

Sensory sluggishness dissociates saccadic, manual, and perceptual responses: An S-cone study

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Sensory information travels to visual and motor areas via several distinct pathways, some of them being fast—like the achromatic magnocellular and retinotectal routes—and others slower—those carrying chromatic signals, in particular S-opponent signals. It is debated whether common visual processing stages are used for different types of responses, such as initiating saccadic or manual responses or making perceptual judgments. The present paper casts new light on this question by comparing the participation of fast and slow pathways across these responses. In the first experiment, we measured manual and saccadic reaction times to luminance and S-cone signals, equated in detectability for each participant and presented on either sides of fixation. Our results show that both manual and saccadic responses are slower for S-cone stimuli. Most interestingly, this reaction time difference was twice as large for saccadic responses as for manual responses, suggesting that saccades rely more on the fast signals, not supported by S-cone stimuli, than do manual responses. In a second experiment, our participants performed temporal order judgments on pairs of luminance and S-cone stimuli. Our results show no evidence of perceived time discrepancy between the two signals, which may imply that perceptual judgments utilize different signals from either manual or saccadic responses.

Keywords: eye movements, color vision, superior colliculus/optic tectum, temporal vision

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Introduction

Common visual processing for different responses?

How are simple actions initiated in response to visual stimuli? Typical models for visuomotor behavior propose that a visual event produces an internal response, which rises with time until its intensity reaches a decision threshold and triggers the motor response (e.g., Carpenter, 1981). The most parsimonious of these models would state that a common source of information is used for perception and all types of motor responses and that the same decision thresholds apply to all responses. Reaction time would then be the sum of stimulus processing time and motor latency, the latter being the only source of difference between response types. Although this model appears simplistic, parsimony makes it the default solution until evidence is brought against it. For instance, Taylor, Carpenter, and Anderson (2006) manipulated stimulus contrast and found similar dependencies for manual and saccadic reaction times, a result they conclude to be compatible with a common target detection stage for both responses.

A more active, though classic, debate concerns the relationship between motor and perceptual responses. Studies have classically compared the differences in

manual reaction times obtained for two different stimuli to the point of subjective simultaneity measured in a temporal order judgment task (TOJ). As recently reviewed in Cardoso-Leite, Gorea, and Mamassian (2007), most studies report TOJ to be less affected than RTs when the two stimuli differ along various dimensions (e.g., salience, spatial frequency or duration). Thus, subjective simultaneity appears to be closer to physical simultaneity than would be predicted from manual responses, and this has led to the conclusion that motor and perceptual responses share only partial processing. For instance, Tappe, Niepel, and Neumann (1994), after showing that TOJ were far less affected than RTs by spatial frequency, concluded that the signals must diverge early, either projecting directly to the motor system for speeded manual responses or allowing longer “integrative processes” for TOJ (for similar conclusions on the effects of attentional cues, see also Neumann, Esselmann, & Klotz, 1993). Models with a later dissociation have also been proposed, a common internal response being followed by distinct decision processes for motor responses and TOJ (Miller & Schwarz, 2006). Correlation found between differences in RT and subjective simultaneity, as well as between their respective variability, has been proposed to support such a serial model (Cardoso-Leite et al., 2007).

In the present paper, we aim to bring new light to this debate by stimulating different pathways that are thought to

differ in their processing speed. If different responses, such as manual and saccadic responses, or motor and perceptual responses, share a common target detection stage, they must all rely on the same combination of the different pathways. This could be achieved if signals from all pathways were gathered in a common “collector,” on the basis of which any responses would be triggered. This model predicts all responses to be equally affected by pathway sluggishness, so that the same delay between chromatic and achromatic stimuli should show up in all types of response. Alternatively, different responses may be differently affected by pathway speed, which would suggest some separation in the visual processing for each response.

Different pathways, different times

Visual perception results from the combination of different pathways, defined both anatomically and on the basis of their sensitivity to certain signals—chromatic or achromatic contrasts in particular. Projecting from retina to visual cortex, via the lateral geniculate nucleus (LGN), are magnocellular, parvocellular, and koniocellular pathways. The magnocellular pathway responds most to luminance stimuli, combining signals from both long-wavelength-sensitive (L) and middle-wavelength-sensitive (M) cones. The parvocellular pathway responds also to luminance edges and additionally to chromatic differences between L- and M-cone signals. Among the koniocellular pathways are cells that compare the signal in short-wavelength-sensitive (S) cones with those of L- and M-cones. There is also a direct retinotectal projection (to the superior colliculus), which, like the magnocellular pathway, responds to luminance stimuli and is not color opponent. Each pathway imposes a different transmission speed, and it is thought that pathways carrying achromatic signals—magnocellular and retinotectal routes—are the fastest, while chromatic signals are available only later. Moreover, tradition holds that the S-cone signals are the slowest (Cottaris & De Valois, 1998; Mollon & Polden, 1976; for a review, see Mollon & Krauskopf, 1973).

The following sections review evidence for these different processing times and their—still somewhat unclear—consequences on motor responses and conscious experience. In all studies that aim to compare responses along different sensory dimensions, a critical aspect is the way the stimuli are equated across dimensions. It is well established that reaction times and perceived times of events are closely related to visibility. Therefore, in the following review, we emphasize studies that based their comparison on measured detectability, rather than other metrics, such as physical intensity or cone contrast. Additionally, appropriate separation of the pathways is an essential criterion for the comparison to be conclusive, especially when no or only small differences are obtained.

Few studies have directly compared luminance and S-cone signals (e.g., Anderson, Husain, & Sumner, 2008;

Perron & Hallett, 1995; Smithson & Mollon, 2004). Many papers focus on the comparison between achromatic and chromatic signals, the latter being usually limited to red-green signals (e.g., Maunsell & Gibson, 1992; Satgunam & Fogg, 2005; Schwartz, 1992; van Asten, Gielen, & de Winkel, 1988), while the remaining studies are concerned with the effect of varying color for equiluminant stimuli (e.g., Cottaris & De Valois, 1998; Krauskopf, 1973; McKeefry, Parry, & Murray, 2003; Mollon & Polden, 1976). However, for our purposes, the comparison between S-cone and luminance pathways is of particular interest. A first practical reason is that S-cones contribute only marginally to the magnocellular pathway (see Chatterjee & Callaway, 2002; Stockman, MacLeod, & DePriest, 1991). Therefore, it is possible to calibrate psychophysically well separated S-cone and luminance stimuli. Another reason is that the difference in processing time is thought to be maximal between luminance and S-cone signals (Cottaris & De Valois, 1998; McKeefry et al., 2003).

S-cone signals are sluggish?

Electrophysiology studies have shown L/M-opponent signals to arrive later in V1 than luminance signals (Maunsell & Gibson, 1992; Nowak, Munk, Girard, & Bullier, 1995; Schmolesky et al., 1998). Typical delays reported between signals originating in magnocellular or parvocellular layers of the LGN are about 10 to 20 ms. Additionally, several studies suggest that S-opponent signals are even slower than L – M signals. For instance, Cottaris and De Valois (1998) presented neural response distributions in response to L – M and S-cone signals in macaque monkey V1. Neural responses to S-cone signals were on average 20 ms longer, and their distribution was spread over a longer time period. More evidence for S-cone sluggishness has been provided by visually evoked potentials (Krauskopf, 1973; Rabin, Switkes, Crognale, Schneck, & Adams, 1994; Robson & Kulikowski, 1998). These studies all report differences in the latency of first peak between short- and middle- or long-wavelength signals when stimuli are equated on the basis of their detection threshold. Reported delays vary between 20 and 100 ms across conditions.

S-cone signals produce sluggish motor responses?

Sluggish manual responses?

Sluggish signals are expected to produce delayed motor responses. Indeed, different studies agree that longer reaction times (RTs) are obtained in response to chromatic versus achromatic signals (Nissen & Pokorny, 1977; Schwartz, 1992; Ueno, Pokorny, & Smith, 1985). In particular, Schwartz (1992) reports RT distributions that are about 90 ms longer in response to chromatic stimuli.

Further, many studies have addressed the influence of wavelength or color on manual RTs for equiluminant stimuli, where care has been taken to eliminate achromatic intrusion (for a review, see McKeefry et al., 2003). For instance, McKeefry et al. (2003) obtained RT differences around 40 ms between $S - (L + M)$ and $L - M$ signals scaled to multiples of detection threshold. Smithson and Mollon (2004) compared RTs to $L + M$, $L - M$, and $S - (L + M)$ signals, all at 75% detection threshold. They obtained average RTs longer by 16 ms and 34 ms for $L - M$ and $S - (L + M)$, respectively, with respect to $L + M$. Interestingly, however, the difference vanished when stimuli were embedded in luminance noise in order to control for luminance intrusion. This is surprising because luminance noise is assumed to ensure the good separation of chromatic and achromatic pathways (Birch, Barbur, & Harlow, 1992; Mollon, 1982) and was therefore expected to maximize the difference between the three pathways. On the other hand, as the authors suggest, too much luminance noise may saturate the magnocellular (and to some extent also the parvocellular) pathway and would therefore slow down responses to luminance stimuli.

Sluggish saccadic responses?

As for manual responses, sluggish signals are also expected to produce delayed saccadic responses. There is also reason to expect the saccadic delay for chromatic signals to be larger than for manual responses. After the retina, in addition to the geniculostriate pathways to visual cortex, luminance signals are also conveyed by the retinotectal route directly to the superficial layers of superior colliculus. This pathway is thought to be important for saccades, potentially providing a fast route to the cortical eye fields, as well as making (possibly weak) connections to the deeper layers of the colliculus that are known to play a major role in the generation of saccades (Bell, Meredith, Van Opstal, & Munoz, 2006; Dorris, Paré, & Munoz, 1997; Everling, Dorris, Klein, & Munoz, 1999; Isa, 2002; Schmolesky et al., 1998; Sparks, 1986). The retinotectal pathway appears to be color-blind (Marrocco & Li, 1977; Schiller & Malpeli, 1977) and, consistent with this, various saccade-related phenomena that occur for luminance stimuli behave differently for S-cone stimuli: The oculomotor distractor effect and saccadic inhibition of return have been reported absent for S-cone stimuli (Sumner, Adamjee, & Mollon, 2002; Sumner, Nachev, Vora, Husain, & Kennard, 2004; see also Sumner, 2006), and the reaction time difference between anti-saccades and pro-saccades is strongly diminished for S-cone stimuli (Anderson et al., 2008).

A few studies have compared saccadic latencies to achromatic and different chromatic stimuli. In particular, saccade latencies for red or green isoluminant stimuli were found to be 20–25 ms longer compared to achromatic stimuli, all presented at 1.5 times detection threshold (van Asten et al., 1988). Similar differences

were confirmed more recently by Satgunam and Fogt (2005), who referred to the CIE Lab space to match in contrast achromatic and isoluminant stimuli. White, Kerzel, and Gegenfurtner (2006) also obtained saccade latencies about 20 ms shorter when adding luminance information to red or green stimuli. However, Perron and Hallett (1995) failed to show any clear difference between achromatic and red-green stimuli in a sequential tracking paradigm, using the uniform chromaticity CIE 1976 space to equate their stimuli across dimensions. Interestingly, they obtained clearly longer (50 ms on average) latencies for blue and yellow stimuli and found tritanopic purity to be the best predictor for saccade latency.

It is worth noting that these studies did not generally take into account the fact that while all color spaces are designed to describe foveal vision, saccadic targets must be presented in the periphery. Because of the decrease in density of the macular pigment with eccentricity (Sharpe, Stockman, Knau, & Jägle, 1998), axes in foveal color spaces cannot be relied on to separate early visual pathways for the periphery, especially in the case of the S-cone (tritan) dimension. Additionally, the density of macular pigment varies individually, so that careful study of chromatic stimuli should ideally always involve individual psychophysical calibration. One exception is the study by Anderson et al. (2008), who obtained a 30-ms difference between luminance and S-cone stimuli, which were individually calibrated and equated in subjective saliency (all stimuli were clearly visible, rather than being equated using detection threshold).

Are there perceptual consequences of S-cone sluggishness?

Up to recently, S-cone motion signals were thought to be delayed compared to luminance stimuli. In the Mollon-Polden effect (1976), a vertical bar consisting of blue and red halves is moved across a yellow field and observers report that the blue half lags behind the red half and persists longer. However, recent findings (Land, Blake, & Mollon, 2007) reveal that when the chosen background guarantees equal adaptive states for S- and L-cones, the effect is greatly diminished and would not exceed 5 ms. Therefore, contrary to a long-standing view, there may in fact be very little perceptual delay between S-cone and luminance stimuli.

How sensory sluggishness can dissociate manual, saccadic, and perceptual responses

From the above review, it seems that S-cone signals (1) are processed slower than luminance signals, (2) trigger slower manual and saccadic responses, and (3) are not perceived consistently later than luminance signals. However, direct comparisons of manual, saccadic, and

perceptual responses to luminance and S-cone signals have not been made in the same study. The present article proposes to carefully measure the effect of sensory sluggishness on each response type, using the same stimuli and participants, to allow these comparisons to be made. In this study, S-cone stimuli are used as a tool in order to determine whether sensory sluggishness affects different responses equally, as predicted if the responses share common visual processing stages, or reveals dissociations between response types.

Two experiments were conducted in the present paper. The first experiment measured manual and saccadic reaction times (RTs) to luminance and S-cone stimuli, which were previously equated in detectability. The second experiment required the same group of observers to make temporal order judgments between luminance and S-cone stimuli, using the same stimuli as in [Experiment 1](#). Conclusions could then be driven from comparing the effect of sensory sluggishness across response types.

Methods

Observers

Twelve subjects participated in [Experiment 1](#), 7 females and 5 males, aged 27 on average (from 22 to 35), including 10 naïve observers and the two authors. In [Experiment 2](#), the same 10 naïve observers participated. All had normal or corrected-to-normal vision, reported no color vision abnormalities, and demonstrated normal color performance in our tritan calibration procedures. All demonstrated normal saccadic behavior.

Material

Stimuli were displayed on a Sony Trinitron 19-inch GDM-F400T9 monitor driven by a Cambridge Research Systems ViSaGe graphics board at 100 Hz, calibrated with ColorCal. Stimuli were presented to the right eye only with 72 cm viewing distance. Eye movements were recorded using the CRS high speed video eyetracker sampling at 250 Hz. The subject's head was stabilized by a chin rest and a head rest. Their left eye was covered with an eye patch. The same experimental setup was kept for all the preliminary and main experiments.

Stimuli

The background was gray (MacLeod-Boynton coordinates, MB, 0.643, 0.021) with mean luminance 25 cd/m^{-2} , modulated with spatiotemporal luminance noise, which consisted of an array of squares (7×33 squares of 30×30 pixels at 1024×768 resolution), whose luminance

changed randomly every 10 ms within the range $24\text{--}26 \text{ cd/m}^{-2}$. This luminance noise ensured that the color changes described below could be detected only by a chromatic channel. Luminance and S-cone stimuli were obtained by increasing respectively the luminance or the S-cone contrast of one background square, at 8 deg eccentricity either on the left or on the right of the fixation point.

To account for individual differences and differences across the visual field, individual equiluminance and tritanopic settings at 8 deg eccentricity on the left and on the right of fixation were preliminarily calibrated psychophysically. Equiluminance values were obtained using the minimum motion technique (Anstis & Cavanagh, 1983; Cavanagh, MacLeod, & Anstis, 1987), and tritan lines were determined using the method developed by Smithson, Sumner, and Mollon (2003). A detailed description of the two techniques can be found in Smithson and Mollon (2004).

Equating detectability for S-cone and luminance stimuli

To ensure that luminance and S-cone stimuli were equally detectable, a preliminary 2-interval forced choice experiment was conducted on each participant to measure 80% detection threshold, for left and right peripheries (i.e., nasal and temporal visual hemifields). Two successive 30-minute blocks were performed for luminance and S-cone contrasts, in a counterbalanced order across participants. Regular breaks between and during the blocks at fixed intervals were imposed to prevent excessive saturation of luminance pathways by the luminance noise. In each block, 7 contrast levels were presented 16 times each in a randomized order. Each trial consisted of two 1800-ms intervals, separated by a 200-ms pause, marked by a stop in the spatiotemporal luminance noise. A stimulus appeared for 250 ms on every trial, either on the left or right, in the first or second interval, after 800 ms of luminance noise. Participants were asked to indicate whether the stimulus appeared in the first or second interval. Percentages correct were fitted with two sigmoids for left and right sides separately, and contrast levels giving 90% of correct responses (80% detection thresholds) were extracted. These individual values were then used as stimuli in [Experiments 1](#) and [2](#). Note that no threshold difference was found between the nasal and temporal hemifields, either for S-cone or for luminance stimuli.

Procedure

Experiment 1: Manual and saccadic reaction times

The temporal sequence in [Experiment 1](#) is illustrated in [Figure 1](#). One stimulus appeared at a time, randomly on the left or on the right, and participants were required either to press the left or right button accordingly or to perform an eye movement to fixate the stimulus. Either

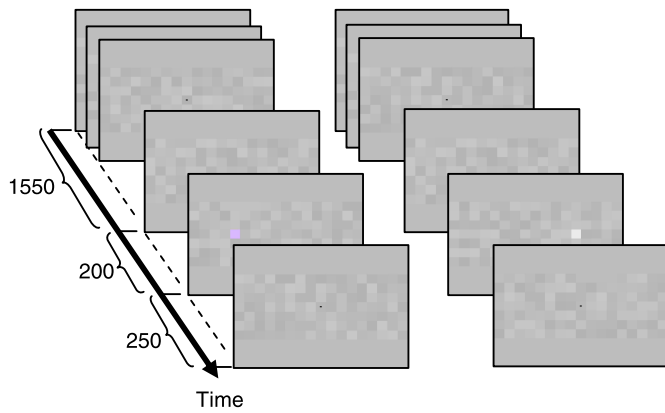


Figure 1. Illustrative temporal sequence in [Experiment 1](#). Trials consisted of spatiotemporal luminance noise in which one stimulus appeared every 2 s for 250 ms. Such stimuli were produced by increasing the chromatic or luminance contrast of one of the background squares. The left panels illustrate a trial with an S-cone stimulus appearing on the left. The right panels illustrate a trial with a luminance stimulus appearing on the right. In half the blocks, participants were asked to give a manual left/right response. In the other half, they were asked to perform an eye movement in the direction of the stimulus. Note that the fixation point disappeared 200 ms before the target. The grid of squares formed spatiotemporal luminance noise in order to ensure the S-cone stimulus was detected only by chromatically opponent channels.

luminance or S-cone stimuli were presented for 250 ms and separated by 1550 ms of spatiotemporal luminance noise. A fixation point was displayed in the center of the screen throughout the block, except during the 200-ms preceding each stimulus.

In manual response blocks, participants were instructed to keep their eyes on the fixation point and press the button as fast as they could. In saccadic response blocks, observers were asked to keep their eyes on the fixation point until the stimulus appeared and then to move their eyes as fast as they could in the direction of the stimulus. In both manual and saccadic blocks, subjects were instructed to respond only when they saw the target and not to guess when they could not see it (note that all stimuli were expected to be detected on 80% of trials). They did not receive feedback.

Stimulus and response types were blocked, the four types of blocks being carefully alternated, in a counter-balanced order across participants. Each block was 2 minutes long, and unlimited breaks were offered between each block. All participants performed four replications of the four block types, allowing us to collect 160 reaction times for each type of trial (80 on each side).

Experiment 2: Temporal order judgments

The temporal sequence of a trial in [Experiment 2](#) is illustrated on [Figure 2](#). On each trial, one luminance

stimulus appeared on one side and one S-cone stimulus appeared on the other side. A variable delay was introduced between them (0 to 150 ms by 30 ms steps), so that the S-cone stimuli could either be presented synchronous with the luminance stimuli (delay 0), before it (delays 30 to 150 ms) or after it (–150 to –30 ms). The first stimuli appeared after 500 to 1000 ms of luminance noise and both stimuli appeared for 250 ms. Stimuli appearance was again followed by luminance noise until the end of the trial, whose total duration was fixed at 1800 ms. The participants were asked to indicate which, of the left or right stimuli, appeared first. If the participant failed to see one or both stimuli, they could use an alternative key to exclude the trial.

Responses for each of the 11 delays (–150 to 150 ms) were measured 20 times, 10 times with S-cone stimuli on the left and luminance stimuli on the right, and 10 times the other way round. Observers were instructed to keep their eyes fixed on the fixation point, which remained present during the whole trial. Participants were not given feedback. The next trial started as soon as the participant gave an answer.

Analyses

Saccades were first detected automatically off-line and then checked visually and corrected if necessary. Saccadic latencies were defined as the duration between the appearance of the stimuli and the onset of the eye saccade. We calculated the median for each reaction time distribution, separately for each participant, stimulus type,

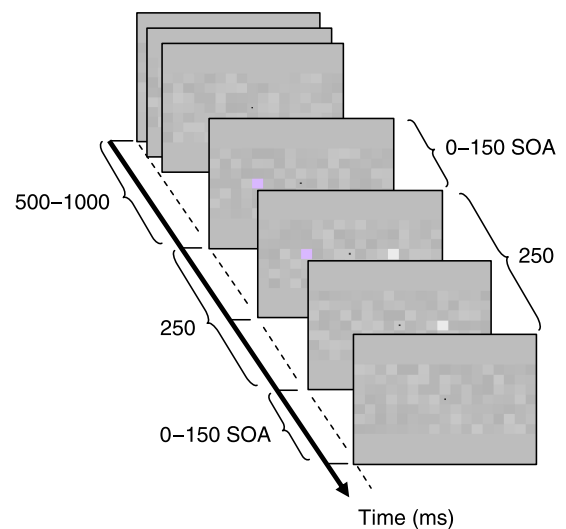


Figure 2. Illustrative temporal sequence in [Experiment 2](#). After a variable delay the stimuli appeared for 250 ms each with a variable SOA between them (the example shows a positive SOA of 150 ms: S-cone stimulus first). Participants were asked to judge which stimulus, left or right, came first.

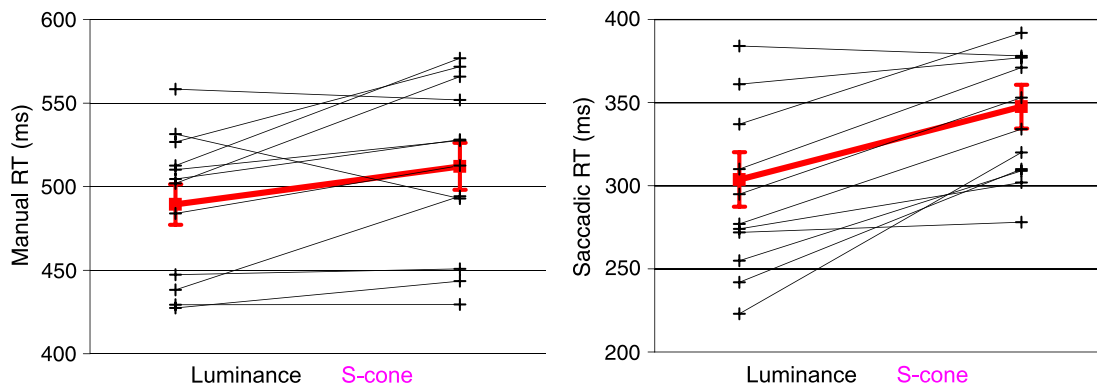


Figure 3. Individual (black) and average (red) median reaction times (RTs) for manual (left) and saccadic (right) responses in [Experiment 1](#). Data points are averaged over left and right responses. Red error bars are standard errors calculated over the 12 participants.

response type, and stimulus side. We kept all reaction times up to 1 s and removed those shorter than 75 ms for saccades and 200 ms for button presses, which were considered to be anticipations. Considering means instead of medians did not alter the pattern of results. However, because reaction time distributions are skewed, relying on means would give an unjustifiably larger weight to long latencies compared to short latencies and make our results more sensitive to outliers and therefore to arbitrary filtering criteria. Using medians, our results were very robust to filtering, so that the results remained virtually the same with or without filtering anticipation values.

In all subsequent analyses, median reaction times were extracted for each subcondition (stimulus side, signal, and response type) for each participant. The summary results for each main factor (signal and response type) were calculated by averaging across secondary factors (stimulus side and/or participant).

Results

Experiment 1

Manual responses

The left panel of [Figure 3](#) illustrates the manual reaction times, calculated for each participant for luminance and S-cone stimuli. Median reaction times (on average across participants and stimulus sides) were 489 ms for luminance stimuli and 512 ms for S-cone stimuli, producing a difference of 23 ms between them (paired-samples two-tailed t test, $t(11) = 2.5$, $p < 0.05$). No difference was found between left and right responses.

The reaction time difference between signals is also illustrated on the left panel of [Figure 4](#), showing the manual response distributions, from our twelve participants together, for luminance and S-cone stimuli. It can be

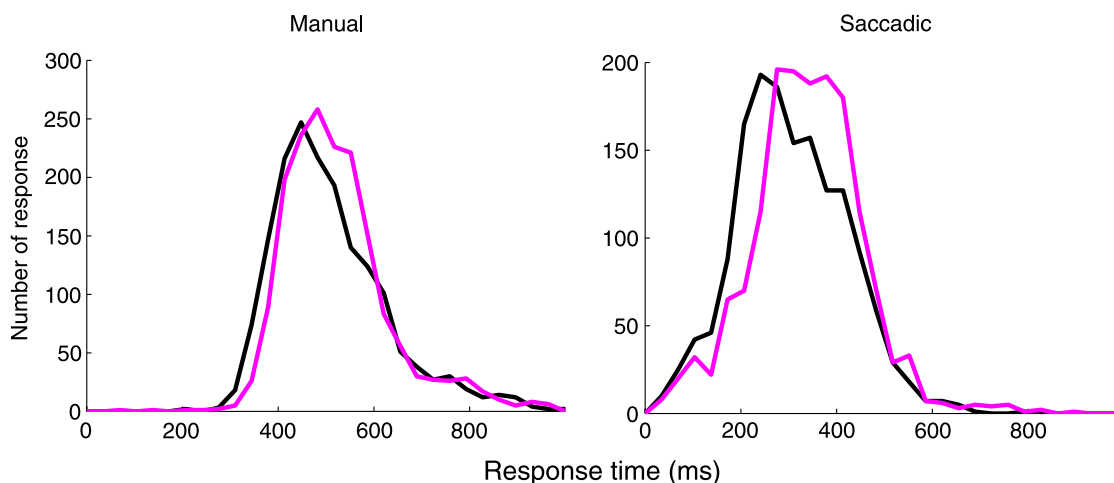


Figure 4. Reaction times distributions in [Experiment 1](#), with bin size = 30 ms, compared for luminance (black) and S-cone stimuli (magenta), in manual (left panel) and saccadic (right panel) conditions.

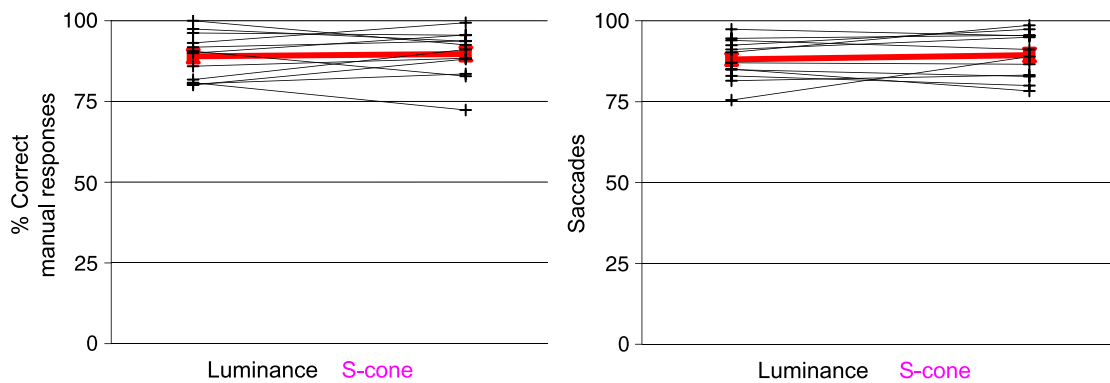


Figure 5. Individual and average proportion correct for luminance and S-cone stimuli, with standard error. Left: manual response blocks. Right: saccadic blocks.

noticed that the two distributions differ over most of their range, except for the very longest responses.

The left panel of Figure 5 presents the proportion of correct answers for luminance and S-cone stimuli. It suggests that the preliminary experiment succeeded in minimizing detectability differences between luminance and S-cone signals and makes it unlikely that the reaction time difference resulted from a difference in mean visibility.

Eye movements

The right panel of Figure 3 illustrates saccade latencies for luminance and S-cone stimuli. Median saccadic latencies (on average across stimulus side and participants) were 304 ms for luminance stimuli and 348 ms for S-cone stimuli, producing a difference of 44 ms between them ($t(11) = 5.2$, $p < 0.001$). Additionally, we noted that, for S-cone stimuli only, left saccades—directed to nasal visual hemifield—were significantly faster than right saccades—directed to temporal hemifield—(mean difference across participants = 31 ms, $p < 0.05$). Therefore, we performed our statistical tests on each side separately and obtained significant differences between responses to luminance and S-cone stimuli for both left and right sides ($t(11) = 3.3$, $p < 0.01$ and $t(11) = 5.0$, $p < 0.001$, respectively).

Figure 4 (right panel) shows the distribution of saccadic latencies for the two signals. As for manual responses, the distributions differ over most of their range and are similar only for the longest saccades. We observe that both distributions show a distinct early mode, corresponding to the very fastest saccades. Although our participants made less than 10% of incorrect saccades, we have analyzed their distributions and verified that they spread equally all along the range of latencies observed for correct saccades, rather than clustering around the earliest part of the latency distribution (data not shown). This confirms that the observed early bump is not produced by the anticipation saccades that are correct just by chance. Therefore, the observed early mode seems to correspond to “express saccades,” which have been well described in the literature in response to luminance stimuli (Fisher &

Ramsperger, 1984). Their presence in response to S-cone signals is of particular interest (see Discussion).

The right panel of Figure 5 confirms that the proportion of correct answers for luminance and S-cone stimuli showed no evidence of differing. Thus, differences in visibility are unlikely to account for the observed latency differences.

Manual and saccadic reaction times compared

Most interestingly, our results showed a significant interaction between response type and stimulus type, the difference between S-cone and luminance signals being twice as large for saccadic (ΔRT_{sacc}) than for manual (ΔRT_{manu}) responses ($t(11) = 2.24$, $p < 0.05$). No significant correlation was found between ΔRT_{sacc} and ΔRT_{manu} ($R^2 = 0.19$, $F(1,11) = 2.3$, $p > 0.1$, see Figure 6). These findings suggest that saccadic and manual responses

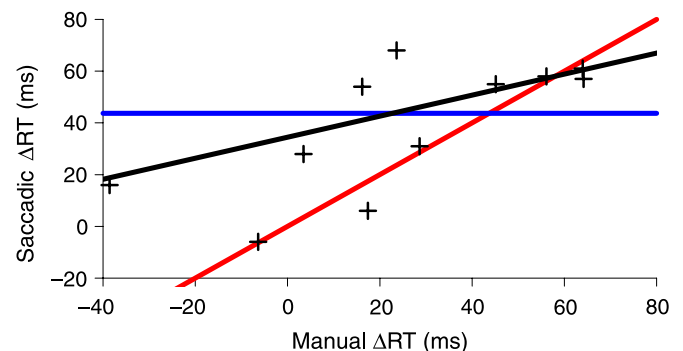


Figure 6. Correlation across participants between response time differences (S-cone – luminance) for saccadic and manual RTs. Data points are individual ΔRT s for the twelve participants, each calculated from the average median response times across left and right responses. The black line shows the linear regression curve. Colored lines represent two extreme predictions: The one system model (red) predicts a perfect dependency, i.e., a high correlation, with regression onset at 0 and slope at 1; the two-independent-systems model (blue) predicts complete independence, i.e., no correlation, regression curve having therefore a null slope and onset at the mean ΔRT_{sacc} .

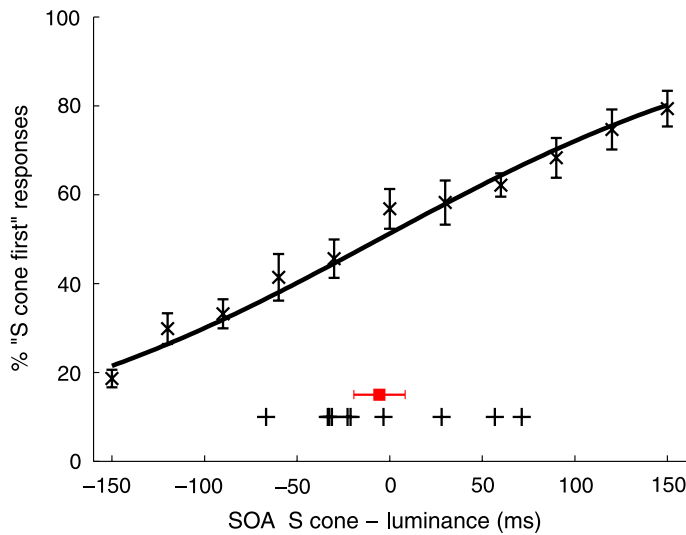


Figure 7. Results of Experiment 2. Average percentage across the 10 participants of “S-cone first” responses as a function of the delay between S-cone and luminance stimuli (x), with individual (+) and average (red square) points of subjective simultaneity. Error bars are standard errors. Positive SOAs correspond to trials in which the S-cone stimulus was presented first.

rely on different combinations of fast and slow pathways, saccades relying more than manual responses on the faster pathways, from which S-cone signals are excluded. Note also that even if slight differences in visibility remained between the luminance and S-cone stimuli, they could not account for this result because, for each participant, identical sets of stimuli were used in the manual and saccadic conditions.

Experiment 2: Temporal order judgments

The proportion of responses in which the S-cone stimulus was reported first was calculated for the 11 delays introduced between S-cone and luminance stimuli for each participant. The corresponding curves were

then fitted individually with a sigmoid (fixed lower and upper values at 0% and 100%, center and slope were the two free parameters) to define the individual points of subjective simultaneity (PSS). The average curve (with mean center and slope across participants) is represented together with individual PSSs in Figure 7. Positive PSS values indicate that S-cone stimuli were perceived later than luminance stimuli (the direction expected from the manual and saccadic results reported above), while negative PSS values represent S-cone stimuli perceived earlier than luminance stimuli. The mean PSS was in fact -5 ms and not significantly different from zero ($t(9) = 0.38, p > 0.1$). These results provide no evidence for a perceived temporal discrepancy between S-cone and luminance signals, especially not in the expected direction.

Motor and perceptual times compared

If the same visual processing was involved for perceptual judgments and motor responses, then any difference in perceived times between two signals should not differ from the difference in response times. To test this, we performed two paired sample t test to compare the PSSs obtained in Experiment 2 with the differences in reaction time (ΔRT_{manu} and ΔRT_{sacc}) from Experiment 1 on the 10 observers who did both experiments. PSSs appear to be significantly smaller than both manual and saccadic effects (paired-samples one tail t test, $t(9) = 2.2, p < 0.05$ and $t(9) = 4.2, p < 0.01$, respectively).

Correlations between perceptual and motor responses

Even if PSSs are significantly smaller than differences in reaction times, the two measures could still show some degree of correlation, which would suggest they rely partly on the same visual processes. Figure 8 illustrates the relationship between PSSs and differences in reaction times (ΔRT) obtained between S-cone and luminance signals for manual and saccadic responses. PSSs were significantly

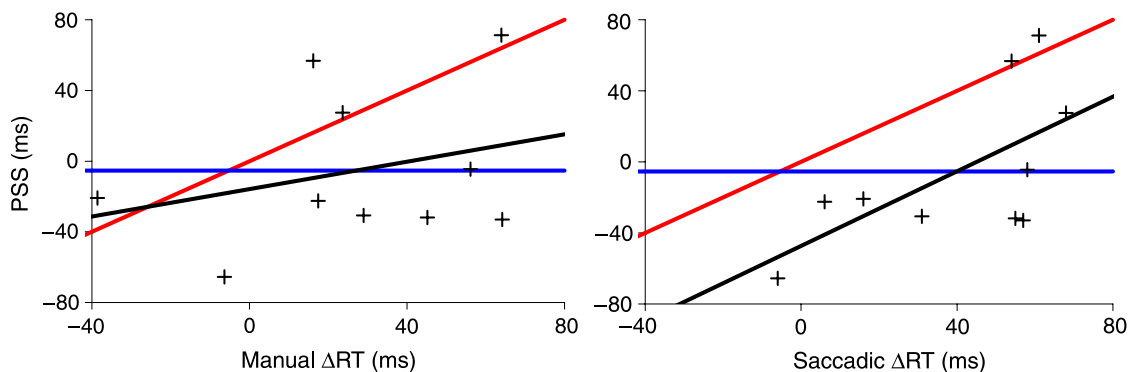


Figure 8. Points of subjective simultaneity (PSS) as a function of manual (left panel) and saccadic (right) differences in RTs (S-cone – luminance). Data for each subject are plotted (+) and the black lines show the linear regression curves. Colored lines represent the predictions of two extreme models: One-system model (red) and two-independent-models (blue), as in Figure 6.

correlated to ΔRT_{sacc} (PSS = $1.05 \Delta RT_{\text{sacc}} - 47$, $R^2 = 0.40$, $F(1,9) = 5.4$, $p < 0.05$) but not to ΔRT_{manu} (PSS = $0.39 \Delta RT_{\text{manu}} - 16$, $R^2 = 0.08$, $F(1,9) = 0.74$, $p > 0.1$). It is surprising that PSSs are better predicted by ΔRT_{sacc} since, in our study, PSSs are on average closer to ΔRT_{manu} (with a difference of 28 ms between mean PSS and mean ΔRT_{manu} , against 48 ms for ΔRT_{sacc}).

Discussion

Sluggish responses to S-cone signals

A first, straightforward, conclusion to this study is that both manual and saccadic responses are slower for S-cone than for luminance signals. This had already been shown for manual responses, though never successfully when using spatiotemporal luminance noise (Smithson & Mollon, 2004). It is noteworthy that the amplitude of luminance noise used in the present study ($\pm 1 \text{ cd/m}^2$ around 25 cd/m^2) was smaller than that employed by Smithson and Mollon (2004; $\pm 3 \text{ cd/m}^2$ around 22.5 cd/m^2). Smithson and Mollon concluded that luminance noise causes saturation of the luminance pathways, which slows them down and reduces the latency difference between them and the S-cone pathway. We therefore limited the range of our luminance noise in an attempt to limit such saturation. However, the presence of some luminance noise may always reduce any observed differences in latency between luminance and chromatic stimuli, and thus our measured differences for both manual and saccadic responses may be underestimated.

Previous studies have also reported differences in saccadic latency between luminance and S-cone stimuli (Anderson et al., 2008; Perron & Hallett, 1995), but this is the first time they have been measured for S-cone stimuli that were carefully calibrated for peripheral vision and also whose detectability was psychophysically matched with that of the luminance stimuli. Anderson et al. (2008) used clearly visible stimuli equated in subjective saliency and found a difference of 20–30 ms (with a luminance noise range slightly smaller than ours: $\pm 0.6 \text{ cd/m}^2$ around 25 cd/m^2). Thus, it seems that using hardly visible stimuli equated on the basis of detectability, as we did here, may enhance the reaction time difference.

Express saccades

Interestingly, our results show evidence for express saccades in response to S-cone stimuli—the early mode at around 100 ms visible in the saccadic latencies in Figure 4. This finding is complementary to that reported by Weber, Fischer, Bach, and Aiple (1991) for red-green contrasts. The presence of express saccades for chromatic stimuli is not consistent with the long-standing view that the

retinotectal route is responsible for their production. A similar conclusion has been reached by Carpenter (2001), who suggests that express saccades, rather than being the consequence of a particular mechanism, are a product of trial order. Carpenter found that the early mode was produced almost exclusively by trials in which the target appeared on the opposite side from the preceding trial, suggesting that saccades are facilitated when they have the same direction as the return saccade from the preceding trial. Our results confirm a significant tendency for saccades to be shorter when a saccade in the opposite direction was performed on the preceding trial, for both luminance (by 29 ms on average, $t(11) = 2.9$, $p < 0.05$) and S-cone signals (18 ms, $t(11) = 4.5$, $p < 0.01$). However, in our results, express saccades did not appear to be exclusively produced by trial order since they were present in both distributions formed respectively by trials in the same direction or in the opposite direction as the trial that preceded them. This result suggests that while trial order can be a source of variability in saccade latency, it cannot be the only explanation for express saccades.

Manual and saccadic responses: same processes?

Most interesting is our second main finding that the difference in reaction times to S-cone and luminance signals is larger for saccade latencies than for manual responses. This result suggests that saccades can take better advantage of fast signals when these are available. Thus, the result is not compatible with the parsimonious “one system” model, in which the same target detection stage is used for manual and saccadic responses.

A less parsimonious model could maintain the hypothesis of a common collector stage, where signals from all pathways are brought together, but allow different decision thresholds to apply for different responses. An internal response to sensory stimulation is usually described as an increasing function that saturates as the response gets close to its maximum. Consequently, the delay between two internal responses would tend to diminish with time, as both responses get closer to their maximum. Thus, earlier decisions, based on signals far from their maxima, could be more sensitive to latency differences between pathways. According to this hypothesis, our results could be compatible with a lower decision threshold for saccades than for manual responses. However, our results fail to support any of the further predictions proposed by such a model. First, there was no evidence for a correlation between ΔRT_{sacc} and ΔRT_{manu} , as would be expected if both responses relied on the same combination of signals. Secondly, different decision criteria would predict different proportions of correct answers for manual and saccadic speeded detections (note that the stimuli were identical for manual and saccadic blocks and were calibrated on a preliminary

manual 2AFC task). Last, in the standard race or diffusion models (Gold & Shadlen, 2001; Smith & Ratcliff, 2004), the variance of the internal signal is thought to increase over time. Therefore, a higher decision threshold is expected to lead to a higher response variability, but no variability difference was found between saccadic and manual reaction time distributions ($\sigma_{\text{manu-S}} = 101$ ms, $\sigma_{\text{manu-L}} = 111$ ms, $\sigma_{\text{sacc-S}} = 109$ ms, $\sigma_{\text{sacc-L}} = 108$ ms).

Our results suggest that manual and saccadic responses rely on different combinations of signals, fast signals playing a larger role for saccade generation than for manual responses. A straightforward explanation for this would be that saccade generation benefits from signals in the retinotectal pathway projecting directly from the retina to the superior colliculus (SC), which is known to play a major role in saccades. However, this pathway projects to superficial layers of the SC, while saccade-related cells lie in the deeper layers, and the connections between the SC layers may be surprisingly weak (Isa, 2002). Thus, it is not clear whether signals in the retinotectal pathway can have a strong direct impact on saccade cells in the SC. Instead, the importance of the retinotectal route for saccades may lie in the onward projections to the pulvinar, frontal eye fields (FEF) and intraparietal sulcus (IPS), which in turn project back to deeper layers of SC (e.g., Paré & Wurtz, 1997). It is also likely that the magnocellular pathway plays a crucial role because it feeds projections from visual cortex to the SC (Schiller, Malpeli, & Schein, 1979) and also because it is likely to supply fast signals to FEF and IPS. Thus, saccades are likely to utilize fast signals from both retinotectal and magnocellular pathways to both frontal and parietal cortex, and our results imply that these fast signals, which S-cone stimuli do not supply, are relatively more important for saccades than for manual responses.

Temporal order judgments and motor reaction times: Same processes?

Our last result is the absence of perceived discrepancy between S-cone and luminance signals. At first sight, this seems surprising given the accumulating evidence that S-cone signals are sluggish relative to luminance signals (Cottaris & De Valois, 1998; Krauskopf, 1973; Rabin et al., 1994; Robson & Kulikowski, 1998) and produce delayed motor responses (as shown again in Experiment 1). However, *perceptual* S-cone sluggishness has rarely been tested. The main evidence has been the Mollon–Polden effect, in which the motion of a blue bar is perceived to lag behind a physically aligned red bar when both are presented on a strong yellow adapting field (Mollon & Polden, 1976). However, it has recently been reported that when the background adapts S- and L-cones equally, the effect is greatly diminished and movement of the bars is perceived as nearly synchronous (Land et al., 2007). Thus, there is converging evidence that the perceptual delay of S-cone stimuli is actually much smaller than would be

predicted by the delays measured physiologically or with speeded motor responses.

Several studies have found that subjective simultaneity is less affected than motor response time by changes in stimulus attributes such as salience, spatial frequency, or duration, although PSS and Δ RT generally appeared to be related (Jaśkowski, 1992; for a review, see Cardoso-Leite et al., 2007). However, some striking dissociations have been reported. Tappe et al. (1994) found that variations in the high spatial frequency range produced a marked effect on RT but left TOJ completely unaffected. Adams and Mamassian (2004) found that while motion changes were detected faster than color changes in an RT task, color changes are perceived to occur earlier than motion changes in a TOJ task. They argue that the processing times for various attributes, rather than being considered as absolute and fixed, could depend on the required task.

Inconsistencies between motor and perceptual responses can be interpreted with reference to the hypothesis that vision is dissociated into two streams, anatomically and functionally independent, for perception and action purposes (Milner & Goodale, 1995). In particular, Adams and Mamassian (2004) explained their results in terms of a dorsal stream for action that is most sensitive to motion and less to color, whereas TOJ would be mediated by the ventral stream, devoted to vision for perception and thought to be more sensitive to color. According to this framework, our results suggest that the difference in processing time between S-cone and luminance signals is larger for the dorsal than for the ventral stream, which would be consistent with relatively greater influence from magnocellular and retinotectal routes in the dorsal stream. However, while this framework could explain larger S-cone delays for motor responses than perceptual judgments, it still leaves unexplained why the delay to S-cone signals measured physiologically at V1 is not translated into a measured perceptual delay at all.

Fundamental differences between motor and perceptual responses can also be expressed in terms of feedforward versus feedback processes. Lamme and Roelfsema (2000) proposed that, while bottom-up feedforward projections can subserve many processes including motor action, additional top-down feedback connections are necessary for a stimulus to be consciously perceived. Such a proposal is supported, for instance, by evidence from a transcranial magnetic stimulation study, in which awareness of visual motion was prevented when the feedback from human area MT+/V5 to V1 was disrupted (Pascual-Leone & Walsh, 2001). The involvement of feedback projections for perceptual judgments but not for speeded responses could explain inconsistencies between RTs and TOJ by two ways. First, because they take time, feedback recurrent connections could “wash out” the delay between S-cone and luminance pathways into noise, so that any delay becomes far harder to measure. Also, feedback connections from higher level areas could correct the discrepancy between pathways and allow the recovery of

synchrony between them. Such a compensatory mechanism could result from learning the usual correlations and delays between pathways from natural stimuli, which are usually visible to all chromatic and achromatic pathways. Since the pathways normally covary strongly in time, their relative delays could be learnt and used in perception to automatically recover physical synchrony.

Both dissociations, between dorsal and ventral streams and between feedforward and feedback, would allow some partial overlap between the mechanisms involved in motor and perceptual responses and could therefore account for a certain level of correlation observed in the literature between the two measures (e.g., Cardoso-Leite et al., 2007). In our results PSS correlated with ΔRT_{sacc} but not with ΔRT_{manu} . We tried to disambiguate this result by testing a prediction of Cardoso-Leite et al. regarding σ_{TOJ} —the standard deviation of the Gaussian distribution underlying the temporal order judgments—and σ_{RT} —the standard deviations of reaction time distributions for each signal presented alone. If both responses rely on a common internal response, σ_{TOJ}^2 is expected to be correlated to $\sigma_{\text{RT-S}}^2 + \sigma_{\text{RT-L}}^2$. We observed no hint of such correlation, neither for manual responses nor for saccades, bringing no further support to an overlap between mechanisms involved for motor and perceptual responses.

Conclusion

In summary, the present study focuses on two types of signals, S-opponent and luminance signals, that show a relative delay in their transmission and finds that they are not equally involved in three types of responses: manual and saccadic speeded responses and perceptual judgments. Although both speeded responses are affected by sensory sluggishness, saccade generation seems to take better advantage of fast luminance signals than do manual responses. This result could indicate a relatively more important role in saccadic initiation for the magnocellular and retinotectal pathways to the SC, FEF, and IPS. On the other hand, subjective simultaneity did not appear to be affected by sensory sluggishness. This dissociation is consistent with a fundamental difference between the way motor responses are initiated and perceptual judgments are made.

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