



Gain adaptation of exogenous shifts of visual attention

Sally A. McFadden^{a,*}, Afsheen Khan^b, Josh Wallman^b

^a *Department of Psychology, The University of Newcastle, Newcastle, NSW 2308, Australia*

^b *Department of Biology, City College, CUNY, New York, NY 10031, USA*

Received 25 June 2001; received in revised form 12 June 2002

Abstract

Gain adaptation of saccadic eye movements is the process whereby the size of the saccade is gradually modified if the target is consistently and surreptitiously displaced during the saccade. Because one attends to the saccade target before each saccade, we asked whether covert shifts of exogenous attention might themselves be adaptable. We did this by presenting a peripheral cue and then displacing it by 3 deg after an interval equal to the average time required for attention to shift from a central to a peripheral cue. This interval, as well as the location at which attention landed, was determined by a modification of the line-motion illusion, in which a line appears to shoot from a previously cued location. We found that this adaptation paradigm produced consistent gradual reductions (for back-steps) or increases (for forward-steps) in the magnitude of the shifts of attention. Like saccadic adaptation, adaptation of shifts of attention could be manipulated independently for rightward and leftward shifts. Furthermore, the backward adaptation paradigm also decreased the magnitude of subsequent saccades, even though no saccades had been made during the attentional adaptation. This argues that saccades are targeted to the locus of attention, and when this locus is systematically shifted, so too are subsequent saccades. In conclusion, the adaptability of shifts of attention suggests that attentional shifts, like saccades, are recalibrated using a spatial error signal.

Crown Copyright © 2002 Published by Elsevier Science Ltd. All rights reserved.

Keywords: Adaptation; Visual attention; Shifts of attention; Saccade; Motion illusion

1. Introduction

Shifts of attention are similar to eye movements in a number of ways: First, both attention and the eyes appear to move in two distinct modes. Like the eyes during saccadic eye movements, attention may, after a delay, shift suddenly and at high speed to the location of a visual object or a visual transient (Yantis, 1988); like the eyes during smooth pursuit, attention can also pursue a moving object, matching its velocity to that of the target (Cavanagh, 1992). Second, when the brain moves the eyes to pursue an object, it produces an efference copy signal, which when added to the visual motion signal results in a veridical assessment of the object's speed, whether the eye is still (so all the motion is on the retina) or is tracking the object (so there is little motion on the retina). Tracking an object with attention can greatly facilitate measuring the speed of a moving object amidst other moving objects, suggesting that an attentional ef-

ference copy signal also exists (Cavanagh, 1992). Third, eye movements can be summoned either by a visual transient such as an object suddenly appearing or moving (exogenous saccades) or by an act of will, as during search or reading (endogenous saccades). Similarly, the locus of attention can be shifted by exogenous or endogenous cues (Yantis & Jonides, 1990). Fourth, the time to initiate saccades or to shift attention can be reduced if the fixation point is extinguished some time before the stimulus is presented (Fischer & Weber, 1993; Mackeben & Nakayama, 1993). Fifth, during search tasks, the size of the attentional field and the average saccade size are similar (Motter & Belky, 1998), and there is a similar effect of priming on saccade latency and focal attentional deployment in visual search tasks (McPeck, Maljkovic, & Nakayama, 1999).

These similarities between shifts of attention and eye movements, especially saccades, are probably not fortuitous. When a change occurs somewhere in the visual field, it attracts first one's attention, and, a bit later, one's gaze. Because of this attentional shift, discrimination is better and faster at the saccade target (and elsewhere in the target hemifield, Crovitz & Daves, 1962),

* Corresponding author.

E-mail address: sally.mcfadden@newcastle.edu.au (S.A. McFadden).

even if one is instructed to make a different discrimination elsewhere (Chelazzi et al., 1995; Posner, Snyder, & Davidson, 1980; Shepherd, Findlay, & Hockey, 1986). Indeed, saccades cannot be made without attention at the target location, and, conversely, one generally cannot attend elsewhere just before making a saccade (Deubel & Schneider, 1996; Kowler, Anderson, Doshier, & Blaser, 1995).

There are two distinct ways that this obligatory coupling might work: Attention might simply alight on visual features and thereby select them for the oculomotor system, which would calculate their location independently. Alternatively, saccades might be targeted specifically to the locus of attention. In this case any errors in the position of attention would produce corresponding errors in saccadic targeting. There is little evidence that bears on which of these two views is correct.

If the saccade targeting is derived from the locus of attention, one can interpret this tight coupling between the attentional and oculomotor systems in several ways. The most extreme one holds that shifts of attention are outcomes of the programming of saccades, even when the eyes do not move (Rizzolatti, Riggio, Dascola, & Umiltà, 1987). A difficulty with any model that makes attentional shifts an epiphenomenon of saccadic programming, is that it leaves unexplained why attention should possess the attribute of spatial extent as well as location, while saccades are only location based. A more moderate position holds that attention is manifested as a peak of activation on a saliency map. Competition among neurons in this map gives rise to a single winning location that corresponds to the most salient object, which then becomes the input to the saccade generator (Clark, 1999; Koch & Ullman, 1985).

How attention shifts is controversial. One view is that attention moves in a continuous (“analog”) fashion, as do the eyes, that is, moving at a finite velocity and passing over intermediate points (Shulman, Remington, & McLean, 1979). Early studies using the Posner (1980) paradigm of comparing reaction time or discrimination enhancement between a previously cued versus non-cued location supported the notion of analog shifts (Tsal, 1983), at speeds of 125 deg/s. An alternative view, based on experiments with better control of the cuing and the effects of stimulus eccentricity, is that attention moves in discrete, abrupt steps, such that shifts of various magnitudes take the same amount of time (Henderson & Macquistan, 1993; Kwak, Dagenbach, & Egeth, 1991; Remington & Pierce, 1984; Sagi & Julesz, 1985). Shifts of auditory attention have also been found to be distance invariant (Mondor & Zatorre, 1995). A third view of attentional shifts considers that attention does not shift from one point to another, but zooms in on one locus and then zooms back out before going on to another (Eriksen & St. James, 1986). Finally, one

might view the “movement” of attention as illusory, being a manifestation of different points on a map gaining ascendancy over the other points. This would be true whether selective attention is an interaction among feature maps, each of which implicitly encode stimulus saliency (Desimone & Duncan, 1995), or if saliency is encoded in separate topographic maps (Itti & Koch, 2000). Whether attentional ascendancy emerges through binding or saliency, clearly the locus of attention can change. We refer to such changes in spatial locus as “shifts” of attention. Our interest in this paper is whether these “shifts” are adaptable. In particular, we demonstrate that a salient feature of the motor programming of saccades—gain adaptation—also applies to shifts of attention.

In the case of saccades, it is clear that visual information present after the saccade can influence the size of subsequent saccades. This is evident from a long line of experiments starting with those of McLaughlin (1967), in which the experimenter surreptitiously moves the target back towards its previous location while the eye is in mid-flight with vision impaired. As a result, the brain is fooled into thinking that an accurate saccade had been too large. Over many saccades this results in the saccade amplitude being gradually reduced so that the saccades land progressively closer to the displaced position rather than the initial position of the target. By similar procedures, one can cause the saccade amplitude to be increased (Albano, 1996; Semmlow, Gauthier, & Vercher, 1989; Straube, Fuchs, Usher, & Robinson, 1997) or the saccade vector to be rotated (Deubel, 1987; Noto, Watanabe, & Fuchs, 1999). Saccade adaptation is specific to the particular directions (Deubel, 1991; Semmlow et al., 1989) or amplitudes (Miller, Anstis, & Templeton, 1981; Noto et al., 1999; Straube et al., 1997). Furthermore, adaptation is specific to the type of saccade (Deubel, 1999; Erkelens & Hulleman, 1993, but see Fuchs, Reiner, & Pong, 1996), that is, adaptation of exogenous saccades does not transfer to endogenous (scanning or memory guided) saccades, perhaps because adaptation can take place in any of several saccade-generating brain pathways (Deubel, 1999; Ganvarz & Grossberg, 1999).

To look for a similar adaptational change in shifts of attention, we examined whether the magnitude of shifts of attention could be changed by a method similar to that used to demonstrate saccade adaptation. To do this, we presented to subjects, whose eyes stayed on a fixation point, a peripheral cue and then, when we estimated that their attention was shifting, we moved the cue back by 30% so that the attentional shift would appear to have been too large. Using this back-step paradigm, we examined the magnitudes of the attentional shifts to see whether the size of the attentional shift changed gradually over many trials. Furthermore, if saccades were made to the locus of attention, one might expect that if

the attentional shifts were smaller after adaptation, then subsequent saccades would also be smaller.

Because we cannot continuously measure the location of attention, as we can measure eye position, we needed to use indirect methods to determine (a) the time when attention shifts and (b) the spatial (landing) location of attention after an attentional shift. We addressed both of these needs by using different variants on the line-motion illusion of Hikosaka, Miyauchi, and Shimojo (1993), which is strongly influenced by the locus of attention. In this illusion, if attention is drawn or directed to a cue, and a line is then presented adjacent to the cue, the line appears to grow (or “shoot”) from the end nearest the cue; if the line is centered on a previous cue, the line appears to shoot outwards in both directions from the cue location. This illusory motion is seen whether attention is drawn to the cue through visual, auditory or tactile means (Shimojo, Miyauchi, & Hikosaka, 1997). This illusion has been explained as a result of attention speeding the processing of visual information, so that the attended part of the line is perceived first (Hikosaka et al., 1993). We found that a psychophysical paradigm using the line-motion illusion gives reliable estimates of both the latency to shift attention and the location of attention. Using this paradigm, we were able to track the magnitude of shifts of attention over time.

Our principal results are, first, that by utilizing the back-step paradigm, we gradually reduced the magnitude of attentional shifts and, second, that this adaptation reduced the size of subsequent saccades. By stepping the cue forward, instead of back, we increased the size of attentional shifts. Finally, we adapted shifts to the right without affecting those to the left. All of these characteristics have been also observed in saccadic adaptation.

2. Methods

2.1. Subjects

The subjects were 21 naive volunteers (City College students of both sexes) and one of the authors (AK). Self-selection eliminated those who were not of a patient disposition. In addition, we discarded the data of subjects whose performance on the line-motion task during the pre-adaptation phase did not pass a criterion (line-motion origin reported as more than 0.5 deg from the actual cue location or standard deviation greater than 0.5 deg). Fourteen subjects participated in Experiment 1; three of these were in both Experiments 2 and 3; and seven subjects participated in Experiment 4.

2.2. Stimuli and apparatus

Stimuli were displayed on a 21 in. green monochrome monitor at 200 frames/s and were viewed at 51 cm by

subjects using a chin-rest in a dimly lit room. The fixation spot and cue were 0.33 deg in diameter; all the stimuli were light green (≈ 37 cd/m²) on a darker green background (≈ 3 cd/m²) and were generated by a computer running VisionWorks (Vision Research Graphics Inc., Durham, NH). The timing of the stimuli and the collection of the subjects' keyboard responses were controlled by a second computer using routines written under SuperScope (GW Instruments, Somerville, MA, USA). Display timing was accurate to within 10 ms. A foot pedal was used by some subjects to initiate a trial sequence or to temporarily halt the task for brief rest periods.

2.3. Monitoring eye movements

To monitor fixation and to assess whether the adaptation of attentional shifts also affects saccadic gain (Experiment 4), we measured eye movements with an infrared limbus tracker (Model 5400, Microguide Inc., Downers Grove, Illinois, USA). The eye tracker was mounted on a frame, and head stabilisation was aided with a chin and forehead rest. Data acquisition was controlled by a SuperScope program on a Macintosh computer. The output of the eye tracker was linearized by having the subject pursue a spot moving through one cycle of a sinusoid with an amplitude of 34 deg and a frequency of 0.04 Hz. This method of calibration minimized the number and size of saccades that the subject made, thereby permitting us to recalibrate the eye movement apparatus after the lengthy attention adaptation procedure, without introducing more than a few saccades that might reverse the effects of any saccadic adaptation that had occurred.

The amplitude of each saccade was measured by the experimenter, using a computer-assisted data analysis program. Each trial was calibrated by measuring the eye position before the target step and after the eye reached its eventual stable position near the end of the 1.6-s trial. We regarded this distance as equal to the distance that the target moved. The saccadic gain was calculated as the amplitude of the saccade divided by this estimate of change in target position.

On five subjects (three of whom are included here), we monitored the eye movements during the attention adaptation experiments, to see whether fixation was maintained. We found that the subjects did not make any saccades during the adaptation experiment.

2.4. Determining time required to shift attention

To determine for each subject the time required for a shift in attention, we used a two-alternative forced-choice discrimination task using the line-motion illusion. With the subject fixating on the centrally located

fixation point, a cue stimulus identical to that used during the adaptation experiment was displayed at 10 deg randomly to the right or left. After a randomly selected delay of 60–200 ms, the cue was followed by a horizontal rectangular line stimulus (10 deg wide by 0.3 deg high), which spanned the distance between the cue and the fixation point.

If the stimulus onset asynchrony (SOA) between the cue and the line was sufficiently long for the subject to shift attention from the fixation to the cue location, the line would appear to shoot from the end located at the cue position. If the SOA was briefer, the line would appear to originate from the fixation point or would appear, veridically, to come on simultaneously across its length. The subject was instructed to identify the origin of the line-motion as either from the inner end (near the fixation point) or from the outer end (near the cue location) by selecting one of two keys on a standard keyboard. If the motion did not appear to originate from near the line's extremities, subjects were instructed to select the key associated with the inner position, since attention had not yet shifted to the outer cued location.

The psychometric functions of the probability of the perceived line-motion origin being at the outer end of the line vs. the SOA were plotted and the raw responses were fitted with a sigmoidal curve (see example subjects in Fig. 1). The average steepness of these functions was 44 ms between the 20% and 80% points and was quite consistent (SD = 15 ms, $n = 10$). These results support the validity of using the line-motion illusion to determine the latency of shifts of attention, as has been previously reported (Hikosaka et al., 1993).

Approximately one day before each adaptation experiment, we calculated the attentional shift latency by an approximate psychometric function obtained by fitting the raw data with a Lowess non-linear smoother (see Section 2.7). An individual subjects' shift time (that

is, the time taken for attention to be changed from the fixation point to the target cue location) was obtained by locating the SOA equivalent to the 50% inward line-motion on this function. The mean attentional shift time was 116 ms.

2.5. Experimental design

In saccadic adaptation experiments, the target is surreptitiously and consistently displaced during the saccade, causing the eye to land beyond or short of the target. We used a similar experimental design to determine whether the magnitude of shifts in visual attention can also adapt to visual feedback. However, in our experiments the subject maintained fixation on a central 0.33 deg fixation spot while tracking an identical cue spot with covert attention. In brief, the cue stepped to the right or left of the fixation spot, and then, after the average latency for that subject to shift attention, the cue briefly turned into a grating of the same size and then returned to being a spot. The subject's task was to identify the orientation of this grating which briefly replaced the cue. This task was designed to ensure focal attention at the cue location. During adaptation, the cue either stepped back (e.g., leftward after a rightward step) or stepped forwards by 3 deg at the moment it became the grating. Thus in this situation the cue could be described as signalling the appearance of the grating 3 deg away.

Interleaved with these grating trials (usually making up 87% of the trials) were line-motion trials (usually 13%) in which a modification of the line-motion illusion was used to identify where attention landed after a shift of attention. The trials are described in detailed in Section 2.6.

We conducted four experiments, each of which required multiple sessions: a series of training sessions (see Appendix A), a session measuring an individual subject's attentional shift time (as described in Section 2.4) and finally the experimental session.

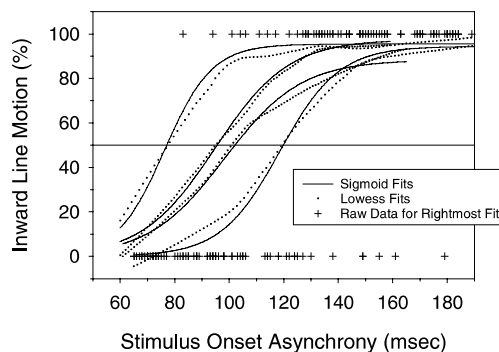


Fig. 1. Time to shift attention. Raw data for one subject (+ symbols at 0% denote reports of outward motion; those at 100% denote inward motion) and the corresponding Lowess and sigmoidal fits for this subject (rightmost curve) and 3 other subjects.

2.5.1. Experimental session

The experimental session of each of the 4 experiments consisted of three phases (Fig. 2): (I) a pre-adaptation baseline phase (mean across subjects = 277 trials, SD = 88 trials); (II) the adaptation phase (mean = 734 trials, SD = 142 trials); and (III) a post-adaptation recovery phase (mean = 367 trials, SD = 117 trials). These three consecutive phases were identical except that during phase II the cue stepped back or forward, after an interval corresponding to the subject's latency to shift attention, whereas in the pre- and post-adaptation phases the cue remained at the location where it first appeared (i.e., either 9 deg or, in Experiment 3, 7 deg).

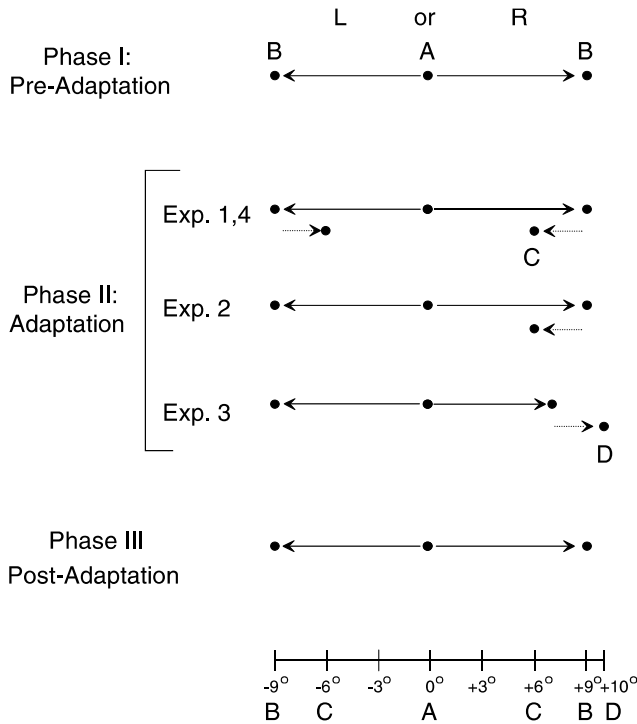


Fig. 2. Cue position during the different phases of each experiment. Subjects fixated a 0.33 deg diameter circular fixation point (A), and were instructed to shift their attention (but not their eyes) to an identical cue stimulus when it appeared at position B. B was located at 9 deg (randomly to the right or left) in all phases of Experiments 1, 2 and 4, or at 7 deg in all phases of Experiment 3. During the adaptation phase only, after a predetermined interval (the attention shift latency), the cue was displaced by -3 deg to position C (6 deg from A) either on both sides (Experiment 1) or one side (Experiment 2) or stepped forward by $+3$ deg to position D (Experiment 3). The cue briefly changed into a small grating upon reaching its final position (position B in phases I and III or at C or D during phase II).

2.5.2. Experiment 1: Adaptation to back-steps in both directions

During the adaptation phase of this experiment we stepped the cue 9 deg either to the right or left of the fixation spot and then, at a time corresponding to the subject's latency to shift attention, stepped it backwards by 3 deg. At the moment of the step-back, the cue was briefly replaced by a grating, before returning to a spot. We tested whether the magnitude of the attention shift decreased over time.

2.5.3. Experiments 2 and 3: Directional specificity of adaptation

In Experiment 2, we examined the directional specificity of the adaptation by stepping back the cue only during trials in which it had initially stepped to the right. In Experiment 3, we tested whether the magnitude of the shifts of attention could be increased (instead of decreased) by presenting the cue at 7 deg right or left and then stepping the cue forward by 3 deg only during the rightward trials.

2.5.4. Experiment 4: Effect of adaptation of attention on saccade adaptation

In this experiment we measured the gain of saccades before the pre-adaptation phase and again after the adaptation phase of an attention adaptation experiment like Experiment 1, except that the frequency of line trials was reduced to 5% to minimise their possible attenuation effect on the adaptation. To assess the gain of saccades, targets were stepped across the screen in 9–11 deg steps for 100–150 trials. When the computer detected the start of a saccade (based on a velocity criterion), the target was extinguished for 300 ms, so that the oculomotor system received minimal feedback as to the accuracy of the saccades. We chose this interval because saccadic adaptation is reduced by two-thirds if the target is not present for 300 ms after the saccade (Fujita, Amagai, Minakawa, & Aoki, 2002).

2.6. Trial descriptions

2.6.1. Grating trials

During these trials, the cue appeared randomly either 9 deg to the right or left of the continuously available fixation point (Fig. 3). After an interval corresponding to the previously determined attentional shift time (see Section 2.4), the cue was replaced for 50–100 ms with a square-wave grating, (Fig. 3, frame 3b; diameter = 0.3 deg, spatial frequency = 6 cpd) randomly chosen from one of four orientations. The Michelson contrast (0.3–0.4 for the two oblique orientations and 0.2–0.3 for horizontal and vertical orientations) was established for each subject during a training session to yield 75%

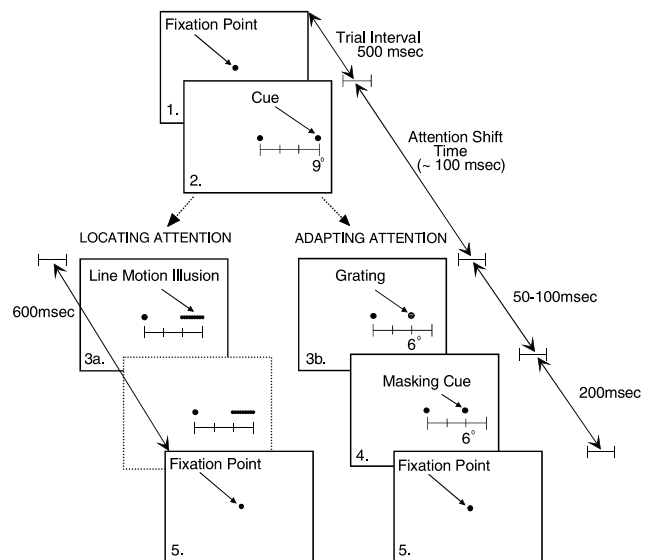


Fig. 3. Sequence and timing of events. Frames indicate the sequence for the two types of trials, those used to assess the location of attention (line-motion task, frames 3a–5) and those used to hold attention on the cue (grating task, frames 3b–5) during the adaptation phase in Experiments 1 and 2.

accuracy. This level of performance was maintained during the experiment by modifying the grating duration and contrast. After the grating intervals, the cue, now acting as a mask, returned for 200 ms. Subjects selected the grating orientation with a keyboard response.

It is worth noting that in addition to requiring our subjects to maintain fixation, our experimental protocol would have discouraged saccades because the grating to be discriminated appeared about 100 ms after the target step and was masked 100 ms later. Thus most saccades would not reach the grating cue while it was present, and the grating would not have been discriminable during the saccade. Indeed, no saccades were detected on those subjects whose eye movements were monitored. Thus, the task involved covert attentional shifts only.

The grating and mask were at the initial cue location of 9 deg to the right or left of the fixation spot (7 deg in Experiment 3) during the pre-adaptation and post-adaptation phases, but were displaced by 3 deg during the adaptation phase, either back towards the fixation point (Experiments 1, 2 and 4) or forward (Experiment 3).

2.6.2. Line-motion trials

The principal innovation in these experiments is the use of a modification of the line-motion illusion to track where attention landed after attention shifted from the fixation spot to the cue. To do this we expanded the response to the line from being a two-alternative forced-choice (“from which end did the line grow?”) to being a nine-alternative forced-choice by having the “line” be a row of nine adjacent filled circles, each 0.33 deg in diameter, and having the subject judge from which of the filled circles the line appeared to originate (examples of stimulus conditions from different experiments are shown in Fig. 4). This procedure yielded a consistent percept in trained subjects that the line originated from the perceived location of a previously flashed cue, and thus, we infer, from the location to which exogenous attention had been drawn.

Like the grating trials, the line trials began with the cue appearing 9 deg (7 deg in Experiment 3) randomly either to the right or left of the fixation point. After an interval corresponding to the attentional shift time for that subject, the cue was replaced for approximately 600 ms by the line stimulus, which spanned 3 deg (Fig. 3, frame 3a).

In Experiment 1, for the first half of the subjects the line was positioned so that the outermost filled circle was aligned with the initial cue location (9 deg right or left), thus spanning the 3 deg between the initial and step-back cue locations (Fig. 4A). In the second half of the subjects and in Experiments 2 and 4, the third circle from the outer end was aligned with the cue location, so that changes in response variability would not cause shifts in response position because of truncation (Fig. 4B). In Experiment 3, in which the cue stepped forward,

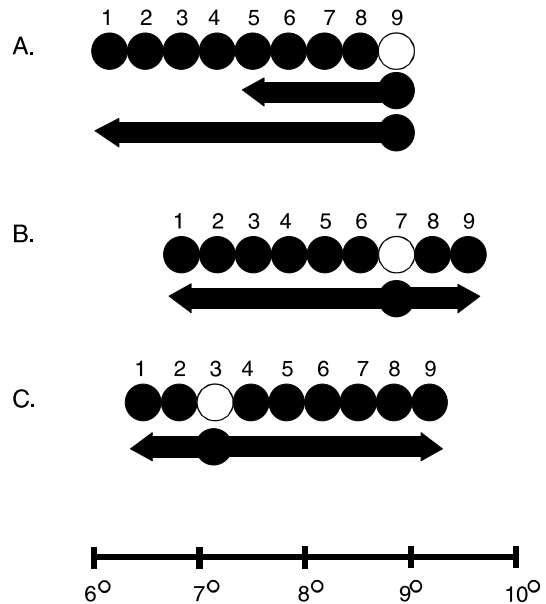


Fig. 4. Modified line-motion illusion. (A) If a single cue (at position 9) precedes a line (composed of a 3 deg row of 9 identical circles), the line appears to shoot from the cue location in the direction of the arrows. (B) If the cue preceding the line is at a position within the line (here position 7, as used in Experiments 1, 2 and 4) the illusory motion flows in two directions but is strongest for the longer line segment (here to the left). (C) If the cue is located at position 3 (as in Experiment 3 in which forward-steps from 7 to 10 deg were used during adaptation), line-motion is seen mostly to the right. In all cases subjects were trained to locate accurately the origin of line-motion to one of the 9 circles.

the cue started at 7 deg and stepped to 10 deg, a position chosen because the cue’s stepping forward from 9 to 12 deg made the grating discrimination too difficult. In this experiment, the third circle from the inner end of the line was aligned with the cue location (Fig. 4C).

2.6.3. Catch trials

In contrast to the training on the line-motion task, in which each of the 9 circles that made up the line was cued with equal probability, during the experiment the line origin remained constant over many consecutive trials (e.g., at position 9). Thus, subjects might bias their responding to the expected cue location. To minimize this effect, which would cause the degree of adaptation to be underestimated, we interleaved an equal number of catch trials with the line-motion trials. These catch trials lacked predictability about the location of the apparent line origin because the line was offset with respect to the cue by a random amount, so that the line-motion appeared to originate with equal probability from each of the eight circle positions other than the actual cue position. The responses on these catch trials were not used in our estimates of adaptation, but were used to ascertain the accuracy of the line-motion task during the experiment.

2.6.4. Frequency of line-motion, catch and grating trials

Because the line was present for much longer than the attentional shift time, each shift to it tends to counter the adaptation produced by the grating trials. Thus, if the frequency of the line trials is higher, our ability to track the locus of attention is better, but the adaptation is weaker. In Experiment 1, the correlation (r) between the degree of adaptation and the frequency of line trials experienced by each subject was 0.82. For this reason, we varied the proportion of line and grating trials in different experiments.

The frequency of the line trials (half of which were normal line-motion trials and half of which were catch trials) was 25% for the first 7 subjects in Experiment 1, after which it was decreased to 13% (for the remaining 7 subjects and for Experiments 2 and 3) to minimize interference of the line trials with the adaptation. In order to maximise the degree of adaptation in Experiment 4, in which the primary measurement was saccadic gain, the number of line-motion and catch trials was further decreased to 5%. Therefore, the ratio of the percentage of line-motion:catch trials of all trials was 25:0% for the first 7 subjects of Experiment 1; 6.5:6.5% for the remaining subjects in Experiments 1 and 2; and 2.5:2.5% in Experiment 4.

2.7. Data presentation

The principal data presented here are the changes in the location of attention immediately after a shift of attention in response to steps of the cue. On each line trial, the subject reported the circle from which the motion appeared to originate. We converted these responses into a percentage of the 3-deg step-back or step-forward. Thus a reported origin of line-motion of 0% corresponded to the actual cue location (B in Fig. 2), -100% corresponded to the backward step location (C in Fig. 2) and +100% corresponded to the forward-step location (D in Fig. 2). The raw data were smoothed using a Lowess smoother as implemented in Sigma-Plot® (SPSS Inc., Chicago) or Data Desk® (Data Description Inc., Ithaca, NY). This non-linear iterative fitting function involves computing a regression line within a window around each y -value and assigning each point a weight inversely proportional to its distance from the fitted line. Because the line-motion trials occurred at only occasional and random trial numbers in each subject, to average across subjects, we interpolated the smoothed data for each subject to yield data at each trial number. The number of trials was not the same for each subject, so for statistical purposes we compared individual trials during the first 180 trials of the pre- and post-adaptation phases and the first three consecutive blocks of 180 trials during the adaptation phase.

3. Results

Because our results rely on the use of the line-motion illusion to determine the location of the focus of attention, we first present results which demonstrate the accuracy of this method. We then show that the shifts of attention measured in this way can be adapted if the target is systematically displaced to a new spatial location at the time of the initial attentional shift. Finally we explore the directional specificity of such attentional adaptation and its effect on subsequent saccadic eye movements.

3.1. Accuracy and reliability of assessments of locus of attention

Our assessments of the adaptation of shifts of attention rely on the accuracy and reliability with which subjects correctly identify the location from which the line-motion originates. Our subjects were able to locate the origin of the line-motion to less than 0.57 deg during training, during which correction trials were given. Furthermore, we tested one of the authors (AK) under extended conditions for 1794 consecutive trials on the line-motion task with the cue randomly presented at all possible positions on the line. We found that the slope of the line relating the perceived locus of line initiation to the actual cue location was very close to 1. After removing the correction trials, $r = 0.83$ (Fig. 5A) and the mean accuracy was 0.76 deg (SD = 0.18 deg).

Over the 2 h time-course of this experiment, we found that the error (the absolute value of the deviation of the reported line origin from the cue location) was stable. This indicates that the repeated use of the line-motion illusion without adaptation does not by itself appreciably change the apparent origin of line-motion. So too in our experimental subjects, as will be seen, we also find that the locus of attention is relatively stable in the long series of over 1000 baseline trials in Experiments 2 and 3, and during the shorter pre-adapt baseline phase in Experiment 1.

To assess the reliability of the line-motion trials during the experimental conditions, in which the task demands were much greater because the line-motion trials occurred infrequently and without warning, we looked at the performance on the catch trials (in which every position on the line was cued) for subjects in Experiment 1 (Fig. 5B). Even under these conditions, the mean accuracy was quite high at 0.72 deg (SD = 0.4 deg).

A curiosity of our origin of line-motion data is the slight displacement in the direction of the line-motion, resulting in the baseline measures being slightly less than zero. This might be a manifestation of the Frohlich illusion, in which one sees the origin of motion of a

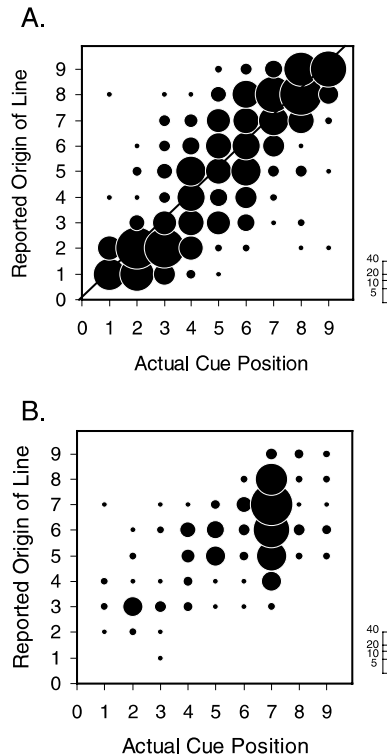


Fig. 5. Accuracy in locating attention with the line-motion illusion. (A) Example of one of the authors (AK) tested with a very long series of line-motion trials (1794) in which the cue was randomly placed with respect to a subsequent line stimulus (composed of 9 circles) spanning from 6 to 9 deg of eccentricity. The circle reported as the origin of the line-motion is highly correlated with the actual cue location. (B) Accuracy during the pre-adaptation phase for the 7 subjects from Experiment 1 who had both the normal line-motion trials (cue at the seventh circle position) and catch trials (cue randomly occurred at one of the other 8 positions). This task was more difficult since the line-motion trials were interlaced with the grating trials and occurred intermittently and unexpectedly. In both cases, frequency of responses is represented by the area of the black circles.

moving stimulus displaced in the direction of the motion (Kirschfeld & Kammer, 1999).

3.2. Experiment 1: Adaptation to back-steps in both directions

3.2.1. Example of raw data

The general result of the adaptation experiment was that once each step of the cue was followed by a back-step at the attention-shift-latency, the magnitude of the shift of attention gradually decreased. Thus the location where attention landed (as measured by the origin of line-motion) became closer to the point to which the cue back stepped. An example of the raw data and its Lowess smoothed function from one subject is shown in Fig. 6. The subject's judgement of the apparent line origin was fairly stable during the pre-adaptation baseline period. During the adaptation phase, the apparent line origin shifted over several hundreds of trials in the

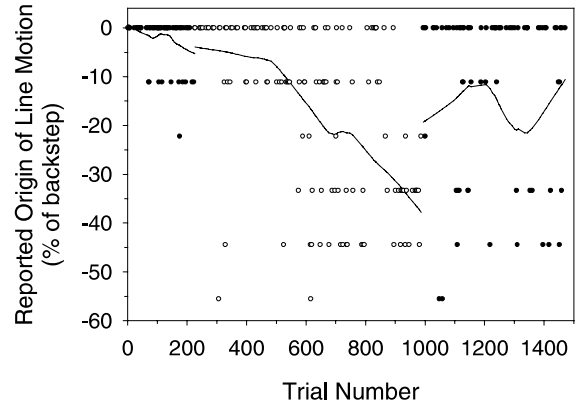


Fig. 6. Example of raw data showing a shift in the locus of attention during adaptation. Raw responses for the reported origin of line-motion are shown for the adaptation phase (open circles) and the pre- and post-adaptation phases (filled circles) of subject F (see Table 1) in Experiment 1, with the corresponding Lowess smoothers fitted to the data of each phase (solid lines). Trial numbers shown on the x-axis include both grating and line-motion trials. In this subject, approximately 20% of total trials were line-motion trials (circles). During the adaptation phase, the reported origin of line-motion moved gradually from the original cue location (0%) toward the step-back location (-100%). Trial Number shows all trials rather than the 180 trial blocks presented in Table 1 and Fig. 9.

direction of the back-stepped location with a clear downward trend to a maximum of approximately 40% of the size of the 3 deg back-step. Once the adaptation was discontinued in the post-adaptation phase, the apparent line origin shifted substantially back toward the original cue location (0%).

3.2.2. Magnitude and consistency of adaptation

Every one of our 14 subjects significantly decreased the size of their attentional shifts by the third block of 180 adaptation trials compared to the first 180 pre-adaptation trials (Fig. 7A and Table 1; mean shift = -16.6%, SD = 8.9; Kruskal-Wallis ANOVA and Dunn's Comparison, $p < 0.01$ for each subject; 12 of these subjects showed a significant shift using t -test comparisons of raw responses during these periods: in 9 subjects $p < 0.001$ and in 3 subjects $p < 0.05$). Both the mean and the mode of the magnitude of the shifts of attention changed with adaptation. Thus the adaptation was not a consequence simply of an increase in the frequency of the subject selecting the adapted position with a concordant decrease in the frequency of selecting the unadapted position (Fig. 8). Notice that the principal difference between the first (Adapt 1) and third (Adapt 3) blocks of the adaptation was the decrease in the frequency of the unadapted position (0%) and the increase in the frequency with which the circles three (-33%) and four (-44%) positions away were chosen. It is important to note that even after adaptation our subjects never reported that the line started at the position representing full adaptation (-100%).

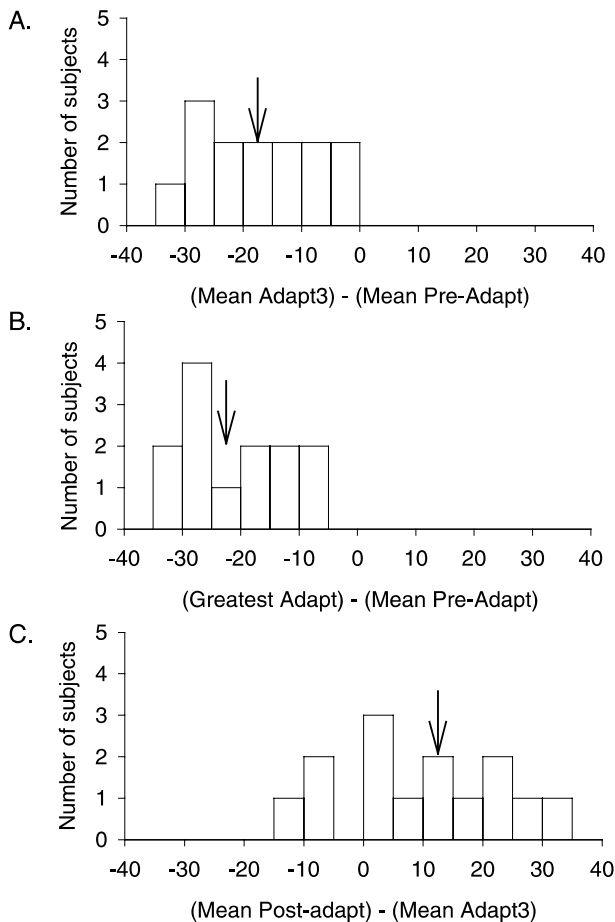


Fig. 7. Distribution of the degree of adaptation in individual subjects in Experiment 1. (A) The mean origin of line-motion over the third block of 180 adaptation trials after subtracting the mean of the pre-adaptation phase. (B) The greatest adaptation as shown by the minimum point on the smoothed curve of responses minus the average of the pre-adaptation phase (Fig. 7B). The median amount of adaptation so measured was 22.5%. Furthermore, all but three of our subjects shifted in the opposite direction during the post-adaptation phase (Fig. 7C and Table 1; mean shift = +10.1%, SD = 14.1; Dunn's Comparison, $p < 0.01$, $n = 11$).

Averaging across subjects as above underestimates the degree of adaptation because of individual differences in time course. Therefore we also show the greatest degree of adaptation shown by each subject (in the third block of 180 adaptation trials) relative to the average of the pre-adaptation phase (Fig. 7B). The median amount of adaptation so measured was 22.5%. Furthermore, all but three of our subjects shifted in the opposite direction during the post-adaptation phase (Fig. 7C and Table 1; mean shift = +10.1%, SD = 14.1; Dunn's Comparison, $p < 0.01$, $n = 11$).

Averaged across all 14 subjects (Fig. 9), the magnitude of attentional shifts clearly decreased during the adaptation phase of the experiment compared to the pre-adaptation baseline phase (by 17.5% of the back-step size during the third block of 180 adaptation trials)

and then increased again (by 11.4%) during the post-adaptation phase (Fig. 9 insert). Subjects who had catch trials but fewer line trials showed slightly greater amounts of adaptation than those subjects who did not have catch trials, but not significantly so (difference between the adaptation phase III and pre-adaptation was -13.5% for subjects A–G and -19.8% for subjects H–N, Table 1, $p > 0.05$). Statistically, the averaged magnitude of attentional shifts across all subjects differed significantly among the three experimental phases (Kruskal–Wallis ANOVA, $H = 794.5$, $df = 4$, $p < 0.001$) and was significantly different between the pre-adaptation and the adaptation or each of the three blocks of the adaptation phase (Dunn's Comparisons, $p < 0.01$ in all cases).

3.2.3. Time-course of adaptation

An important attribute of saccadic gain adaptation is that it is gradual. We find this is also true of adaptation of shifts of attention. From the averaged change in the perceived origin of the line-motion across all subjects (Fig. 9), the regression of apparent line origin on trial number during the adaptation phase shows a significant downward linear trend (slope = -2.19% per 100 trials; $r = 0.99$, $p < 0.001$) and a reversal of that trend when the adaptation trials were discontinued in the post-adaptation phase (slope = +2.81% per 100 trials; $r = 0.77$, $p < 0.001$). These changes from the pre-adaptation baseline were not due to variability during the pre-adaptation control period, because performance was relatively stable (slope = -0.64% per 100 trials) and accuracy during this period was high—the average perceived position of the origin of the line-motion was 0.25 deg away from the actual cue location.

Although Fig. 9 shows that the average adaptation is progressive, this does not necessarily imply that adaptation in individual subjects is progressive; the same curves could have resulted from each subject suddenly adapting but after different numbers of trials. The full adaptation curves of each subject (Fig. 10) show that adaptation is not sudden. Rather, the adaptation curve of most subjects proceeds more or less steadily downward, and regression fits give negative slopes in all but one case (Subject N in Fig. 10). Additionally, the mean level of adaptation relative to the pre-adaptation period in individual subjects does not differ significantly during the first block of the adaptation period, but does by the second and third blocks (ANOVA, Tukey comparison, $p < 0.001$). Eleven of the 14 subjects significantly decreased further between the first 180 trials and the third block of 180 trials (Kruskal–Wallis ANOVA and Pairwise Dunn's Comparisons, $p < 0.001$ for $n = 11$, Table 1). When the adaptation trials were discontinued during the post-adaptation phase, slopes were positive in 10 of 14 subjects.

Table 1

Mean and standard deviation of the reported origin of line-motion in the first 180 trials of the pre-adaptation phase I, 540 trials of the adapt phase II (divided into 3 equal blocks of 180 trials), and 180 trials of the post-adaptation phase III for Experiment 1

Subject	Shift time (ms)	Pre-adapt phase I		Adapt phase II						Post-adapt phase III	
		Mean%	SD	1		2		3		Mean%	SD
				Mean%	SD	Mean%	SD	Mean%	SD		
A	150	-9.68	2.80	-33.93	3.68	-40.96	1.59	-34.74	1.73	-6.62	2.65
B	140	-15.92	3.81	-15.71	0.62	-18.94	2.27	-19.40	0.54	-12.12	3.66
C	140	-4.39	2.11	-4.03	0.74	-7.49	4.82	-26.63	3.82	-2.04	1.51
D	130	-11.38	0.86	-12.40	0.60	-14.28	2.41	-22.89	1.41	-18.49	4.74
E	100	-16.93	3.62	-18.20	0.24	-19.97	1.85	-27.27	1.18	-10.09	2.72
F	130	-1.48	1.06	-4.84	0.58	-8.68	2.64	-19.79	2.38	-15.36	2.42
G	78	-9.24	1.52	-15.54	2.65	-17.45	1.74	-12.77	0.47	-25.71	10.92
H	93	-12.85	2.45	-24.76	3.52	-35.93	2.99	-37.92	0.45	-23.45	3.04
I	130	-0.48	4.83	-6.80	8.96	-24.72	1.27	-21.92	0.18	-27.92	7.00
J	118	3.34	3.93	-7.10	1.31	-11.25	0.76	-12.43	1.20	-1.47	5.55
K	105	-1.17	2.97	-17.59	2.24	-27.97	3.99	-32.42	1.74	-9.33	2.03
L	90	-6.3	1.50	-18.57	1.47	-17.55	0.95	-15.73	0.98	-24.13	4.30
M	95	-9.97	3.10	-26.80	0.55	-27.28	1.81	-36.58	1.97	-3.67	3.21
N	123	-1.16	7.11	-8.05	0.50	-6.42	0.66	-9.92	0.44	-9.11	6.08
Mean	116	-6.97	2.98	-15.31	1.98	-19.92	2.13	-23.60	1.32	-13.54	4.27
SD	22	6.25	1.67	8.90	2.32	10.47	1.20	9.30	0.98	9.06	2.49

The upper group of subjects (A–G) were those with 25% line-motion trials and with position 9 of the line aligned with the cue, while the lower group (H–N) had 6.5% line-motion trials and position 7 was aligned with the cue (see Section 2). Data are expressed as the percentage of the 3 deg back-step. Full adaptation would be -100%. Shift time is the estimated time taken by each subject to shift attention to a brief peripheral cue (see Section 2.4).

3.2.4. Coupling between leftward and rightward adaptation steps

Because the time-course of adaptation differs among individuals (or among experiments), we looked to see whether, in individual subjects, the course of adaptation to rightward and leftward steps of the cue was similar. In 9 subjects, the linear regressions of the smoothed interpolated values in the two directions were well correlated (mean $r = 0.77$, $SD = 0.2$), while the remaining subjects had weak or no coupling (mean $r = 0.22$, $SD = 0.04$). The degree of correlation between the left and right sides was not related to the magnitude of the mean adaptation in individual subjects.

3.3. Experiments 2 and 3: Directional specificity of adaptation

A salient feature of saccadic adaptation is that adaptation to rightward steps does not transfer to leftward steps. To see whether the rightward and leftward shifts of attention could also be adapted independently, for 3 subjects we had the cue step either backward (Experiment 2) or forward (Experiment 3) during the adaptation phase, but only during trials in which the initial step was to the right. When the cue appeared on the left side, there was no displacement, with the grating and the cue remaining in their initial location for the duration of the trial.

We found that rightward attentional shifts can be adapted without affecting leftward shifts. Furthermore,

it is clear that the magnitude of attentional shifts can be increased as well as decreased by our adaptation paradigm. These unidirectional effects are evident both in the time-course of adaptation averaged over the three subjects (Fig. 11) and the differences between the means of the entire adaptation period for leftward and rightward steps in individual subjects (Fig. 12; ANOVA and Tukey comparisons, $p < 0.001$ in all cases).

Specifically, highly significant shifts of attention were observed for the rightward direction for the averaged performance during the adaptation phase when compared with either the rightward baseline trials during the pre-adaptation phase or with the leftward (non-adapting) trials during the adaptation phase (Dunn's Pairwise Multiple Comparison after Kruskal–Wallis ANOVA; backward steps, $Q = 20.1$ and 23.2 , forward-steps, $Q = 6.1$ and 28.6 respectively, $p < 0.01$ in all cases). No adaptation occurs in the leftward (non-adapting direction) (Dunn's Pairwise Multiple Comparison after Kruskal–Wallis ANOVA; backward steps, $Q = 1.34$, forward-steps, $Q = 1.39$, not significant in both cases). This finding confirms that the change shown in Fig. 9 during the adaptation phase of Experiment 1 is specific to the adaptation condition, rather than being one that would be observed for any long series of attentional steps. Like saccadic gain, the magnitude of attentional shifts may be decreased more easily than increased, as the mean change during the adaptation phase relative to the pre-adaptation baseline phase was greater for backward shifts (mean = -19.1,

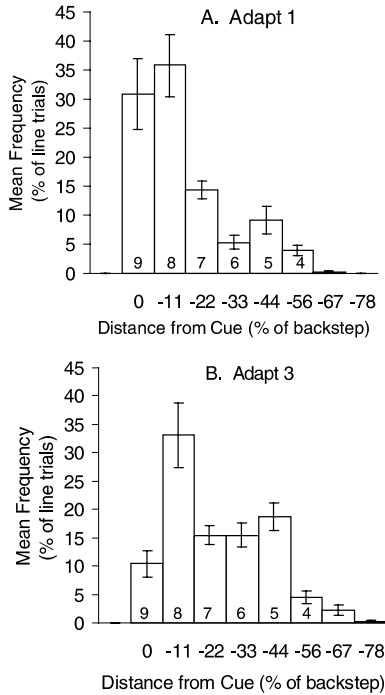


Fig. 8. Mean frequency distribution for the origin of line-motion during the adaptation phase for the first seven subjects in Experiment 1 (for whom the line spanned the cue (0%) and back-step (–100%) locations). (A) First 180 trials of the adaptation phase and (B) last 180 trials of the adaptation phase. The circle location numbers (as in Fig. 4A) are shown at the bottom of each bar. Notice that adaptation did not arise because of a change in the relative ratio in which only the cue and back-stepped locations were selected. Instead there was a shift in preference away from the initial cue location towards (but never at) the back-stepped location.

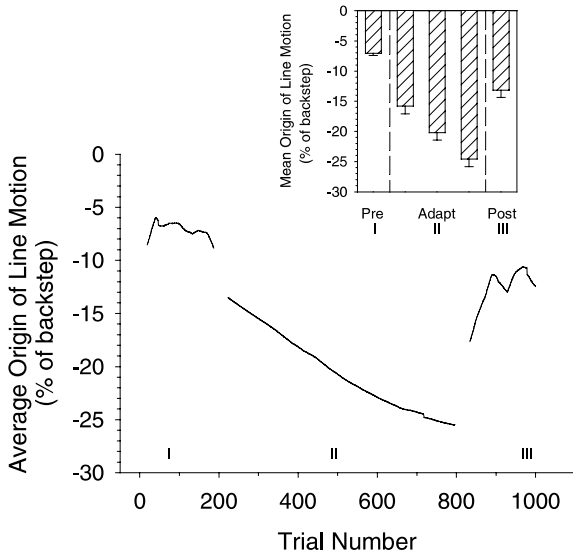


Fig. 9. Average changes in the locus of attention during Experiment 1. The location of attention, as measured with the line-motion illusion, was averaged for all 14 subjects during the first 180 trials of the pre- and post-adaptation phases and for the first 540 trials of the adaptation phase of Experiment 1. The inset shows the mean position for each 180 trial block.

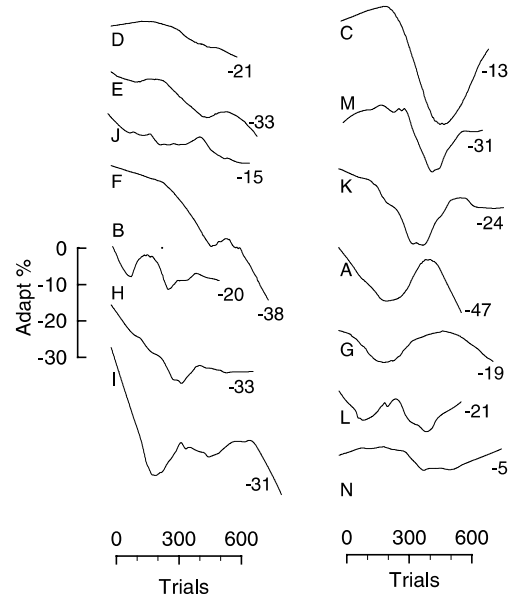
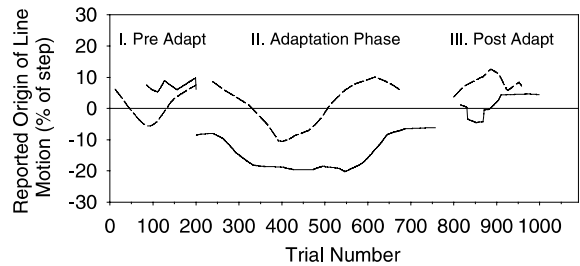


Fig. 10. Smoothed adaptation curves during the adaptation phase for each subject in Experiment 1. The numbers at the end of each curve show the amount of adaptation (in terms of the percentage of the back-step) at the last point on the curve. A–N labels refer to the subject number as listed in Table 1.

A. Backward Adapt Steps Drive Attention Gain Down



B. Forward Adapt Steps Drive Attention Gain Up

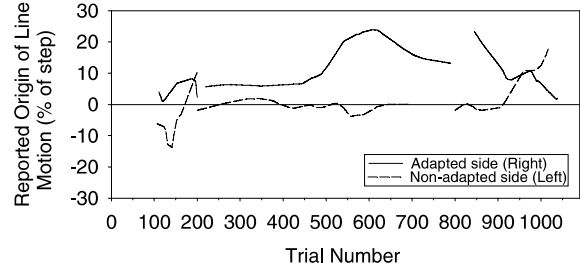


Fig. 11. Unidirectional adaptation of shifts of attention. Line origin reported during experiments in which the cue stepped backward (A—Experiment 2) or forward (B—Experiment 3) only on trials in which the cue stepped to the right (solid lines). Adaptation occurred in both cases. On trials in which the cue stepped first to the left and remained in its new position for the rest of the trial (dashed lines), responses were similar during the pre-adaptation (left curves), adaptation (middle curves) and post-adaptation (right curves) phases. Data averaged across 3 subjects.

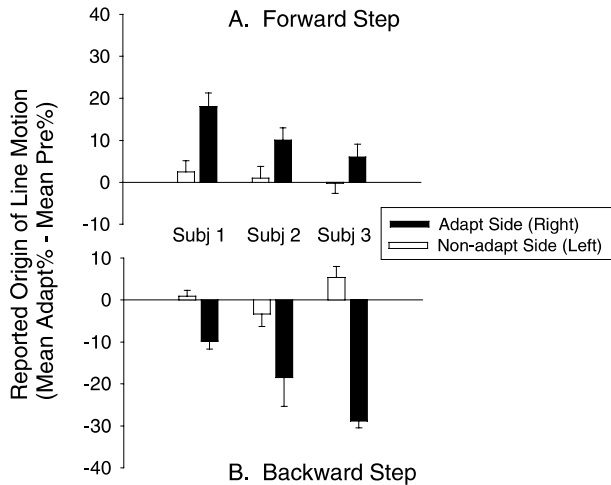


Fig. 12. Adaptation causes both increased and decreased shifts of attention in individual subjects. Mean changes of origin of line-motion during the adaptation phase relative to the pre-adaptation baseline phase in (A) Experiment 3 and (B) Experiment 2. Positive changes indicate increases in the magnitude of attentional shifts. Error bars are standard error of the mean.

SD = 9.5, $n = 3$) than for forward shifts (mean = +11.4, SD = 6.1, $n = 3$).

3.4. Experiment 4: Effect of adaptation of attention on saccade size

Because attention shifts to the saccade target before the eye moves, it is possible that the location of attention defines the saccade target. If this were so, adapting attention so that a target at 9 deg causes attention to move 8 deg might cause saccades to that target to be 8 deg as well, even though during the adaptation no saccades took place (the eyes were always on the central fixation point). We found that in 5 out of 7 cases of adaptation of the shifts of attention similar to Experiment 1 there was subsequently a statistically significant reduction in the saccadic gain (0.064 ± 0.026 s.e.m., $p < 0.05$; two-sample paired t -test; Fig. 13). We are uncertain, however, whether there was a relationship between the magnitude of adaptation of attention and the size of the subsequent saccades ($r = 0.54$), because to maximize attentional adaptation, very few line-motion trials were included during the adaptation. It is also likely that during the measurement of the saccade gain, the attentional shifts gradually disadapted back toward their original value because we left the target on for about 200 ms (until the saccade was initiated). As a consequence, once attention had shifted to the adapted location the target would have remained on at the original location for an additional 100 ms before the saccade. If adaptation of attentional shifts is like saccadic adaptation, having the stimulus at the unadapted location just after the attentional shift would reverse the effects of the

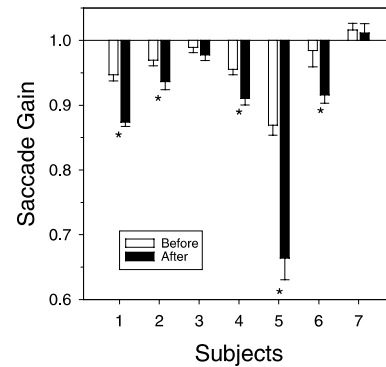


Fig. 13. Adaptation of shifts of attention transfers to saccade gain. Mean and standard error of changes in the gain of saccadic eye movements before (open bars) and after (filled bars) an attention adaptation experiment in seven subjects. Open loop saccades were measured before the pre-adaptation phase and again after the adaptation phase. In 5 of the subjects the saccadic gain decreased significantly after backward attention adaptation, $*p < 0.001$. In subject 2, the line-trials were not interleaved with the grating trials but were presented as a block at the end of each phase.

adaptation. A more definitive test of the relation between adaptation of attention and saccades would be to interleave attentional adaptation trials with trials requiring a saccade to a briefly flashed target (suggested by Laurence Harris, York University).

4. Discussion

We have shown that when a subject views a cue that steps back (or forward) around the time that the subject usually shifts his or her attention, the amplitude of the attentional shift gradually decreases (or increases). As such, these adaptational changes resemble those that take place in saccadic eye movements during experiments in which a target is stepped backwards or forwards during a saccade. To evaluate the similarity of these two adaptational phenomena, we will consider first the differences in methods of producing these two forms of adaptation and then the differences in the magnitude of adaptation obtained. Finally, we will discuss the implications of adaptation of attentional shifts for understanding saccades and for understanding how the locus of attention shifts.

4.1. Appropriateness of the line-motion illusion for measurement of the location of attention and of the time to shift attention

Our results rest on our use of a modification of the line-motion illusion to evaluate where visual attention is at a particular point in time. It has been proposed that non-attentional visual factors may contribute to the shooting line illusion (Downing & Treisman, 1997; but see Schmidt, 2000). However, the fact that the direction

of the illusory line-motion can be determined by which end of the line attention has been drawn to, whether by visual, auditory or tactile stimuli or by verbal instructions (Shimojo et al., 1997) suggests that the attentional component of this illusion is at least strong enough to warrant its use in our task.

In particular, we find that the line-motion illusion has four properties that are useful for our purposes: (a) It locates attention with considerable precision. Using our 9-circle line, our subjects could be trained to identify the origin of the line-motion to less than 0.5 deg. (b) The long-term accuracy of the apparent line origin was stable. When we gave a subject nearly 1800 line-trials over 2 h, the origin of the line-motion was discriminable to within 0.68 deg of the actual cue position over the whole period. (c) The shifting of “attention” from one location to another, as assessed by the line-motion, is rapid and orderly. We find that the standard deviation (across subjects) of the SOA that elicits 50% inward line-motion is 22 ms. (d) The latencies that we measure are similar to other reports on the exogenous shifting of attention (Eriksen, Webb, & Fournier, 1990; Remington, 1980; Yantis & Jonides, 1990).

Because of the limitation that we have only one method for measuring the locus of attention with the precision we require, we cannot be entirely sure that non-attentional factors might not participate in the adaptation we report. If our judgement is incorrect with respect to the line-motion illusion being predominantly determined by the locus of attention, one would have to look elsewhere for the cause of the adaptation we report.

4.2. *Alternative explanations of attentional adaptation*

We find that our adaptation situation results in a change in the magnitude of the attentional shift to the onset of a cue at an eccentric location. Is it reasonable to consider this an adaptation like that of saccades subjected to a somewhat similar stimulus situation? We will consider several alternative explanations.

First, one might attribute the changes we observe to a voluntary reallocation of attention, rather than an adaptation of the attentional shifts. Because attention can be voluntarily directed, might not the onset of the cue be taken as a signal to attend to the stepped-back or stepped-forward location, rather than to the cue location? If so, what we are calling “adaptation” would not be a modification of the magnitude of the shift of attention to the cue location, but rather would entail a shift in strategy such that the subject would cancel the shift of attention to the primary cue location and attend directly to the expected location of the grating. In general, our evidence does not support this explanation. Subjects do not suddenly change their locus of attention during the course of adaptation. Rather, it is evident that the changes are generally progressive, both across

subjects (Fig. 9) and in each individual subject (Figs. 8 and 10), as would be expected of an adaptational change, even though some subjects do quickly reduce the size of their attentional shifts at the start the adaptation.

Furthermore, none of our subjects adapted fully to the back-step (or forward-step) of the cue (Fig. 8). If a cognitive strategy had been employed, one might expect that any such endogenous attentional mechanism would have shifted the locus of attention directly to the cue. Instead, it appears that even after hundreds of nearly identical trials, the endogenous attentional mechanism cannot cancel the exogenous shifts of attention. It has been explicitly shown that when conflicting endogenous and exogenous cues are presented, the demands of the exogenous cues cannot be denied (Muller & Rabbitt, 1989; Remington, 1980). The reason for this lack of interaction may be that the exogenous attentional latency is much shorter than the endogenous (less than 100 vs. 300 ms or more—see Eriksen et al., 1990; Hikosaka, Miyauchi, & Shimojo, 1996; Remington, 1980; Yantis & Jonides, 1990). The forms of attention also differ in that exogenous attention does not linger long in one place, whereas endogenous attention can be sustained (Muller & Rabbitt, 1989; Nakayama & Mackeben, 1989; Remington, Johnston & Yantis, 1992). It would be interesting to know how sensitive the adaptation is to the timing of the step-back.

Second, we will consider whether there might be a false impression of adaptation because the cue location is at or close to one end of the line or the other, so that a large increase in the variability of the responses during the adaptation phase of the experiment might cause the mean perceived line origin to shift towards the center of the line (because responses can be much further from the starting point in the direction of the near end of the line than in the direction of the far end of the line). We can exclude increased variability as an explanation for our results for two reasons: (a) The magnitude of adaptation of the 7 subjects for whom the cue location was at the third outermost circle on the line (Fig. 4B) was the same as, or even slightly greater than, that of the 7 subjects for whom the cue location was at the end of the line (Fig. 4A) (mean over 540 trials of -20.4% vs. -18.9% respectively, $p = 0.8$). (b) The variability during the adaptation phase was not correlated with the degree of adaptation. We computed the square of the residuals of the fit to the Lowess function for each subject and correlated this variance-like measure to the amount of adaptation. The correlation coefficients had an average value of -0.09 ($SD = 0.17$, $n = 14$).

Third, the adaptation is not a consequence of progressive changes in the apparent line origin that would have occurred even if the cue had not stepped backwards or forwards. In Experiments 2 and 3 where adaptation occurred only for rightward steps, the shifts of attention to leftward steps did not differ from the

pre-adaptation baseline phase and were relatively stable throughout all phases. Also, the single experiment with 1794 consecutive line-trials showed no tendency of a progressive shift in line-origin that could account for the adaptation that we have observed.

4.3. *What is necessary to produce adaptation?*

In our experiments we required an explicit orientation task of our subjects. Thus, although the unpredictable appearance of the cue summoned attention exogenously, the task also would have been aided by an endogenous shift of attention to the back- (or forward-) stepped location. As just discussed, the adaptation measured reflected changes in the exogenous shift of attention, because the endogenous shift would not have occurred by the time that the line was presented. One can ask therefore whether the discrimination task was necessary at all. We speculate that the adaptation could have occurred without the discrimination task, but that the discrimination task served to keep the spatial scale of attention narrow, so that all attentional resources were deployed in the small region of the cue and grating. Without this endogenous signalling of the appropriate scale of attention, the attentional focus might have been so broad that both the original cue location and the stepped back location would have been encompassed by a single broad focus of attention. We have evidence that saccade adaptation is sensitive to the size of the attentional field (Wallman, Khan, Yun, & McFadden, 2001).

4.4. *Does adaptation of attention require that attention actually moves?*

Our interpretation of both the latency and the adaptation of the attentional shift was motivated by the supposition that attention does in fact shift, but the results we have obtained and the conclusions we have drawn from these results do not rest on this supposition. One can take the alternative view that attention does not move in the sense of a spotlight moving, but rather that at the start of each trial attention is diffuse and then after the cue is presented it becomes focused in one region (that is, it zooms in to the cued location) (Eriksen & St. James, 1986; Shepherd & Muller, 1989). This view does not demand a change in our interpretation of our results. Rather, we would say that our results imply that after attention is focused, some process assesses whether it zoomed accurately to the cue location, and, if not, the zoomed location is altered over hundreds of trials. Similarly, our finding of an orderly sigmoidal curve when we assessed the time to shift attention could be interpreted as the time necessary to focus attention to the cued location. This interpretation would, however, require that, before the cue is presented, attention is somewhat more intense at the fixation point than it is

elsewhere in order to account for the illusory line-motion being in the direction away from the fixation point. Indeed, the fact that the line-motion does shift in direction with time after moving the cue argues that at least the centroid of attention must move from one spot to another, an interpretation that borders on saying the locus of attention itself moves.

4.5. *Comparison of the magnitude of attentional adaptation with that of saccadic adaptation*

The adaptation we measure in the magnitude of shifts of attention is similar to saccadic adaptation in three respects: It is gradual, it is specific to the direction of target step (right vs. left), and it is specific to the sign of the subsequent target shift (backwards vs. forwards). However, the adaptation seems to differ from saccadic adaptation in being slower or smaller in magnitude. During saccadic adaptation in humans, the system adapts from 20% to 25% (Straube & Deubel, 1995) up to 90% (McLaughlin, 1967). In our attentional adaptation experiments, we found that on average, the amount of adaptation was about 20%, although individual subjects adapted up to 35%.

There are several possible explanations for why our attention adaptation values are towards the lower range found in saccadic adaptation experiments. First, our method of assessing the location of attention itself interferes with the degree of attentional adaptation. That is, we found that the mean amount of adaptation increased as the proportion of line-motion trials decreased. If we extrapolate this function to 0% line-motion trials then the amount of attentional adaptation would be on average approximately 30% of the back-step size. The reason for this interference may be that during the line-motion trials, the visual stimuli are on the screen for longer than the attention shift-time and attention is free to move about, so that these shifts are not adapted. Furthermore, if the subjects had a tendency to persist in responding to the key representing the cue-location, this might bias their responses in the direction opposite to adaptation. However, we did not find any difference in degree of adaptation between subjects who had catch trials and those who did not. More generally, unlike saccade adaptation experiments, in which one can instruct the subjects not to make extraneous eye movements and one can monitor their compliance, in attention adaptation experiments this is, of course, not possible. Second, if one views the attention adaptation procedure like that of a saccade adaptation experiment, the deficiency in the shift-of-attention adaptation procedure is that we cannot tell when the attention shifts during a given trial and then step the target forward or back at that time. Instead, we must step the target at the average attention-shift-latency, meaning that in most cases we shift the target either

before or after the attention shifts. Presumably this causes a smaller adaptational change than would have been the case if we shifted the target at just the right moment, as can be easily done with saccades by monitoring the eye movements continuously. Third, in saccade experiments one typically measures the eye position at the moment when it comes to rest at the end of the saccade. In the case of our attention experiments we measure the location of attention (on our line-motion trials) at a fixed time after the target step, the same time we use to step back the target during the adaptation phase. If attention moves continuously across the visual field (Shulman et al., 1979) at a finite velocity (e.g., 125 deg/s; Tsai, 1983), as proposed by some authors, we may have assessed the location of attention while it was still moving, at least in some proportion of trials. Whether attention moves at a finite velocity is, however, a matter of some debate (Yantis, 1988). The magnitude of this underestimation would depend on unknown aspects of the dynamics of the line-motion illusion.

Whether the degree of attentional adaptation is small for fundamental or methodological reasons, it should be noted that the degree of saccadic adaptation in humans, even after many trials, also is typically considerably less than that which would bring the eye directly onto the displaced target. Miller et al. (1981) have suggested that there are fast and slow adaptive processes, of which only the fast process is adapted during these experiments.

4.6. *Implications for saccade targeting and adaptation*

Our finding that adaptation of shifts of attention transfers to saccades implies that saccades are directed specifically to the locus of attention, rather than to stimuli identified by attention but targeted by independent means. This in turn implies that saccadic adaptation, as it is usually defined, could result from either adaptation of attentional shifts or from saccadic adaptation at the motoric level, or both. We conjecture that these two levels of adaptation are independent, because the brain would need a way to compensate for specific changes in the strength of the eye muscles without affecting covert shifts of attention.

Does this mean that saccade adaptation experiments might actually be adapting the shifts of attention that precede saccades? We think not. Our experiment was unusual in that the cue remained in its initial location only long enough for attention to move there, whereupon the back-step occurred. In normal saccade adaptation experiments the target spot is on for approximately twice as long, allowing time for an attentional shift to the target and a corrective step before the saccade occurs. Therefore the fact that the target subsequently steps back during the saccade should not stimulate adaptation of attentional shifts. Recently, an explicit study of the locus of attention before saccades

showed that it was not shifted by saccadic adaptation (Ditterich, Eggert, & Straube, 2000). Indeed, the step-back during the saccade may well be registered by the attentional system as simply another target step, not signalling an error in attentional localization. In other situations, however, either attentional or saccadic adaptation might take place. For example, in memory guided saccades to briefly presented targets, adaptation might be either at the attentional or motoric level. This possibility extends the view that saccadic adaptation can take place at several different levels of the visual and oculomotor systems (Deubel, 1999).

4.7. *At what level might adaptation of exogenous shifts of attention occur?*

As mentioned in the Introduction, exogenous spatial attention has been characterized in several ways, including being the peak on a map of perceptual saliency and being an intrinsic component of saccadic eye movements (although the eye movement itself may be cancelled after the shift of attention). At first glance, it might appear that the finding that the magnitude of shifts of attention can be adapted argues that attention lies clearly on the motoric side of the continuum, because it is easy to see the adaptation in terms of changing a motoric gain term, as in saccadic adaptation. However, in both the cases of saccades and attention, there are at least four levels at which adaptation might occur. We will consider the possibilities for saccadic adaptation and then consider which might apply to adaptation of attention.

First, the adaptation could involve a warping of the visual map, so that stimuli at 10 deg right are mapped at 8 deg right. Presumably such a remapping would not affect all visual maps. If it did, the perceived geometry of the visual world would be influenced by saccadic gain adaptation provoked by such things as weakness of an eye muscle. There is evidence against visual remapping being the basis of saccadic adaptation (Wallman & Fuchs, 1998). Second, the transformation between the visual map and the premotor spatial map used in selection of the saccadic target might be altered. In the case of neurons with large motoric fields, such as those in the superior colliculus, a simple spatial gradient of modulatory input across the map could cause a consistent shift in the location of the peaks of activity. Such gain modulation effects (gain fields) have been proposed to account for the effect of attention on cortical areas (Connor, Preddie, Gallant, & Van Essen, 1997; Salinas & Abbott, 1997). Third, saccadic eye movements involve a transformation from a spatial coordinate scheme, in which the saccade is planned, to a temporal coordinate scheme, in which the amplitude of the saccade is coded in the duration of the burst of firing of the ocular motor neurons that will get the eye to the desired target. Saccadic adaptation might be manifested by a change in

the duration of this burst. There is evidence of changes in the dynamics of saccades as a result of adaptation (Abrams, Dobkin, & Helfrich, 1992; Straube & Deubel, 1995) as well as evidence that the fastigial nucleus might produce saccadic adaptation by changing the duration of saccades (Scudder, 1998). Fourth, although in one sense saccades are entirely pre-programmed in that the saccadic endpoint cannot be influenced by visual signals acquired en route, in another sense the eyes' path can be considered to be guided by internal feedback in that the oculomotor system is thought to keep track of where it calculates the eye is during the saccade and to terminate the saccade when it estimates that the target has been reached (Van Gisbergen, Robinson, & Gielen, 1981). Saccadic adaptation might act at the level of this efference feedback calculation.

By similar reasoning we can consider the possibility that adaptation of shifts of attention might occur at the same four steps. First, if saccadic alternations can be remappings at the level of visual maps, surely this would affect shifts of attention as well. Second, if one views spatial attention as peaks on a saliency map achieved by a winner-take-all process, one would have to accept that there is some process that transforms the raw visual map into this saliency map. Alterations of this transformation could constitute adaptation. The third possibility of temporal changes in the motoric signal is least likely to apply to attention, in that we have no evidence for such a spatial-to-temporal transformation in the case of shifts of attention. In the case of the fourth possibility, there is evidence of something like an efference feedback pathway for attention (Cavanagh, 1992); this might be involved in adaptation both of saccades and of shifts of attention.

5. Conclusions

We have shown that shifts of attention, like saccades, can be adapted if the target is spatially displaced during the time of the initial attentional shift. This finding can be added to the list of similarities between attention and saccades presented in the Introduction. The fact that the targeting of attention is plastic suggests that it represents the output of on-going spatial computations, rather than being an inherent attribute of the visual image in the brain. The fact that this targeting appears to be linked to saccadic targeting suggests that saccades may be directed to the locus of attention, rather than to targets identified by attention. In some situations adaptation might be effected by changes at the level of either attention or saccades or both.

Acknowledgements

This research was supported by PSC-CUNY grants, DIST Bilateral Sci and Tech 96/7597 and by NIH

RR03060. We are grateful to Frederick A. Miles and Albert F. Fuchs for careful critiques of an earlier draft.

Appendix A

We trained subjects on the grating identification task and the line-motion task in separate sessions 1–3 days before the experiment. Subjects required approximately 550 line-motion training trials and 150 grating training trials.

A.1. Training for line-motion trials

In order to effectively discriminate the location of the origin of the shooting line, subjects required three types of training. First, they were trained to type a key corresponding to particular circles on the line. For this phase, the cue appeared at a random position between 2 and 5 deg right or left of the fixation point, and stayed on for 320 ms, after which it was replaced (for 600 ms) by the row of circles, spanning the distance from 2 to 5 deg from the fixation point. At first the subject was told in advance which circle would be turned on until 10 consecutive correct responses had been made. Thereafter, correct responses were signalled by a beep, and errors caused the subsequent trials to have the cue appear in the same location until the correct response was made (correction trials).

In the second training phase, this task was made more difficult by first moving the range of cue-locations to span 4–7 deg from the fixation point and then 6–9 deg. Finally, in the third training stage, the duration of the cue (the SOA) was reduced from 320 to 100 ms in 2 steps. Each change in eccentricity and reduction in duration occurred once the 10-point running average of the difference in the number of circles between the reported origin and the actual cued location fell below 0.7 circles (0.57 deg), including the correction trials. The line training was concluded when the subject maintained this criterion for approximately 40 trials, with the final stimulus location (spanning 6–9 deg) and final SOA (100 ms; Fig. 3, frame 3a). In practice, most subjects achieved an accuracy less than 0.57 deg. On the day of the experiment, immediately before the experiment began, the subject was given brief refresher training on the line-motion illusion. This training began with the 6–9 deg line span with a 320 ms cue duration which, once criterion was passed, was decreased to 100 ms.

At the end of the training on the line-motion illusion, subjects were able to accurately locate the origin of line-motion, the locus of which could not be predicted since each cued position appeared randomly and with equal probability. During the actual experiments, the same line-motion task was used to assess the perceived origin of line-motion, except that the line-motion trials oc-

curred only occasionally rather than on each successive trial as in training. When a line-motion trial did occur during the experiment, subjects were unable to predict the cue location as it occurred at a random position on the catch trials, and the catch trials were themselves randomly interspersed with the normal line-motion trials.

A.2. Training for grating trials

The grating trials were introduced so that focal attention was required at the cue location. These trials required the subject to identify the orientation of a small briefly presented grating. To perform this task required some training and required setting the grating parameters for a criterion level of performance for each subject.

Training trials presented stimuli like those in the grating trials described in Section 2.6.1, except that the difficulty of the task was increased in several steps. At the beginning of the training, the grating stimulus was 1.0 deg in diameter (9.0 mm), with a contrast of 1.0, a duration of 250 ms and a spatial frequency of 6.0 cpd. These stimulus parameters were used until the subject made 20 consecutive correct responses. During successive steps in the training the duration was decreased to 100 ms, the diameter was decreased to 0.33 deg (the same size as the cue), and the contrast was reduced to 0.3–0.4 for the oblique orientations and 0.2–0.3 for the vertical and horizontal orientations until performance was stable at approximately 75% (over 20 trials for an individual subject). The grating properties at this performance level were used at the start of the experiment for that subject.

References

- Abrams, R. A., Dobkin, R. S. & Helfrich, M. K. (1992). Adaptive modification of saccadic eye movements. *Journal of Experimental Psychology: Human Perception and Performance*, 18, 922–933.
- Albano, J. E. (1996). Adaptive changes in saccade amplitude: oculocentric or orbitocentric mapping? *Vision Research*, 36, 2087–2098.
- Cavanagh, P. (1992). Attention-based motion perception. *Science*, 257, 1563–1565.
- Chelazzi, L., Biscaldi, M., Corbetta, M., Peru, A., Tassinari, G. & Berlucchi, G. (1995). Oculomotor activity and visual spatial attention. *Behavioural Brain Research*, 71, 81–88.
- Clark, J. J. (1999). Spatial attention and latencies of saccadic eye movements. *Vision Research*, 39, 585–602.
- Connor, C. E., Preddie, D. C., Gallant, J. L. & Van Essen, D. C. (1997). Spatial attention effects in macaque area V4. *Journal of Neuroscience*, 17, 3201–3214.
- Crovitz, H. F. & Daves, W. (1962). Tendencies to eye movement and perceptual accuracy. *Journal of Experimental Psychology*, 63, 495–498.
- Desimone, R. & Duncan, J. (1995). Neural mechanisms of selective visual-attention. *Annual Review of Neuroscience*, 18, 193–222.
- Deubel, H. (1987). Adaptivity of gain and direction in oblique saccades. In J. K. O'Regan & A. Levy-Schoen (Eds.), *Eye movements: from physiology to cognition* (pp. 181–190). Elsevier.
- Deubel, H. (1991). Plasticity of metrical and dynamic aspects of saccadic eye movements. In J. Requin & G. E. Stelmach (Eds.), *Tutorials in motor neuroscience* (pp. 563–579). Kluwer.
- Deubel, H. (1999). Separate mechanisms for the adaptive control of reactive, volitional, and memory-guided saccadic eye movements. In D. Gopher & A. Koriat (Eds.), *Attention and performance XVII* (pp. 697–721). Cambridge: MIT Press.
- Deubel, H. & Schneider, W. X. (1996). Saccade target selection and object recognition: evidence for a common attentional mechanism. *Vision Research*, 36, 1827–1837.
- Ditterich, J., Eggert, T. & Straube, A. (2000). Relation between the metrics of the presaccadic attention shift and of the saccade before and after saccadic adaptation. *Journal of Neurophysiology*, 84, 1809–1813.
- Downing, P. E. & Treisman, A. M. (1997). The line-motion illusion: attention or completion? *Journal of Experimental Psychology: Human Perception and Performance*, 23, 768–779.
- Eriksen, C. W. & St. James, J. D. (1986). Visual attention within and around the field of focal attention: a zoom lens model. *Perception and Psychophysics*, 40, 225–240.
- Eriksen, C. W., Webb, J. M. & Fournier, L. R. (1990). How much processing do nonattended stimuli receive? Apparently very little, but. *Perception and Psychophysics*, 47, 477–488.
- Erkelens, C. J. & Hulleman, J. (1993). Selective adaptation of internally triggered saccades made to visual targets. *Experimental Brain Research*, 93, 157–164.
- Fischer, B. & Weber, H. (1993). Express saccades and visual attention. *Behavioral and Brain Sciences*, 16, 553–567.
- Fuchs, A. F., Reiner, D. & Pong, M. (1996). Transfer of gain changes from targeting to other types of saccade in the monkey: constraints on possible sites of saccadic gain adaptation. *Journal of Neurophysiology*, 76, 2522–2535.
- Fujita, M., Amagai, A., Minakawa, F. & Aoki, M. (2002). Selective and delay adaptation of human saccades. *Cognitive Brain Research*, 13, 41–52.
- Ganvarz, G. & Grossberg, S. (1999). A neural model of saccadic eye movement control explains task-specific adaptation. *Vision Research*, 39, 3123–3143.
- Henderson, J. M. & Macquistan, A. D. (1993). The spatial distribution of attention following an endogenous cue. *Perception and Psychophysics*, 53, 221–230.
- Hikosaka, O., Miyauchi, S. & Shimojo, S. (1993). Focal visual attention produces illusory temporal order and motion sensation. *Vision Research*, 33, 1219–1240.
- Hikosaka, O., Miyauchi, S. & Shimojo, S. (1996). Orienting a spatial attention—its reflexive, compensatory, and voluntary mechanisms. *Brain Research Cognitive Brain Research*, 5, 1–9.
- Itti, L. & Koch, C. (2000). A saliency-based search mechanism for overt and covert shifts of visual attention. *Vision Research*, 40, 1489–1506.
- Kirschfeld, K. & Kammer, T. (1999). The Frohlich effect: a consequence of the interaction of visual focal attention and metacontrast. *Vision Research*, 39, 3702–3709.
- Koch, C. & Ullman, S. (1985). Shifts in selective visual attention: towards the underlying neural circuitry. *Human Neurobiology*, 4, 219–227.
- Kowler, E., Anderson, E., Doshier, B. & Blaser, E. (1995). The role of attention in the programming of saccades. *Vision Research*, 35, 1897–1916.
- Kwak, H. W., Dagenbach, D. & Egeth, H. (1991). Further evidence for a time-independent shift of the focus of attention. *Perception and Psychophysics*, 49, 473–480.
- Mackeben, M. & Nakayama, K. (1993). Express attentional shifts. *Vision Research*, 33, 85–90.
- McLaughlin, S. (1967). Parametric adjustment in saccadic eye movements. *Perception and Psychophysics*, 2, 359–362.

- McPeck, R. M., Maljkovic, V. & Nakayama, K. (1999). Saccades require focal attention and are facilitated by a short-term memory system. *Vision Research*, 39, 1555–1566.
- Miller, J. M., Anstis, T. & Templeton, W. B. (1981). Saccadic plasticity: parametric adaptive control by retinal feedback. *Journal of Experimental Psychology: Human Perception and Performance*, 7, 356–366.
- Mondor, T. A. & Zatorre, R. J. (1995). Shifting and focusing auditory spatial attention. *Journal of Experimental Psychology: Human Perception and Performance*, 21, 387–409.
- Motter, B. C. & Belky, E. J. (1998). The zone of focal attention during active visual search. *Vision Research*, 38, 1007–1022.
- Muller, H. J. & Rabbitt, P. M. (1989). Reflexive and voluntary orienting of visual attention: time course of activation and resistance to interruption. *Journal of Experimental Psychology: Human Perception and Performance*, 15, 315–330.
- Nakayama, K. & Mackeben, M. (1989). Sustained and transient components of focal visual attention. *Vision Research*, 29, 1631–1647.
- Noto, C. T., Watanabe, S. & Fuchs, A. F. (1999). Characteristics of simian adaptation fields produced by behavioral changes in saccade size and direction. *Journal of Neurophysiology*, 81, 2798–2813.
- Posner, M. I. (1980). Orienting of attention. *Quarterly Journal of Experimental Psychology*, 32, 3–25.
- Posner, M. I., Snyder, C. R. & Davidson, B. J. (1980). Attention and the detection of signals. *Journal of Experimental Psychology*, 109, 160–174.
- Remington, R. W. (1980). Attention and saccadic eye movements. *Journal of Experimental Psychology: Human Perception and Performance*, 6, 726–744.
- Remington, R. & Pierce, L. (1984). Moving attention: evidence for time-invariant shifts of visual selective attention. *Perception and Psychophysics*, 35, 393–399.
- Remington, R. W., Johnston, J. C. & Yantis, S. (1992). Involuntary attentional capture by abrupt onsets. *Perception and Psychophysics*, 51, 279–290.
- Rizzolatti, G., Riggio, L., Dascola, I. & Umiltà, C. (1987). Reorienting attention across the horizontal and vertical meridians: evidence in favor of a premotor theory of attention. *Neuropsychologia*, 25, 31–40.
- Sagi, D. & Julesz, B. (1985). Fast noninertial shifts of attention. *Spatial Vision*, 1, 141–149.
- Salinas, E. & Abbott, L. F. (1997). Invariant visual responses from attentional gain fields. *Journal of Neurophysiology*, 77, 3267–3272.
- Schmidt, W. C. (2000). Endogenous attention and illusory line motion reexamined. *Journal of Experimental Psychology: Human Perception and Performance*, 26, 980–996.
- Scudder, C. A. (1998). Discharge of fastigial nucleus neurons is altered during adaptive modification of saccade size. *Society for Neuroscience Abstracts*, 24, 60.15, 147.
- Semmlow, J. L., Gauthier, G. M. & Vercher, J. L. (1989). Mechanisms of short-term saccadic adaptation. *Journal of Experimental Psychology: Human Perception and Performance*, 15, 249–258.
- Shepherd, M., Findlay, J. M. & Hockey, R. J. (1986). The relationship between eye movements and spatial attention. *Quarterly Journal of Experimental Psychology A*, 38, 475–491.
- Shepherd, M. & Muller, H. J. (1989). Movement versus focusing of visual attention. *Perception and Psychophysics*, 46, 146–154.
- Shimojo, S., Miyauchi, S. & Hikosaka, O. (1997). Visual motion sensation yielded by non-visually driven attention. *Vision Research*, 37, 1575–1580.
- Shulman, G. L., Remington, R. W. & McLean, J. P. (1979). Moving attention through visual space. *Journal of Experimental Psychology: Human Perception and Performance*, 5, 522–526.
- Straube, A. & Deubel, H. (1995). Rapid gain adaptation affects the dynamics of saccadic eye movements in humans. *Vision Research*, 35, 3451–3458.
- Straube, A., Fuchs, A. F., Usher, S. & Robinson, F. R. (1997). Characteristics of saccadic gain adaptation in rhesus macaques. *Journal of Neurophysiology*, 77, 874–895.
- Tsal, Y. (1983). Movements of attention across the visual field. *Journal of Experimental Psychology: Human Perception and Performance*, 9, 523–530.
- Van Gisbergen, J. A., Robinson, D. A. & Gielen, S. (1981). A quantitative analysis of generation of saccadic eye movements by burst neurons. *Journal of Neurophysiology*, 45, 417–442.
- Wallman, J. & Fuchs, A. F. (1998). Saccadic gain modification: visual error drives motor adaptation. *Journal of Neurophysiology*, 80, 2405–2416.
- Wallman, J., Khan, A., Yun, R. & McFadden, S. (2001). The spatial scale of attention affects adaptation of saccadic gain. *Journal of Vision (Vision Sciences Society Meeting)*, B258 (Abstract).
- Yantis, S. (1988). On analog movements of visual attention. *Perception and Psychophysics*, 43, 203–206.
- Yantis, S. & Jonides, J. (1990). Abrupt visual onsets and selective attention: voluntary versus automatic allocation. *Journal of Experimental Psychology: Human Perception and Performance*, 16, 121–134.