
Distinguishing Subcortical and Cortical Influences in Visual Attention

Subcortical Attentional Processing

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Purpose. The purpose of the study was to investigate the role of subcortical processing in human visual attention. The midbrain contribution to visual attention is unclear. Although evidence exists for a subcortical attentional advantage in ocular motor tasks, such an advantage has not been shown in perceptual tasks. Because retinotectal projections arise predominantly from nasal retina (i.e., temporal hemifield), subcortical attention should be distributed asymmetrically for monocular viewing conditions with an advantage to the temporal hemifield.

Methods. To test for a subcortical attentional effect, the authors compared the results of binocular and monocular viewing conditions using the split priming motion induction paradigm. In this perceptual attention paradigm, priming cues are presented to the left and right of fixation followed by an instantaneously presented horizontal bar. As a result of attention to the priming cues, motion is perceived within the bar as it appears to draw in from the two lateral cues toward a central collision point. Asymmetrically distributed attention results in an asymmetry in the perception of motion within the bar, and thus the perceived collision point will be shifted away from the center.

Results. In two separate studies, one with and one without control of eye movements, the authors found significant differences between the results for monocular and binocular presentation. When the stimulus configuration is presented to the left eye, the perceived collision point is shifted toward the center consistent with a subcortical attentional effect. However, presentation of the stimulus configuration to the right eye yields the same results as those of binocular presentation.

Conclusions. This pattern of results can be explained by a separate and additive interaction between cortical and subcortical attentional effects in the visual field. Dominance of the left visual field for cortical attention and dominance of the temporal visual field for subcortical attention act together when the initial priming cue occurs in the temporal (left) visual field of the left eye. However, these influences compete when the same stimulus configuration is presented to the right eye, where cortical attention predominates in the left visual field and subcortical attention predominates in the temporal (right) visual field. *Invest Ophthalmol Vis Sci.* 1997;38:364–371.

The visual system is a limited capacity processor that must, of necessity, be selective in the allocation of resources. A visual scene presents the observer with innumerable potential objects of regard, all of which

are subject to some limited degree of processing with more detailed processing confined to targets at specific locations within the visual field. It is the attentional system that is responsible for selecting targets and locations that will receive more detailed processing while, at the same time, deemphasizing targets in other locations.^{1,2} Attention may be thought of as focusing a beam or spotlight of attention within the visual field with detailed processing within the center of the beam and a tapering of attention the further one moves from the center of the beam.^{3,4} Treisman^{5,6}

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Submitted for publication March 28, 1996; revised October 7, 1996; accepted October 8, 1996.

Proprietary interest category: N.

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has proposed that when an object differs from its neighbors by a single feature (e.g., color or orientation), that object will pop out independent of the number of distractors. This processing is said to occur automatically or preattentively. However, when an object differs from its neighbors by a conjunction of two or more features, processing is slower and dependent on a serial search of all distractor elements. Looking at attention somewhat differently, Posner et al⁷ have proposed a three-stage process in which the attentional system must be capable of engaging a target, disengaging from that target, and shifting onto a new target. Generally, saccadic eye movements accompany shifts in attention so that foveated targets receive maximal processing. However, covert shifts of attention without foveation are possible.

There is evidence for both cortical and subcortical influence on attention. Colby⁸ comments that "there is hardly any region of cerebral cortex beyond the primary sensory and motor regions that can't be shown to participate in some kind of attentional process." All cortical sites with visual field representation seem to play a role in visual attention. Clinically, deficits in visual attention result most commonly from lesions of the parietal lobe.⁹ Neglect and extinction of contralateral hemispace arise commonly from right-sided parietal lesions but only rarely from left-sided lesions.¹⁰ Thus, the right parietal lobe appears to be dominant for attention.¹¹ In the model by Posner et al,⁷ parietal lesions affect the disengage function. In the Treisman paradigm, parietal lesions impair the serial processing required for conjunction tasks while sparing the parallel processing required for feature detection.¹²

In addition to cortical structures, there is mounting experimental and clinical evidence for a midbrain influence on visual attention. Neurons in the superior colliculus show an enhanced response to the presence of a stimulus when that stimulus is to serve as the target of a saccadic eye movement¹³⁻¹⁵ and may provide the visual signal for exogenous shifts of attention even in the absence of a saccadic eye movement.¹⁶ These results suggest that a subcortical attentional effect can be dissociated from ocular motor function in the midbrain. In addition to these findings, Posner et al¹⁷ have found a deficit in shifting attention to cued targets in patients with progressive supranuclear palsy, a degenerative disease affecting midbrain structures including the superior colliculus. Furthermore, Rafal et al¹⁸ have suggested that inhibition of return (i.e., the bias against returning attention to a location that has been attended recently) is mediated by midbrain pathways.

Although the striate cortex receives input from both nasal and temporal retinas, the midbrain receives predominant input from the nasal retinas.¹⁹ This

means that the two visual hemifields are represented equally in the cortex but that the temporal hemifield is over-represented in the midbrain. This neuroanatomic arrangement can be exploited to separate out the cortical and subcortical contributions to visual attention. The subcortical attentional effect only will be apparent under monocular testing conditions, because the binocular visual field will be symmetric with respect to both cortical and subcortical representations (Fig. 1). Therefore, demonstration of a temporal hemifield advantage in attention tasks using monocular stimulus presentations is indicative of midbrain processing. Rafal et al²⁰ have shown a monocular temporal hemifield advantage in a reaction time task to the onset of a peripheral target by either a manual button press or a saccadic eye movement to the target. Although these results show that subcortical attention can influence a motor response, this effect has not yet been shown to influence the perceptual component of attention.

Hikosaka et al²¹ showed illusory motion within a bar instantaneously drawn at brief intervals after presentation of a lateralized cue. The basic paradigm is to present a cue followed after a short time delay by the presentation of a horizontal bar. Despite the instantaneous presentation of the bar, the perception is that of motion within the bar such that the bar appears to *draw* away from the cue down the attentional gradient created by the cue. The cue is considered to prime the end of the bar that appears closest to it. When two cues are presented simultaneously on each side of fixation (Fig. 2), the bar appears to draw in from both sides toward the center with a perceived central collision point (split priming effect).²² When the cues are presented asynchronously, the two bars appear to draw in from the cues with a collision point that varies with intercue asynchrony. With long intercue asynchronies, the collision point is closer to the initial cue because the final cue has the greatest attentional gradient. With short intercue asynchronies, the collision point is closer to fixation. von Grunau and Faubert²³ have concluded that this motion induction (MI) effect results from attentional priming to the cues.

Under monocular conditions, the subcortical attentional effect will be greatest in the temporal hemifield. If this effect is evident in the MI paradigm, we predict that under monocular conditions, cues presented in the temporal hemifield will result in a greater attentional gradient than cues presented in the nasal hemifield. Thus, when the initial cue is presented in the monocular temporal hemifield, the result will be a closer temporal integration between the cue and the subsequent bar, effectively decreasing the intercue asynchrony. As a result, the apparent colli-

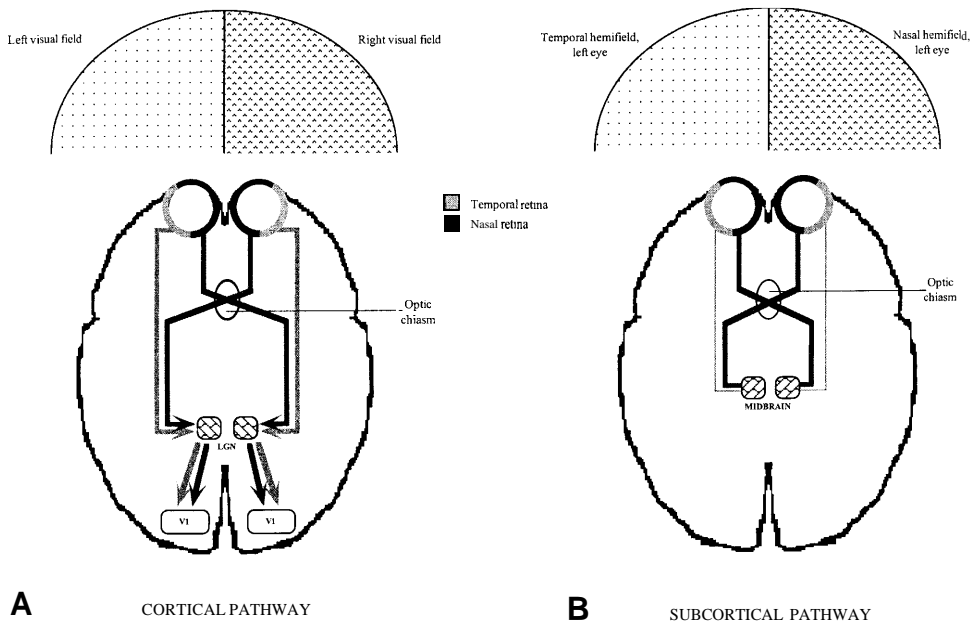


FIGURE 1. Schematic representation of projections from retina to cortex and midbrain. Retinal projections undergo an approximately 50:50 hemidecussation in the optic chiasm. The geniculostriate pathway, therefore, contains relatively equal projections from the corresponding points in the nasal and temporal retinas of the two eyes (A). The midbrain predominantly receives a crossed input (*thick line*) from the nasal retina of the opposite eye and a lesser input (*thin line*) from the temporal retina of the ipsilateral eye (B).

sion point will be closer to central fixation than when the same stimulus presentation is viewed binocularly.

MATERIALS AND METHODS

Materials

Two studies were performed using the MI paradigm. Study A used monocular stimulus presentations on an RGB monitor controlled by a Macintosh Quadra 950 computer and did not control for eye movements. Study B, presented on a TTX SVGA monitor controlled by a 486 PC, compared monocular and binocular viewing conditions. Eye position was monitored with the ISCAN RK-416 pupil-tracking system (ISCAN, Cambridge, MA) with noise-reduction software and eye magnification optics. The occurrence on any given trial of an eye movement greater than 0.25° , either vertically or horizontally, led to the rejection of that specific trial. The horizontal resolution of the pupil-tracking system, corresponding to a 1-unit change in its response, was 0.065° , or approximately 4 minutes of arc. A 0.25° eye movement generated a 3.9-unit response, easily detectable by the system. By eliminating trials in which fixation was unstable, we were able to ensure that hemifield presentation was accurate and that the effects observed did not involve an ocular motor response.

Subjects

Ten subjects participated in study A and eight subjects participated in study B. All subjects were between 20 and 45 years of age and had normal or corrected-to-normal vision, with no evidence of amblyopia or

strabismus. The research followed the tenets of the Declaration of Helsinki and was approved by the Ottawa General Hospital Research Ethics Committee. Subjects were compensated minimally and were required to provide informed consent before their participation in the study.

Stimuli and Procedure

Figure 2 illustrates the basic stimulus presentation used in both studies. Table 1 lists the stimulus parameters for the two studies. In brief, the first cue was presented on the left side of the bar on half the trials and on the right side on the other half (random order). The second cue was presented on the opposite side at varying intercue asynchronies while the first cue remained on the screen. After a brief delay after the second cue, the horizontal bar instantaneously appeared on the screen. The cue-bar interval was selected on the basis of a preliminary study that showed that it produced the strongest MI effect for the particular stimulus configuration used in each study. The cues remained on the screen during the presentation of the bar. The perceptual effect is that of inward motion from both cues toward the center. At the end of each trial, the whole display remained on the screen while a cursor appeared under the bar. Subjects moved the cursor to the perceived collision point and pressed a button to record that position ($-e1.00$ to $+1.00$). In study A, conducted monocularly, 30 trials were run for each asynchrony (15 right cue first and 15 left cue first) for a total of 240 trials. In study B, conducted both monocularly and binocularly, 10 trials per asynchrony were run (5 for each first cue location), for a total of 50 trials per viewing condition.

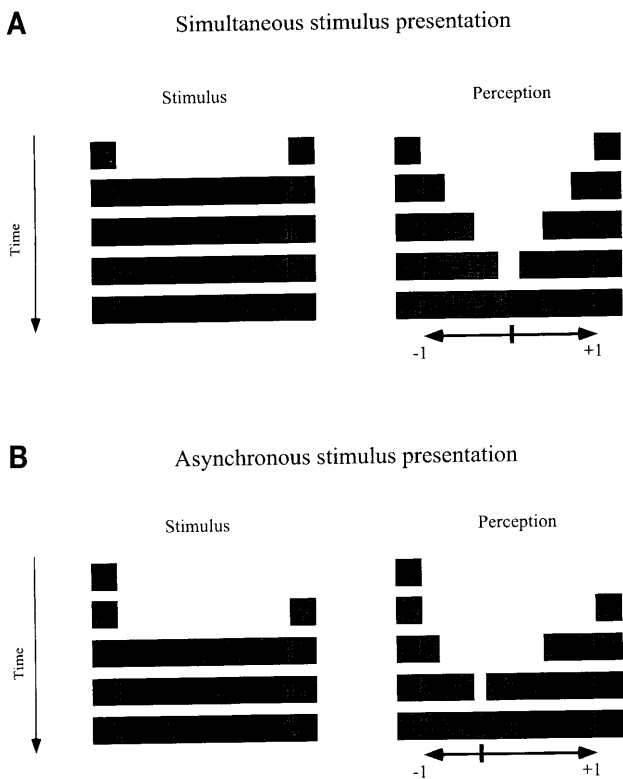


FIGURE 2. Schematic representation of the stimulus configuration and perceptual results. Time is represented along the vertical axis. The horizontal axis represents the horizontal extent of the stimuli. When two spots of light are presented simultaneously followed by an instantaneously presented horizontal bar, the perception is that of two bars growing in from both cues toward the center with a collision point in the center (A). When the two cues are presented asynchronously, the collision point is closer to the initial cue with the location dependent on the intercue asymmetry (B).

RESULTS

The results for studies A and B are shown in Figure 3. Panels A and B show the results for monocular stimulus presentations in study A. Panel C shows the results for both monocular and binocular stimulus presentations in study B. In study A, 6 of 10 subjects showed MI (Fig. 3, panel A). The results for the four subjects who did not show evidence of MI are pre-

sented in Figure 3, panel B. In study B, seven of eight subjects showed evidence of MI. In both studies, the subjects who experienced the MI effect are considered as *responders*, whereas those who did not experience the effect are considered as *nonresponders*. Other investigators (S. Shimojo and J. Faubert, personal communication, 1995) similarly have found that not all subjects are capable of discerning the MI effect.

Analysis of variance (ANOVA) was performed on the results shown in Figure 3. For both studies, the data were divided into two groups: left cue presented first and right cue presented first. In study A, the ANOVA was performed on two levels of viewing condition (right eye and left eye) and on eight levels of cue asynchrony. In study B, three levels of viewing condition (right eye, left eye, and binocular) and five levels of cue asynchrony were analyzed. In both studies, when the left cue was presented first, a significant main effect was found for viewing condition ($P \leq 0.01$) and for cue asynchrony ($P \leq 0.01$), whereas no significant interaction between the two variables was found. When the right cue was presented first, no main effect of viewing condition was found. Cue asynchrony produced a significant main effect ($P \leq 0.01$), but no interaction between viewing condition and cue asynchrony was found (Table 2). In both studies, the perception of the location of the collision point was shifted increasingly toward the initial cue as the intercue asynchrony increased. Viewing condition, however, had a significant effect under both monocular and binocular conditions only when the initial cue appeared on the left. Based solely on the ANOVA, we cannot conclude whether the MI effect was decreased in the left eye or whether it was increased in the right eye.

A multiple comparison test (Tukey) was therefore performed in study B to determine whether the left cue first presentation decreased the MI effect in the left eye or whether it increased the effect in the right eye. The binocular condition was used as a baseline measure. The Tukey test showed a significant difference between left eye and binocular presentations ($P \leq 0.05$) and no such difference between right eye and binocular presentations. The Tukey test indicates that

TABLE 1. Summary of Stimulus Configuration for Studies A and B

| Study | Size Cue/Bar (Degree of variance) | Color Stim/Back | Background Luminance (cd/m^2) | Cue-Bar Luminance (cd/m^2) | Cue-Bar Interval (msec) | Intercue Asynchrony (msec) |
|-------|--------------------------------------|--------------------|---|--|----------------------------|----------------------------------|
| A | 0.95/22.04 | Red/green | 30 | 4.8 | 75 | 0 to 210 (30 msec increments) |
| B | 0.95/16.80 | Blue/black | 0.26 | 19.13 | 100–150 | 0 to 200 (50 msec increments) |

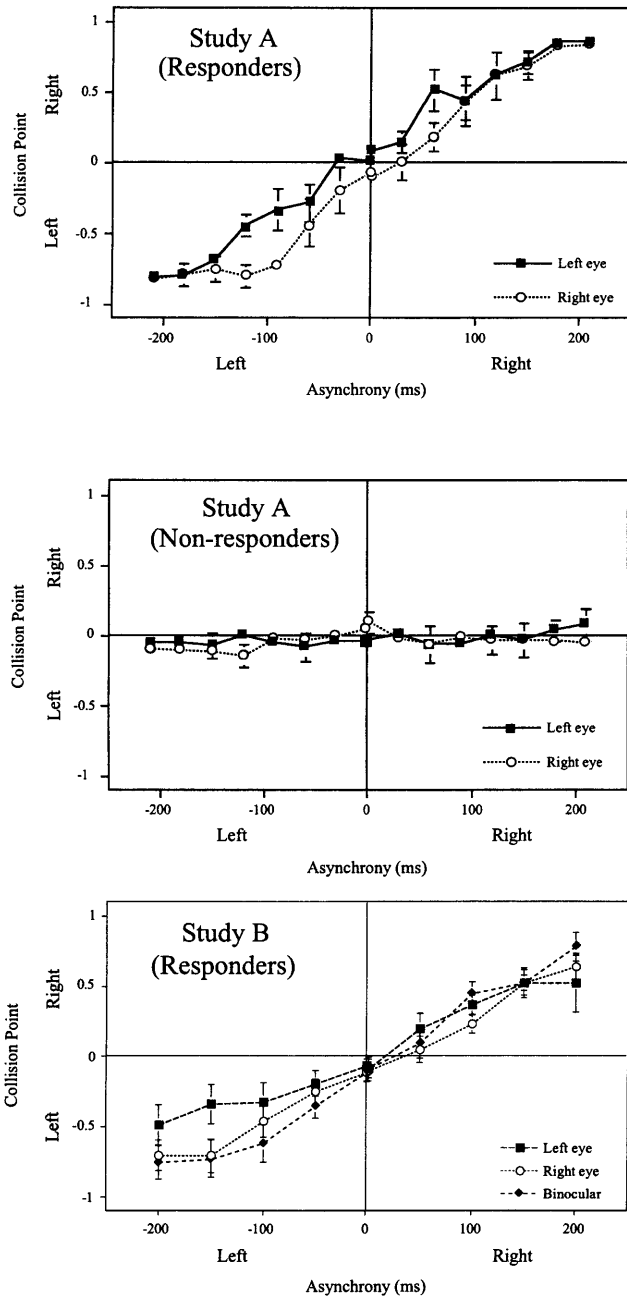


FIGURE 3. Perceived collision point versus intercue asynchronies for *responders* and *nonresponders* in studies A and B. Intercue asynchrony is represented along the x-axis (negative and positive values indicate initial cue presentation on the left or right, respectively). Perceived collision point is represented along the y-axis (negative and positive values indicate perceived collision point to the left or right of center, respectively).

the MI effect was decreased in the left eye when the left cue was presented first.

Figure 4 shows the difference between the collision point for left eye and right eye presentation for individual subjects at intercue asynchronies of ± 120

msec (study A) and ± 150 msec (study B). These asynchronies were selected because they produced the largest differences between viewing conditions. The results for all subjects are shown regardless of the strength of the MI effect they showed. All subjects in study A, and all but one subject in study B, showed a consistent shift in collision point for left eye stimulation when the initial cue was in the temporal hemifield. The difference in collision point for left eye minus right eye stimulation was not consistent when the initial cue presentation was in the right temporal hemifield. These results are independent of whether the subjects experienced the MI effect.

In summary, the MI effect is decreased for the left eye when the initial cue is presented to the left of fixation, that is, the perceived collision point is closer to fixation when the initial cue is presented in the temporal hemifield of the left eye than when it is presented in the left visual field for binocular presentations or in the nasal field for right eye presentations. No equivalent decrease of the MI effect was found in the right eye when the right cue was presented first. In this case, the location of the collision point coincides with the collision point of binocular stimulus presentations.

The results from the two studies are similar, indicating that the effects we observed are not specific to a particular stimulus configuration. Furthermore, because we monitored fixation in study B and obtained the same results as in study A, it is clear that eye movements did not play a role in this effect.

DISCUSSION

In this study, we have shown a shift in the MI effect consistent with activation of midbrain attentional mechanisms. This generally is similar to what one would expect based on the conclusions of Rafal et al.²⁰ However, our results are different in two respects:

1. Our task emphasized the perceptual component of attention rather than a motor response to an attentional cue.
2. The effect we observed was limited to stimulus presentations to the left eye.

There is an asymmetric projection to the midbrain from nasal and temporal hemiretinas with a preponderance of midbrain input from the nasal hemiretina. Thus, stimuli presented to the temporal hemifield will have greater representation in the midbrain than stimuli presented to the nasal hemifield. The impact of this asymmetric midbrain representation on visual attention can be observed only under monocular testing conditions. Our objective in this study was to find evidence for a midbrain role in attentional processing

TABLE 2. Statistical Analyses for Studies A and B

| <i>Source</i> | <i>SS</i> | <i>df</i> | <i>MS</i> | <i>F Value</i> | <i>P Value</i> | <i>F Critical</i> |
|----------------------------|----------------------------|-----------|-----------|----------------|--------------------|-------------------|
| Study A | | | | | | |
| ANOVA: left cue first | | | | | | |
| Viewing condition | 0.60 | 1 | 0.60 | 11.10 | 0.001 | 6.96* |
| Asynchrony | 8.07 | 7 | 1.15 | 21.43 | <0.001 | 2.87* |
| Interaction | 0.49 | 7 | 0.07 | 1.31 | 0.258 | 2.87 |
| Within | 4.30 | 80 | 0.05 | | | |
| ANOVA: right cue first | | | | | | |
| Viewing condition | 0.19 | 1 | 0.19 | 3.07 | 0.084 | 3.96 |
| Asynchrony | 9.03 | 7 | 1.29 | 20.62 | <0.001 | 2.13* |
| Interaction | 0.31 | 7 | 0.04 | 0.70 | 0.669 | 2.13 |
| Within | 5.00 | 80 | 0.06 | | | |
| Study B | | | | | | |
| ANOVA: left cue first | | | | | | |
| Viewing | 399.84 | 2 | 199.92 | 5.92 | 0.004 | 4.85* |
| Asynchrony | 1773.57 | 4 | 443.39 | 13.14 | <0.001 | 3.53* |
| Interaction | 148.99 | 8 | 18.62 | 0.55 | 0.814 | 2.72 |
| Within | 3037.78 | 90 | 33.75 | | | |
| ANOVA: right cue first | | | | | | |
| Eye | 52.72 | 2 | 26.36 | 0.97 | 0.384 | 3.10 |
| Asynchrony | 3030.19 | 4 | 757.55 | 27.78 | <0.001 | 2.47* |
| Interaction | 144.42 | 8 | 18.05 | 0.66 | 0.724 | 2.04 |
| Within | 2454.70 | 90 | 27.27 | | | |
| <hr/> | | | | | | |
| <i>Comparison</i> | <i>Difference of Means</i> | | <i>p</i> | <i>q</i> | <i>P < 0.05</i> | |
| <hr/> | | | | | | |
| Tukey test: left cue first | | | | | | |
| Left eye vs. binocular | 4.22 | | 3 | 4.58 | Yes* | |
| Left eye vs right eye | 3.01 | | 3 | 3.27 | No | |
| Right eye vs binocular | 1.21 | | 3 | 1.32 | No | |

*Statistically significant difference.

using a perceptual judgment task, the MI paradigm. A previous study²⁰ showed a similar effect; however, the dependent variable was a motor response. In our studies, subjects judged the perceived collision point of induced motion from lateralized cues toward the center. Consequently, there was no correct response and reaction time was not a relevant variable. Our results, with and without monitoring of fixation, showed a shift in collision point for initial cue presentation to the temporal hemifield of the left eye. We believe this shift in collision point to be the result of a closer temporal integration between the bar and the initial cue when that cue is presented in the monocular left temporal hemifield. There was no equivalent shift for the right eye and no shift in either eye when the final cue was presented in the temporal hemifield.

Because the temporal hemifield has greater mid-brain representation than does the nasal hemifield, a subcortical attentional advantage would be expected when cues appear in the temporal hemifield. When the initial cue is presented in the temporal hemifield, it causes a larger attentional gradient than when the equivalent cue is presented in the nasal hemifield. We believe that initial cue presentation to the monocular

temporal hemifield offsets the impact of the temporal proximity of the final cue to the bar. The attentional advantage of the temporal field is translated into a shift in the perceived collision point away from the initial cue. The initial cue and the bar seemingly are brought closer together in time. The analogy would be that of a magnet: the creation of an attentional field by the priming cue *attracts* subsequent stimuli to that cue, and therefore they appear to have been presented closer in time to the priming cue. This effect particularly is obvious at stimulus asynchronies of 120 to 150 msec. This may be because the attentional gradient does not have time to fully develop at shorter asynchronies.

Other investigators also have found evidence of subcortical attentional processing. Experimentally, lesions of the superior colliculus result in a mild deficit in saccade initiation and accuracy.²⁴ In a patient with a lesion involving the superior colliculus, it was suggested that the prolonged saccadic latency may be because of a defect in disengagement of visual attention from the object of regard.²⁵ Animal studies suggest that the superior colliculus may aid in shifts of attention,¹⁵ and human studies have shown a midbrain

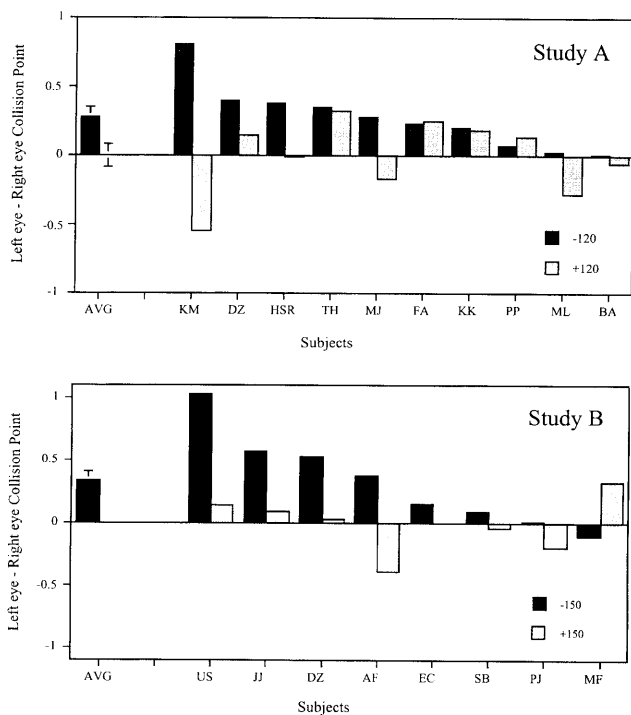


FIGURE 4. Difference in perceived collision point for left eye and right eye presentation for individual subjects is shown for ± 120 msec asynchrony (study A) and at ± 150 msec asynchrony (study B).

attentional advantage to a manual button keypress in the absence of a saccadic eye movement.²⁰ Although these studies indicate a role for the superior colliculus in the attentional shift required for a saccadic eye movement, what has been less well known is the ability of the superior colliculus to influence attention in the absence of eye movements. Recently, Robinson and Kertzman¹⁶ have used the Posner paradigm to show a role for the superior colliculus in exogenous shifts of attention even in the absence of eye movements. In our study, we eliminated trials in which an eye movement occurred. We therefore believe our results support the dissociation between the midbrain attentional system and a saccadic eye movement response by showing the presence of a midbrain attentional effect in a nonmotor attentional task.

The subcortical attentional effect should be manifested as a shift in collision point when the initial cue presentation occurs in the temporal hemifield under both right eye and left eye viewing conditions. However, our results suggest an attentional advantage for the monocular temporal hemifield only for left eye stimulus presentations. We believe this indicates a role for cortical attentional processing.

Strong evidence exists in favor of a hemispheric asymmetry in attentional mechanisms. Recent positron emission tomography data²⁶ indicate that shifting

attention to the right visual field activates both the left and right superior parietal lobules, whereas shifting attention to the left visual field significantly activates only the right superior parietal lobule. The right parietal cortex is therefore able to attend both ipsilaterally and contralaterally. Heilman and Van Den Abell¹⁰ similarly have shown, by the use of electroencephalogram recordings, that the right hemisphere is able to attend to both left and right hemisphere, whereas the left hemisphere is capable of attending only to right hemisphere.

These studies suggest that the right hemisphere dominates cortical attentional processing. If our results were caused solely by a right cortical attentional effect, one would expect to see an attentional advantage whenever the initial cue was presented in the left visual field, that is, not only for initial cue presentation in the monocular left temporal hemifield but also for initial cue presentation to the right nasal hemifield and for binocular presentation to the left visual field. This was not observed. Neither was the temporal advantage seen in both monocular hemifields as would be expected if the results were caused solely by a subcortical attentional effect. We believe the particular pattern of results obtained in our studies only can be explained by an interaction between subcortical and right hemisphere attentional mechanisms.

When the initial cue is presented binocularly in the left visual hemifield, it activates dominant right hemisphere resources but not midbrain attentional resources. This does not appear to be sufficient to create the asymmetry in the attentional gradient required to produce the effect we obtained. It is only when an additive interaction occurs between cortical and subcortical attentional effects that we obtain an asymmetry in the attentional gradient. This condition only can be satisfied by monocular stimulus presentation to the left eye. We believe that initial stimulus presentation to the temporal visual field of the right eye activates midbrain attentional resources but not those of the dominant right hemisphere, whereas initial stimulus presentation to the temporal hemifield of the left eye activates the attentional resources of both the midbrain and the dominant right hemisphere, and this is the only stimulus configuration that does so.

In summary, our results show the influence of subcortical attentional mechanisms on a perceptual judgment task. The fact that the subcortical attentional effect is limited to left eye viewing rules out the possibility that our results can be explained by a nasotemporal asymmetry in photoreceptor and ganglion cell density that is similar in the two eyes. Rather, this study suggests an interaction between cortical and subcortical attentional mechanisms. Under binocular

viewing conditions, we believe that the midbrain attentional effect is negated by the interaction between projections from the temporal hemifield of one eye and the nasal hemifield of the other eye. Thus, subcortical and cortical contributions to attention are separable and demonstrable with the appropriate viewing conditions.

Further, the difference between monocular and binocular results illustrates the importance of monocular testing in visual attention paradigms. The binocular field consists of overlapping points from nasal and temporal hemiretinas and, thus, binocular testing in tasks of visual attention will tend to mask any subcortical effect. Such an effect only can be shown by monocular testing in which the effect of cues presented in nasal and temporal retinas can be dissociated and compared.

Key Words

motion induction, parietal lobe, superior colliculus, visual attention, visual pathways

Acknowledgments

The authors thank Basil Al Zeerah and Alice Funke for their help with data collection and Greg Craig for his assistance with programming.

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