Signals Invisible to the Collicular and Magnocellular Pathways Can Capture Visual Attention

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Summary

The retinal projection to the superior colliculus is thought to be important both for stimulus-driven eye movements and for the involuntary capture of attention [1–5]. It has further been argued that eye-movement planning and attentional orienting share common neural mechanisms [6–12]. Electrophysiological studies have shown that the superior colliculus receives no direct projections from short-wave-sensitive cones (S cones) [13–15], and, consistent with this, we found that irrelevant peripheral stimuli visible only to S cones did not produce the saccadic distractor effect produced by luminance stimuli [16, 17]. However, when involuntary orienting was tested in a Posner cueing task [18, 19], the same S-cone stimuli had normal attentional effects, in that they accelerated or delayed responses to subsequent targets. We conclude that involuntary attentional shifts do not require signals in the direct collicular pathway, or indeed the magnocellular pathway, as our S-cone stimuli were invisible to this channel also.

Results and Discussion

Spatial attention is often studied using a cueing paradigm introduced by Posner [18]: reaction times to targets that can appear in more than one location are generally shorter if a peripheral "cue" is presented 100–200 ms before the target appears at the same position, whereas responses are longer if the subsequent target appears away from the cued location [19]. The facilitation and inhibition of target detection persist even if the cues bear no relation to where the target will appear and if the subjects are instructed to ignore them. This type of involuntary effect is known as "exogenous orienting of attention". It is widely held that the superior colliculus, SC, is important for attentional orienting; the supporting evidence comes from brain-damaged patients [20–22], animal lesions [23], and, most compellingly, from interactions of attentional cues with saccades [9, 10]. In addition, the effects of exogenous orienting have been found to be larger when the cue appears in the

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temporal, rather than the nasal, visual field, and this asymmetry was attributed to the predominance of crossed fibers within the retinotectal projection to the SC [5]. Thus, it has been argued that the direct retinotectal pathway, rather than a cortical pathway, mediates automatic attentional capture. However, Williams et al. [24] have reported that, in macaques, the mean nasotemporal ratio in the collicular projection (1.57) is no different from the ratio of 1.54 for the whole optic nerve, which is dominated by the cortical projection. Therefore, nasotemporal asymmetry cannot be uniquely diagnostic of retinotectal mediation, and we present below a novel way to test whether an effect is mediated via the direct retinotectal route.

In the present experiments, we exploit the fact that electrophysiological studies have reported that there are no projections to the SC from color-opponent cells in the retina and, specifically, no projections from short-wave (S) cones at all [13–15]. In fact, S-cone signals may also be excluded from the magnocellular pathway [25, 26]. The S cones are thought primarily to subserve color perception [27], and their signals are carried by morphologically distinct types of retinal ganglion cells, which project to the koniocellular layers of the lateral geniculate nucleus and thence to layers 2 and 3 of the striate cortex [28, 29]. If there is S-cone input to the magnocellular pathway, as has been suggested by some researchers [30, 31], or even to the collicular pathway, it is small and, more importantly, it is not chromatically opponent and can therefore be masked using luminance noise [32, 33].

Our main finding, reported in experiment 2, is that luminance-masked chromatic S-cone signals produce normal involuntary attentional effects in a Posner cueing task. Thus, in contrast to a previous belief [5], signals in the direct pathway to the SC are not necessary for involuntary shifts of attention. But first we report an experiment on a different effect, the oculomotor distractor effect, which is also thought to be mediated by the direct collicular pathway. In this case, we obtained results consistent with direct collicular mediation.

Experiment 1: Oculomotor Distractor Effect

If subjects are asked to move their gaze to a target as soon as it appears and ignore all other stimuli, responses tend to be slower if an irrelevant stimulus appears simultaneously with the target. This is known as the "oculomotor distractor effect" [16, 17], and it is assumed that involuntary processing of the irrelevant stimulus must interfere with the planning and initiation of the saccade to the target. The superior colliculus (SC) is known to have a role in the initiation of saccadic eye movements [1, 2], and it has been suggested that SC cells activated by distractor stimuli inhibit SC cells activated in response to the saccade target [3]. The direct pathway to the SC has been held responsible for the distractor effect because the effect has been found for the blind field of cortically damaged hemianopes [4]. In addition, the
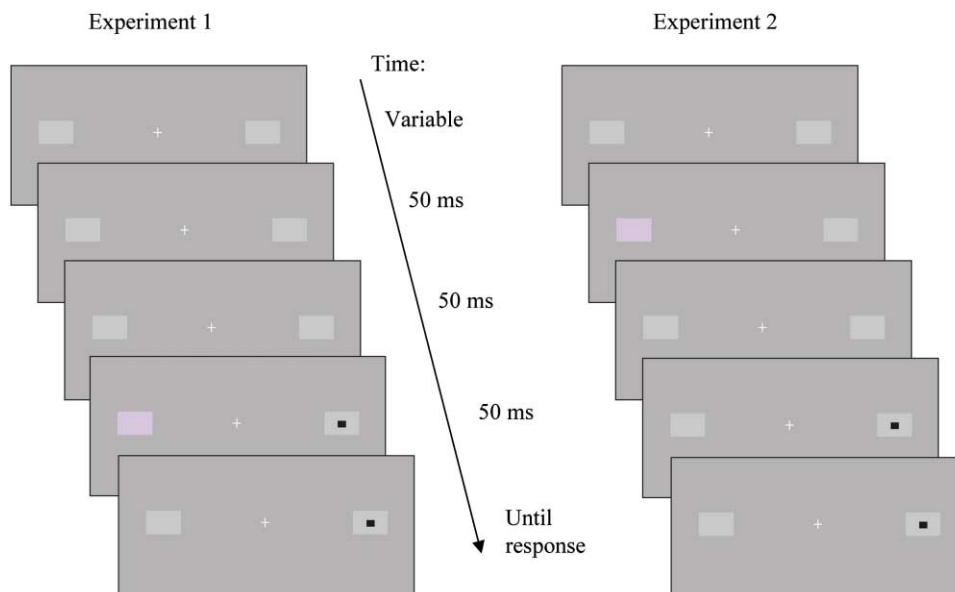
Experiment 1

Experiment 2

Figure 1. Comparison of Trials in Experiments 1 and 2

In both cases, the targets were small black rectangles, and the subjects were instructed to ignore all other stimuli. In Experiment 1, subjects made discriminatory saccades to the location of the target appearance. In Experiment 2, subjects responded with a single button release wherever the target appeared. Both of the examples shown have a contralateral S-cone task-irrelevant stimulus.

effect has been found to be larger when the distractor appears in the temporal, rather than the nasal, visual field [4, 17]. However, as discussed above, nasotemporal asymmetry may not be diagnostic of the retinotectal pathway, and, furthermore, Walker et al. (2000) [17] did not find the distractor effect in hemianopes. Therefore, the neural pathway mediating the distractor effect remains debated.

In experiment 1, we tested whether task-irrelevant stimuli visible only to S cones, and thus invisible to the direct retinotectal pathway, would produce an oculomotor distractor effect like that found for task-irrelevant luminance stimuli. Subjects were required simply to move their gaze as quickly as possible to small black targets that could appear either to the left or right of fixation and to ignore any other stimuli (see Figure 1). In 25% of the trials, the target was accompanied by a brief luminance increase either around the target location or on the opposite side of fixation. In another 25% of the trials, the target was similarly accompanied by a brief color change, which had been individually calibrated for each subject beforehand to be visible only to S cones by using the procedure of Smithson et al. [34]. The presence of temporal luminance noise ensured that the color changes could be detected only by a chromatic channel, and not by any luminance channel to which S cones might possibly contribute.

Since the error rate was very low (<3%) and there were no significant differences between conditions, the distractor effect for each kind of task-irrelevant stimulus can be defined as the difference between saccade latency with and without that stimulus. Figure 2 shows that only the contralateral luminance stimuli produced any effect (t = 4.2, df = 11, p < 0.01). The clear lack of a distractor effect from the S-cone stimuli is consistent

with mediation of the effect by either the direct retinotectal pathway or the magnocellular division of the geniculostriate pathway. Experiment 2 will show that it cannot be the case that the S-cone stimuli were simply much less salient than the luminance stimuli, and subjects reported that the irrelevant color changes were in fact much more salient than the irrelevant luminance stimuli. It is interesting in and of itself that our luminance stimuli produced an effect at all, despite the addition of temporal luminance noise, which might have acted as continuously presented distracting stimuli occurring even in "no-distractor" trials.

We also tested manual discriminatory (left/right) responses instead of eye movements and found no significant effects (data not included in figures: both ipsi- and contralateral luminance task-irrelevant stimuli slightly lengthened RT, but these effects were not reliable and were clearly different from the large and reliable effect for the saccade responses that occurred for only the contralateral distractor). This is consistent with previous research [4], and the fact that the effect depends on response modality supports the idea that the distractor effect is not a perceptual phenomenon but is caused by interference in the process of saccade planning [3]. In addition, we tested for a saccade distractor effect when the task-irrelevant stimuli were presented 100 ms after target onset, and, consistent with previous results [35], we found no effects. However, in contrast to previous studies [4, 17], we found no evidence of nasotemporal asymmetry for the simultaneous luminance distractors.

Experiment 2: Exogenous Orienting of Attention

The results of experiment 1 were entirely consistent with the standard view that initiation of saccades depends

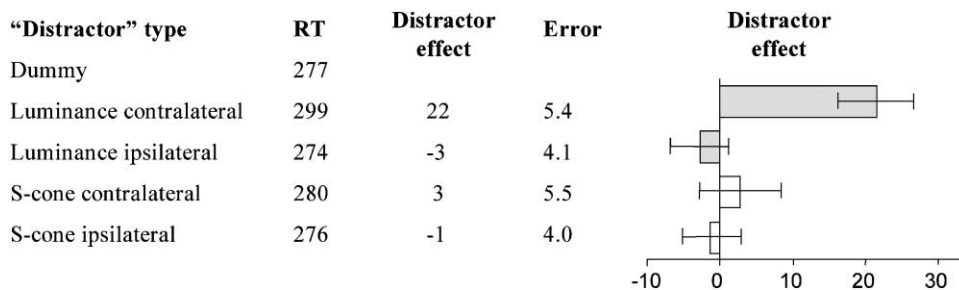| "Distractor" type	RT	Distractor effect	Error	Distractor effect
Dummy	277			
Luminance contralateral	299	22	5.4	
Luminance ipsilateral	274	-3	4.1	
S-cone contralateral	280	3	5.5	
S-cone ipsilateral	276	-1	4.0	

Figure 2. Summary of Results, in ms, for Experiment 1

The color and luminance of the dummy task-irrelevant stimuli were within the range of the constantly present luminance noise, and, thus, this was the no-distractor condition. Mean saccadic RT in the no-distractor condition is subtracted from mean RT in the other conditions to obtain the distractor effect for each type of irrelevant stimulus, and the third column shows the standard error of these differences for each subject. The distractor effects and their standard errors are illustrated in the bar chart.

on the SC and that signals from S cones do not gain direct access to the SC. Experiment 2 used a highly similar procedure (see Figure 1) to test whether task-irrelevant stimuli visible only to S cones would, like luminance cues, produce effects in an exogenous orienting paradigm: the task was again to detect black targets that could appear to the left or right of fixation, but, this time, the response was to release a single button as quickly as possible whenever and wherever a target appeared. Subjects were again instructed to ignore any other stimuli that might occur; but, in 25% of the trials, the targets were preceded by a brief increase in luminance in either the left or right location, and in another 25% of the trials, there was a brief change in color that had been calibrated to be visible only to that subject's S cones. As in experiment 1, these task-irrelevant stimuli (or cues) bore no relationship to where the target would appear. There was also a luminance decrement stimulus (25% of trials). The luminance changes (increments and decrements) were expected to replicate the exogenous cueing effects previously found, and the color changes that could be detected only by S cones were our test of direct collicular mediation.

Reaction times following ipsi- and contralateral task-irrelevant stimuli were compared in order to calculate the cueing effect (each type of cue could not be compared to the no-cue condition since the latter lacks the warning or arousing element produced by a stimulus that precedes a target. The no-cue condition was needed, however, for calculation of any nasotemporal asymmetries). Figure 3 shows that stimuli visible only to S cones pro-

duced an exogenous cueing effect (t = 3.29, df = 7, p < 0.01) comparable to that produced by luminance cues (increment, t = 2.03, df = 7, p < 0.05; decrement, t = 2.61, df = 7, p < 0.05). Thus, purely chromatic signals originating in the short-wave cones influence not only an observer's subjective judgements but also his or her covert orienting behavior — as defined operationally by the Posner cueing task — and we conclude that signals in the direct pathway to the superior colliculus are not necessary for the triggering of exogenous orienting. Our results would equally contradict a model in which exogenous orienting in the Posner task required a signal in the magnocellular pathway. There is some evidence that S cones may contribute slightly to the *luminance* signal in the magnocellular pathway [30, 31], and we do not rule out this possibility for the retinotectal route also. Even if this were the case, however, these pathways would still not be able to distinguish our S-cone stimuli from the luminance noise – only a chromatic pathway could do that.

The important result is that the S-cone stimuli produced an effect at all: we do not draw any strong conclusions from the relative sizes of the cueing effects because there is no secure way of matching luminance and chromatic stimuli (for example, multiples of threshold may be an inappropriate metric for stimuli that are not close to threshold). Unlike Rafal et al. [5], we found no evidence of nasotemporal asymmetry for either luminance or S-cone cues.

It has been argued by many researchers, especially on the basis of single-cell recordings, that the orienting

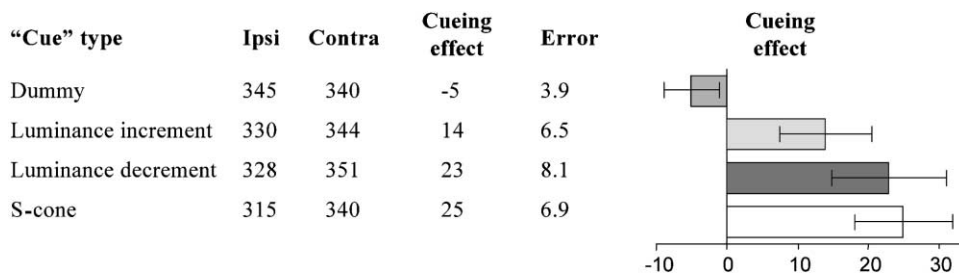| "Cue" type	Ipsi	Contra	Cueing effect	Error	Cueing effect
Dummy	345	340	-5	3.9	
Luminance increment	330	344	14	6.5	
Luminance decrement	328	351	23	8.1	
S-cone	315	340	25	6.9	

Figure 3. Summary of Results, in ms, for Experiment 2

The cueing effect, shown in the third column, is the difference between the mean manual RTs to targets following ipsi- and contralateral task-irrelevant stimuli (cues), and the fourth column shows the standard error of these differences for each subject. The cueing effects and their standard errors are illustrated in the bar chart.

of attention and the planning of eye movements share neural mechanisms (whether or not the direct retinotectal route is essential) [6–12]. Consistent with this idea are many reports of saccade-related cortical areas, such as frontal eye fields and parietal areas, being activated in attentional tasks [36–40]. Behaviorally, it has been found that both attention and eye movements are captured by stimuli that have an abrupt onset [41]. One might therefore expect that any stimulus capable of capturing attention should produce the oculomotor distractor effect, and vice versa, especially when the experimental conditions used are highly similar, as in the experiments reported above. However, we have found a dissociation between the effects of S-cone stimuli on saccade execution and on attentional orienting. Thus, while some attentional effects may share mechanisms with eye-movement control, it appears that others do not. One important difference between attentional mechanisms may lie in the distinction between automatic "exogenous" orienting and volitional "endogenous" orienting. Some imaging studies have suggested that the same or similar cortical areas are activated in the two types of task [42, 43], but the resolution of imaging is limited, and, behaviorally, distinctions between the effects of exogenous and endogenous orienting on manual and saccadic responses have been reported [44].

In summary, stimuli visible only to S cones did not produce a saccade distractor effect but did produce an exogenous cueing effect, while our luminance stimuli produced results similar to those of previous studies of saccade distraction and exogenous orienting, despite the addition of temporal luminance noise. Our strongest conclusion is that exogenous orienting does not require a signal in either the direct retinotectal pathway or in the magnocellular pathway.

Experimental Procedures

Both Experiments
Subjects monocularly viewed a Sony Trinitron 19 inch GDM-F400T9 monitor driven by a Cambridge Research Systems VSG 2/2 graphics board at 100 Hz. The screen background was gray (MacLeod-Boynton coordinates, MB, 0.643, 0.021) at a luminance of 12 cd m^{-2}, and two solid "guide boxes" (0.8° by 0.4°) were continuously displayed 5.5° to the left and right of fixation. These were the same chromaticity as the background and had a luminance that changed every 50 ms to a value drawn randomly from the range 24.2–27.8 cd m^{-2}. This luminance noise ensured that the color changes described below could be detected only by a chromatic S-cone channel [33]. The intertrial interval took a value randomly between 1000 and 2000 ms, but subjects saw constantly flickering guide boxes with the appearance of occasional targets rather than perceiving the trials as discrete units. Each novel calibration or experimental block was preceded by automated instructions and practice trials.

Because monitors and graphics boards show nonadditivities, and because the optics and absorption properties of the individual's eyes differ, equiluminant and S-cone matches were determined psychophysically for each stimulus in the appropriate retinal position and were determined for each eye of each subject by using the method developed by Smithson et al. [34] (additionally, our calibration procedure would have detected any color vision deficiency). Chromaticities and luminances were calculated from the spectra of each stimulus, which was measured directly with a PhotoResearch PR650 telespectroradiometer.

Experiment 1
In each trial, a small black target (0.4° by 0.3°) appeared in the center of one of the guide boxes and remained present until a response was made. Simultaneous with target presentation (the effect has been found to be largest for simultaneously presented distractors [35]), one guide box took, for 50 ms, a chromaticity and luminance value associated with one of three types of task-irrelevant-stimulus: 1) "dummy": gray with luminance within the noise limits (50% of trials); 2) "luminance increment": gray at 32 cd m^{-2} (25% of trials); 3) "S cone": a color change visible only to S cones (25% of trials). Each of the 12 naïve and untrained subjects (5 male, 7 female, aged between 15 and 56) performed 8 blocks of 64 trials. Eye movements were monitored with a Skalar IRIS limbal tracker, which was head mounted and secured to the chair back to prevent head movement. The left and right eyes were used alternately; in four consecutive blocks, the response required was a saccade to the target, and in the other half, a discriminatory manual key press (left or right) was required (subjects were instructed not to move their eyes). The starting response and starting eye were counterbalanced across subjects. For each response type, paired t tests separately compared the mean RT for the "dummy distractor" condition to the mean RT for each "distractor" type (ipsilateral luminance, contralateral luminance, ipsilateral S cone, contralateral S cone), and Bonferroni corrections for multiple tests were applied. All analyses on means were repeated for medians, and the same results were obtained.

Experiment 2
The targets were identical to those in Experiment 1, but subjects released a single Morse key to either target, rather than making a discriminatory response. One third of the trials were "catch trials" in which a target did not appear. In each trial, 100 ms before target onset, one guide box took, for 50 ms, a chromaticity and luminance value associated with one of four types of task-irrelevant stimulus (each 25% of trials): 1) "dummy" or "no-cue": gray with luminance within the noise limits; 2) "luminance increment": gray at 32 cd m^{-2}; 3) "luminance decrement": luminance of 20 cd m^{-2} and chromaticity shifted in the L-M direction by three times the maximum possible L-M error in the "S-cone" cue; 4) "S-cone": a color change visible only to S cones. Eight naive and untrained subjects (3 male, 5 female, aged between 20 and 30) performed two blocks of 240 trials with each eye in a counterbalanced order. An infrared camera was used to check that fixation was maintained on the central cross. A chin rest stabilized the head. Separately for each cue type, paired t tests compared the mean RT for ipsilateral and contralateral cues. All analyses on means were repeated for medians, and the same results were obtained.

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