

MIDBRAIN MECHANISMS FOR ORIENTING VISUAL ATTENTION

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ABSTRACT

The role of midbrain visual centers for orienting attention was studied in chronometric experiments measuring the effect of pre-cues on simple reaction time to detect a peripheral luminance change. Two types of cues were tested: Exogenous cues--a peripheral luminance change which did not predict target location; and Endogenous cues--a central arrow which predicted the likely target location. Patients with peri-tectal midbrain degeneration from progressive supranuclear palsy showed deficits in orienting to both types of cues. In normal human subjects tested monocularly, we compared orienting into the temporal hemifield (which has more direct access to the midbrain superior colliculus) with orienting into the nasal hemifield. Exogenous cues produced equivalent speeding of detection at cued locations in both hemifields; but nasal cues produced more slowing of detection at uncued locations. Endogenous nasal cues produced earlier speeding of detection at cued locations than temporal cues; and at later intervals, they produced more slowing of detection at uncued locations. Both cortical and subcortical visual systems appear to be integrated in orienting to both exogenous and endogenous information. Whereas the subcortical pathway receives input mainly from the temporal hemifield, the cortical system is biased in orienting to the nasal hemifield; and its commitment produces more slowing of detection at unattended locations.

The selectivity of visual perception is guided by brain mechanisms which orient attention in the visual field. One manifestation of visual orienting is overt, consisting of movements of the head and/or eyes to achieve foveation of the attended spatial position. Covert orienting of attention can occur independent of motor activity, and serves to align internal attention systems with a spatial location. Neurophysiologic studies in behaving primates have indexed this covert orienting in terms of selective enhancement in neuron firing

rate in response to a visual cue which prepares the animal, while maintaining fixation, to detect a forthcoming target, or to prepare a saccade toward it (Wurtz, Goldberg & Robinson, 1980). Similarly, covert orienting can be studied in humans by measuring facilitations and inhibitions in simple reaction time (RT) performance resulting from preliminary visual cues which either correctly prepare the subject to detect the target at the cued location, or which summon attention elsewhere in the visual field (Posner, 1980).

In one study using this approach, normal humans maintained fixation at the center of a video display, and made simple RT keypress responses on detecting a target which appeared, with equal probability, in either of two flanking boxes located equidistant to left or right. On each trial the target was preceded by a precue which was the brief brightening of one of the flanking boxes. This cue predicted, with 80% probability, that the target would appear at the contralateral location. The results were quicker detection RTs at the location of the cue at early cue-target intervals; whereas for targets appearing more than 200 msec. following cue onset, RTs were quicker for targets contralateral to the cue, i.e. where the subjects had expected the target. This result suggests that attention may be summoned automatically by exogenous sensory signals, or it may be deployed endogenously based on a strategic set (Posner, Cohen & Rafal, 1982)

In the same communication we reported that covert orienting of visual attention was slowed in patients with progressive supranuclear palsy (PSP), and attributed this deficit to lesions of the phylogenetically older visual system of the midbrain superior colliculus and peri-tectal region. PSP, and the more frequently occurring Parkinson's disease, share the clinical and pathological features of degeneration of the substantia nigra and other basal ganglia structures. However, PSP is distinguished from Parkinson's disease pathologically by a conspicuous degeneration of the superior colliculi and peri-tectal regions; and clinically by a distinctive impairment in making voluntary eye movements which affects vertical more than horizontal eye movements. Our experiment demonstrated that attention movements were also slower in the vertical plane. The cue used in that experiment, however, was the brightening of a peripheral box which predicted, with 80% probability, that the target would appear at the cued location. Since the exogenous and the endogenous contributions of the cue were redundant, we could not specify whether midbrain visual centers were involved in exogenous orienting, endogenous orienting, or both.

The main goal of the present experiments was to determine the role of midbrain visual centers in exogenous and endogenous orienting. The first experiment examined covert attention orienting in PSP patients and, as in the previous study of Posner Cohen & Rafal (1982), attention movements in the vertical plane were compared with those in the horizontal plane. However, two different types of precue conditions were also compared. In one condition, the exogenous cue condition, the precue consisted of the brightening of a peripheral box which did not predict (50% probability) the position of the target. Any effect of the cue on detection RT could, therefore, be attributed to automatic, stimulus driven orienting. In another condition, the endogenous cue condition, a

central arrow was used which predicted, with 80% probability, the position at which the target would appear. Since the arrow appeared at fixation and cued a peripheral locus only by its symbolic meaning, this condition was assumed to reflect endogenous control mechanisms.

Experiments 2 and 3 examined the effects of these two types of cues on covert orienting in normal human subjects tested under monocular conditions. These experiments took advantage of the different neuroanatomical connections of the subcortical retino-tectal pathway and the cortical geniculostriate system. The geniculostriate system is binocular, and the temporal and nasal hemiretinas of both eyes are equally represented in the occipital lobe cortex. In contrast, the extrageniculate visual system is essentially monocular; this subcortical retino-tectal pathway is dominantly crossed, and each superior colliculus receives input mainly from the contralateral eye. Moreover, in each superior colliculus, the visual field of the contralateral eye is asymmetrically represented such that the receptive fields of the temporal hemifield dominate, whereas little input from the nasal hemifield is mapped on the colliculus. Therefore, under monoptic viewing conditions, a difference in covert orienting into the nasal and temporal hemifields should provide insight into the contributions of subcortical visual centers, which are relatively blind to signals occurring in the nasal hemifield.

EXPERIMENT 1

Subjects:

Six patients with progressive supranuclear palsy volunteered to participate in the study. Each patient had a moderate to severe impairment in the ability to move the eyes vertically, but little or no difficulty moving the eyes in the horizontal direction.

Apparatus and Procedure:

In a quiet, darkened room subjects faced a black and white TV monitor placed 37 cm in front of the patient at eye level. The index finger of the preferred hand rested on a single response key placed on a table between the subject and the TV monitor. The TV monitor and response board were interfaced with a microcomputer which controlled the stimulus display and the recording of RT.

Subjects fixated a central plus sign which was flanked by four unfilled, square boxes, one degree across, which were plotted 10 degrees of visual angle above, below, to the right and to the left of fixation. Subjects were instructed to maintain fixation at the central plus sign, and to respond with a quick manual keypress response whenever a target appeared in any of the boxes. The target was a large bright asterisk filling the box, and each of the four boxes was equally likely to contain the target on each trial. However, 50, 150, 350, or 550 msec prior to the onset of the target, a cue was presented to prepare the patient for target detection. In one precue condition, the

exogenous cue condition, the precue consisted of the brightening of one of the peripheral boxes for 300 msec. This cue did not predict the location of the forthcoming target; the target was equally likely to occur at the location of the cue, or opposite to this position. Cues and targets were always in the same plane, i.e. horizontal or vertical. Trials in which the cue correctly indicated the target position are referred to as valid trials, and trials in which the cue incorrectly predicted the target position are referred to as invalid trials. Two blocks of 160 trials were run. In another precue condition, the endogenous cue condition, a central arrow, one degree of visual angle in length, was used to signal the position of target occurrence; e.g. a right directed arrow would indicate that the target would be likely to occur to the right of fixation. Eighty percent of trials were valid and 20% were invalid. Four blocks of 160 trials were run for each subject. The order of blocks with exogenous and endogenous cues was randomized within patients.

Results and Discussion:

Trials in which target detection responses were less than 150 msec or longer than 3500 msec. were excluded from analysis. Median RTs from the remaining trials for each subject in each condition were calculated and subjected to a repeated measures analysis of variance (ANOVA). The within subjects' factors were type of precue (peripheral brightening vs. central arrow), validity (correct vs. incorrect signaling of the target position), direction (horizontal vs. vertical), and interval (50, 150, 350, and 550 msec).

Two of the main effects, validity and interval, were significant; $F(1,5)=14.21, p<.025$ and $F(3,15)=26.29, p<.001$; respectively. Detection RTs were shorter on valid trials than invalid trials, and decreased as the cue-target interval increased. Specifically, RTs were 952 msec, 910 msec, 882 msec, and 849 msec, for the 50 msec., 150 msec, 350 msec, and 350 msec, cue-target interval conditions, respectively. The main result was a significant interaction between validity and direction; $F(1,5)=6.71, p<.05$. Valid trials were responded to faster when cue and target appeared in the horizontal direction than when they appeared in the vertical direction (Table 1). There was, however, no difference between vertical and horizontal target detection RTs on invalid trials. This interaction was not qualified by the type of precue, and was present under exogenous and endogenous precue conditions.

These results reveal a direction specific impairment of covert attention orienting in our PSP patients. Covert orienting to the cued location occurred more effectively when the target occurred in the horizontal plane than when it occurred in the vertical plane, and this was true for both exogenous and endogenous cues. These findings suggest that the subcortical visual system of the midbrain contributes to covert shifts of attention activated by either exogenous or endogenous information.

TABLE 1: ORIENTING IN PSP

		Cued	Uncued	Difference
Box Cue	Horizontal	793	904	111
	Vertical	868	898	30
	Difference			81
Arrow Cue	Horizontal	871	983	112
	Vertical	935	991	56
	Difference			56
Both	Horizontal	832	943	111
	Vertical	902	945	44
	Difference			67*

Mean RT in msec for PSP patients in Experiment 1 for horizontal and vertical targets appearing at cued and uncued locations. * $p < .05$

EXPERIMENT 2

In Experiment 1, we found that intact collicular function is necessary for normal orienting to both exogenous and endogenous cues. In a second experiment, endogenous orienting was examined under monocular conditions in normal subjects. A central arrow cue was used to indicate the peripheral position at which a target was likely to occur. Since this cue required endogenous processing, and since the central position of the cue provided information equally available to both superior colliculi, differences in orienting between temporal and nasal hemifields should reflect biases of cortical systems for orienting attention.

Subjects:

Fourteen neurologically unimpaired adults were paid to participate.

Apparatus and Procedure:

The apparatus and procedure of Experiment 2 were the same as the endogenous (arrow) cue of Experiment 1 except that only horizontal cues and targets were used. Cue duration was 200 msec, and cue-target stimulus onset asynchronies (SOA) were intervals of 50, 150, 300 and 500 msec. Subjects were tested monoptically by patching of one eye before each experimental block. The order of left versus right eye patching was counter-balanced across successively tested subjects who participated in four blocks of 160 trials each.

Results and Discussion:

After excluding RTs of less than 100 msec. and greater than 2500 msec, mean RTs for each subject in each condition were analyzed in an ANOVA. Within factors were: hemifield toward which the cue summoned attention (temporal versus nasal); cue (valid or invalid); and interval (50, 150, 300, 500 msec.). The mean RT for all fourteen subjects in each condition are shown in Fig. 1. As in Experiment 1, there were main effects of interval and of cue validity. RT decreased as the cue-target interval increased ($F(3,39) = 56.6, p < .001$.) RTs were faster at the validly cued locations at all intervals ($F(1,13) = 23.8, p < .001$.) The hemifield cued (nasal versus temporal) interacted with interval such that responses to targets which followed nasal cues were quicker at the two short intervals; whereas responses to targets which followed temporal cues were faster at the long two intervals ($F(3,39) = 3.3, p < .05$). The data from the two short intervals were cast into a separate ANOVA. This confirmed that RT to targets that followed nasal cues (whether the cues were valid or invalid) were significantly faster than those which followed temporal cues ($F(1,13) = 7.45, p < .05$). This advantage for targets which followed nasal cues was due to faster RTs on valid trials in which a cue summoning attention to the nasal hemifield was followed by a nasal target ($F(1,13) = 5.03, p < .05$). Reaction times to targets appearing in the temporal hemifield following nasal hemifield cues were also faster than those to uncued targets appearing in the nasal hemifield, but this difference was not significant ($F(1,13) = 1.29, p = n.s.$). The data from the two long intervals (300 msec and 500 msec) were also cast into a separate ANOVA which confirmed that, at these intervals, RTs following nasal cues were slower than those which followed temporal cues ($F(1,13) = 5.25, p < .05$). Fig. 3 shows that the faster RTs for targets following temporal cues were primarily a result of the invalid cue condition: nasal cues followed by targets in the temporal hemifield resulted in slower RTs than targets which appeared in the nasal hemifield following temporal cues.

The results of this experiment seem to indicate that endogenous control mechanisms for orienting attention are biased for orienting toward the nasal hemifield. This bias is reflected by the quicker responses to nasal targets following nasal cues at early cue-targets intervals; and by slower disengagement from the nasal hemifield to respond to temporal targets following invalid cues at the later intervals. Since the subcortical visual system of the midbrain can maintain surveillance of the visual periphery, but has little input from the nasal hemifields of either eye, such a bias by the cortical system toward the nasal hemifield seems to be to be a reasonable arrangement for efficient functioning of the visual system as a whole.

In Experiment 3, we examined orienting to exogenous signals in the temporal and nasal hemifields in normal subjects under monocular conditions. Since the nasal hemifield is relatively blind to the superior colliculus, we wanted to determine whether the cortical attention system was competent in responding to exogenous signals presented in the nasal hemifield.

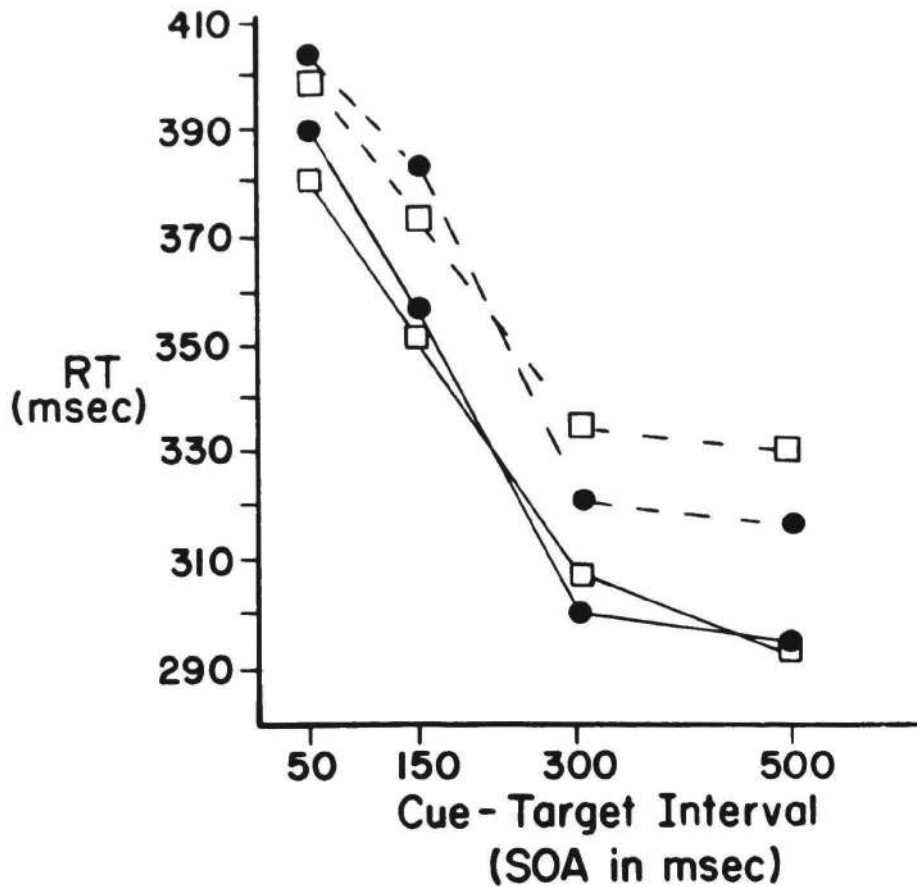


FIG. 1: ENDOGENOUS ORIENTING IN EXPERIMENT 2. Mean RT as a function of interval for target detection following arrow cues pointing toward temporal (solid circles) and nasal (open squares) hemifields. Solid lines indicate targets appearing at the cued location (valid trials); dashed lines indicate targets appearing contralateral to the cued location (invalid trials).

EXPERIMENT 3

Subjects:

Twenty-five neurologically unimpaired subjects were paid to participate, and were tested under monocular conditions as in Experiment 2.

Apparatus and Procedure:

The apparatus and procedure of Experiment 3 were the same as in Experiment 2, except that the cue was brightening of one peripheral box which did not predict (50% probability) target location.

Results and Discussion:

RTs shorter than 100 msec. and longer than 2500 msec were excluded from analysis. This led to an exclusion of approximately 2% of the data. The results from the remaining trials are shown in Fig. 2. Responses were faster on valid trials than on invalid trials ($F(1,24) = 6.05, p < .025$); and RTs decreased as the cue-target interval increased ($F(3,72) = 19.9, p < .001$). The two variables, validity and interval, interacted ($F(3,72) = 3.90, p < .025$), such that valid cues produced faster responses than invalid cues at the short intervals. This cue effect was reduced at the two longer intervals. Furthermore, validity interacted with hemifield ($F(1,24) = 4.37, p < .05$): Invalid trials resulted in slower responses when the cue appeared in the nasal hemifield and the target appeared in the temporal hemifield, than when the opposite sequence occurred. Inspection of Fig. 2 reveals that this interaction was present only at the two short cue-target intervals (50 msec and 150 msec). The interaction of validity and hemifield thus complements the finding of Experiment 2 which showed a deficit in the reorienting of attention in a temporal direction. In Experiment 2, this interaction was present at the longer cue-target intervals, presumably because the use of an endogenous cue required more time to fully commit attention, and encouraged subjects to maintain attention at the cued position. In Experiment 3, the interaction was present at the shorter cue-target intervals, presumably because the stimulus driven orienting of attention occurred relatively quickly and lasted briefly.

The major finding of this experiment is that exogenous signals which have no direct access to the superior colliculus do summon attention. This finding implies that cortical systems are involved in exogenous orienting. Their commitment, however, results in greater slowing to reorient to unattended locations.

GENERAL DISCUSSION

Attention may be oriented to facilitate the processing of information either internally in memory, or of events occurring at the sensory surface. When orienting to facilitate the processing of visual information, attention may be summoned either by an exogenous sensory signal, as when we turn toward a sudden movement seen out of the corner of the eye; or may be allocated endogenously, under internal control, in order to prepare to detect an expected stimulus, as when we decide to look both ways before crossing the street. In the studies reported here, we have attempted to relate both exogenous and endogenous mechanisms for orienting attention to neural systems; and specifically to determine what role the retino-tectal pathway of the phylogenetically older extrageniculate, midbrain visual system plays in visual orienting.

The results of the first experiment in patients with progressive supranuclear palsy were clear cut. Midbrain degeneration, including the superior colliculus and peri-tectal region, produced a deficit in orienting to

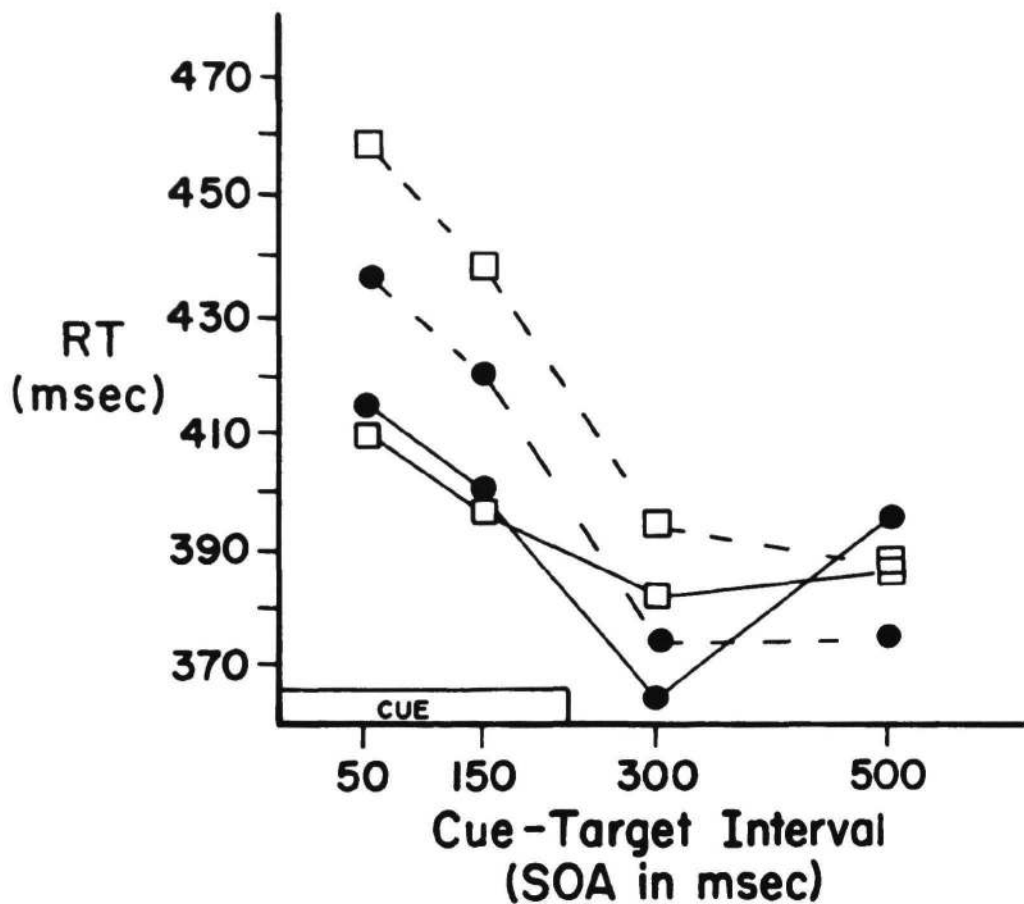


FIG. 2: EXOGENOUS ORIENTING IN EXPERIMENT 3. Mean RT as a function of interval for targets following a box brightening cue in the temporal (solid circles) and nasal (open squares) hemifields. Solid lines indicate targets appearing at the cued location (valid trials); dashed lines indicate targets appearing contralateral to the cue (invalid trials).

both exogenous and endogenous cues. Covert orienting of attention was found to be impaired in the direction in which eye movements were more limited in these patients. Moreover, the deficit in covert orienting was clearly related to the fact that cues summoning attention in the clinically affected direction produced less advantage for targets appearing at the cued locations; whereas there was no difference in reaction time to detect targets at the uncued locations. This result is consistent with the concept that the superior colliculus is involved in the operation of moving covert attention. It contrasts strikingly with observations in patients with cortical lesions of the parietal lobe in whom the opposite pattern was found: *viz* RTs to detect targets at cued locations were not greatly different in the visual fields ipsilateral and contralateral to the lesion; rather the differences found were at the uncued locations, implicating a disorder in disengaging attention to reorient toward the field contralateral to the lesion (Posner, et al, 1984).

In the PSP patients tested in Experiment 1, we found that collicular lesions affect both exogenous and endogenous orienting. In the hemifield experiments in normal subjects, we sought to determine how the retino-tectal system might contribute to exogenous and endogenous orienting, and what kinds of orienting behavior could occur independent of this system. We have recently found this hemifield method to be a useful approach which can provide converging evidence with patient studies. Posner and Cohen (1984) showed that an exogenous sensory signal which first summons attention, results in a subsequent inhibition of return which slows detection of targets at the recently cued location. We have shown that this inhibition of return is deficient in patients with progressive supranuclear palsy (Posner, et al, 1985). Recently we have also found that this inhibition of return effect is greater in the temporal than in the nasal hemifield of normal human subjects under monocular conditions (Rafal and Calabresi, unpublished). This same result is, in fact, reflected in our current results in Experiment 3, as may be seen from a close inspection of Fig. 2. At the 500 msec interval RTs at the validly cued location are slower than at the uncued location in the temporal hemifield, whereas this is not true for cues summoning attention into the nasal hemifield. We have reason to feel, therefore, that this hemifield method can be useful in examining the role of the retino-tectal pathway, and can converge with studies of patients with lesions of the superior colliculus.

We began these investigations with the hypothesis that exogenous orienting is specifically linked to the colliculus, whereas endogenous orienting is a cortical function. Our results cannot be interpreted to support such a simple division of labor. Collicular lesions affected both exogenous and endogenous orienting. In normals, hemifield differences were found for orienting to both exogenous and endogenous information. The pattern that emerges from these results is that cortical and subcortical mechanisms interact with one another in orienting in response to both exogenous and endogenous information.

Because of its neuroanatomic connections, the collicular system is competent to orient only to signals in the temporal hemifield. In animals the nasal hemifield has little representation in the colliculus (Hubel et al, 1975; Pollack & Hickey, 1979). Newborn human infants, in whom the retino-tectal pathway is well established, but who lack a fully developed geniculo-striate pathway, seemed to orient with saccadic eye movements only to stimuli in their temporal hemifield (Lewis et al, 1979). In considering a system in which cortical and subcortical centers interact, it would seem to be appropriately adaptive that cortical systems might compensate for the lack of nasal hemifield competence of the collicular system by being biased toward the nasal hemifield. The results of Experiment 2, using a central arrow (endogenous) cue, are consistent with such an arrangement. Orienting toward the nasal hemifield occurred more quickly and required more commitment of limited capacity attention resources.

In Experiment 3, we sought to determine whether the cortical system, operating on information from geniculo-striate input, played a role in

orienting to exogenous sensory signals which had no predictive value. Since nasal hemifield cues summoned attention (as indexed by speeding of RT to targets following valid cues) as efficiently as temporal hemifield cues, we concluded that cortical systems are involved in exogenous orienting. The commitment of the cortical system to exogenous orienting was found, again, to require relatively greater limited capacity attention resources resulting in greater slowing to reorient to unattended locations.

In summary, the results of these experiments in neurological patients and normal human subjects support a model in which cortical and subcortical visual centers interact in orienting to both exogenous and endogenous information. Since subcortical centers have more direct access to input from the temporal hemifield, cortical centers are biased to orient toward the nasal hemifield. Furthermore, commitment of the cortical system appears to require limited capacity attention resources to a greater degree than does the subcortical midbrain system, and its commitment results in slower reorienting to detect targets elsewhere.

This model must be considered to be tentative. In our hemifield experiments, no neutral cue was used, so that we did not measure costs and benefits directly. We did conduct a control experiment in six normal subjects tested monocularly in which no cue was given. No difference was found in RT to detect targets in the nasal and temporal hemifields. Nevertheless, in our cue experiments, we could not be sure whether the effects of cueing on detection in the two hemifields were due to the direction toward which attention was summoned by the cue, or were related to the hemifield toward which attention had to be reoriented after the appearance of the target. It will be necessary to measure the effects of nasal and temporal orienting on the reorienting to detect central targets to resolve this question. Finally, our use of the term "cortical" and "subcortical" are somewhat arbitrary. The colliculus and striate cortex are connected with one another both directly, and through relays through pulvinar nucleus of the thalamus. While our results suggest an interaction between cortical and subcortical centers, specification of the neural basis for this interaction will require further investigation. The approach of seeking converging evidence from chronometric studies of neurological patients and normal subjects offers a promising avenue of investigation in attacking this kind of fundamental issue in cognitive neuroscience.

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