Visual Attention Mechanisms Show a Center–Surround Organization

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The sudden onset of a cue triggers visual attention, which then enhances visual processing in the zone near the cue. This enhancement causes a motion illusion in subsequent stimuli presented near the cue. At greater separations from the cue, the illusory motion reverses direction, indicating prolonged processing speed. Measurements of the strength and direction of illusory motion at increasing separations from the cue reveal an attentional 'perceptive field' with an excitatory center at the focus cued and an inhibitory surround subtending the remaining visual field. These findings help explain the traditional attentional 'benefits' and 'costs' of attention.

Visual attention    Apparent motion    Motion induction    Focal attention    Psychophysics    Line motion
Spotlight

INTRODUCTION

For a brief period of time following the sudden onset of a visual cue, attention is focused on that region of the visual field immediately surrounding the cue. Within this attentional focus, two beneficial effects occur. First, reaction times for detection of visual targets presented subsequent to the cue are decreased. Second, the ability to correctly discriminate these targets is improved. These benefits allow quick detection and response to sudden changes in the visual field. This type of reflexive bottom-up attention response generated by a visual cue is the same as 'transient focal attention' reported by Nakayama and Mackeben (1989).

Attentional responses can be produced by a wide variety of cues, such as: the brightening of a box around the area where the target is to appear (Posner & Cohen, 1984), a frame that flashes (Nakayama & Mackeben, 1989), or the onset of a dot (Nakayama & Mackeben, 1989; von Grünau & Faubert, 1992), square (von Grünau & Faubert, 1995) or horizontal line beneath the position where target is to appear (Kröse & Julesz, 1989; Eriksen & James, 1986). Improved performance and reaction times in response to attentional cues have been measured for a wide range of visual targets, including: luminance detection (Posner, Cohen & Rafał, 1982; Eriksen & Collins, 1969; Downing & Pinker, 1985; Sagi & Julesz, 1986), letter recognition (Tsai, 1983; Eriksen & James, 1986; Kröse & Julesz, 1989), target orientation discrimination (Downing, 1988; Nakayama & Mackeben, 1989), vernier targets (Mackeben & Nakayama, 1993), and combinations of target orientation and color (Nakayama & Mackeben, 1989).

The benefits of focal attention do not come without costs. The first of these costs is noted immediately following the onset of a cue. Whereas reaction times within the attentional focus are decreased, reaction times for targets outside of the attentional focus are prolonged (Posner & Boies, 1971; Posner, 1975; Posner & Snyder, 1976; Posner et al., 1982; Downing & Pinker, 1985; Kröse & Julesz, 1989). The second cost of focal attention occurs much later. The time period over which visual processing is enhanced by focused attention is brief, lasting only about 200 msec. Following this period until about 1000 msec after the initial cue, the reaction times for subsequent targets will be longer (Hikosaka, Miyachi & Shimojo, 1993a; Posner & Snyder, 1976; Posner & Cohen, 1984).

The nature of the attentional focus is not yet fully understood. It has been compared to a beam of light which is switched on in response to a cue and illuminates the region containing and adjacent to the cue (Posner, Snyder & Davidson, 1980). When this beam is activated, beneficial effects of attention are experienced within the area of the beam. The shape of the attentional beam has been described as round (Eriksen & James, 1986) or elongated (Sagi & Julesz, 1986). Attention is best 'captured' by the sudden onset of a visual cue (Jonides & Yantis, 1988), and the greatest enhancements of visual processing occur closest to the cue (Hikosaka et al., 1993a), then taper off gradually. The size of the attentional focus increases as a function of cue eccentricity, so that the beam produced in response to a
cue at 4 deg from a target is twice as large as that elicited by the same cue presented at a separation of 2 deg (Sagi & Julesz, 1986).

While the area and strength of the attentional focus may be manipulated, the temporal properties of visual attention remain constant. Following the cue onset, attention is recruited rapidly. By as short as 50 msec following the cue (cue lead time) optimal reaction times and discrimination performance have already been achieved. This is true regardless of the cue type or the retinal location cued (Nakayama & Mackeben, 1989). The strength of the beam of attention then slowly 'fades', and performance drops off with longer temporal delays between the cue and the target.

The onset of the attentional focus can be observed directly as an illusory motion within a line. The illusion is as follows: immediately following the onset of a visual cue (such as a small dot), a line is displayed (see Fig. 1). Even though the line is physically displayed all at once, it does not appear to have been presented instantaneously. The portion of the line closest to the dot appears first; then, each successively more distant portion of the line comes into view slightly later than the its neighbor. In other words, the line seems to ‘grow’ with its leading edge moving away from the cue. This illusion was originally observed by Kanizsa (1951) who dubbed it ‘polarized gamma motion’. Recently Hikosaka, Miyachi and Shimojo (1991, 1993b) suggested that the induced motion in the line occurs because the cue serves to prime attention, which in turn accelerates visual processing speed in the zone surrounding the cue. The differential processing speed, faster for portions of the line close to the cue relative to portions more distant, induces the illusion of motion. Recent studies have referred to this illusion as either the ‘line-motion illusion’ (Hikosaka et al., 1991; Miyachi, Hikosaka & Shimojo, 1992; Hikosaka et al., 1993b) or ‘motion induction’ (Faubert, 1992; von Grünau & Faubert, 1992, 1995). The term ‘line-motion’ is somewhat of a misnomer, since the same illusion can also be observed moving along other shapes, such as curves, or circles (Faubert, 1992). We will use both terms interchangeably to preserve consistent terminology with existing papers.

Studies which have measured visual attention using the line-motion illusion have confirmed many properties of visual attention previously reported using reaction time or percent correct measurements. The line motion illusion is best elicited by the sudden onset of a visual cue. Induced motion, like decreased reaction times, can be produced in response to many types of cues, including cues defined by luminance, color, motion and stereopsis (von Grünau & Faubert, 1992, 1995). The strongest percept of line motion occurs at the same cue lead time at which the strongest facilitation of reaction times is observed (50 msec) (Hikosaka et al., 1993b). In addition, both discrimination performance (Nakayama & Mackeben, 1989) and induced motion illusions (Hikosaka et al., 1993b) have also been produced consciously by directing attention to a particular stimulus.

The advantage of being able to directly observe attentionally produced changes in visual processing speed makes the line-motion illusion a promising new tool to learn more about the nature of visual attention. However, to fully utilize the line-motion illusion as a research tool, a precise method to measure and quantify the percept of illusory motion must be developed.

To date, only one laboratory has directly measured induced motion. Miyachi et al. (1992) broke the line down into a series of small segments. Following presentation of the cue, the line segments were displayed in order successively closer to the cue, producing phi motion towards the cue, and thus against the attention-based motion induction. Phi motion velocities were varied until the oppositely-directed line-motion produced by the cue was nulled. Using this method, they mapped out the extent of the attentional visual field to about 3.5 deg from the cue. Beyond this cue-line separation, no further illusory line-motion away from the cue occurred.

The nulling technique of Miyachi et al., although promising, is limited in its usefulness as a tool for measuring the full scope of visual attention. Their measurement technique makes the assumption that the direction of the line motion illusion will always be away from the cue. However, this may not be the case. Line motion away from the cue occurs only when visual processing speed is accelerated. In other words, this method is only useful for measuring processing speed under conditions where attentional benefits occur. It is not capable of determining changes in visual processing speed linked to attentional costs. A better measurement technique would be capable of nulling line motion in either direction. In this study we have revised Miyachi et al. (1992)’s technique to do this. Perception of line phi motion both with and without a preceding attentional cue.
were compared. An attention index which reflected the change in perception produced by the attentional cue was calculated. The attention index has the advantages of being able to measure both: (1) the direction of the induced motion; and (2) the strength of the percept of line motion. Attention index scores were used to investigate the effect of a cue at increasing spatial and temporal separations from a line. A large range of cue-line separations were included.

METHODS

Subjects

Five subjects participated in this study. Their ages ranged between 22 and 42. One author (BS) served as a subject (in spite of having the same initials, subject SS was not one of the authors). The remaining volunteer subjects, who were naïve as to the purpose of the experiments, were students at the University of Missouri School of Optometry. These observers were paid for their participation. All five subjects had no ocular diseases, normal binocular vision, and best-corrected visual acuity of 20/20 or better in both eyes.

Apparatus and stimuli

A Macintosh computer with an AppleColor high resolution monitor was used to present stimuli and record subjects’ responses. A 57 cm long viewing tunnel was used to shield the monitor from glare, and provide a constant viewing distance.

Figure 2 depicts a typical stimulus presented in this study. A small cross served as a fixation point and remained constantly on in the center of the screen throughout all trials. Two main stimulus conditions were employed: (1) in the Cued condition a small dot appeared followed after a variable delay by the appearance of a target line; and (2) in the No Cue condition the target line appeared without the cue. The target line was broken down into segments which were presented sequentially, generating phi motion with velocities of 5, 10, 15, 44, 89 and \( \infty \) (one segment presented at one time) deg/sec.

The fixation cross, cue, and line were all black (0.87 cd/m²) with a Michelson contrast of 97.7% relative to a white background (70.6 cd/m²). The fixation cross subtended a visual angle of 0.5 deg \( \times \) 0.5 deg at a 57 cm viewing distance. The target line was a rectangle whose overall dimensions were always 1.5 deg horizontally by 0.4 deg vertically. The line segments were generated by breaking the line down into 2, 3, 6, 12 or 20 equal sections. For example, in a line with 20 segments, the horizontal dimension of each segment would be 1/20 the horizontal dimension of the entire line (4.5 min arc).

The target line was always displayed centered 0.6 deg below the fixation cross. We used a line target at a constant location and a peripheral cue with varying position because: (1) It is easier to interpret data from a cue scaled in size with eccentricity than for a line with inherent and perceived motion that would need to be scaled in both size and velocity with eccentricity; and (2) there may be peripheral motion directional biases that are less evident centrally (Ball & Sekuler, 1981) which would influence our data to different degrees with a peripheral line target at various eccentricities.

The cue was a solid circle presented directly to the left or the right of the line. The distance between the cue and the center of the target line (cue-line separation) was varied by presenting the cue more peripherally on the screen in 1.5 deg increments up to 9 deg (unless otherwise specified). As the cue-line distance increased, the cue size was increased to be equally visible to the subject. The scaling of the cue was 15 times the Snellen acuity for the retinal eccentricity stimulated (Westheimer, 1979).

Procedure

(a) Cued condition. Subjects fixated a central cross and initiated each trial by pressing a key. At least 1000 msec later, the cue was presented. To prevent the subject from anticipating the exact onset time of the cue, the cue onset time was incremented by random values between 0 and 167 msec. After a fixed cue lead time, the line was presented. Phi motion in the line was generated towards the cue by drawing segments of the line progressively closer to the cue. The subject’s task was a two-alternative forced choice paradigm, in which the direction of the line

![Figure 2](image-url)
motion was indicated by pressing either the left (←) or right (→) arrow key on the keyboard. If no line motion was detected, subjects were instructed to guess.

Within each block of trials the cue-line distance remained constant. Presentation of the cue to the right or left of the target line, as well as the velocity of the phi motion generated in the line, were randomly varied from trial to trial. Each block consisted of 360 trials (2 cue positions × 6 phi motion velocities × 30 measurements).

(b) No cue condition. To establish a baseline for the subjects' sensitivity to leftwards vs rightwards phi motion, one block of trials was presented without a preceding cue. In these 'no cue' trials, phi motion of different velocities was generated in the target line randomly in a rightward or leftward direction.

Attention index calculation

An example of the calculation of an attention index score (using hypothetical data) is presented in Fig. 3. The target line was designed to induce a percept of phi motion in a constant direction (towards the cue), but the subjects' percept could be of motion in either the same or the opposite direction. The percentage of presentations in which motion is perceived in a direction opposite to that of the stimulus phi motion is plotted as a function of the velocity of that phi motion. Percentages below 50% represent a percept of line motion in the same direction as the stimulus line's phi motion, while percentages above 50% represent a percept of motion in the opposite direction.

In the No Cue condition, the strength of the subjects' percept of motion would diminish with increasing phi motion velocity, until subjects reached an asymptotic performance of approx. 50% motion reported in either direction. The lowest velocity yielding a 50% directional response was determined to be the cut-off velocity.

Plots for the Cued condition reflect the additional effect of an attentional cue on the percept of line motion. In the absence of the attentional cue, velocities faster than the phi motion threshold would yield no consistently-directed motion percept. However, if a cue is presented prior to the target line, line motion would still be seen even at these high velocities. A percept of directed motion at these velocities (or when the line is instantaneously presented) must be caused by the attentional effect of the cue. If the line motion is seen as going away from the cue, asymptotic levels would be much greater than for the No Cue condition.

To calculate the attention index score, the cut-off velocity for apparent motion is first determined. For all velocities faster than this threshold, the mean No Cue condition scores ($X_{NCUE}$) are subtracted from the mean Cued condition scores ($X_{CUE}$). The calculation for Fig. 3 is:

\[
\text{Attention Index} = \left( \frac{85 + 90 + 87}{3} \right) - \left( \frac{50 + 48 + 49}{3} \right) = +38.
\]

Assuming that there is no subject bias for responding that motion was in any particular direction (i.e. 50% in the no-cued condition), the maximum possible attention index is +50 and the minimum possible attention index is −50. An attention index score with a magnitude of +40 to +50 would indicate a strong line-motion percept; a magnitude of +10 to +20 would indicate a weak percept; and a score of 0 would indicate that the cue has no effect on the line. If the attentional cue produced a line-motion illusion which moved towards the cue, i.e. in the same direction as the phi motion, the result would be a negative attention index score.

If subjects had any small biases for tending to report motion in one direction over another, they were removed by attention index calculation. For example, if at velocities above the cut-off velocity a subject responded that 53% of the time the line motion went 'left' in the No Cue condition and that 70% of the time the line motion went 'left' in the Cued condition, the attention index score would be +17. By subtracting the No Cue response in calculating the changes, we remove the influence of motion direction perceptual biases.

This approach for removing small subject biases created the potential problem of ceiling and floor effects. For example, if the above subject reported 100% line motion in one direction, the maximum score possible would be +47 and the minimum possible score would be −53, rather than the range from +50 to −50 for subjects with no bias. This could create a potential problem for subjects with large biases for reporting motion in one direction. For example, a subject who responded in the No Cue condition 80% of the time that motion was perceived in one direction could never demonstrate a large

![Figure 3](https://example.com/fig3.png)

FIGURE 3. Calculation of the attention index. The direction of the line phi motion becomes more difficult to discriminate as velocity increases. In the No-Cue condition when phi motion velocities in the line are too fast to be seen (velocities higher than the cut-off velocity), subjects guess the line motion direction, resulting in asymptotic performance of 50%. In the Cue condition, attentionally induced changes in processing speed produce an illusory line motion which persists regardless of the velocity of the line phi motion, so that at velocities above the cut-off velocity only the illusory motion is seen. The strength of the illusory motion percept is proportional to the difference between the Cue and No Cue scores at velocities above the cut-off velocity. If the illusory line motion moves away from the cue a positive score results (positive attention). Alternatively, illusory line motion towards the cue would generate a negative score (negative attention).
attention index. To prevent this possibility, subjects with biases > 55% or <45% were excluded from participating in the study.

In addition to potential response biases in the No Cue condition, it is also possible that some subjects might have had a response bias in the Cue condition such that they would tend to respond that the motion was either mostly towards or mostly away from the cue. The use of naive subjects prevented preconceived notions as to which direction the motion should be relative to the cue. Additionally, we added in another control. In some trials the velocity of the phi motion inherent within the line was slow (5–10 deg/sec) and distinguishable in both the Cue and the No Cue conditions. In these trials subjects would be expected to report motion towards the cue. These slower velocities were used to generate a psychometric response curve for each block of trials as shown in Fig. 3. If, during a block of trials, a subject responded that motion was ‘away from the cue’ on every individual trial, the responses would no longer vary with line phi motion velocity, but would show a constant 100% ‘motion away from the cue’ response at all velocities; the opposite response would produce a similar response at 0%; and, random guessing would produce such a response at 50%. Blocks of trials which demonstrated straight line response curves rather than psychometric response curves were excluded.

Separate calculations were made for trials with rightward and leftward cues. Within each block of Cue trials, those trials with rightward cues (in which the inherent phi motion in the line is rightward) were compared to No Cue trials with rightward phi motion; a similar comparison was made for leftward cues.

RESULTS

No Cue condition

The mean velocity cutoff threshold for line phi motion in the absence of a cue was 18.7 ± 2.8 deg/sec. Subjects responses for reporting motion in one direction for trials above their motion cutoff velocities ranged from 45–53%, indicating only mild response biases favoring line motion in one direction over another. When these responses were pooled, motion was reported in the opposite direction from the phi motion on 47.6% ± 1.45% of the trials, a performance level not significantly different from the predicted chance level of 50% (*t* = −1.651, *P* = 0.1076). For all greater velocities, performance remained near the chance level. Rightward vs leftward phi motion yielded similar response curves (*F* = 0.5671, *P* = 0.4532); i.e. subjects did not exhibit a directional response bias.

Cue condition

Subjects did not show a bias for making choices based on the presence or absence of the cue, as indicated by sigmoid psychometric functions being generated on 100% of the Cue Trials. The presence of the cue did, however, tend to change the percentage of directional responses relative to the cue at all velocities, except for the 5 deg/sec velocity where nearly 100% of the responses were always directed towards the cue. The influence of the cue on the responses changed depending on its temporal and spatial relationship to the line, as reported below.

Attention index scores

Attention index scores for cues presented at separations of 1.5–9.0 deg from the target line, and for cue lead times of 17–200 msec are plotted as a series of three-dimensional graphs in Fig. 4. The attention index scores changed significantly over both the cue lead time (*F* = 17.7, *P* < 0.0001) and cue position (*F* = 6.04, *P* < 0.0001). At each cue lead time, independent regions in which both positive and negative attention index scores occurred were found, whose locations were dependent upon the cue position. Results for these positive and negative regions are discussed separately below.

The attentional focus

Positive attention index scores (motion perceived as going away from the cue) are depicted as values above the baseline of Fig. 4. We will refer to the production of line motion away from the cue as the positive attention effect or positive attention. Positive attention indices were found consistently in a region surrounding the locus where the cue was presented. This zone can be thought of as the area of the visual field in which attentional cueing produced accelerated visual processing speed; i.e. this zone corresponds to the classical attentional focus. The magnitude of the attention indices decreased with greater cue–target separations until positive attention index scores were no longer produced.

Within the central positive attentional focus, there was
a strong tendency for attention index scores to be highest at both close spatial and temporal separations from the cue. The strength of the attentional effect diminished with increasing cue lead times or cue-line separations. Maximal attention index scores (+41) were produced at a 17 msec cue lead time by cues 1.5 deg from the target line. Under these conditions time, cues to the right and to the left of the target line produced similar scores. However, all cue-line separations > 1.5 deg produced different responses to leftward vs rightward cues. This resulted in the shape of the function being skewed to the left; i.e. cues presented to the right of the target did not elicit as strong a response as cues presented to the left.

When the cue lead time was increased beyond 50 msec, the amplitude of the peak of the positive attention response declined. The decline was much greater for rightwards cues than for leftwards cues. For 1.5 deg leftwards cues, the peak response declined to a minimal attention index score of +29 at 200 msec, while the response to cues in the 1.5 deg rightwards position declined to a minimal score of +12. This asymmetric difference in the rate of decline was a result of a narrowing of the diameter of the positive attentional focus, as illustrated in Fig. 5. The spatial extent of the attentional focus was maximal at the 17 and 50 msec cue lead times. At 17 msec, the total diameter of the positive attentional zone subtended 10.1 ± 1.3 deg. By a 50 msec cue lead time, the zone increased in size to 12.8 ± 1.6 deg by 50 msec, but this diameter was not significantly larger than that found at 17 msec (P > 0.05, Student–Newman–Keuls). At longer temporal separations the size of the attentional focus narrowed dramatically, reaching only 5.3 ± 0.45 deg by 200 msec.

**Attentional costs—**negative** attention

Cues presented beyond the greatest eccentricity that yielded positive attention effects did not simply fail to elicit an attentional response. Rather, the attention index scores for cues in these locations fell below zero. In other words, the perceived direction of illusory motion reversed—subjects now saw the line moving towards the cue. The production of line motion towards the cue will be referred to as the **negative attention effect or negative attention**. Contour plots comparing the magnitude and spatial extent of positive and negative attention are shown in Fig. 6(A) and 6(B). Attention indices fell significantly below zero (t = −0.4595, P = 0.0001) for all cues presented to the right of the line beyond the zone of positive attention. There was no corresponding negative attention zone for cues presented within 9 deg to the left. The attention index scores just dropped below zero for cues presented at 9 deg left, but this reduction was not statistically different from zero (t = −0.306, P = 0.7624).

The properties of the negative attentional effect differed radically from those of positive attention. While positive attention effects were maximal close to the cue, negative attention exerted increasing influence with **greater separations from the cue**. However, the amplitude of the negative attention effect was much smaller than that of the positive attention effect. Figure 7 shows the attention index scores as a function of cue lead time for cues presented at separations of ±1.5 deg and 9 deg to the right of the target line. These two separations represent loci at which positive attention and negative attention each exerted large effects on processing speed. The mean negative attention index score in response to the 9 deg rightward cue was −12.4, almost a third of the positive index produced by cues at a 1.5 deg separation (attention index = +35.9). While positive attentional effects are maximal by a 17 msec cue lead time and decline steadily afterward, negative attentional effects remain constant for all delays following cue presentation until the longest measured cue lead time (200 msec).

**Visual attention outside of the focus**

The absence of negative attention index scores elicited by cues presented to the left of the target line did not preclude the possibility that a zone of negative attention might be noted for leftward cues at greater eccentricities. Although the average scores pooled across all subjects were positive, negative scores in response to leftward cues were observed for some subjects. Figure 8 shows the individual spatial characteristics of visual attention for all five subjects at the 50 msec cue lead time. A focused zone of positive attention surrounding the cue with symmetrical flanking areas of negative attention in response to cues on both sides of the line was observed for subject LF. Subjects BB and DC also demonstrated negative scores for leftward cues at eccentricities to the left of the focus.

Two questions were raised by the shape of the response curves within the limits of ±9.0 deg cue line separations: (1) Do zones of negative attention exist for all subjects if greater separations are used for cues presented on both sides of the target line? and (2) What is the full extent of

![Figure 5](image-url) **FIGURE 5.** The diameter the zone of positive attention. The diameter of the zone over which positive scores are elicited (that is, line motion is perceived away from the cue) is greatest immediately after cue presentation, and then declines with greater cue lead times. Data for subjects BC, BB, DC and LF are included. Data for subject SS were excluded, due to a positive zone which was too wide to accurately determine boundaries.
FIGURE 6. Contour plots of the zones of positive and negative attention. (A) The zone of positive attention index scores ($\geq 0$) is plotted, indicating spatial and temporal separations between the cue and target line where processing speed is accelerated, producing a percept of line motion growing away from the cue. The perceived line motion is strongest at spatial locations nearest to the cue. For the initial 50 msec following the cue the attentional focus is wide, then over time it narrows. (B) The zone of negative scores ($\leq 0$) is plotted, indicating perceived motion towards the cue. The zone of negative attention flanks the zone of positive attention, becoming wider as the positive zone narrows. Negative attention scores become greater with increasing distance from the cue.
the zone of negative attention—in other words, how far does the cue have to be separated from the line before no further negative attention is produced? In order to answer these questions, additional data were gathered for three observers (BS, DC and SS) at extended cue-line separations up to 90 deg. Greater cue eccentricity was achieved by moving subjects closer to monitor and scaling the stimulus dimensions for acuity (Westheimer, 1979). Data were collected for the cue lead time which had the maximum attentional response (50 msec). The resulting attention index scores are plotted as a function of cue line separations in Fig. 9. The general shape of the spatial visual attention functions for all three subjects was that of a sharp, central positive attentional focus in the zone immediately surrounding the cue, encircled by extended flanking zones of negative attention. The most robust negative attention responses occurred for cues presented at a distance of 10–30 deg from the line. At greater eccentricities, weaker line motion was reported. The response function climbed back up to nearly zero in the far periphery, producing an attentional response curve similar in shape to that of an antagonistic center-surround receptive field.

To better characterize the mean attentional function, it was fitted to a difference-of-gaussian (DOG) function using the formula described by Enroth-Cugell and Robson (1966):

\[ y = K_c \cdot \exp\left(-\frac{r}{r_c}\right)^2 - K_s \cdot \exp\left(-\frac{r}{r_s}\right)^2. \]

In the DOG equation, \( K_c \) and \( K_s \) represent the amplitudes of the center and surround regions, respectively. Likewise, \( r_c \) and \( r_s \) represent the radii of the center and surround. The responses at any given spatial position are given by \( r \).

DOG functions have been used successfully to model the spatial properties of receptive fields of visual neurons in which a center response is flanked by an antagonistic surround response (Enroth-Cugell & Robson, 1966). In the case of visual attention, the positive effects at the attentional focus may be likened to the center response, while the negative attentional effects correspond to its surround response.

DOG functions were used to provide estimates of the width and amplitude of the positive and negative effects of attention. In Fig. 9 the mean attention index scores are signified by open circles, and the line indicates the best-fitting DOG curve. The attentional function was well fitted by a DOG curve (\( r = 0.83 \)). The values obtained for the positive center portion of the function were an amplitude (\( K_c \)) of 57, and a radius (\( R_s \)) of 4.2 deg. For the negative surround function the amplitude was 15 (\( K_s \)) and the radius (\( R_c \)) was 172 deg.

**DISCUSSION**

The spatiotemporal characteristics of the line motion illusion are comparable to those of previous measures of attention. Our data show a rapid activation of attention, as evidenced by the fast initial rise of positive attention to a maximum, followed by a slow decline in strength. A similar pattern of activation of visual attention has been found in previous studies of the temporal nature of attention using other stimulus configurations and measurement techniques. Previous studies have noted the presence of a maximal attentional effect by 50 msec following cue presentation (Tsai, 1983), followed by a slow decline (Nakayama & Mackeben, 1989). The temporal course of the positive peak noted in the current study indicates that attention is fully active by as short as 17 msec. While this time precedes the peak found in many
studies, Mackeben and Nakayama (1993) and Shimojo and Tanaka (1994) have reported similar results.

The strength of the positive attentional response is greatest when the target line is close to the cue and falls off with increasing cue-line separations. The maximum diameter for the positive attentional focus was $12.8 \pm 1.6$ deg (50 msec cue lead time). This does not necessarily imply that the diameter of the focus will always be this size, as the focus can vary depending on the type of attentional stimulus used (Hughes & Zimba, 1987). For example, Miyauchi et al. (1992) reported a maximum diameter of 7.2 deg. We have experimented with other types of cues and found that the diameter of the focus tended to decrease as the luminance contrast between the cue and the background decreases (Steinman, Steinman & Lehmkuhle, 1994). We also noted that the general pattern of maximal positive attentional responses temporally and spatially close to the cue held true for many types of cues.

We are unaware of any studies of attention which have probed attentional effects at large spatial separations between cue and target. It was these more peripheral spatial probes of attention that produced the most intriguing data. As the spatial separation between cue and target increased beyond the limits of the central attentional focus, the line-motion illusion reversed direction. That is, the percept of the illusory motion was now directed towards the cue (negative attention).

The best explanation for this change in the direction of the illusory motion is that beyond the distance between cue and target where attention has an excitatory effect on processing speed, is a zone where attention exerts an inhibitory influence. A slowing down of visual processing speed in this zone would result in an oppositely-directed motion percept in the line. This explanation would account for previous reports of the faster reaction times for stimuli in the zone immediately surrounding a preceding attentional cue (the beneficial effect of attention) and slower reaction times for stimuli in the remaining visual field (the cost of attention) (Downing & Pinker, 1985). To our knowledge this is the first report of attentionally induced line motion being used to observe the inhibitory effects of attention on loci distant from a cue.

Another possible argument is that the onset of the probe line itself could serve as an attentional cue, setting up a second spotlight of attention which would generate an additional line motion illusion away from itself. Since it is unlikely that inhibitory effects from the previously-exposed first cue would completely prevent the line from itself triggering attention again, it is possible that the line could induce a second illusory motion away from itself. However, this could not account for the subjects' reports of illusory line motion within the line towards the original cue, for the following reason: Attentional line motion is not seen within the cue (Hikosaka et al., 1993a), nor does it occur when the cue and probe line are displayed simultaneously (Hikosaka et al., 1993b). If the line served as a second cue to activate attention, any motion illusion produced would only be observed if another probe line were presented, after a sufficient delay.

Due to the pervasiveness of opponent receptive fields in the visual system, including higher visual cortical areas such as MT (Allman, Miezin & McGuinness, 1985) and IT (Gross, Rocha-Miranda & Bender, 1972), one might...
expect that such an organization would exist in the pathways responsible for visual attention as well. Our data support this notion. When the magnitude of evoked attention is plotted as a function of cue-line separation, the positive effects are centered in a small zone around the point in which the cue was presented. A region in which negative attentional effects occur surrounds the zone of positive attentional effects and persists throughout the entire remaining visual field. The resulting function is a bimodal curve with a shape very similar to an on-center/off-surround physiological receptive field, which can be fitted with a DOG curve. Curve fitting with DOG functions provided several important pieces of information about the visual attention function:

(1) The positive portion of the function extends for a radius of 4.2 deg surrounding the cue.

(2) The peak magnitude of the positive response is three to four times greater than that of the negative response.

(3) The radius of the negative response is larger than the maximum extent of the visual field, indicating that when the central positive response to an attentional cue occurs, the entire remaining visual field is suppressed by the negative attentional surround.

In other words, presenting a cue at one location results in accelerated processing of visual information in the zone surrounding the cue and decelerated processing of all visual information throughout the remaining visual field.

The finding that the negative effects of attention continue to inhibit visual processing even when positive attention has nearly totally dissipated supports the notion that positive and negative attention are mediated by separate mechanisms. We postulate that the sudden onset of a visual cue triggers both mechanisms. An excitatory positive attention mechanism accelerates visual processing speed in a small zone surrounding the cue (attentional focus). At the same time, an inhibitory negative attention mechanism slows visual processing speed across the entire visual field. Initially, for the first 50 msec the positive attention has a much greater magnitude than negative attention, so its effects are dominant near the cue, producing an attentional focus of accelerated processing speed that corresponds to the center of the ‘perceptive field’. The entire remaining visual field corresponds to the inhibitory surround and had decelerated processing speed. This configuration would ensure that targets at the cued location are preferentially processed initially. After 50 msec, the transient, excitatory mechanism would begin to decline, but the inhibitory effects would linger, allowing negative attention to exert a stronger influence. Eventually at cue lead times beyond 200 msec the positive effect would dissipate to the point where the negative effect would predominate. The resulting inhibition would reduce the ability of subsequent cues at the same location from continuing to summon visual attention, freeing attention to move to new locations.

Our model is supported by Posner and Cohen’s (1984) finding that after cueing a location, the initial decrease in reaction times (for cue lead times under 200 msec) is followed by a subsequent increase in reaction times (for cue lead times from 200 to at least 1500 msec). Nakayama and Mackeben’s (1989) report that a cue flickering at 7.5 Hz does not produce a prolonged attentional response may be interpreted as further evidence for the negative effects of the attentional response over time. The flicker rate they used corresponds to the presentation of a cue at the same locus every 133 msec. Our data demonstrate that negative attention remains at the same value for at least 200 msec. If a second cue were presented during this refractory period, any positive attentional effects produced by the second cue presentation would be (at least partially) suppressed. In other words, negative attentional effects produced by a preceding cue could inhibit a second cue from exerting as strong a positive attentional response as it would have if the preceding cue had not been presented. The full positive attentional response could not occur again until after the negative attentional effect had run its course and returned to its baseline level at some cue lead time longer than the 200 msec period we measured. The finding of a prior cue inhibiting the response to a subsequent cue is reminiscent of neuronal responses measured during refractory periods reported by Ikeda (1965). When two consecutive subthreshold flashes were presented within an interval from 0–40 msec their inputs were summated, however, if the delay between them was longer (40–80 msec) the second stimulus was inhibited.

We are unable to explain the asymmetry between responses for cues displayed to the left vs those displayed to the right. This effect is not the result of the computer’s method of drawing lines; i.e. it is not due to the lines being drawn in a leftward-to-rightward fashion. First, there was no significant difference between subject’s detection thresholds for rightward vs leftward line phi motion. Second, even if there were such a difference it would have been eliminated when the difference between the Cue and No Cue condition were calculated. More importantly, the perceived direction of motion of the line changes direction when the cue is presented on the opposing side of the line. This would not happen if the response were a subject bias for motion in only one direction. Therefore, the left–right asymmetry for cue effectiveness is not the result of subject bias for selecting rightward line motion. Furthermore, a similar left–right asymmetry was found at another lab using the same paradigm (Shimojo, 1994).

In summary, the traditional ‘benefits’ and ‘costs’ of visual attention, as measured by reaction times, can be explained by differences in visual processing speed which occur at various separations from the cue. These differences can be measured directly via the strength and direction of perceived motion in the line motion illusion. Within a restrictive region surrounding an attentional cue (the so-called attentional focus) processing is accelerated, producing line motion away from the cue. Outside of this region, the line motion illusion reverses in direction, indicating decelerated processing. Our data suggest two distinct regions of attentional activation with opposing effects. Within a small region centered around the cue, the processing speed of a novel stimulus is enhanced; in the surrounding visual field, processing is inhibited reducing
the effectiveness of existing stimuli. Such organization suggests that visual attention does not merely direct our processing faculties towards a target of interest, but also actively directs it away from other stimuli.

We propose that visual attention mechanisms exhibit an opponent center–surround receptive field-like organization similar to that found elsewhere in the visual system. The large size of the attentional 'perceptive field' is consistent with extrastriate visual cortical areas such as MT playing a role in visual attention and orientation as postulated by Hikosaka et al. (1993a).

REFERENCES


