Oculomotor Distraction by Signals Invisible to the Retinotectal and Magnocellular Pathways

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Bompas A, Sumner P. Oculomotor distraction by signals invisible to the retinotectal and magnocellular pathways. J Neurophysiol 102: 2387–2395, 2009. First published August 5, 2009; doi:10.1152/jn.00359.2009. Irrelevant stimulus onsets interfere with saccade planning to other stimuli, prolonging saccadic latency (the oculomotor distractor effect) or eliciting directional errors (saccadic capture). Such stimulus-driven interference has been associated with the retinotectal pathway, the direct pathway from retina to superior colliculus. Consistent with this theory, the distractor effect has not been found for stimuli visible only to the short-wave cones in the retina (S cones), which are thought not to contribute to the retinotectal pathway. However, S-cone signals are generally slower than luminance signals and such differences in temporal dynamics have not been taken into account when investigating the saccadic distractor effect. Here, by varying the delay between target and distractor, we found that S-cone stimuli do in fact produce a distractor effect, but the optimal delay is generally different from that for luminance distractors. The temporal dynamics of the distractor effect conform to a general framework of saccadic competition that takes sensory transmission time into account. Additionally, we observe that S-cone stimuli are able to produce saccadic capture in our paradigm. We conclude that stimulus-driven oculomotor interference does not rely on the retinotectal pathway, or indeed the magnocellular pathway, which is also blind to our S-cone stimuli.

INTRODUCTION

Sensorimotor competition and the oculomotor distractor effect

Initiating saccades (fast eye movements) is believed to entail competitive interactions between neurons representing different potential saccade directions. This competition involves a complex interplay between goal-directed factors and more automatic stimulus-driven impulses. The automatic impact of simple stimulus onsets can be seen, for example, by their effect when a saccade is required to a different location. An irrelevant stimulus (often called a “distractor”) generally delays the intended saccade and can sometimes entirely “capture” the saccade, so that it is directed toward the distractor, not the target. Such delays and errors are often referred to as the oculomotor distractor effect, remote distractor effect (RDE, because the distractor is remote from the target), or oculomotor capture and have been widely used as measures of sensorimotor competition and interference in the eye movement system (e.g., Born and Kerzel 2008a; Graupner et al. 2007; Griffiths et al. 2006; Honda 2005; Lévy-Schoen 1969; Ludwig et al. 2005; Theeuwes 1994; Theeuwes et al. 1998; Walker et al. 1995, 1997; White et al. 2005). Here we refer to the slowing of latency to the target as the “RDE” (or simply the distractor effect) and refer to saccades toward the distractor as “capture.”

A key structure for saccade planning and competition is the superior colliculus (SC), a midbrain center that makes the major input into the brain stem saccadic generator (Dorris et al. 1997; Sparks 1986). The SC contains a motor map of saccade endpoints and it is thought that when activity in one part of this map reaches some criterion level, a saccade to the corresponding location is initiated. Thus lateral inhibition between cell populations in the SC has been proposed as the source of the RDE, by delaying the buildup of activity favoring a saccade to the target (Findlay and Walker 1999; Godijn and Theeuwes 2002; Munoz and Itsvan 1998; Ollevier et al. 1999; Trappenberg et al. 2001; Walker et al. 1997). Capture would occur if activity for the distractor actually reaches threshold before activity for the target does (see e.g., Godijn and Theeuwes 2002; Leach and Carpenter 2001; Theeuwes et al. 1998).

Retinotectal mediation?

To have an impact on motor planning, visual signals must gain efficient access to the motor competition process even when they are irrelevant. The direct visual pathway from retina to colliculus is a natural candidate by which this might occur. This retinotectal pathway is phylogenetically older than the geniculostriate route, which is fully present only in mammals, and the retinotectal pathway has long been associated with various nonconscious and “low-level” stimulus-driven phenomena (e.g., Posner and Cohen 1980; Rafal et al. 1990; Weiskrantz 1986). Three pieces of evidence have specifically linked the RDE to the retinotectal pathway. First, the effect was found for the blind field of cortically damaged hemianopes (Rafal et al. 1990). Second, the effect has been found to be larger when the distractor appeared in the temporal visual field, rather than the nasal visual field (Rafal et al. 1991; Walker et al. 2000). Such nasal–temporal asymmetry was assumed to arise from the anatomical asymmetry in the retinotectal projection and became used as a behavioral marker for retinotectal mediation (Berger and Henik 2000; de Gelder and Stekelenburg 2005; Dodds et al. 2002; Lewis and Maurer 1992; Perry and Cowey 1984; Posner and Cohen 1980; Rafal et al. 1989; Rothbart et al. 1990). Third, Sumner et al. (2002) reported the effect absent for stimuli visible only to short-wave cones (S cones), which do not appear to make any contribution to the retinotectal projection (de Monasterio 1978; Marrocco and Li 1977; Schiller and Malpeli 1977).

However, there are wrinkles in this neat story. The retinotectal pathway does not in fact provide direct access to the motor map in the intermediate layers of the SC; instead, it projects to the superficial layers of the SC. Although the

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sensory map thus created in the superficial layers appears to be aligned with the motor map beneath (Schiller and Stryker 1972), it remains unclear how well these layers communicate and the connections may be surprisingly weak (e.g., Isa 2002; Moschovakis et al. 1988). However, this does not necessarily rule against an important role for the retinotectal route in the RDE because saccadic competition is also associated with the cortical eye fields, which strongly influence the SC motor map (see DISCUSSION in Dorris et al. 2007). Onward projections from the retinotectal pathway may be important for providing the very rapid visual responses in these cortical areas (e.g., Schmolesky et al. 1998).

The second wrinkle concerns the actual evidence supporting retinotectal mediation. Although Rafal et al. (1990) found the RDE in the blind field of hemianopes, Walker et al. (2000) did not. Such interpatient variability may have stemmed from differences in cortical sparing, rather than the retinotectal route that was spared in all. Next, the interpretation of nasal–temporal asymmetry has been undermined by both anatomical (Williams et al. 1995) and behavioral studies (Bompas et al. 2008), indicating that it is not a safe diagnostic test for retinotectal mediation—at most, nasal–temporal asymmetry can be considered consistent with retinotectal influence.

This leaves the S-cone evidence provided by Sumner et al. (2002). In this study color changes visible only to S cones and hidden in luminance noise did not produce the RDE, whereas luminance distractors produced the RDE under the same experimental conditions. Such S-cone stimuli are thought to be invisible to the retinotectal pathway and so the absent S-cone RDE is exactly what would be expected if stimulus-driven saccadic interference is retinotectally mediated. Furthermore, the result was taken to support a dissociation between saccades and attention (e.g., Derrington 2002; Hunt and Kingstone 2003; see also Sumner 2006; Sumner et al. 2004), since in the same study Sumner et al. (2002) found that S-cone stimuli did produce exogenous attentional orienting (e.g., Jonides 1981; Posner 1980). However, finding an effect absent is of course not as strong evidence as finding it present. Moreover, although the RDE is normally measured with simultaneous presentation of target and distractor, recent evidence (Bompas and Sumner, unpublished data) has shown that this is not sufficient for making comparisons between different distractors (e.g., luminance and S-cone).

Sensory delays

Distractor-related activity is expected to be transient and its ability to interfere with saccadic planning will be limited to a certain time window (e.g., Godijn and Theeuwes 2002; Trappeenberg et al. 2001). Thus the amplitude of the RDE is expected to be reduced for distractors presented either too early, at a time when the target signal has not yet arrived, or too late, when target activity is already reaching the initiation threshold. However, the arrival time of signals at the motor competition will depend not only on stimulus presentation time, but also on how rapidly the sensory signals are transmitted. This is a potential problem for any study comparing RDE amplitude between distractors with different stimulus properties (e.g., size, contrast, spatial frequency, or color; Born and Kerzel 2008a; Irwin et al. 2000; Ludwig et al. 2005; Sumner et al. 2002; White et al. 2005). Such stimulus changes are known to influence sensory processing speed, which in turn will affect the time at which the signals arrive at the motor competition and thus influence how much RDE is observed. In our case, S-cone signals are delayed relative to luminance signals (for a review see Bompas and Sumner 2008) and produce longer saccadic latencies even when the stimuli are matched on detectability (Bompas and Sumner 2008) or subjective salience (Anderson et al. 2008). Thus simultaneous presentation may not be optimal for investigating the distractor effect with S-cone stimuli. Rather, such stimuli are likely to benefit from a head start relative to luminance stimuli.

Study overview and predictions

Our main question in this study was simply whether there is an S-cone distractor effect. Since S-cone stimuli take longer to produce responses than do luminance signals, testing the S-cone distractor effect only for simultaneous presentation is incomplete. Here we measure the distractor effect at multiple stimulus onset asynchronies (SOAs) for both S-cone and luminance distractors and take a psychophysical approach of obtaining many measures per participant. Our second main question was whether S-cone stimuli produce saccadic capture. To obtain an estimate of whether directional errors toward S-cone stimuli are truly stimulus driven—or simply incorrect anticipations of the target—we compare the error rates during trials with and without distractors.

We can also make subsidiary predictions concerning the temporal dynamics of any distractor effects we measure (Bompas and Sumner, unpublished data). We cannot say beforehand what the optimal delay will be for any particular distractor or participant because this depends on a host of factors that may vary between stimuli and between participants. However, the optimal delay for each distractor should not be arbitrary and should correspond systematically with the difference in processing speed for target and distractor signals. If we make the assumption that arrival times of signals into the competition process are correlated with the latencies of saccades to the same visual stimuli (Bell et al. 2006), then the difference in saccadic latency for two stimuli should correlate with the delay maximizing the RDE when one is used as a distractor and the other one as a target. For this purpose, we also measured saccadic latency in blocks in which the stimuli used as distractors in the main experiment were now used as targets.

A second subsidiary prediction concerns the relationship between latency effects (the RDE) and capture (errorneous saccades toward the distractor). If capture results when the distractor signal actually reaches motor threshold and elicits a saccade, then there is a crucial difference between this and latency effects: the latter require interference between two signals, whereas capture does not. Thus although the RDE will be maximal when the two signals maximally overlap in the competition process and thus maximally interfere with each other, capture will be maximal simply when the distractor signal has the best chance of reaching motor threshold. This will occur when it minimally overlaps with the target signal, so that it receives little inhibition from the target-related activity, i.e., when the distractor appears much earlier than the target.
METHODS

Participants

Five observers participated in this experiment, four female and one male. All were students at the School of Psychology, Cardiff University, and naïve to the purpose of the experiment. All had normal vision and received payment for their time.

Equipment

Stimuli were displayed on a Sony Trinitron 19-in. GDM-F400T9 monitor, driven by a Cambridge Research Systems (CRS) ViSaGe graphics board at 100 Hz, calibrated with a CRS ColorCal and associated software. Viewing distance was 72 cm. Eye movements were recorded using the CRS high-speed video eye-tracker sampling at 250 Hz. The subject’s head was stabilized by a chin rest and a head rest. Stimuli were presented monocularly (to the right eye only), to ensure optimal calibration of S-cone stimuli. The left eye was covered with an eye patch.

Stimuli

The target stimulus was a small dark gray square (10 cd/m², occupying 0.25 deg²), presented at 8° eccentricity either on the left or on the right of fixation. The fixation point was a small light gray square (32 cd/m², occupying 0.1 deg²). To ensure correct isolation of the S-cone pathway, background and distractors were modulated with spatiotemporal noise that consisted of an array of squares (7 × 33 squares of 30 × 30 pixels, at resolution 1,024 × 768) whose luminance changed randomly every 10 ms within the range 24–26 cd/m² (MacLeod–Boynton coordinates: 0.643, 0.021). Luminance distractors were defined by superimposing a luminance increment on the luminance noise of the square opposite the target stimulus. S-cone distractors were defined by superimposing a chromatic step along the tritan dimension, while keeping luminance signals equal (Fig. 1). To account for individual differences and differences across the visual field, individual equiluminance and tritanopic settings at 8° eccentricity were preliminarily calibrated psychophysically. Equiluminance values were obtained using the minimum motion technique (Anstis and Cavanagh 1983) and tritan lines were determined using the Smithson–Sumner–Mollon method (Smithson et al. 2002, 2003). The intensity of luminance distractors was individually matched in salience with that of our S-cone stimuli in a preliminary experiment (see following text).

Procedure

MAIN EXPERIMENT. Each trial started with the reappearance of the central fixation point. After a fixed 700-ms delay, the target appeared randomly on the left or right of fixation, for 300 ms. The fixation point disappeared together with the target offset and reappeared some 500 ms later at the start of the next trial. Participants were instructed to move their eyes as fast as they could to the target, ignoring any other stimuli.

On half of the trials, the target appeared alone and in the other half a distractor appeared opposite to the target (Fig. 1) for 50 ms. Distractors were presented with nine different SOAs, ranging from 80 ms before to 80 ms after the target in steps of 20 ms, resulting in 36 distractor conditions (distractor color × SOA × target direction). These distractor-present conditions were randomly ordered and mixed with no-distractor trials. Each distractor condition was presented 45 times, resulting in 90 saccades per condition after averaging across direction and a total of 3,240 trials per participant.

MEASURING SACCADE LATENCY TO THE DISTRACTORS. We also determined the saccadic latency to the stimuli used as distractors in the main experiment. Each trial consisted of the presentation of either the luminance or S-cone stimulus on the left or right of fixation and for the same duration as that in the main experiment (50 ms), 700 ms after the beginning of the trial. The same background of luminance noise squares was used. Participants were instructed to make a saccade as fast as they could to the stimulus. Color and direction were presented in a randomized order. Each stimulus was presented 80 times for each direction, resulting in 160 saccades per condition after averaging across directions.

MATCHING SALIENCE BETWEEN S-CONE AND LUMINANCE STIMULI. In a preliminary stage, we simultaneously presented one S-cone and one luminance stimulus on each side of fixation, with the same eccentricity and duration as those in the main experiment. Sides for the S-cone and luminance stimuli were randomized. The luminance of the luminance stimulus was adjusted on each trial according

![FIG. 1. Time sequence of trials. Left: on half the trials, the target (small black square) appeared alone randomly on the left or right of fixation. Middle and right: on the other half of the trials, a distractor (larger square) appeared opposite to the target for 50 ms, embedded in spatiotemporal luminance noise, with various delays compared with the target onset. Illustrated here are one condition with an S-cone distractor at negative stimulus onset asynchrony (SOA, middle) and one condition with a luminance distractor at positive SOA (right). The target always appeared at 700 ms and stayed on for 300 ms. A fixation point was present throughout the trial and disappeared together with the target. Sizes of stimuli are enlarged for illustration purposes.](image-url)
to a staircase procedure (one up and one down), as the participant indicated on which side the stimulus appeared more salient. Two staircases with different initial values (one higher and one lower than the expected converging value) were interleaved and both stopped after 10 reversals. This procedure was usually repeated three times for each observer, with various initial values converging toward the point of salience matching.

Eye movement analysis

Saccades were detected automatically off-line and then checked visually and corrected if necessary. Saccades were detected using a velocity criterion of 100°/s and saccade onsets were defined at velocity 24°/s. Saccadic latencies were defined as the duration between the appearance of the target and the onset of the saccade. We calculated the mean of each saccadic distribution separately for each participant and distractor condition (color × SOA × target side). Considering medians instead of means did not alter any of the conclusions in the present study. We removed saccade latencies <75 ms, which were considered to be anticipations, and latencies >500 ms, which were not considered to be true sped-up responses to the target. This excluded <5% of saccades across conditions and participants. In all subsequent analyses, mean reaction times were extracted for each subcondition and then averaged across directions. RDE for each distractor condition was calculated by subtracting the mean latency in the no-distractor condition from the mean latency in the distractor condition.

RESULTS

Distractor effects for S-cone and luminance stimuli

We obtained robust distractor effects in our five participants for both luminance and S-cone distractors, as visible on Fig. 2. On average across all SOAs, the presence of a distractor increased saccade latency significantly for both distractor types [two-tailed paired t-test for luminance distractors: t(4) = 20, P < 0.001; for S-cone distractors: t(4) = 7.7, P = 0.001]. The distractor effect depended on SOA, showing a maximum for intermediate SOAs and decreasing for distractors at the early and late extremes [negative SOAs in Fig. 2 mean that the distractor was presented before the target; main effect of SOA for luminance distractors: F(8,32) = 3.0, P = 0.01; quadratic effect, F(1,4) = 12.2, P = 0.025; for S-cone distractors: F(8,32) = 2.3, P = 0.04, quadratic F(1,4) = 12.3, P = 0.025]. At the group level, significant distractor effects were observed for SOAs ranging from −40 to +40 ms for luminance distractors and from −40 to +20 ms for S-cone distractors (all P < 0.05). At the individual level, in our critical S-cone condition, distractors produced significant increases in saccade latency compared with the no-distractor condition for at least one SOA around the peak of the SOA curve for each participant (p1: [−20, 0]; p2: [−20, 0, 20]; p3: [−40, −20, 0, 20, 40]; p4: [−40]; p5: [−60, −40, −20, 0, 20]). Thus the key results of our study are simply stated: S-cone stimuli do produce a distractor effect, but timing matters.

We fitted the RDE as a function of SOA with a Gaussian curve to extract 1) the center, defining the optimal SOA (“SOAopt”; i.e., the SOA producing the maximum RDE) and 2) the amplitude of the RDE at this optimal SOA (“RDEmax”). We do not make any claim about using a Gaussian in particular because we did not have any reason to choose one bell-shaped curve over another. We used a Gaussian function with three free parameters (center, amplitude, and SD). The fitted curves appear as the continuous curves on Fig. 2, with the solid vertical continuous bars representing the SOAopt. These varied between −36 to +34 ms across conditions and participants. As can be seen, the SOAopt for S-cone stimuli was generally earlier than that for luminance stimuli. At the optimal SOA for each participant, the RDE varied from 20 to 30 ms for S-cone distractors and from 32 to 44 ms for luminance distractors [both significantly differing from zero: two-tailed t-test for S-cone distractors, t(4) = 12, P < 0.001; for luminance distractors, t(4) = 16, P < 0.001].

Relative magnitude of S-cone distraction

Our main result is simply the presence of a reliable distractor effect for both luminance and S-cone distractors. However, this
is not to say that S-cone stimuli are equally effective at distracting saccades as are luminance stimuli. We observed consistently higher distractor effects with our luminance stimuli than with our S-cone stimuli across all participants [paired-sample two-tailed t-test: \( t(4) = 3.8; P = 0.019 \)]. However, we must be cautious here. Our stimuli were matched in subjective salience, which does not guarantee that signals are of comparable intensity at any level relevant for saccade generation. For instance, S-cone stimuli have been shown to be cortically magnified in V1 (Mullen et al. 2007, 2008) and even if this has an equal effect on both subjective salience and saccadic competition, there may be other enhancements at other levels that are relevant only for appearance and not for saccades. This would be consistent with our previous data that the temporal delay measured for S-cone stimuli with saccades does not appear to be relevant for subjective temporal judgments (Bompa and Sumner 2008).

All we can say with certainty is that S-cone stimuli matched in subjective saliency with their luminance counterparts are still less-efficient saccadic distractors even when temporal differences are taken into account. This could suggest that, beyond the latency issue, there is some difference in the efficiency of the two types of distractors—perhaps that the pathways to which S-cone stimuli are invisible make an important contribution to the saccade system above that achievable by the S-cone pathway. An alternative possibility is that the similarity between distractor and target plays a role and light gray distractors are considered (by the saccade system) more similar to black targets than are colored distractors (Born and Kerzel 2008b).

**Optimal SOA and latency differences**

We predicted that the optimal SOA should vary systematically with the relative processing speed of distractor and target and that the latter could be estimated by the difference in saccadic latency to the two stimuli used as target and distractor. The dashed lines in Fig. 2 mark the differences between saccadic latency to the targets in the no-distractor condition of the main experiment and saccadic latencies to the distractor stimuli when they were targets. Thus where the magenta dashed line lies to the left of the black dashed line, saccadic latency was slower for S-cone stimuli than that for luminance stimuli, as expected. Four participants show this pattern and, for these four subjects, the optimal SOA for S-cone distractors was earlier than that for luminance distractors. In other words, the S-cone distractors benefited from a head start, commensurate with their slower processing speed. Participant 5 had slightly shorter latencies to the S-cone stimuli than those to the luminance stimuli, which was not expected, but is not too surprising given that stimuli were equated on subjective salience and therefore subject to variations in criteria between subjects. Importantly, the relative position of SOAopt for S-cone and luminance distractors is also reversed for this subject, maintaining the correspondence between relative latency differences and optimal distractor timing. Thus over all participants there was a clear relationship between latency differences and optimal distractor SOA (Fig. 3). As an indication, taking all participants and distractor types into account gave a regression line: SOAopt = 0.62 × latency difference + 29 (\( R^2 = 0.41; P < 0.05 \)).

![FIG. 3. Optimal SOA as a function of the latency difference between target and distractor for the 5 participants, for S-cone (magenta) and luminance (black) distractors. The magenta and black line is an indicative regression line across participants and distractor types.](http://jn.physiology.org/)

**Oculomotor capture**

The number of saccades directed toward the distractors is plotted in Fig. 4. First, we note that the number of errors in the no-distractor condition was extremely small (<0.38% for all participants, 0.25% on average). When the number of these errors is deducted from the number of errors in the distractor conditions, the remaining number of errors corresponds to saccades directed to the distractor (true oculomotor capture) and not anticipations. The first result is that oculomotor capture clearly occurred for both distractors. Averaging over SOA, the difference between errors in distractor trials and no-distractor trials was significant [one-tailed paired t-test for luminance distractors: \( t(4) = 2.8, P = 0.02 \); for S-cone distractors: \( t(4) = 4.4, P < 0.01 \)] and did not differ significantly between distractor types \( t(4) < 1 \).

The second result is that capture depended strongly on SOA [Fig. 4; for luminance distractors, \( F(8,32) = 4.9, P = 0.001 \); for luminance distractors, \( F(8,32) = 4.2, P = 0.001 \)]. The highest capture rates occurred for SOA of −80 and −60 ms for both luminance and S-cone distractors and did not differ significantly between distractor types.

**Discussion**

**Summary of the main results and conclusions**

Our main conclusion is the presence of a reliable distractor effect for both luminance and S-cone distractors (Fig. 2). Since S-cone stimuli embedded in luminance noise are invisible to the retinotectal and magnocellular pathways, this result suggests that the distractor effect does not rely on these particular pathways exclusively, contrary to the suggestions of previous studies (Rafal et al. 1990, 1991; Sumner et al. 2002).

Second, we found that the S-cone distractor effect was consistently smaller than the luminance distractor effect, even at its optimal SOA. We must be cautious in interpreting this result because the stimuli were matched on subjective salience...
A distractor effect for S-cone stimuli, which are thought to be invisible to the retinotectal and magnocellular pathways, stands in contrast to a previous report (Sumner et al. 2002) and undermines previous conclusions that the distractor effect stems from retinotectal signals. Apart from the experiment carried out by Sumner et al. (2002) with S-cone stimuli, the main behavioral evidence for retinotectal mediation of the RDE came from hemianopic patients (Rafal et al. 1990) and from the nasal–temporal asymmetry thought to be diagnostic of retinotectal mediation (Rafal et al. 1991). However, Walker et al. (2000) did not replicate the hemianopic evidence, suggesting that sparing of the distractor effect may differ between individual patients, which in turn may suggest that it arises from different degrees of cortical sparing. Moreover, it has recently been demonstrated that behavioral nasal–temporal asymmetry is not necessarily associated with the retinotectal pathway (Bompas et al. 2008). Thus it seems that no evidence remains to favor an exclusive retinotectal source for the RDE.

An S-cone RDE is also consistent with other results for S-cone stimuli, such as the presence of fixation-related inhibition, as measured by the fixation offset effect (also called the gap effect) (Sumner et al. 2006). Since fixation-related inhibition and saccadic distraction have been explained by very similar mechanisms and given that the RDE is in fact sometimes measured with stimuli at fixation (Born and Kerzel 2008a; Walker et al. 1997; White et al. 2005), it would have been surprising if S-cone stimuli were capable of eliciting one phenomenon but not the other. This leaves the question of how S-cone signals do gain access to the oculomotor system. The most likely route is extrastriate projections to the frontal eye field (FEF) or parietal eye movement areas, which are presumably relatively efficient given that saccade latency to S-cone stimuli is hardly slower than would be expected by their sensory delays alone (as found here and, e.g., Anderson et al. 2008; Bompas and Sumner 2008). However, this is not simple because FEF sensory cells do not show basic chromatic sensitivity (e.g., Stuphorn and Schall 2002; Thompson and Bichot 2005). Thus presumably by the time S-cone stimuli influence the oculomotor system, their chromatic identity is lost and they gain access as “stimuli of potential relevance for saccades.” For example, Ottes et al. (1987) found that although the initial response in SC does not discriminate color (first 100 ms), when the color of the stimulus is relevant for the saccade, later activity can discriminate the differently colored stimuli. How this route may be gated according to relevance is not understood and the crucial neurophysiological comparisons have not been made (e.g., how FEF and SC responses to chromatic stimuli depend on oculomotor relevance).

However, this is not to say that S-cone stimuli are no different from luminance stimuli for the saccadic system. S-cone signals are generally slower and also less temporally and spatially precise (e.g., Bompas and Sumner 2008; Mollon and Bowmaker 1992; Mollon and Polden 1975). Our data also provide an indication that their access to the saccadic system is relatively less important than their access to perceptual salience, given that their ability to distract did not seem to be commensurate with the subjective salience matching we used. Part of the reason for this may lie in “feature relevance”—that similarity between distractor and target plays a role (e.g., Born and Kerzel 2008b; Ludwig and Gilchrist 2002). This would apply to our study if the saccade system considers colored distractors to be less similar to black targets than light gray distractors are. However, even when S-cone stimuli are task relevant, their ability to reflexively attract saccades may be less strong than that of luminance stimuli. For example, Anderson et al. (2008) found...
that the antisaccade cost (latency for saccading away from a stimulus minus latency for saccadic toward it) was smaller for S-cone stimuli than that for luminance stimuli. This was taken to suggest that S-cone stimuli produce a smaller “visual grasp reflex” than that produced by luminance stimuli and thus this reflex is less difficult to suppress when saccading away from the stimulus. Such a result is clearly consistent with a smaller distractor effect. In Anderson et al. (2008), as in the present study, the S-cone and luminance stimuli were matched for subjective salience. However, note that in the present study, we did not observe less capture (errors) for S-cone distractors (although due to the fewer number of errors, the power in comparing errors is much less than that in comparing latencies).

Last, it is worth asking why Sumner et al. (2002) did not record an S-cone distractor effect. First, it is likely that the S-cone distractors would have benefited from a head start to be fairly compared with luminance distractors. Note that although our data show a significant RDE at SOA = 0, we must be cautious in comparing directly the 0-ms conditions between studies because with different stimuli used the curves of RDE against SOA could be relatively shifted. Second, here we observed that, even at their optimal SOA, S-cone stimuli still appear to be less distractive than their luminance counterparts. Further, it is notable that overall the amplitudes of the RDE in the present study were larger than those in Sumner et al. (2002) even for luminance distractors. The amplitude differences between the two studies most likely stem from differences in the pattern of luminance noise. Here the luminance noise had a range of ±1 cd/m², whereas Sumner and colleagues used a larger range of ±1.8 cd/m². More important, however, here we used an entire patchwork of noisy squares changing every 10 ms, which helps participants treat it as “background,” whereas in Sumner et al. just the potential distractor positions flickered and changed every 50 ms, which is more difficult to ignore. Thus the luminance noise in Sumner et al. (2002) may have acted as a distraction on all trials, including the “no-distractor” condition, which would reduce the calculated RDE and would therefore reduce the chance to observe the RDE for the less-efficient S-cone distractors. In favor of this argument, we note that the saccade latencies in the no-distractor condition were much longer in Sumner et al. (2002) (277 ms on average) than those in the present study (ranging from 174 to 219 ms across participants).

To confirm this, we attempted a replication of the method in Sumner et al. (2002). Targets and distractors appeared at locations indicated by two guide boxes, which flickered in luminance every 50 ms, in which the amplitude of the luminance noise was ±1.8 cd/m². The distractors had the same S-cone contrast and luminance level as those in Sumner et al. (2002) and appeared simultaneously with the target (i.e., zero SOA condition only). Our design differed from that in Sumner et al. in that it used the same target and distractor sizes and eccentricity as those in the present article for better comparison. We tested four participants, all of whom were calibrated individually for equiluminance and tritan line as in the main experiment (two of them were also subjects in the main experiment). This design produced smaller and less-reliable RDEs than those in our main experiment for both distractor types and the result did not differ between S-cone and luminance distractors (RDE for each participant in milliseconds for luminance distractors: [1, 10.5, −1.5, 8]; for S-cone distractors: [8, 10, −8.5, 5.5]; although the effects for luminance and S-cone distractors appear to be on average respectively smaller and larger than in those in Sumner 2002, these do not fall outside of the range of observed values in this original study). We also observed longer saccade latencies in the no-distractor condition (238 to 256 ms) compared with the main experiment (174 to 219 ms), although the targets were identical. Thus we conclude that the luminance noise arrangement in the current study is more appropriate for revealing distractor effects than the arrangement used in Sumner et al. (2002).

Methodological point: measuring RDE at multiple SOAs

One subsidiary conclusion of the present study is that it is not safe to compare distractor effects at only one time point when the manipulated feature is expected to modulate processing speed. Importantly, measuring the RDE at multiple SOAs is safer even if target and distractor are very similar stimuli: in all RDE designs, there has to be some dimension (feature, location, etc.) that allows the participant to distinguish target from distractor and this is expected to favor the task-relevant signal. It is a common assumption that such endogenous (top-down) biases (i.e., “attention”) can modulate the sensory signals at an early level (Carrasco 2006) and therefore target signals would generally reach the motor map earlier than would distractor signals. Thus even with identical stimuli, simultaneous presentation will not necessarily be the optimal SOA. Additionally, for stimuli equated on visibility or salience, delays in the arrival times could occur due to subsequent processing stages not included in the salience judgment.

Conclusions

We have tested the theory that saccade distraction is caused by sensory signals in the retinotectal pathway. We found that stimuli invisible to this pathway cause robust distractor effects and saccade capture and thus these effects do not rely on the retinotectal pathway, or even the magnocellular pathway, which is also blind to S-cone stimuli in luminance noise. Consistent with a competition framework for saccade generation, the optimal timing for distractor presentation differs between stimuli and also between RDE (latency effect) and capture (error rate) measures.

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References


