PERGAMON

Neuropsychologia 37 (1999) 511–520

NEUROPSYCHOLOGIA

The temporal order judgment paradigm: subcortical attentional contribution under exogenous and endogenous cueing conditions

David H. Zackon[a,*], Evanne J. Casson[a], Aftab Zafar[a], Lew Stelmach[b,c], Lyne Racette[a,c]

[a] *University of Ottawa Eye Institute, 501 Smyth Road, Ottawa, Ontario, Canada K1H 8L6*
[b] *Communications Research Centre, 3701 Carling Avenue, Ottawa, Ontario, Canada K2H 8S2*
[c] *Carleton University, 1125 Colonel By Drive, Ottawa, Ontario, Canada K1S 5B6*

Received 28 January 1998; received in revised form 8 October 1998; accepted 8 October 1998

Abstract

The role of subcortical attentional processing was investigated under exogenous and endogenous cueing conditions. As retinotectal projections arise predominantly from the nasal retina i.e., temporal hemifield, subcortical attention should be distributed asymmetrically under monocular viewing conditions with a temporal hemifield advantage. We compared the results of monocular and binocular viewing conditions using a temporal order judgment (TOJ) paradigm. Subjects fixated a centrally located cross and two stimuli were presented with a variable onset asynchrony. Three experiments were conducted: no cue, exogenous cue and endogenous cue. Subjects reported which stimulus seemed to appear first. An effect consistent with subcortical processing was found under exogenous cueing conditions. No such effect was found under endogenous cueing conditions. We believe that subcortical attentional processing in response to an exogenous cue facilitates rapid shifts in attention towards environmental stimuli. We found no evidence for subcortical processing in voluntary directed attention and believe this process to be cortical in nature.

Keywords: Visual attention; Subcortical processing; Visual pathways; Naso-temporal asymmetry

1. Introduction

Visual attention may be allocated in response to either endogenous or exogenous cues [10, 18]. Attention directed towards a peripheral stimulus in response to a symbolic cue presented at fixation is referred to as voluntary or endogenously oriented attention. In contrast, the sudden appearance of a sensory stimulus i.e., exogenous cue, acts to 'draw attention' to that cue. This process of automatically orienting attention towards a novel stimulus has been called exogenous or reflexive attention.

The superior colliculus is crucial for the proper generation of reflexive visually guided saccadic eye movements [7]. Chemical inactivation of the superior colliculus results in numerous deficits in saccadic eye movements including increased latency, decreased velocity and decreased accuracy [5]. In lower animals, it plays an important role in orienting towards a peripheral stimulus i.e., the visual grasp reflex [4]. This reflex is seen in animals with afoveate vision and has been shown to be part of a more general function of the superior colliculus in orienting the entire body towards a stimulus [9].

A similar situation may exist for the attentional system. Robinson and Kertzman [14] demonstrated that cells in the superficial layers of the superior colliculus are involved in the covert shift of attention towards an exogenous stimulus. These cells are activated in the performance of attentional tasks that are independent of eye movements. The response of these cells however is not modulated by endogenous attentional shifts. These results suggest that subcortical attention may function for exogenous rather than endogenous attentional shifts.

Additional evidence for subcortical attentional processing may be found in studies on inhibition of return (IOR). IOR is a phenomenon in which there is a delay in reaction to a stimulus presented at a recently cued location. Neurons in the superior colliculus which are activated in the performance of exogenous attentional shifts also show a delayed reaction to a stimulus presented at a recently cued location. Rafal et al. [12] found evidence in normal subjects for a subcortical origin of inhibition of return. IOR has been demonstrated for visual and auditory stimuli [16], mainly for localization tasks [8]. IOR is not observed when the dependent measure

* Corresponding author. Tel.: +1 613 737 8147; e-mail: dzackon@aix1.uottawa.ca

0028–3932/99/$ - see front matter
PII: S0028-3932(98)00134-1

involves making a perceptual judgment [3, 15]. This is consistent with a subcortical role in localization responses when a subsequent motor response is directed towards the stimulus. No effect has been found when a perceptual judgment as to the nature of the stimulus is required [8].

Indirect evidence for subcortical attentional processing may be found when subjects are tested under monocular conditions. There is a lateralized neuro-anatomic arrangement of retino-tectal fibers that diverges from the arrangement of retino-geniculo-striate projections. Although the striate cortex receives relatively equal projections from both the nasal and temporal retinas, subcortical structures receive predominant input from the nasal retinas i.e., temporal hemifields [6]. As a result, the visual hemifields are equally represented in the cortex but the temporal hemifield is over-represented subcortically (Fig. 1). A subcortical attentional effect should be apparent under monocular testing conditions in which one can compare the results of stimulus presentation to the nasal and temporal hemifields. Demonstration of a temporal hemifield advantage in attention tasks using monocular stimulus presentation is indicative of subcortical processing.

Rafal et al. [13] found a temporal hemifield advantage in a reaction time task in which subjects were asked to respond to a flash of light either by a manual button keypress or by making a saccade towards the light. These tasks were performed monocularly and the appearance of the light was preceded by a peripheral cue in either the nasal or the temporal hemifield. A temporal hemifield advantage was found for these tasks (which both required a motor response from the subjects) indicating a role for the midbrain in overt orientation movements towards a stimulus. They proposed that the superior colliculus was involved in such attentional shifts in humans. The finding of a temporal hemifield advantage in these tasks provides additional support for a subcortical role in overt orientation movements towards a stimulus. The question remains as to whether subcortical activity is limited to the processing required to enable motor activity or whether subcortical structures play a role in attentional shifts in isolation from motor responses.

Recently, we found evidence of subcortical attentional processing in isolation from motor responses using a motion induction task [21]. We used a split priming motion induction paradigm in which priming cues are

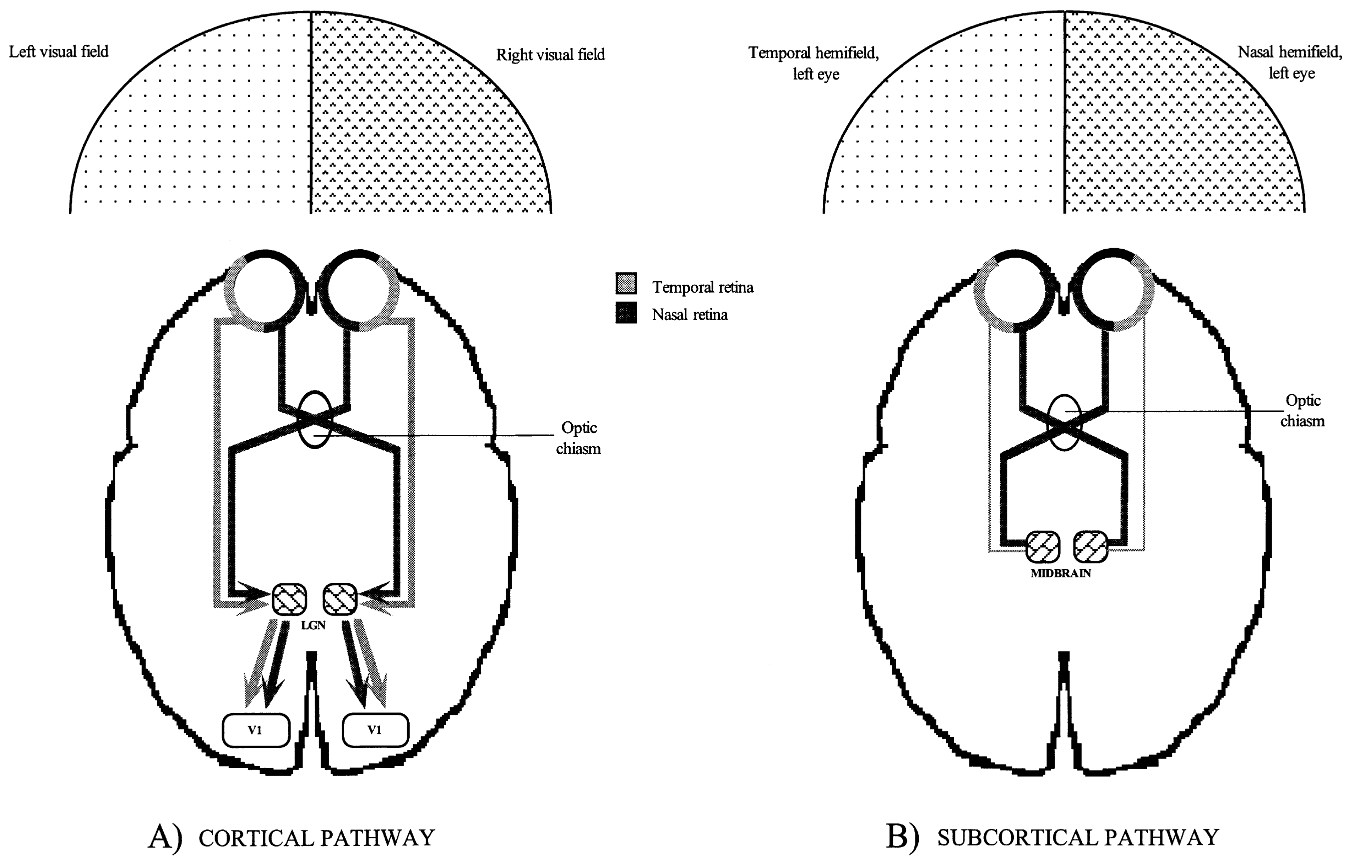

Fig. 1. Schematic representation of projections from retina to cortex and subcortical structures. Retinal projections undergo an approximately 50 : 50 hemi-decussation in the optic chiasm. The geniculo-striate pathway therefore contains relatively equal projections from the corresponding points in the nasal and temporal retinas of the two eyes (Panel A). Subcortical structures receive predominantly 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 (Panel B).

presented to either side of fixation followed by an instantaneously presented bar. As a result of attention to the priming cues, motion is perceived within the bar as it appears to draw in from two lateral cues towards a central collision point. Using monocular stimulus presentations, we found results consistent with subcortical attentional processing when the initial cue presentation was in the temporal hemifield of the left eye. This task was purely perceptual and no motor response was called for. Trials in which a saccade occurred were eliminated from the data. We interpreted our results as indicating a complex interaction between subcortical and cortical processing. Indeed, it has been shown that the resulting motion percept can be altered by exogenous or endogenous attentional manipulations. It remains controversial whether this apparent motion effect is due to attention or to a mediating effect of attention upon the binding, or impletion process, of the cue to the succeeding line to give a unitary percept of a single object in apparent motion [2].

These results suggest that subcortical structures are involved in attention in isolation from eye movements. The observed naso-temporal asymmetry was thought to implicate the superior colliculus of the midbrain in attentional processing [13, 21]. However Williams et al. [20] failed to show any naso-temporal asymmetry in retinal projections to the midbrain. They suggest that other subcortical structures such as the pulvinar and the accessory optic nuclei receive asymmetric projections from the nasal and temporal retinas.

The purpose of the present study was to further define the role of subcortical structures in human attention. Visual search is accomplished by both exogenous shifts of spatial attention in response to the sudden occurrence of an external event (i.e., a flash of light, a sound or a movement) and also by voluntary shifts of attention resulting from cognitive processing. We designed this study to look for evidence of subcortical processing in a temporal order judgment (TOJ) task under both exogenous and endogenous cueing conditions.

Kustov and Robinson [9] have shown that subcortical structures are important in shifts of attention when followed by a motor response to the stimulus. When the attentional shift results from an exogenous cue, the response is strong and early suggesting a close linkage between the stimulus and the subsequent motor response. Endogenous cues result in a more gradual response suggesting involvement of cortical processing. We used a TOJ paradigm to determine the role of subcortical structures in a purely perceptual task in which no eye movements are called for. While Posner and Cohen [11] did not find a temporal hemifield effect in a TOJ task in which attention was not manipulated, the TOJ paradigm has been found to be sensitive to attentional manipulations [17].

We presented two flashes of lights, one to either side of fixation, either simultaneously or with a variable interstimulus asynchrony. Stimulus onset was preceded either by an exogenous cue presented at the location of one of the stimuli or by a central arrow pointing towards one side and thereby inducing voluntary directed attention (endogenous cue). Under monocular conditions, the subcortical attentional effect should be greatest in the temporal hemifield. If this effect is evident in the TOJ paradigm, cues presented in the temporal hemifield should produce a greater attentional shift than cues presented in the nasal hemifield. It was our hypothesis that a subcortical attentional effect would be found for exogenous but not for endogenous cues.

2. Materials and methods

2.1. Materials

Stimuli were presented on an IBM Tektronix 608 point plotter equipped with P15 phosphor and controlled by a 486 PC. Eye movements were monitored with the ISCAN RK-416 pupil-tracking system (ISCAN, Cambridge, MA, U.S.A.) with noise-reduction software and eye magnification optics. Trials on which an eye movement (horizontal or vertical) greater than 0.25° occurred were rejected. The horizontal resolution of the pupil-tracking system, corresponding to a 1-unit change in its response, was 0.065° or approximately 4 min of arc. A 0.25° eye movement generated a 3.9-unit response, which was easily detectable by the system. Trials on which fixation was unstable were rejected and re-run at a later point within each session. Monitoring eye movements ensured that hemifield presentation was accurate, and that the effects observed did not involve an ocular motor response.

2.2. Subjects

Ten subjects were tested in each experiment (with six subjects participating in all three experiments). All subjects were between 16 and 26 years of age. The mean age was 22.4 years in Experiment 1 (no cueing) and Experiment 2 (exogenous cueing) and 22.1 years in Experiment 3 (endogenous cueing). Subjects 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 minimally compensated and were required to provide informed consent prior to participation in the study.

3. Experiment 1 (No cue)

3.1. Stimuli and Procedure

The temporal order judgment (TOJ) paradigm was used in all three experiments. In this paradigm, subjects report which of two stimuli seems to appear first. The basic temporal order judgment paradigm (Fig. 2) was used in Experiment 1 to show that, in the absence of priming cues, subjects were able to make temporal order judgments without any bias related to hemifield of presentation. Subjects were required to fixate on a centrally located cross (0.37° of visual angle), and to initiate each trial by clicking a specific button on a button box. Two stimuli then appeared in the centre of an area delimited by markers (dashed lines which formed a square). Stimuli were presented either simultaneously or with a 25, 50, 75, 100, 150, or 200 ms asynchrony. The left and right stimuli were presented first equally often, in random order. Five trials were run for each of the resulting 13 conditions. Overall 65 trials were run in each session. Subjects were tested under both monocular (left eye and right eye) and binocular viewing conditions. A total of 130 trials were run for each viewing condition, and each subject was tested in 390 trials. Subjects were required to indicate, in a forced-choice manner, which stimulus seemed to appear first by depressing either the left or right button on a button box. All experiments were conducted in a dimly lit room with the head positioned in a headrest located 38.5 cm in front of the display.

3.2. Results and discussion

A two-way analysis of variance (ANOVA) was run on the data from Experiment 1, which are illustrated in Fig. 3. Thirteen levels of inter-stimulus asynchrony were included in the analysis (0, and left and right stimuli presented first by 25, 50, 75, 100, 150 and 200 ms). Three levels of presentation hemifield were tested (temporal, nasal and binocular). The dependent variable was the number of correct responses i.e., the number of times subjects correctly reported either the left or right stimulus as having appeared first. The results show a significant effect for inter-stimulus asynchrony ($F(12,351) = 27.04$, $P < 0.001$). As the asynchrony between the two stimuli increased, subjects made increasingly more accurate temporal order judgments. This shows that overall, subjects were able to perform the TOJ task appropriately. No significant difference was found for presentation hemifield in the absence of priming cues. No significant interaction was found between inter-stimulus asynchrony and presentation hemifield. These results replicate those of Posner and Cohen [11] indicating that in the absence of an attentional manipulation, temporal order judgments do not show a temporal hemifield effect.

4. Experiment 2 (Exogenous cue)

4.1. Stimuli and procedure

The procedure in Experiment 2 was identical to that of Experiment 1, with the exception that an exogenous attentional cue was introduced. The cue consisted in the

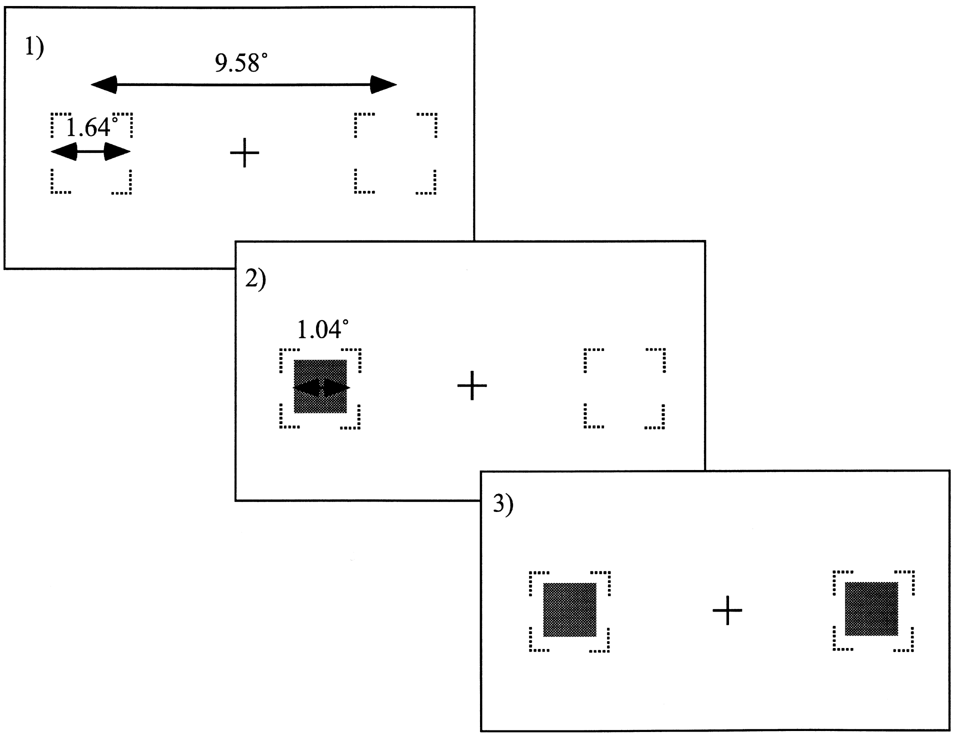

Fig. 2. Illustration of the basic temporal order judgment paradigm used in Experiment 1 (no cues). Subjects fixated on the centrally located cross and initiated each trial. Two stimuli were presented either simultaneously or with a variable onset asynchrony. The left and right stimuli appeared first equally often and in random order. Subjects reported which stimulus was perceived as having appeared first. Eye movements were monitored.

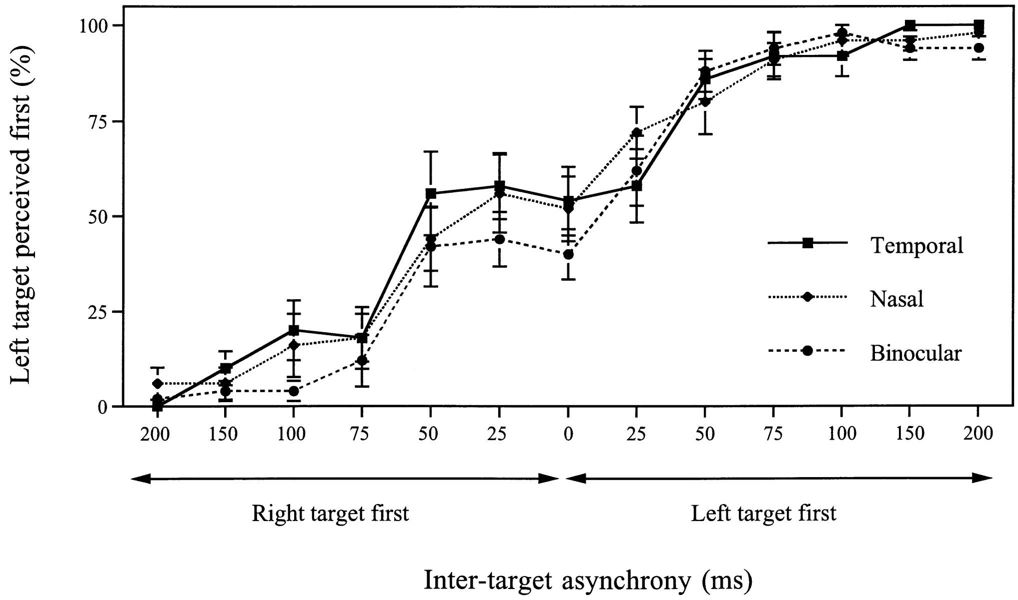

Fig. 3. Percentage left stimulus perceived first as a function of inter-stimulus asynchrony for temporal, nasal and binocular presentation hemifield presentation in Experiment 1 (no attentional cue). The right stimulus appeared first on half the trials and the left stimulus appeared first on the other half.

brightening in one of the markers surrounding the stimulus (Fig. 4, Panel A). The cue was presented randomly either to the left or right side of fixation at various cue-stimulus asynchronies (either simultaneously, or with a 50, 150 or 300 ms asynchrony). The two stimuli were presented either simultaneously or with a 60 ms asynchrony equally often to the right and left of fixation. Subjects were tested both monocularly and binocularly and had to indicate in a forced-choice manner which stimulus seemed to appear first by depressing either the left or right button on a button box. Two sessions were run for each viewing condition (right eye, left eye and binocular presentations). The order of the six sessions was randomized and each session consisted of 64 trials

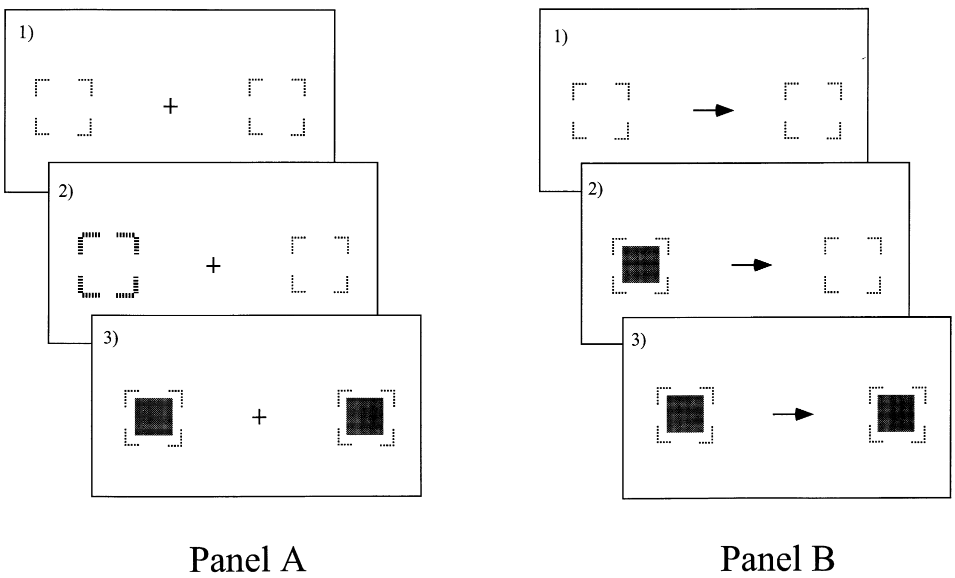

Fig. 4. An illustration of the temporal order judgment paradigm with exogenous (Panel A) and endogenous (Panel B) attentional cues. The exogenous cue consisted of a brightening of one of the markers surrounding the stimulus. In the endogenous condition, subjects were required to shift attention to the side towards which a central arrow was pointing. In both attentional conditions, stimuli were presented either simultaneously or with a variable onset asynchrony. Subjects reported which stimulus appeared first.

(32 for simultaneous stimulus presentation and 32 for asynchronous presentations). Overall, 384 trials were conducted per subject.

4.2. Results and discussion

The results for temporal, nasal and binocular hemifield presentations for simultaneous stimulus presentation are illustrated in Fig. 5 (the dependent variable is the percentage of left stimulus perceived first). The results for all inter-stimulus asynchronies and viewing conditions are presented in Table 1. For the purposes of Table 1 and of the statistical analysis, the dependent variable is the percentage of cued stimulus perceived first i.e., the percentage of left stimulus perceived first when the attentional cue was presented to the left and the percentage of right stimulus perceived first when the cue was presented to the right. The results for the 60 ms asynchrony were not included in the analysis, as the attentional effect is better isolated in simultaneous stimulus presentations. To determine the effect of cue-stimulus asynchrony on temporal order judgments, a one-way ANOVA was conducted on the data for simultaneous stimulus presentations. Seven levels of cue-stimulus asynchrony were included in the analysis (simultaneous cue-stimulus presentations, 50, 150 and 300 ms to both the left and right side of fixation). A significant effect of cue-stimulus asynchrony was found ($F(6,233) = 14.95$, $P < 0.001$). This result shows that the attentional effect of the cue becomes greater with increasing cue-stimulus asynchrony.

To determine whether stimulus presentation to the monocular temporal hemifield increases this attentional effect, a Wilcoxon signed rank test was performed on the data from the simultaneous condition (this non-parametric procedure was used as both the normality and equal variance assumptions of the ANOVA were violated). The Wilcoxon signed rank test compared the temporal and nasal hemifield results to those obtained under binocular viewing conditions. This analysis showed that temporal hemifield presentations differ significantly from binocular presentations ($W = -491$, $P < 0.05$). No such difference was observed between nasal and binocular presentations. Therefore, a temporal hemifield advantage was found with exogenous cueing which suggests that subcortical structures are involved in exogenous attentional processing.

5. Experiment 3 (Endogenous cue)

5.1. Stimuli and procedure

Experiment 3 was identical to Experiment 2, with the exception that an endogenous rather than an exogenous cue was used. The central fixation cross was replaced by an arrow which randomly pointed either to the left or to the right (Fig. 4, Panel B). Subjects were instructed to shift their attention to the stimulus indicated by the direction in which the arrow was pointing. When ready, subjects initiated each trial by depressing a button on a button box. Stimuli were presented either simultaneously or with a 60 ms asynchrony. When an asynchrony was introduced between the two stimuli, the left and right stimuli appeared first equally often. Subjects had to

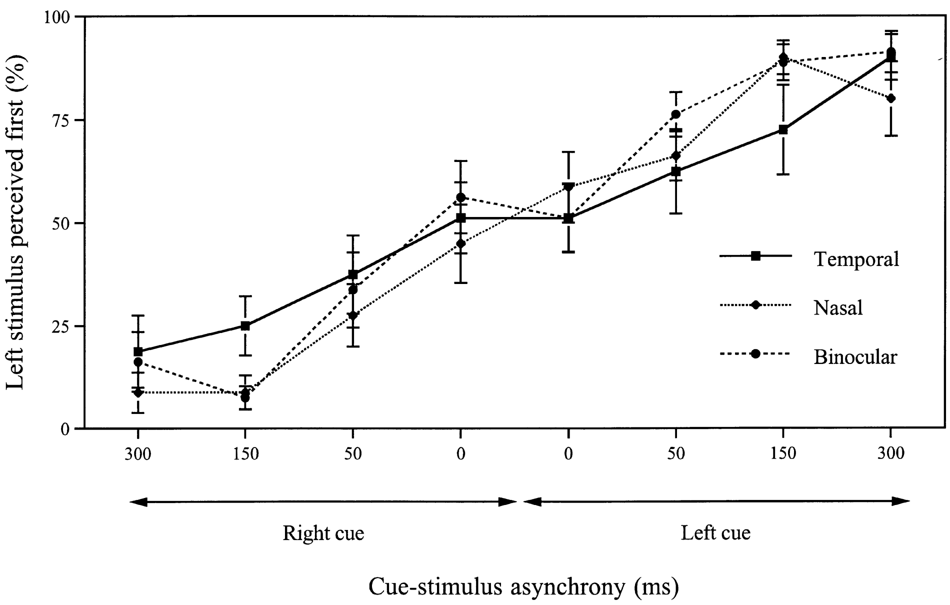

Fig. 5. Results from simultaneous stimulus presentations in Experiment 2 (exogenous cue), showing the percentage of cued stimulus perceived first as a function of the cue-stimulus asynchrony. Results for temporal, nasal and binocular viewing conditions are presented for both right and left cue presentation.

Table 1
Mean and standard error of cued stimulus perceived first (%) for all conditions in Experiment 2 (exogenous cues)

Inter-stimulus (ms)	Cue-stimulus (ms)	Temporal hemifield Mean (%)	SE	Nasal hemifield Mean (%)	SE	Binocular Mean (%)	SE
−60	−300	90.00	4.08	97.50	2.50	97.50	2.50
	−150	95.00	3.33	95.00	3.33	92.50	3.82
	−50	70.00	9.72	90.00	5.53	82.50	7.50
	−0	72.50	8.70	65.00	7.64	87.50	5.59
	0	37.50	10.70	35.00	10.67	45.00	9.72
	50	67.50	9.90	67.50	8.38	55.00	10.41
	150	77.50	10.17	77.50	7.86	70.00	9.72
	300	70.00	12.80	75.00	9.86	75.00	12.91
Mean		72.50	3.60	75.31	3.31	75.63	3.44
0	−300	90.00	5.53	80.00	8.98	91.25	4.95
	−150	72.50	10.83	90.00	4.08	88.75	4.35
	−50	62.50	10.21	66.25	5.91	76.25	5.42
	−0	51.25	8.43	58.75	8.55	51.25	8.22
	0	48.75	8.63	55.00	9.54	43.75	8.79
	50	62.50	9.50	72.50	7.64	66.25	9.14
	150	75.00	7.22	91.25	4.19	92.50	2.76
	300	81.25	8.79	92.50	5.00	83.75	7.23
Mean		67.97	3.33	75.78	2.85	74.22	3.00
+60	−300	72.50	14.17	80.00	10.41	82.50	7.50
	−150	85.00	8.50	82.50	5.34	80.00	7.27
	−50	47.50	12.61	60.00	9.28	60.00	6.67
	−0	40.00	12.47	45.00	11.67	57.50	8.38
	0	80.00	6.24	80.00	8.17	80.00	10.41
	50	82.50	6.51	80.00	8.98	77.50	8.70
	150	92.50	3.82	97.50	2.50	97.50	2.50
	300	90.00	5.53	85.00	6.67	95.00	3.33
Mean		73.75	3.80	76.25	3.30	78.75	2.89

report which stimulus seemed to appear first. Three viewing conditions were tested (temporal hemifield, nasal hemifield, and binocular presentation). Two sessions per viewing condition were run. Each session consisted of 48 trials (16 simultaneous stimuli, 16 left stimulus first and 16 right stimulus first). Overall, each subject underwent 288 trials.

5.2. *Results and discussion*

One concern in the endogenous condition was to ascertain that subjects were indeed shifting attention to the side indicated by the arrow. If subjects did not shift their attention, the results would be meaningless with regards to an attentional effect. To ensure that subjects were shifting attention according to the arrow, a two-way ANOVA was conducted on the data obtained for simultaneous stimulus presentation. The dependent variable was the percentage of left stimulus perceived first. A significant effect of attentional locus (left or right of fixation) was found ($F(1,234) = 162.21$, $P < 0.001$), indicating that a greater percentage of left stimulus were perceived first when the arrow pointed left and that a greater percentage of right stimulus were perceived first when the arrow pointed to the right.

It is possible that a response bias was introduced by the arrow cue i.e., subjects may have reported perceiving more left stimulus first when the arrow was pointing left, and more right stimulus first when the arrow was pointing right, based solely on the direction of the arrow. To rule out this possibility, a Wilcoxon signed rank test was performed on the data from those trials on which the first stimulus appeared on the side opposite to where the arrow was pointing (under asynchronous stimulus presentation conditions). If a bias associated with the arrow was present, the response pattern should be consistent with the direction to which the arrow was pointing (and not with which stimulus appeared first). We hypothesized that more left stimuli would be perceived first when the left stimulus was presented 60 ms prior to the right stimulus (arrow pointing right); similarly more right stimuli would be perceived first when the right stimulus was presented 60 ms prior to the left stimulus (arrow pointing left). The results indicate that when a 60 ms inter-stimulus asynchrony is introduced, subjects subjectively perceive the initial stimulus as appearing first, even when the arrow is pointing in the direction opposite to the first stimulus ($W = -393$, $P < 0.001$). This indicates that no response bias was associated with the arrow cue. Furthermore, this suggests that subjects were indeed shifting attention to the side indicated by the arrow (in both the simultaneous and 60 ms inter-stimulus asynchrony conditions). Considering the anatomical asymmetry between retino-tectal and retino-striate projections and the fact that endogenous attention was indeed engaged in the task, the lack of a temporal hemifield advantage suggests the absence of subcortical involvement in endogenously oriented attention.

Figure 6 illustrates the percentage of right stimulus perceived first in the simultaneous stimulus presentations in Experiment 3. The complete data set is presented in Table 2. A one-way ANOVA on ranks (Kruskal-Wallis) was conducted on the data obtained in the simultaneous stimulus presentation. Three levels of viewing condition were included in the analysis: temporal, nasal and binocular presentations.

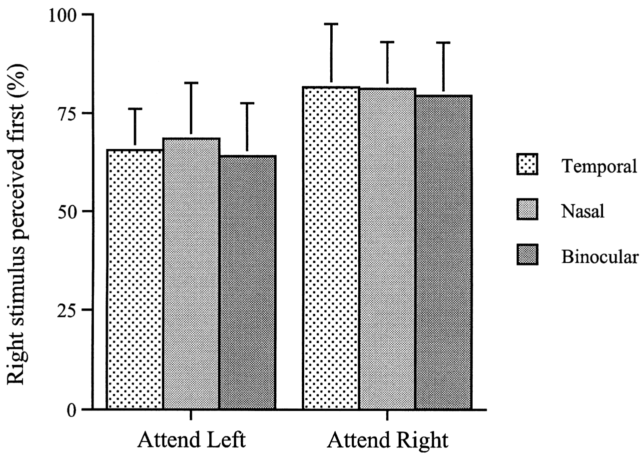

Fig. 6. The results for simultaneous stimulus presentations in Experiment 3 (endogenous cue) are illustrated. The percentage of right stimulus perceived first is plotted as a function of viewing condition (temporal, nasal and binocular).

No significant effect of presentation hemifield was found. This negative result was predicted and indicates the absence of a temporal hemifield advantage when endogenous cueing is used in a temporal order judgment task. Endogenous cues require that subjects voluntarily shift attention to a specific location, and such a complex process does not seem to be influenced by subcortical processing.

6. General discussion

The purpose of this study was to further delineate the role of subcortical structures in attentional processing—specifically to determine if these structures function in the attentional response to both exogenous and endogenous cues. We have previously shown a role for subcortical processing in the induced motion paradigm where the response was a perceptual judgment [21] rather than a motor response.

In the absence of a cue (Experiment 1), there was no perceptual hemifield advantage, and subjects performed equally well under both monocular and binocular viewing conditions. That is to say, that there was no bias towards either side and that there was no difference in response under temporal, nasal or binocular viewing conditions. This experiment demonstrates that our results are not artifactual in nature, but rather due to the cueing conditions. Accuracy improved as the inter-stimulus asynchrony increased. The absence of a temporal hemifield effect indicates that, in the absence of a cue, subcortical processing does not affect the judgment of temporal order.

Experiments 2 and 3 demonstrated that if attention is drawn towards one side by the presentation of a cue—either exogenous or endogenous—prior to the onset of two simultaneously presented stimuli, subjects tend to perceive the stimulus on the attended side as having appeared first. These results replicate previous work [17] showing that perception of temporal order is sensitive to attentional manipulation. We further showed that there is no difference in results between cue presentation to

Table 2
Mean and standard error of cued stimulus perceived first (%) for each inter-stimulus asynchrony in Experiment 3 (endogenous cues)

Inter-stimulus (ms)	Attentional locus (ms)	Temporal hemifield Mean (%)	SE	Nasal hemifield Mean (%)	SE	Binocular Mean (%)	SE
−60	Left	85.63	4.76	85.63	6.53	86.88	5.31
	Right	75	7.10	74.38	3.89	88.75	6.10
0	Left	68.75	4.37	63.13	5.47	73.75	5.50
	Right	36.88	8.36	43.75	7.34	41.25	5.98
+60	Left	29.38	9.41	31.25	7.68	25.63	8.86
	Right	13.75	4.55	17.50	6.44	7.5	3.20

the monocular nasal hemifield vs cue presentation in the binocular condition in either the exogenous or endogenous cue conditions.

In Experiment 2, when the exogenous cue was presented to the monocular temporal hemifield, we observed a shift in the response curve towards shorter cue-stimulus asynchronies—that is to say that the attentional effect of cue presentation seems to bring the cue and the stimulus closer together in time. For example in Experiment 2, at 150 ms, subjects' temporal order judgments were similar to that seen at shorter cue-stimulus asynchronies. It has been suggested that the effect of attention is to increase the speed of transmission of visual information [17] such that attended stimuli reach the cortical visual areas prior to non-attended stimuli. If the subcortical attentional effect was due to faster transmission speed of the cued stimulus, we would have recorded more right first responses when the cue was presented in the temporal hemifield of the right eye and more left first responses when the cue appeared in the temporal hemifield of the left eye. However the opposite was observed: a lesser number of stimuli were perceived as appearing first when the cue was presented to the temporal hemifield.

We observed this effect in the motion induction paradigm as well [21]. The analogy we used in that paper applies here as well. The creation of an attentional field by a cue acts as a magnet to attract subsequent stimuli to that cue, such that cue and stimulus appear to have been presented closer together in time. Exogenous cues seem to 'compress' the time interval between the cue and stimulus, linking them closer together in time. And so increased speed of processing does not account for the results obtained in our previous study [21], nor those obtained in the present study. Subcortical attention does not appear to influence the speed at which information is processed and transmitted, but rather appears to jointly affect the processing of both cue and stimulus such that both are perceived as having been presented closer together in time.

Notwithstanding the usual concurrence of fixation and attention upon the same object, both animals and humans must remain alert (attentive) to exogenous stimuli appearing within the peripheral visual field which may call for a shift in attention. In Posner's three step theory of attention [10], a shift in attention would necessarily be precipitated by either the exogenous appearance of a peripheral stimulus or by an internally generated command. We suggest that the circuitry responsible for voluntary directed attention is dependent upon cortical pathways and that this system is superimposed upon an older subcortical platform subserving exogenous orienting of attention.

These two attentional systems likely function in concert. Braun and Sagi [1] demonstrated that it is possible to simultaneously perform two tasks, a discrimination task requiring directed attention and a detection/localization task requiring feature gradient registration. In contrast, two tasks both requiring the allocation of focal attention can be simultaneously performed but must have attention allocated sequentially. The ability to simultaneously process information about salient boundaries and singularities in one location while allocating attentional resources towards an object elsewhere in the environment suggests the ability to sample information from more than one spatial location with the limitation that detailed processing can only be allocated to one location. This corresponds with our everyday experience that while driving, for example, one generally directs focal attention to a central area while retaining the ability to rapidly redirect attention and gaze to other stimuli present in the periphery. Anatomically, simultaneous processing of detection tasks on the one hand and discrimination tasks on the other may be due to subcortical and cortical processing respectively.

Similar implications may be drawn from a study by Yantis and Jonides [18]. They looked at the extent to which abrupt onsets automatically draw attention towards the spatial location of the cue. The effectiveness of the cue was manipulated by varying either its duration or its predictive validity. They found that the attentional state of the subject determines the extent to which an abrupt onset stimulus will automatically capture attention. When subjects are in a diffuse attentional mode, a strong effect of abrupt onset is seen. On the other hand, when subjects are in a highly focused attentional state, attention is less likely to be captured by a suddenly appearing cue. Taken together, these two studies indicate that attention is not a unitary process. Exogenous suddenly appearing stimuli are subject to some degree of attentional processing even while one is engaged in another task necessitating voluntary directed attention.

Although subcortical processing largely remains in the shadow of dominant cortical voluntary attentional processing, it may assume a more dominant role in disease states where cortical processing becomes impossible. The phenomenon of blindsight in which patients with lesions involving striate cortex retain the ability to detect stimuli in their subjectively blind hemifield may be due to preservation of subcortical projections to extra-striate cortex [19].

In summary we have shown that perception of temporal order is influenced by exogenous cue presentation to the monocular temporal hemifield. Endogenous cue presentation directing attention to the monocular temporal hemifield does not influence temporal order judgments. These results indicate a role for subcortical attentional processing when attention is drawn by an exogenous cue but not for voluntary directed attention. We believe that subcortical processing enables one to rapidly redirect attention in response to suddenly appearing exogenous cues. Voluntary directed attention is presumably dependent upon cortical processing. Both systems likely interact to facilitate fast shifts of attention towards an environmental stimulus requiring immediate processing while maintaining cortical control to both override inappropriate attentional shifts and to direct attention to stimuli chosen as a result of cognitive processing.

Acknowledgements

This research was supported in part by the University of Ottawa Medical Research Fund. The authors wish to thank Greg Craig for his assistance with programming.

References

[1] Braun J, Sagi D. Vision outside the focus of attention. Percept Psychophys 1990;48:45–58.
[2] Downing PE, Treisman AM. The line-motion illusion: attention or impletion? J exp Psychol: Hum Percept Perform 1997;23:768–79.
[3] Gibson BS, Egeth H. Inhibition and disinhibition of return: Evidence from temporal order judgments. Percept Psychophys 1994;56:669–80.
[4] Hess WR, Bårgi S, Bucher V. Motorische funktion des tektal—und segmentalgebietes. Monatsschr Psychiatr Nevrol 1946;112:1–52.
[5] Hikosaka O, Wurtz RH. Modification of saccadic eye movements by GABA-related substances. I. Effect of muscimol and bicuculline in monkey superior colliculus. J Neurophysiol 1985;53:266–91.
[6] Hubel DH, LeVay S, Wiesel TN. Mode of termination of retinotectal fibres in macaque monkey: An autoradiographic study. Brain Res 1975;96:25–40.
[7] Keating EG. Impaired orientation after primate tectal lesions. Brain Res 1974;67:538–41.
[8] Klein RM, Taylor TL. Categories of cognitive inhibition with reference to attention. In: Dagenbach D, Carr TH, editors. Inhibitory Mechanisms in Attention, Memory and Language. New York: Academic Press, 1994.
[9] Kustov AA, Robinson DL. Shared neural control of attentional shifts and eye movements. Nature 1996;384:74–7.
[10] Posner MI. Orienting of attention. Q J Exp Psychol 1980;32:3–25.
[11] Posner MI, Cohen Y. Attention and the control of movements. In: Stelmach GE, Requin J, editors. Tutorials in motor behavior. Amsterdam: North Holland Publications, 1980.
[12] Rafal RD, Calabresi PA, Brennan CW, Sciolto TK. Saccade preparation inhibits reorienting to recently attended locations. J exp Psychol: Hum Percept Perform 1989;15:673–85.
[13] Rafal RD, Henik A, Smith J. Extrageniculate contributions to reflex visual orienting in normal humans: a temporal hemifield advantage. J Cognit Neurosci 1991;3:322–8.
[14] Robinson DL, Kertzman C. Covert orienting of attention in macaques. III. Contributions of the superior colliculus. J Neurophysiol 1995;74:713–21.
[15] Schmidt WC. 'Inhibition of return' is not detected using illusory line motion. Percept Psychophys 1996;58:883–98.
[16] Schmidt WC. 'Inhibition of return' without visual input. Neuropsychologia 1996;34:943–52.
[17] Stelmach LB, Herdman CM. Directed attention and perception of temporal order. J exp Psychol: Hum Percept Perform 1991;17:539–50.
[18] Yantis S, Jonides J. Abrupt visual onsets and selective attention: voluntary versus automatic allocation. J exp Psychol: Hum Percept Perform 1990;16:121–34.
[19] Weiskrantz L. Blindsight: A case study and implication. Oxford: Oxford University Press, 1986.
[20] Williams C, Azzopardi P, Cowey A. Nasal and temporal retinal ganglion cells projecting to the midbrain: implications for 'blindsight'. Neuroscience 1995;65:577–86.
[21] Zackon DH, Casson EJ, Stelmach L, Faubert J, Racette L. Distinguishing subcortical and cortical influences in visual attention. Invest Ophthalmol Vis Sci 1997;38:364–71.