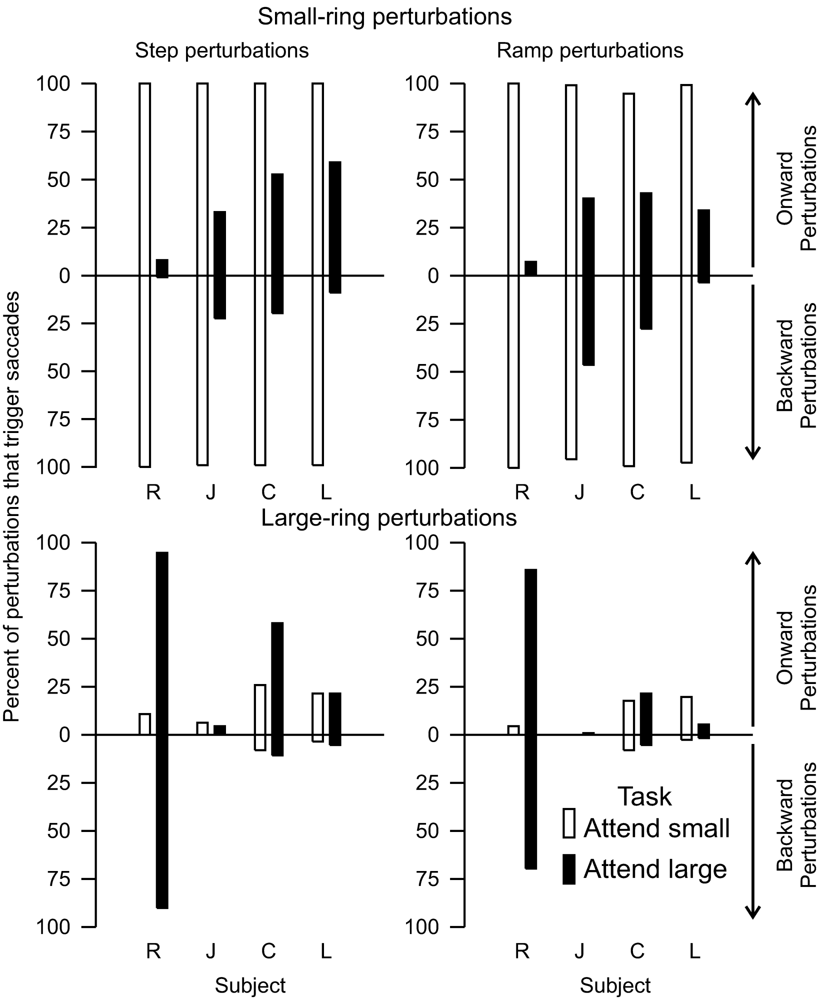

Fig. 7. Percentage of trials with saccades when only one ring was perturbed (experiment 3): The perturbations in the onward direction are plotted above the abscissa, the ones in the backward direction, below the abscissa. The unfilled bars are for the attend-small conditions, the filled ones are for the attend-large conditions.

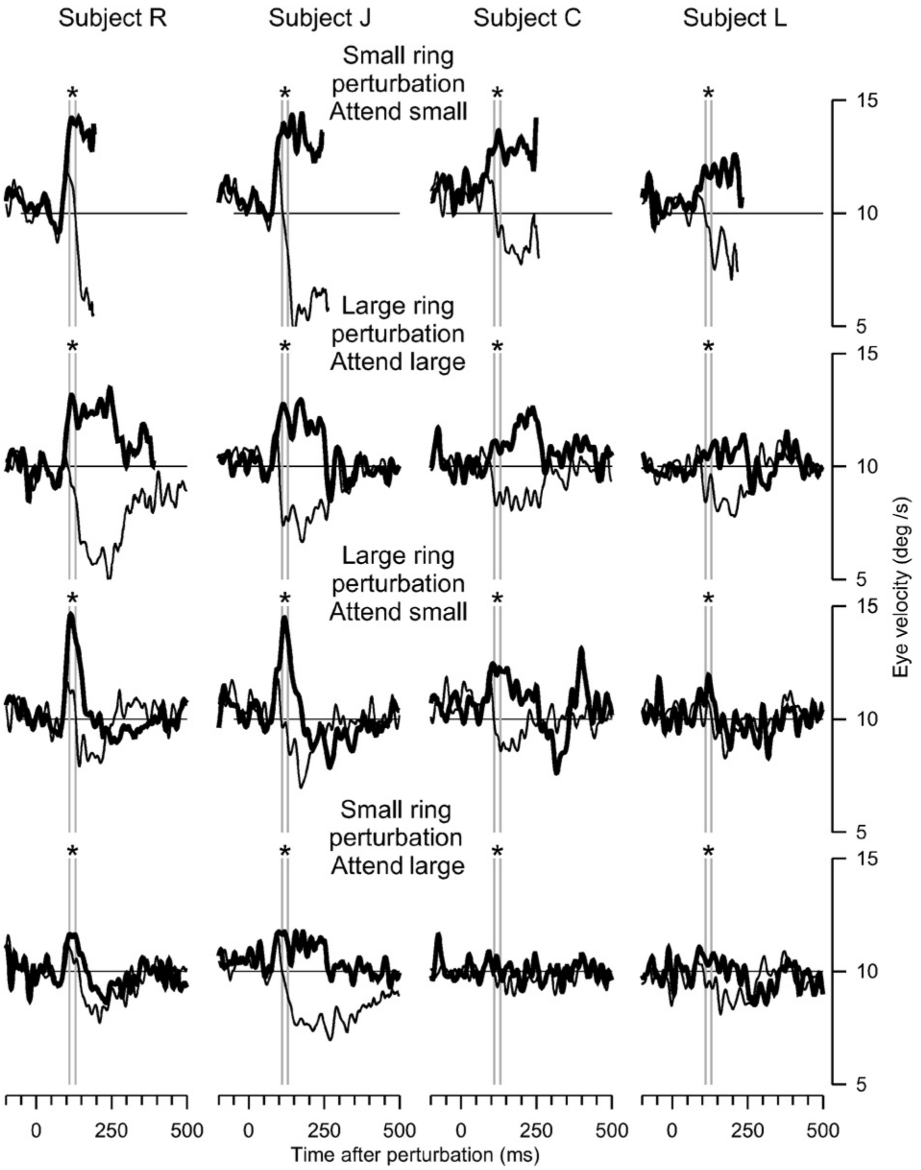

Fig. 8. Average eye velocity during trials in which motion of only one ring was perturbed (experiment 3): Bold lines, onward ramps (+10 deg/s); thin lines, backward ramps (−10 deg/s). The pair of vertical lines indicates 110–130 ms after the perturbation. *Significant differences between average velocities for that interval. All traces start as an average of 112 trials, but this number decreases over the course of the trace because each velocity trace was averaged only until the first saccade following the perturbation.

ing large. These smooth eye velocity responses were even stronger in subject J, even though she made no saccades following perturbations of the large ring when she was attending to the small ring. The changes in smooth eye velocity were systematically larger when the unattended (and perturbed) ring was the large ring than when it was the small ring if the perturbation was a forward ramp (Wilcoxon rank-sum test, $p < 0.001$), but not if it was a backward ramp. The responses to the unattended ring were clearly more transient than responses to perturbations in the attended ring (Fig. 8, subjects R and J, large ring perturbation; compare attend-small and attend-large conditions).

4. Discussion

We have shown that instructing subjects to attend to different spatial aspects of a stimulus affects the oculomotor responses to a perturbation of the stimulus motion. When the subjects attended to a ring smaller than the size of the step perturbation, saccade latencies were half as short, and the probability of making a saccade was higher, than when they attended to a ring much larger than the perturbation step. This was true during both fixation and pursuit of the stimuli. Furthermore, the gain of the ongoing pursuit eye movements (i.e., the ratio of eye velocity to target velocity) was also greater when attending to the small ring, as was the initial pursuit gain at the start of stimulus movement. Finally, when only the unattended ring had its motion perturbed, subjects had greater difficulty suppressing saccades to the small ring than to the large, but had greater difficulty suppressing pursuit responses to the large ring than to the small one, with marked differences among subjects. Because neither the stimulus nor its motion differed between the two attentional conditions, and because we balanced the direction, size, and type of perturbation (ramp or step), we infer that the attentional instruction affected the oculomotor responses to the stimulus.

These results are consistent with a long history of effects of attention on reaction times, including saccadic reaction times (e.g., Shepherd et al., 1986). In these studies, summoning attention to the location of the saccade target reduced the saccade latency by 20–30 ms. What is remarkable about the results we present is that the latency differences are about five-fold larger than those shown by the earlier studies. Indeed, the spatial attention effects shown here is so great that the observation of a single saccade allows one to classify with 94% certainty whether the subject was attending to the ring larger or smaller than the size of the target displacement.

Because of the surprising magnitude of the effect of these spatial attention instructions, we will first discuss possible alternative explanations of our findings, then we will discuss what these results say about saccadic decision processes, what form of attention might be involved here, how attention might be deployed differently for pursuit and saccades, and finally, what functional explanation there might be for the spatial aspects of attention having such large effects.

4.1. Explanations unlikely to account for the present results

4.1.1. Non-attentional factors

Factors other than attention might have been responsible for the observed changes in the oculomotor responses. First, it is possible that the differences in saccade latencies were a consequence of differences in saccade amplitude between attend-small and attend-large conditions. This appears unlikely because the average amplitude difference was very small (0.15° on average in the second experiment, see Table 2) and the direction of the amplitude differences varied from subject to subject and condition to condition, whereas the latency difference was large and consistent (125 ms on average in the second experiment). Furthermore, saccadic latencies have been shown to have little dependence on amplitude over the range from 0.75° to 12° (Darrien, Herd, Starling, Rosenberg, & Morrison, 2001; Fuller, 1996; Kalesnykas & Hallett, 1994).

Second, one could argue that the observed changes in pursuit were responsible for the effects on saccades. However, we found similar effects of attentional scale on saccade latency when the stimulus was stationary and being fixated before the perturbation (158 vs. 314 ms) as when it was moving and being pursued (165 vs. 304 ms, step perturbations in both cases). Furthermore, we found similar effects on saccade latency whether the perturbation was a ramp or a step. The saccade latency was, however, longer for the ramp than for the step. This is to be expected, because the position error develops gradually for the ramp perturbations, but appears suddenly for the step perturbations.

Third, the accuracy of tracking might have been greater in the attend-small condition, and this could have been responsible for the observed differences in saccadic latency and pursuit gain. However, we found only small and inconsistent differences between the position error during tracking in the two attentional conditions (Table 3). This also reveals that subjects were looking at the center of the stimulus at the time of the perturbation in both attentional conditions.

4.1.2. Non-spatial attentional factors

Other factors, related to attentional processes, could also account for our data. First, it could be argued that the difference in latency was the result of a difference in the quantity of attentional resources mobilized, rather than in the spatial deployment of attention. To minimize this factor, we adjusted for the speed of rotation of the inner and outer ring to equate the difficulty of the attend-small and attend-large tasks. The success of this matching is indicated by the similar performance on the different attentional tasks (Table 1).

Second, one could hypothesize that in the attend-large tasks attention was divided, either simultaneously or sequentially, between the tracked small ring and the attended large ring, whereas in the attend-small tasks, attention was undivided, and that it was the dividing of attention, rather than its spatial scale, that was responsible for the observed changes. For this to be the cause of the doubling of saccade latency when attending to the large ring, one might expect that attending to the large ring would allow one to report the number of segments in the small ring much more often than the reverse case. This was not the case: subjects were at chance in discriminating either unattended ring (Table 1). Furthermore, the latency distributions in the attend-large condition did not show a peak in the short latencies, as one might expect if attention was sometimes allocated to the small ring (Fig. 4). Finally, an analysis now underway of saccadic latencies to steps of various sizes of single rings, carried out with the same attentional task as in the experiment presented here, did not find them to be different from the two-ring situation: for instance the latencies of subject L to a 1° step of an 8° ring alone were similar to those for the same subject reported here to a 1.5° step, with both rings present (448 vs.

390 ms, respectively; Madelain, Harwood, Krauzlis, & Wallman, 2004).

4.2. The LATER model

A simple model of reaction times assumes that saccades are triggered when an internal decision signal reaches a threshold value (Carpenter & Williams, 1995; Reddi & Carpenter, 2000; Reddi, Asrress, & Carpenter, 2003). By applying this model to our latency data, we were able to show differences among subjects in the patterns of responses associated with changes in latency. Although previous studies using this model have generally identified only changes in threshold or changes in the rate of the decision signal, our data suggest that the attentional instruction in our task might affect both factors (see Kurata & Aizawa, 2004 for similar effects), or might involve a change in the variability of the rate. As discussed in the Results, the LATER model does not fully disentangle the effects of changes in these three factors.

Nonetheless, the changes we found associated with decreased latencies in the attend-small condition fell into two classes. Two of the subjects (R and J) showed principally a parallel shift of the reciprobit curves, implying that their saccades in the attend-small condition were associated with higher rates of rise of the decision variable (albeit with a small change in reciprobit slope, suggesting either an increase in threshold or a small decrease in the rate variability). Perhaps these subjects were able to more effectively monitor the relevant visual information in the attend-small condition, resulting in higher rates of rise of the decision signal and a concomitant decrease in the variability of those rates. The other two subjects (C and L) showed principally a swiveling of the curves about the infinite-time intercept, implying a decrease in threshold (albeit with a change in rate or rate variability). For these subjects, the primary change in the attend-small condition might have been a lowering of their decision threshold, and thus affected how the movements were prepared rather than how the visual information was monitored. The distinction between these two classes of behavior is underscored by the fact that none of the subjects showed an increase in rate combined with a decrease in threshold, which would have been the most direct way to decrease the saccade latencies.

The segregation of the subjects based on this analysis is also consistent with other aspects of their data. Subjects R and J showed a similar effect of spatial scale of attention on saccade latencies, and resembled one another both with respect to saccade amplitudes (Table 2) position errors (Table 3), and velocity profiles, in particular in response to backward ramps (Fig. 8). Similarly, subjects C and L also tended to exhibit similar trends in all of these ways. These observations suggest that the oculomotor programming of our subjects fell into two distinct patterns, and that fitting their saccade latencies with the LATER model captured a signature of these patterns.

4.3. What form of attention?

The stimuli we have used here involve a combination of exogenous and endogenous summoning of attention. The endogenous aspect is that the subject is directed to attend to the large or small ring by an arbitrary auditory instruction. The oculomotor response to the perturbation, however, seems to reflect the exogenous effect of the perturbation itself, occurring sooner than the 300 ms or so required for endogenous summoning of attention (Nakayama & Mackeben, 1989; Theeuwes, Godijn, & Pratt, 2004). Furthermore, when only the unattended ring had its motion perturbed (experiment 3), putting endogenous attention in conflict with exogenous attention, three of our subjects made saccades when the unattended small ring was perturbed, suggesting that an exogenous cue near the fovea could not be ignored by these subjects. It is our opinion that the strong effects on saccade latency we report here may have been enhanced by the particular stimuli used, in which performance of the required discrimination is greatly facilitated by tracking the rotational motion of the rings with attention, a process that involves "locking" onto the rotating ring being attended. When this occurred, the rings appeared to rotate more slowly and the gaps in the attended ring formed illusory contours extending toward the center of the stimulus. These changes in the appearance of the stimulus during the task (see Carrasco, Ling, & Read, 2004, for another effect of attention on stimulus appearance) may have provided the subjects with feedback as to the intensity of their endogenous attention, and may have contributed to the strong selective attention subjects could give to one of two similar stimuli.

We describe the attentional task used here in terms of the spatial scale of attention, but we cannot be certain whether the relevant factor was that the spatial scale of attention was small or that attention was concentrated at the fovea. Subsequent studies, using different stimuli, have also shown that saccades have shorter latencies when attention is directed to a small part of a stimulus, even when both the small and large part of the stimulus are at 2° of eccentricity (Madelain et al., 2004). Therefore, we are confident that the factors responsible for the observed changes in the oculomotor responses are related to the size and not to the relative position of the attended object.

4.4. Comparison of changes in pursuit and in saccade responses

The effects of attentional state on both pursuit velocity and saccadic latency result in more accurate tracking in the attend-small task. Specifically, when attending small, not only were the pursuit responses to perturbations larger but also the eye velocity at the initiation of pursuit was higher, revealing a higher open-loop gain. We cannot distinguish whether the pursuit gain was increased transiently at the time of the perturbation or whether it was more generally increased by attending small because, except at the onset of pursuit, the closed-loop gain was too close to a value of 1 for the small differences in open-loop gain to be detectable.

When both rings moved together the differences in pursuit velocity were modest in magnitude and statistically significant only for onward perturbations. However, when only the unattended ring had its motion perturbed, there was a clear asymmetry in that the large ring could not be ignored, whereas the small ring could—the opposite of the situation with saccades (compare Figs. 7 and 8). The capability of saccades to ignore unattended movements in the periphery may reflect a greater influence of attention on saccades than on pursuit. Alternatively, the irrepressible changes in eye velocity to perturbations of the unattended large ring may be due to the large area of the outer ring, which, in the absence of stationary visual features, causes the oculomotor system to attempt to stabilize it on the retina. We cannot, of course, distinguish optokinetic from pursuit contributions to these eye-velocity transients.

We find it interesting that the pursuit differences were a matter of magnitude, whereas the saccadic differences were a matter of timing. This could be attributed to the greater costs associated with making saccades because visual contact with the target is transiently lost. Therefore the decision to launch a saccade may be delayed until sufficient information indicates that a perturbation requiring correction has occurred. It would appear from our results that there is a smaller tolerance for position errors when the spatial scale of attention is small than when it is large.

4.5. Why does the spatial deployment of attention affect tracking behavior?

The finding that the spatial scale of attention strongly influences the probability and latency of saccades as well as the pursuit responses raises the question of whether attention acts at the visual or motoric level. To consider the visual possibility first, abundant evidence shows that attention facilitates visual discrimination. When the spatial scale of attention is small, discriminations in that small area are maximally improved; when the spatial scale of attention is large, the improvement accrues to stimuli over a wider area, albeit with less benefit at each stimulus location (Castiello & Umilta, 1990; Eriksen & St James, 1986). Therefore, it might be that when attention is concentrated on the small part of the stimulus its saliency is increased (Cameron, Tai, & Carrasco, 2002) and its spatial uncertainty reduced, increasing the responsiveness to perturbations. Based on our analysis using the LATER model, two of our subjects (R and J) showed changes in saccade latency that were consistent with this possible mechanism—higher rates of rise and lower variability in the decision signal during the attend-small condition. As a further test, one might expect that raising the contrast of the small ring while attending to the large one would have the same effect on saccade probability and latency as attending to the small ring. In preliminary experiments conducted with both rings at contrasts lower than those employed in the present study and with a different set of subjects, we found that raising the contrast of the small ring four-fold had no effect on saccade latency (Harwood, Madelain, Krauzlis, & Wallman, 2003). Because the effect of attention is generally found to be only the equivalent of about a 20% increase in contrast sensitivity (Lu, Jeon, & Dosher, 2004; Pestilli & Carrasco, 2005), we infer that increased visibility is not the only explanation for the effects of attending to the small ring.

Alternatively, attention might act at the level of motor preparation. Because one attends to and tracks stimuli in order to see them better, and because saccades incur the cost of temporarily interrupting seeing the stimulus, it might be the case that the decision process is delayed unless the stimulus moves outside of the "spotlight" of attention. Thus, when attending to a large stimulus, the visual system would be spared the cost of saccades to every minuscule positional error, whereas when a small part of the stimulus is attended, saccades will keep the fovea on the attended region. This hypothesis predicts that saccades will be consistently made with short latencies even if attention is directed to a large stimulus, as long as the size of the perturbation is greater than the size of the attentional field. In the results presented here, we found that when the size of the step was so small as to be similar to the diameter of the small ring, the saccades had longer latencies, more like those when the large ring was attended, and the latency distributions to large and small ring were less discriminable by both the Kolmogorov–Smirnov statistic and by ROC analysis. However, the same step caused short latencies if the stimulus tracked was even smaller. Consistent with this interpretation, the results of our LATER analysis suggested that two subjects (C and L) lowered their decision threshold in the attend-small condition, perhaps by scaling the trigger level according to the size of the attentional field. Finally, in a larger series of experiments in progress we find that the saccade latency depends robustly on the ratio of step-size to the ring diameter, saturating with long latencies at low ratios and falling to a minimum beyond a ratio of 1 (Harwood et al., 2003; Madelain et al., 2004). Therefore, for some subjects it seems that the motor explanation is the correct one. To put the matter in the terms of the recent Carpenter (2004) formulation of saccade latency as a serial process of detection followed by a decision, the influence of attention as studied here may have effects at different levels in different subjects.

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