

Extrageniculate Contributions to Reflex Visual Orienting in Normal Humans: A Temporal Hemifield Advantage

Robert Rafal

Department of Neurology
University of California, Davis and Martinez VAMC

Avishai Henik

Department of Neurology
University of California, Davis and
Department of Behavioral Sciences
Ben-Gurion University of the Negev, Israel

Jean Smith

Brown University Program in Medicine

Abstract

■ Evidence is presented that the phylogenetically older retinotectal pathway contributes to reflex orienting of visual attention in normal human subjects. The study exploited a lateralized neuroanatomic arrangement of retinotectal pathways that distinguishes them from those of the geniculostriate system; namely, more direct projections to the colliculus from the temporal hemifield. Subjects were tested under monocular viewing conditions and responded to the detection of a peripheral signal by making either a saccade to it or a choice reaction time manual keypress. Attention was summoned by noninformative peripheral precues, and the benefits and costs

of attention were calculated relative to a central precue condition. Both the benefits and costs of orienting attention were greater when attention was summoned by signals in the temporal hemifield. This temporal hemifield advantage was present for both saccade and manual responses. These findings converge with observations in patients with occipital and midbrain lesions to show that the phylogenetically older retinotectal pathway retains an important role in controlling visually guided behavior; and they demonstrate the usefulness of temporal–nasal hemifield asymmetries as a marker for investigating extrageniculate vision in humans. ■

INTRODUCTION

The encephalization of visual function in cerebral cortex is a relatively new development in phylogeny. The geniculostriate pathway is fully developed only in mammals. In other vertebrates vision is mediated by input through the retinotectal pathway to the superior colliculus of the midbrain. The demands of increasingly complex visual cognition presumably generated the evolutionary pressures leading to the development of a completely new, parallel visual pathway in mammals. In experimental animals the neurobiologic basis for this dramatic transition has begun to receive attention (Karten & Shimizu, 1989), as has the question of how the “two visual systems” (Schneider, 1969) are integrated.

Recent evidence from three converging sources has shown that extrageniculate pathways contribute to the regulation of visually guided behavior in humans. Studies

of “blindsight” (Weiskrantz, 1986) in hemianopic patients have shown that certain visual functions are preserved when only the retinotectal pathway is available for transmitting visual input. These pathways process information that, while not accessible to conscious awareness, can nevertheless guide orienting responses toward the hemianopic field (Zihl & Von Carmon, 1979). Clinical and experimental observations in patients with lesions of the dorsal midbrain have demonstrated distinctive deficiencies in the allocation of visual attention and in visual search (Rafal & Grimm, 1981; Fisk, Goodale, Burkhart, & Burnett, 1982; Posner, Cohen, & Rafal, 1982; Rafal et al., 1987). A third method of investigating extrageniculate vision in humans, exploited in the current investigation, is based on a lateralized neuroanatomic arrangement of retinotectal pathways that distinguishes them from those of the geniculostriate system; viz. an asymmetry between input from temporal and nasal hemifields.

The retinotectal pathway has more crossed fibers from the contralateral eye, and the temporal hemiretina (nasal hemifield) has a smaller direct input to the superior colliculus (Fig. 1). In cats this pathway is almost entirely monocular. Cats with bilateral occipital ablations in whom extrageniculate vision is restored by intercollicular section orient only toward signals in the temporal hemifield. In monkeys, this anatomic asymmetry is much less complete (Wilson & Toyne, 1970; Hubel, LeVay, & Wiesel, 1975; Pollack & Hickey, 1979; Perry & Cowy, 1984).¹ Nevertheless, the functional relevance of this anatomic asymmetry in humans was shown by demonstrating that newborns (in whom the geniculostriate pathways is not developed) have a strong bias to saccade to signals in the temporal hemifield (Rothbart, Posner, & Boylan, 1991). Even in adults, the bias to saccade toward the temporal hemifield persists under conditions of bilateral, simultaneous stimulation (Posner & Cohen, 1980; Shulman, 1984). This hemifield asymmetry is specific to oculomotor responses; no temporal hemifield advantage was found in a perceptual (temporal order judgment) task (Posner & Cohen, 1980).

Our approach has been to show converging evidence

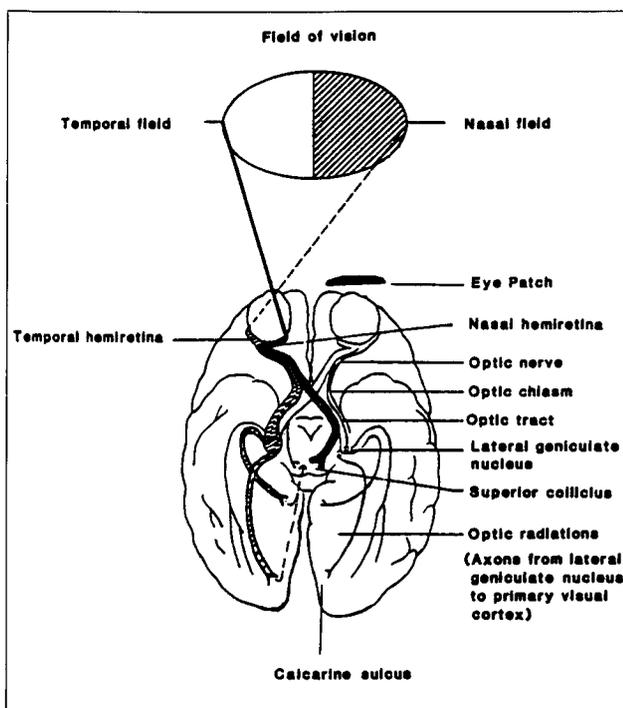


Figure 1. Comparison of the connections of the geniculostriate and the retinotectal pathways. With one eye occluded by a patch, visual information from the open eye is sent through both crossed and uncrossed pathways to project equally to both striate cortices via the geniculate bodies. In contrast the afferents from the open eye to the midbrain are dominantly crossed and project mainly to the superior colliculus contralateral to the open eye; moreover, these projections are asymmetric such that the temporal visual hemifield has a greater representation in the colliculus than does the nasal visual hemifield. (Adapted from Stein, 1982.)

for extrageniculate contributions to orienting visual attention from the demonstration of attention deficits in patients with midbrain degeneration, and from the study of temporal–nasal hemifield asymmetries in orienting attention in normal human subjects. A peripheral visual signal has a biphasic effect on attention (Posner, Cohen, & Rafal, 1982; Posner & Cohen, 1984; Maylor, 1985): First attention is summoned to that location. This early facilitation then is superseded by an inhibition of return which slows responses to signals at that location. Previous work has shown that midbrain lesions interfere both with the initial movement of attention (Posner, Cohen, & Rafal, 1982, Rafal et al., 1989) and with the generation of inhibition of return (Posner, Rafal, Choate, & Vaughan, 1985). We have also shown that inhibition of return is generated more effectively in normal humans when activated by signals in the temporal hemifield (Rafal, Calabresi, Brennan, & Sciolto, 1989).

In the current study, we show that the reflexive orienting of covert attention is more efficiently summoned by signals presented in the temporal hemifield. Subjects were tested with one eye patched. Thus, when the left eye was patched signals in the right field were temporal, and those in the left field were nasal; conversely when the right eye was patched, the left field was temporal and the right was nasal. Subjects were asked to make responses to visual signals presented, with equal probability, in the temporal or nasal hemifield. Attention was manipulated by presenting, on each trial, a precue to summon attention either to one of the two possible target locations, or to the center of the display. This cue was a luminance change that could reflexly summon attention, but that did not predict the target location; that is, the target was as likely to appear in the contralateral field as it was at the location of the cue. Since we wanted to examine the role of midbrain pathways in both oculomotor activation and covert attention movements, each subject performed two tasks tested in separate blocks. In the saccade task the subject maintained fixation at the center of the display and, when the target appeared, executed a saccade to it. In the covert orienting task the subject was required to maintain fixation at the center of the display and make no eye movements; when the target appeared the subject made a choice reaction time (key-press) response.

In this paradigm the efficacy of the cue in summoning attention is indexed both by a facilitation of responses to targets at the cued location—“benefits,” and by inhibitory effects on responding to targets in the contralateral hemifield—“costs.” Benefits are measured as a relative facilitation of detection RT or saccade latency when the target appears at the location of a noninformative peripheral cue (valid cue) compared with the condition where there is a central cue. Costs are measured as a relative slowing of response, compared to the central cue condition, when the target appears contralateral to a peripheral cue (invalid cue). The benefits and costs of

orienting into temporal and nasal hemifield were calculated as described in Table 1 and compared.

It is important to note that one cannot measure the effects of orienting to one hemifield by subtracting the RT to targets in that field in the invalid cue condition from RT to targets in that field in the valid cue condition. For example, the temporal target invalid cue RT minus the temporal target valid cue combines both the benefits of orienting toward a valid *temporal cue*, and the costs of orienting to an invalid *nasal cue*. The costs of orienting to the temporal hemifield are reflected in slower RTs to targets in the *nasal* hemifield following an invalid temporal cue. These must be subtracted from RTs for nasal targets following a central cue to calculate the costs of orienting to an invalid cue in the temporal hemifield.

RESULTS

Mean response latencies for each cue condition (valid, neutral, and invalid) are given in Table 2 and those for each cue-target interval are shown in Figure 2. The results for temporal and nasal targets are plotted separately for saccade and key press response blocks.

Responses are faster for saccade than for keypress [$F(1, 16) = 36.3, p < .0001$], and responses are faster at longer cue-target intervals [$F(3, 48) = 48.6, p < .0001$]. The effect of interval is greater for keypress responses [$F(3, 48) = 3.2, p < 0.05$]. Responses are faster for valid cues than for neutral cues, and are slowest in the invalid cue condition [$F(2, 32) = 70.1, p < 0.0001$]. The effect of cue is greater at longer cue-target intervals [$F(6, 96) = 5.85, p = 0.0001$]. For both saccade and for keypress responses, larger cue effects are produced when the cue is presented in the temporal hemifield [$F(2, 32) = 6.9, p < 0.005$].

Figure 3 shows the costs and benefits of orienting toward temporal and nasal cues. Costs are smaller for eye movements than for manual responses [$F(2, 32) = 6.4, p < 0.005$]. For both kinds of responses, the benefits and the costs are larger for orienting toward cues in the temporal hemifield [$F(2, 18) = 7.8, p = 0.01$].

DISCUSSION

The results show that a peripheral luminance change summons attention to its location, and that the orienting of attention facilitates detection of targets there while inhibiting detection of targets elsewhere in the visual field. The current results also confirm the findings of

Posner, Nissen, & Ogden (1978) that the effects of orienting attention are less for eye movements than for manual responses. They extend those observations to show that facilitatory effects of orienting attention are not different for the two types of responses. The response difference is restricted to the inhibitory component; that is benefits were the same for saccade and keypress task, but costs were greater for manual responses.

The major finding of the current study is that signals in the temporal hemifield are more efficient in summoning attention than are signals in the nasal hemifield. Orienting to signals in the temporal hemifield produced both greater facilitation at the cued location and greater inhibition in the contralateral field. This asymmetry was found for manual responses as well as for saccades, and indicates that there is a temporal hemifield advantage for covert attention movements as well as for eye movements.

Neurophysiologic studies measuring selective enhancement in single unit responses have related the superior colliculus to orienting in which monkeys make saccades, but not in conjunction with attention movements while the eyes remain fixed (Wurtz & Mohler, 1976). It is worthwhile to consider that the reflex orienting of covert attention, as examined in the current study, is different from the endogenous allocation of attention that the selective enhancement paradigm is used to identify. In that paradigm visually responsive cells are first identified, and the experimenter then determines whether the visual response of the cell is enhanced either when the monkey must make a saccade to the signal, or when it must strategically allocate attention to the region of the signal to detect its dimming and to respond with a keypress response. Wurtz and Mohler (1976) showed that collicular units show selective enhancement in the saccade condition, but not in the covert orienting condition. However, the kind of reflex orienting examined in the current study is rather different and occurs even when the subject does not make any response to the cue per se. It occurs automatically when the cue is presented.² Note that in the selective enhancement paradigm the cells selected for study are those which respond to visual signals. Although this response is often construed as a "sensory" effect, it is possible that it might reflect the kind of reflexive orienting to exogenous signals that is being examined here. In any case, the selective enhancement effect used in neurophysiologic studies seems to be related to more endogenous attention mechanisms; and the absence of selective en-

Table 1. Orienting to Temporal and Nasal Hemifield

	<i>Temporal Cue</i>	<i>Nasal Cue</i>
Benefits	Temporal target (central cue – valid cue)	Nasal target (central cue – valid cue)
Costs	Nasal target (invalid cue – central cue)	Temporal target (invalid cue – central cue)

Table 2. Mean Saccade Latencies and Keypress Reaction Times (Standard Deviations in Parentheses)

	Saccade Latency (msec)		Keypress RT (msec)	
	Temporal Target	Nasal Target	Temporal Target	Nasal Target
Valid cue	257 (57)	258 (44)	368 (71)	377 (78)
Central cue	288 (51)	279 (100)	403 (73)	400 (76)
Invalid cue	297 (52)	275 (55)	422 (79)	426 (80)

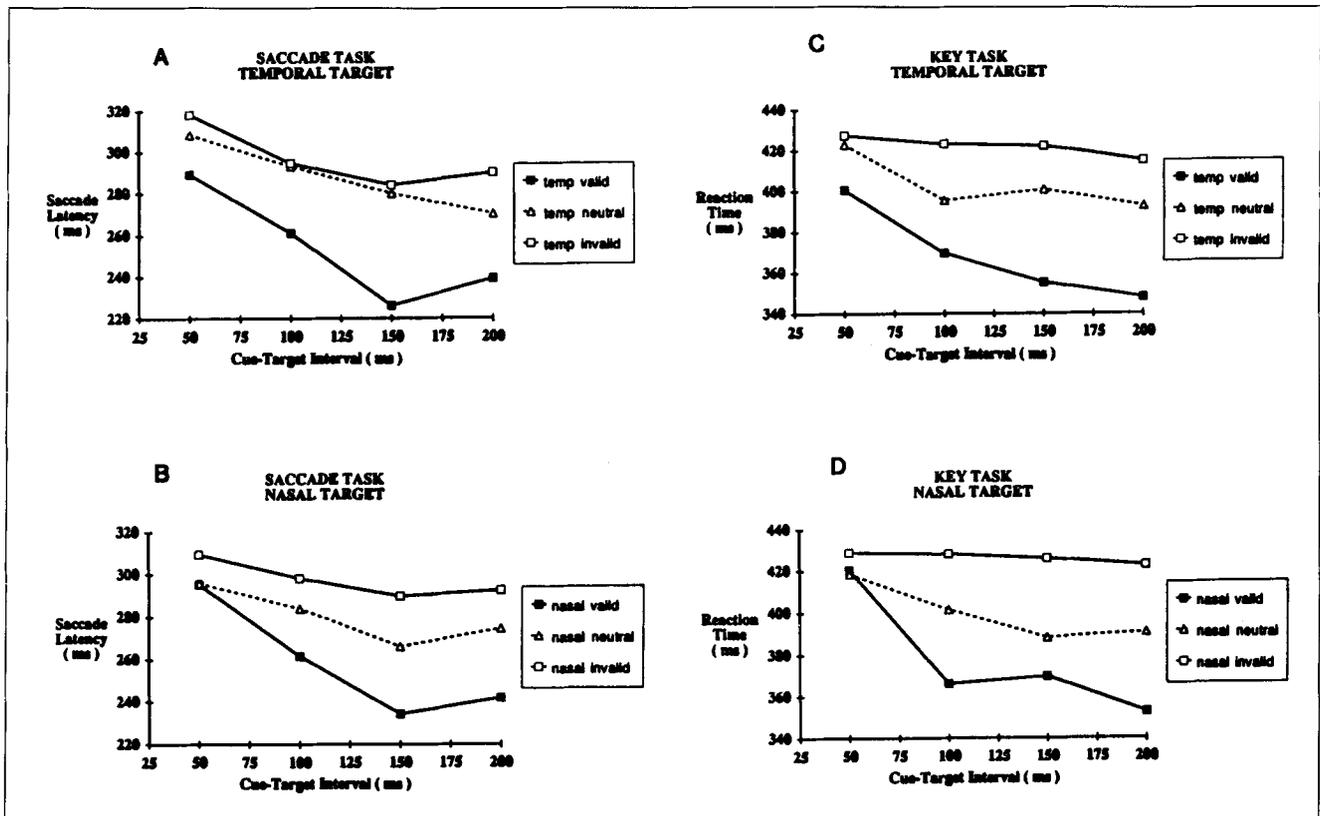


Figure 2. Mean saccade latencies and key press RTs in milliseconds as a function of cue-target interval in the valid cue, invalid cue, and central cue conditions for orienting toward the temporal and nasal hemifields.

hancement in collicular units when no saccade is made is not evidence against a role of this structure in the kind of reflexive orienting being considered here.

A previous study by Shulman (1984) failed to show a statistically reliable temporal hemifield advantage for covert attention shifts. In the current study we focused on the early effects of cueing—within 200 msec, before inhibition of return develops. Shulman's experiment used longer SOAs. Since inhibition of return is also generated more efficiently by signals in the temporal hemifield, the failure of Shulman's study to show a temporal hemifield advantage for covert orienting may have been due to the cogeneration of inhibition of return with the longer SOAs used. Also, the peripheral cues used in

Shulman's study were predictive of the likely target location. These cues may have induced the subjects to allocate attention endogenously using a strategic set; and the experiment may therefore have tapped a different kind of process than the reflexive orienting examined in the current study. Finally, in Shulman's (1984) experiment, the effects of cues on detection of peripheral targets were compared with detection of targets in the center of the display.

The current finding that signals in the temporal hemifield summon covert attention more efficiently suggests that extrageniculate midbrain pathways play a special role in reflex orienting to exogenous signals, and converge with findings in brain injured patients to implicate

center of the display and to make a response only after the target appeared. Eye movement and keypress responses were made in separate blocks of trials. The order in which the tasks were tested was randomized across successive subjects. In the saccade task the subject made a saccade to the target. In the keypress task the subject made a choice RT response, pressing a key with the index finger if the target appeared in the left box, and the middle finger if the target appeared in the right box. Responses of less than 100 msec were considered to be anticipatory. An "ERROR" signal was presented and these trials were excluded from analysis.

The orienting of visual attention was measured in terms of facilitation in detection RT when the target appeared at the cued location ("valid cue" condition) in comparison to trials in which the target appears in the hemifield opposite the cued location ("invalid cue" condition). To compare orienting toward temporal and nasal hemifields, subjects were tested under monocular viewing conditions. Each eye was tested in a separate block with the other occluded by a patch. The eye tested first was randomized across successive subjects. When the display was viewed by the right eye, the right field was temporal and the left nasal. When the left eye was used, the left field was temporal and the right was nasal. For each task condition (saccade and keypress) 240 trials were recorded with each eye. Each subject received 48 practice trials in each response condition.

Apparatus

An Apple 2e microcomputer controlled the display and recorded responses. In the keypress task the subject placed the index finger and middle finger of the right hand on adjacent plastic keys mounted on a keyboard. Light pressure on either key activated a microswitch that recorded RT. In the saccade task eye position was recorded with an Eye-Trac 210 infrared scleral reflectance recording device mounted on spectacle frames. The experimenter monitored an eye position cursor on a separate slave scope that simultaneously showed the same display viewed by the subject. At the beginning of each session the device was calibrated by centering the cursor on the central fixation + while the subject was looking at it; the gain of the device was then adjusted such that when the subject made a saccade to a target on left or right the cursor moved to the position of the target on the slave scope. The Eye-Trac was interfaced with a microcomputer through a device (Greg Laird Associates, Portland, Oregon) that produced a velocity (first derivative) transformation of the Eye-Trac signal, which in turn triggered response recording by the computer.

Stimuli were displayed in black and white on a Magnavox RGB 40 monitor. The boxes had a luminance of 4 cd/m²; the precue was brightening of this box to a luminance of 16 cd/m²; when the target appeared within

the brightened box they had, together, a luminance of 26 cd/m².

Acknowledgments

This study was supported by PHS Grant MH 41544. We thank Anne Boylan who prepared Figure 1.

Notes

1. For the eccentricity of 10° used in the current study, Perry and Cowey (1984) found that the density of ganglion cells in the nasal hemiretina is approximately twice that of the nasal hemiretina. However, light scatter into the more peripheral temporal crescent region (with no representation in the temporal hemiretina) may well have contributed to the asymmetric effects reported here.
2. Recent work by Yantis and Jonides (1990) shows the need to explore the mechanisms by which reflexive orienting of visual attention might be inhibited under endogenous control.

REFERENCES

- Fisk, J. D., Goodale, M. A., Burkhart, G., & Barnett, H. J. M. (1982). Progressive supranuclear palsy: The relationship between oculomotor dysfunction and psychological test performance. *Neurology*, *32*, 698–705.
- Hubel, D. H., LeVay, S., & Wiesel, T. N. (1975). Mode of termination of retinotectal fibres in macaque monkey: An autoradiographic study. *Brain Research*, *96*, 25–40.
- Karten, H. J., & Shimizu, T. (1989). The origins of neocortex: Connections and laminations as distinct events in evolution. *Journal of Cognitive Neuroscience*, *1*, 291–301.
- Lewis, T. L., Maurer, D., & Blackburn, K. (1985). The development of young infants' ability to detect stimuli in the nasal visual field. *Vision Research*, *25*, 943–950.
- Maylor, E. A. (1985). Facilitory and inhibitory components of orienting in visual space. In M. I. Posner & O. S. M. Marin (Eds.), *Attention and performance XI*. Hillsdale, NJ: Lawrence Erlbaum.
- Perry, V. H., & Cowey, A. (1984). Retinal ganglion cells that project to the superior colliculus and pretectum in the macaque monkey. *Neuroscience*, *12*, 1125–1137.
- Perry, V. H., Oehler, R., & Cowey, A. (1984). Retinal ganglion cells that project to the dorsal lateral geniculate nucleus in the macaque monkey. *Neuroscience*, *12*, 1101–1123.
- Pollack, J. G., Hickey, T. L. (1979). The distribution of retinocollicular axon terminals in rhesus monkey. *Journal of Comparative Neurology*, *185*, 587–602.
- Posner, M. I. (1980). Orienting of attention. *Quarterly Journal of Experimental Psychology*, *32*, 3–25.
- Posner, M. I., & Cohen, Y. (1980). Attention and the control of movements. In G. E. Stelmach & J. Requin (Eds.), *Tutorials in motor behavior* (pp. 243–258). Amsterdam: North Holland.
- Posner, M. I., & Cohen, Y. (1984). Components of visual orienting. In H. Bouma & D. Bouwhuis (Eds.), *Attention and performance X* (pp. 531–556). London: Lawrence Erlbaum.
- Posner, M. I., Rafal, R. D., Choate, L., & Vaughan, J. (1985). Inhibition of return: Neural basis and function. *Cognitive Neuropsychology*, *2*, 211–228.
- Posner, M. I., Cohen, Y., & Rafal, R. (1982). Neural systems control of spatial orienting. *Philosophical Transactions of the Royal Society of London*, *B298*, 187–198.
- Posner, M. I., Walker, J. A., Friedrich, F. A., & Rafal, R. D.

- (1987). How do the parietal lobes direct covert attention? *Neuropsychologia*, *25*, 135–146.
- Posner, M. I., Walker, J. A., Friedrich, J. & Rafal, R. (1984). Effects of parietal injury on covert orienting of visual attention. *Journal of Neuroscience*, *4*, 1863–1874.
- Rafal, R., Calabresi, P., Brennan, C., & Sciolto, T. (1989). Saccade preparation inhibits reorienting to recently attended locations. *Journal of Experimental Psychology: Human Perception and Performance*, *15*, 673–685.
- Rafal, R. D., & Grimm, R. J. (1981). Progressive supranuclear palsy: Functional analysis of the response to methysergide and antiparkinsonian agents. *Neurology*, *31*, 1507–1518.
- Rafal, R., Smith, J., Krantz, J., Cohen, A., & Brennan, C. (1991). Extrageniculate vision in hemianopic humans: Saccade inhibition by signals in the blind field. *Science*, in press.
- Rothbart, M. K., Posner, M. I., & Boylan, A. (1991). In J. Enns (Ed.), *The development of attention: Research and theory*. Amsterdam: North Holland, in press.
- Schneider, G. E. (1969). Two visual systems: Brain mechanisms for localization and discrimination are dissociated by tectal and cortical lesions. *Science*, *163*, 895–902.
- Shulman, G. L. (1984). An asymmetry in the control of eye movements and shifts of attention. *Acta Psychologica*, *55*, 53–69.
- Stein, J. F. (1982). *An introduction to neurophysiology* (Fig. 6.9, p. 95). Oxford: Blackwell Scientific.
- Stoerig, P., & Cowey, A. (1989). Residual target detection as a function of stimulus size. *Brain*, *112*, 1123–1139.
- Weiskrantz, L. (1986). *Blindsight: A case study and implications*. Oxford: Oxford University Press.
- Wilson, M. E., & Toyne, M. G. (1970). Retino-tectal and cortico-tectal projections in *Macaca mulatta*. *Brain Research*, *24*, 395–406.
- Wurtz, R. H., & Mohler, C. W. (1976). Organization of monkey superior colliculus: Enhanced visual response of superficial layer cells. *Journal of Neurophysiology*, *39*, 745–765.
- 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.
- Yukie, M., & Iwai, E. (1981). Direct projections from the dorsal lateral geniculate nucleus to the prestriate cortex in macaque monkeys. *Journal of Comparative Neurology*, *201*, 81–97.
- Zihl, J. (1980). Blindsight: Improvement of visually guided eye movements by systematic practice in patients with cerebral blindness. *Neuropsychologia*, *18*, 71–77.
- Zihl, J., & Von Carmon, D. (1979). The contribution of the 'second' visual system to directed visual attention in man. *Brain*, *102*, 835–856.