Dissociation of color and luminance on saccade initiation during target selection in the superior colliculus

Brian J. White¹ and Douglas P. Munoz²,³,⁴

Centre for Neuroscience Studies¹, Departments of Physiology², Psychology³ and Medicine⁴, Queen’s University, Kingston, Ontario, Canada

Corresponding author:
Brian J. White, Tel: 613-533-6360 x78890, Fax: 613-533-6840
Email: brianw@biomed.queensu.ca

Manuscript:
Figures: 4
Abstract: 201 words
Introduction: 762 words
Results: 911 words
Discussion: 825 words
Methods: 1170 words

Supplementary Material:
Supplementary Figures: 5
Supplementary text: 719 words

Acknowledgements:
The authors thank Ann Lablans, Donald Brien, Sean Hickman and Mike Lewis and for technical assistance. This project was funded by the Human Frontiers Science Program, Grant RGP0039-2005-C, and the Canadian Institutes of Health Research Grants MOP-77734 and CNS-90910. DPM was supported by the Canada Research Chair Program.

Keywords: visual search, visuomotor mechanisms, pop-out, saccadic eye movements, feature selectivity
ABSTRACT

One of the primary functions of the primate superior colliculus (SC) is to orient visuospatial attention towards behaviorally relevant stimuli on the basis of such features as color. However, a longstanding view has held that visual activity in the SC arises exclusively from achromatic pathways. We recently reported evidence that the SC is also highly sensitive to signals originating from chromatic pathways, supported by the fact that the arrival time for isoluminant color signals is significantly delayed relative to luminance signals. Here, we examined how this difference in visual arrival time affects processes leading to visual target selection and saccade initiation in the SC. We trained monkeys to perform a simple color-singleton selection task in which stimuli were either luminant or isoluminant relative to the background. While visual responses were significantly delayed at isoluminance, target discrimination time was relatively unchanged, provided that stimulus chromaticity was held constant. However, saccades were triggered sooner in the luminant condition. In other words, the luminance increment triggered the accumulation of SC neuronal activity towards response threshold in advance of the arrival of color-related signals. This implies that different visual mechanisms may act independently on the neural accumulator that triggers a saccadic command in the SC. One mechanism is largely determined by the arrival time of pertinent visual signals, while the other is linked to the target selection process.
INTRODUCTION

The primate superior colliculus (SC) has been implicated as a critical component in the selection of visual targets on the basis of such features as color\(^1^4\). However, a longstanding view has held that visual activity in the SC arises exclusively from achromatic pathways\(^5^6\). Recently, we\(^7\) reported evidence that the SC also receives a significant contribution from chromatic pathways, supported by the fact that its response to isoluminant color stimuli is significantly delayed relative to luminance-defined stimuli. Here we describe a critical consequence of this shift in visual arrival time on the neural processes underlying target selection and saccade initiation in the SC.

During selection of a color singleton (see for example Fig. 1a-c), neurons in brain areas that are actively involved in target selection (e.g., visual area V4\(^8^9\); lateral intraparietal area, LIP\(^10^11\); frontal eye fields, FEF\(^12^13\); SC\(^1^3\)) initially respond indiscriminately to a target or distractor (Fig. 1d). That is, the appearance of an array of visual stimuli generates an initial volley of visual activity that is typically not feature selective (see however\(^14\)). Selection then evolves as target-related activity is enhanced while distractor-related activity is suppressed\(^2^3^12^13\). However, studies investigating neural selection processes with color have typically used stimuli that are not equiluminant with the background, such that they carry significant achromatic and chromatic components. We reasoned that if visual signals from chromatic mechanisms are delayed in brain areas that are involved in the selection of color targets (e.g., the SC), the earliest observed visual volley might represent a task-irrelevant
achromatic response to signals carried along the shortest visual pathways (e.g., retina->SC\textsuperscript{15} or retina->V1->SC\textsuperscript{16}). This raises an interesting question: In a selection task where color is the critical feature, is the selection process tied to the arrival of the earliest achromatic signals or the subsequent task-relevant chromatic signals? If the latter is true, what role does this initial volley of achromatic information play in generating the saccadic command during a target selection task where color is the critical feature?

To this end, we recorded the activity of single SC neurons while monkeys performed a simple color-singleton selection task using three interleaved conditions designed to test the effect of a luminance versus a color manipulation (Fig. 1a-c; see Methods). Briefly, in the “Iso-easy” condition (panel b) all items were isoluminant with the background, with the target easily discernible from distractors. In the “Lum-easy” condition (panel a) everything was identical except that luminance contrast (-36\%) was added to all search items equally (luminance manipulation). In the “Iso-diff” condition (panel c) items were isoluminant with the background but distractor chromaticity was shifted closer to the target color making it less discriminable (color manipulation). These stimuli allowed us to formulate specific predictions based on three critical parameters (Fig. 1d-g), visual response onset latency (ROL), neural discrimination time (DT), and saccadic reaction time (SRT) (see Methods). Using these stimulus manipulations our aim was to independently manipulate the neural parameters, ROL and DT, and then measure their independent contribution on the initiation of a saccadic command.
The predictions may be summarized as follows: First, we expect a delay in ROL in the Iso-easy relative to the Lum-easy condition (luminance manipulation, Fig. 1d) because responses to isoluminant color stimuli in the SC are significantly delayed relative to high contrast luminance stimuli\(^7\). Second, the delay in ROL should produce a corresponding delay in SRT\(^7\) (Fig. 1d, f left panel). In contrast, we expect no difference in ROL between the isoluminant conditions (color manipulation, Fig. 1e and Fig. 1g left panel) because no difference was found previously for equally saturated isoluminant colors derived from these directions in the color space\(^7\). The critical question involves DT. We expect the color manipulation to prolong SRT in the Iso-diff condition by directly prolonging DT due to reduced search efficiency\(^17\) (Fig. 1e, and Fig. 1g right panel). However, for the luminance manipulation, we predict one of two possible outcomes regarding DT (Fig. 1d and Fig. 1f right panel): 1) DT will be delayed along with the predicted delay in ROL. 2) DT will remain constant—or moderately shorter with the luminance pedestal\(^18,19\)—because a shift in stimulus luminance has been shown to have little effect on search performance when stimulus chromaticity is held constant\(^20\). Thus, if SRT is tied to ROL independent of DT for the luminance manipulation, and SRT is tied to DT independent of ROL for the color manipulation, it supports the hypothesis that the pathways carrying chromatic and achromatic signals to the SC can act independently to generate a saccadic command. The following results show that this is precisely the case.

RESULTS
Two rhesus monkeys performed the color-singleton selection task with the three interleaved stimulus conditions previously described: Lum-easy, Iso-easy, and Iso-diff (see Methods and Fig. 1). Fig. 2 summarizes the behavioral results collected from 44 independent recording sessions. As predicted, mean SRTs for correctly directed saccades (Fig. 2b) were significantly delayed in the Iso-easy (red) relative to the Lum-easy (black) condition \( t_{43} = 14.28, p < .00001 \), and delayed further in the Iso-diff (blue) condition \( t_{43} = 7.74, p < .00001 \). The proportion of saccade direction errors (Fig. 2c) also significantly differed between conditions, with more errors in both the Lum-easy and Iso-diff conditions relative to the Iso-easy condition \( t_{43} = 5.59, p < .00001, t_{43} = 11.16, p < .00001 \), respectively). We also observed subtle differences in saccade metrics (supplementary Fig. S1a-c) between stimulus conditions, in particular peak saccade velocity was slightly higher in the Lum-easy condition.

(Figure 2 here)

We then examined the results of 44 visuomotor SC neurons (see Methods for rationale behind neuron-type used). To evaluate the neural selection process across stimulus conditions, we compared target- versus distractor-related SC activity time-locked to the appearance of the search array. Fig. 3 shows the rasters and spike density functions between stimulus conditions for a single visuomotor neuron. The left column illustrates the luminance manipulation (Iso-easy vs Lum-easy), and the right column illustrates the color manipulation (Iso-easy vs Iso-diff). For the example neuron, the target-related response (solid lines) showed a clear delay in ROL for the Iso-easy relative to the Lum-easy
condition (Fig. 3c), which otherwise looked identical. However, the distractor-related responses (dashed lines) were somewhat different. While there was a clear shift in ROL, distractor-related activity was suppressed at about the same rate in both conditions ($t_{43} = 0.27$, $p = .1$ across population comparing average distractor-related activity within shaded region in Fig. 3c). Furthermore, in the Iso-easy condition the target was already partially discriminated early within the initial volley of visual activity. Consequently, this neuron discriminated the target from distractors at about the same time in either condition. In contrast, for the color manipulation, ROL was virtually identical for the target- and distractor-related response in the Iso-easy and Iso-diff conditions (Fig. 3d), but DT was clearly prolonged in the latter, largely because distractor-related activity remained elevated relative to the Iso-easy condition ($t_{43} = 5.23$, $p < .00001$ across population comparing average distractor-related activity within shaded region in Fig. 3d). The single neuron results were replicated in the average spike density functions for the sample of 44 visuomotor neurons (Fig. 3e-f).

In addition, saccade-aligned population responses (supplementary Fig. S1d-g) showed subtle differences between conditions that matched the differences in saccade metrics (Fig. S1a-c) described earlier. In particular, there was a slightly greater peak saccade burst with the luminance increment, which matched the increase in peak saccade velocity for this condition.

(Figure 3 here)

To test directly the predictions laid out in Fig. 1f-g, we derived precise measures of ROL and DT for each visuomotor neuron (see Methods), and
correlated them with the average SRT obtained from each of the 44 recording sessions. Fig. 4a-b shows the results of the luminance manipulation and color manipulation, respectively. For the luminance manipulation, there was a clear positive relationship between ROL and SRT (Fig. 4a left panel) with the median angle of the lines showing a near perfect relationship (45° is perfect, and here median = 43°, SEM = ±2.5°). However, there was a much weaker relationship between DT and SRT (Fig. 4a right panel), with more variability (median = 71°, SEM = ±6.9°). That is, for the luminance manipulation ROL was a far better predictor of the change in SRT than DT. In contrast, for the color manipulation, DT (median = 22°, Fig. 4b right panel) was a better predictor of the change in SRT than ROL (median = 89°, Fig. 4b left panel). This is concisely summarized in Fig. 4c-e. In short, the change in SRT as a result of the luminance manipulation (Fig. 4e, black versus red) was primarily due to the delayed ROL for isoluminant color signals (Fig. 4c, black versus red, $t_{43} = 20.11$, $p < .00001$) and not due to differences in DT (Fig. 4d, black versus red, $t_{43} = 1.6$, $p = .31$). In contrast, the change in SRT as a result of the color manipulation (Fig. 4e, red versus blue) was primarily due to prolonged DT as a result of reduced target-distractor discriminability (Fig. 4d, red versus blue, $t_{43} = 7.9$, $p < .00001$), and not due to differences in ROL (Fig. 4c, red versus blue, $t_{43} = 0.3$, $p = 1$). These results strongly support the hypothesis that the pathways carrying luminance versus color-related signals to the SC can act independently on generating a saccadic command.

(Figure 4 here)
This hypothesis is also consistent with the pattern of saccade direction errors one might expect (Fig. 2c). We predicted a greater proportion of direction errors in the Iso-diff condition simply because of reduced target discriminability. However, if luminance contrast pushed neuronal activity towards response threshold before the arrival of the task-relevant chromatic signals, we would also predict a greater proportion of direction errors in the Lum-easy relative to the Iso-easy condition. This was precisely what we found (Fig. 2c). In other words, the saccade system appears to use the early transient luminance signals to prepare a movement in advance of the arrival of task-relevant chromatic signals at the expense of a moderate increase in error rate.

DISCUSSION

Our results provide strong evidence for a dissociation between visual mechanisms leading to the initiation of a saccadic response in the superior colliculus: For the luminance manipulation, SRT was tied to ROL independent of DT, whereas for the color manipulation, SRT was tied to DT independent of ROL. In other words, if the selection process in the SC were triggered by the earliest arriving visual signals, we would expect selection time to be delayed with the corresponding delay of isoluminant color signals. However, selection time was about the same for the luminance manipulation despite the fact that visual responses were significantly delayed at isoluminance. This suggests that the selection process may instead be tied to the arrival of the task relevant chromatic component of the stimuli. However, while selection time remained constant, saccades were nonetheless triggered earlier with the luminance increment. This
implies that luminance signals contributed to the accumulation of neuronal activity (in a spatially nonspecific manner) towards response threshold in advance of the arrival of the color-related signals. This was very different from the color-manipulation which also had a dramatic effect on behavior and neural processes, but in a clearly different manner, by prolonging the integration time required for discriminating the target, thereby prolonging the distractor-related response leading to later DT.

We have known for some time that the SC is critical for the production of saccadic eye movements21, and more recently that it is directly involved in visual target selection1-4. Here, we have suggested the existence of independent visual mechanisms for the initiation of the saccadic response. One mechanism is linked to the arrival time of pertinent visual signals, and a second mechanism is driven by later arriving visual signals that are associated with the target selection process. One possibility is that visual signals arising from different pathways (possibly representing different stimulus features) may arrive at different times in brain areas responsible for selection. We propose that the initial volley of visual activity in the SC is purely achromatic and arises from the shortest pathways to the SC associated with bottom-up processes (e.g., retina->SC15 or retina->V1->SC16), whereas the isoluminant color responses we have observed in the SC7 arise from relatively longer pathways (e.g., extrastriate->SC22,23, or V4->FEF->SC24).

Anatomically, the SC is known to receive direct projections from various visual sources (e.g., retinotectal15, V116, V225, MT26, V422), with increasingly
higher visual areas projecting to increasingly deeper SC layers\textsuperscript{27}. It is reasonable to presume that these structures do not all carry identical visual signals to the SC. Furthermore, signals arriving from for example V4 should invariably reach the SC later than those arriving from V1\textsuperscript{28}. Consistent with this view, color-related signals in the SC are absent in the retinotectal fibers\textsuperscript{6}, but are found in abundance in the intermediate SC layers\textsuperscript{7}. Alternatively, because color-related activity is absent in the SC of anesthetized monkeys\textsuperscript{5}, color-related signals might be carried via pathways that carry the top–down (goal-related) signal to the SC (e.g., V4->FEF->SC\textsuperscript{24}), which may be disrupted by anesthesia.

Recall that we observed evidence of selection within the earliest epoch of visual activity, in particular for the Iso-easy condition (red curves in Fig. 3), which is in contrast to previous studies\textsuperscript{1-3,8-10,12,13} (see however\textsuperscript{14}). That is, by removing the luminance component, we observed evidence suggesting that selection (or possibly the color discrimination component of the selection process) had begun prior to the arrival of isoluminant color signals in the SC. This is in line with the fact that the SC (like most of the oculomotor network\textsuperscript{1-3,8-10,12,13}) is not feature selective, but better represents the site of the integration of the output of visual feature maps (i.e., a visual salience map\textsuperscript{29}, or a priority map\textsuperscript{30}). This is consistent with the finding that single SC neurons show little unique color specificity\textsuperscript{7}. Alternatively, this early selection we observed might reflect the sort of experience-dependent feature selectivity described by Bichot and colleagues\textsuperscript{14}. Bichot and colleagues showed that while FEF neurons do not typically exhibit feature selectivity, extensive training exclusively with targets of one color can
produce feature selective responses within the initial volley of visual activity. Because this selective response occurs so soon after the appearance of the stimulus array, Bichot and colleagues proposed that it reflects a form of experience-dependent plasticity that mediates the learning of stimulus-response associations. Our results might reflect a similar process in the SC because our monkeys were trained continuously with the same stimulus color configurations (see Methods). Most importantly, the three stimulus conditions were randomly interleaved while this early selectivity was most pronounced in the Iso-easy condition (Fig. 3, see also supplementary Fig. S2). This suggests the intriguing possibility that the experience-dependent plasticity described by Bichot and colleagues may be specific to the task-relevant pathways (in this case, the pathways carrying color-related signals to the SC). Consequently, we would expect it to be less pronounced when the target-related signals are less discernible (Iso-diff condition), or are contaminated by visual signals arising from achromatic mechanisms (Lum-easy condition).
METHODS

Data were collected from two Rhesus monkeys (*Macaca mulatta*, 11 and 12 kg). Surgical procedures and extracellular recording techniques were previously described\(^3\).

**Stimuli and Equipment**

Stimuli were presented on a CRT monitor at a screen resolution of 1024 x 768 pixels (75Hz non-interlaced), subtending a viewing angle of 54 x 44 deg. The voltage-to-luminance relationship (gamma) for each of the monitor's phosphors was linearized using the UDT instruments (San Diego, CA, USA) S471 optometer with a model 265 photopic filter. The monitor's color properties were measured using the PR-655 (Photoreserch, CA, USA), and corrections were made for the Judd-Vos modified luminosity function \(^{32,33}\). Stimulus presentation and data acquisition were controlled by a UNIX-based real-time data control system (REX; Hays, Richmond and Optican, 1982). Spikes, eye position data and event data were sampled at 40KHz, and recorded in a multi-channel data acquisition system (Plexon Inc., Dallas, Texas, USA).

Stimuli were circular disks whose color properties were derived from the DKL color space\(^3\) (Fig. 1a-c). This color space corresponds closely to the type of segregation that exists along the geniculostriate pathway in early vision\(^35\). One pathway sums the inputs of the long- and middle-wavelength cones (L+M), producing a luminance channel that is mostly sensitive to stimuli varying along the “black-white” dimension in the DKL space. A second pathway computes the difference between the inputs of the L and M cones (L-M), and is mostly sensitive
to stimuli varying along the “red-green” dimension in the DKL space. A third pathway computes the difference between the inputs of the short-wavelength cones (S-cones) with the sum of the L- and M-cones (S-(L+M)), and is mostly sensitive to stimuli varying along the “blue-yellow” dimension in the DKL space. These three channels form the primary visual-cortical inputs via the magno-, parvo-, and koniocellular layers of the LGN, respectively.

Monkeys performed a simple four-item color-singleton selection task (a target of one color amongst distractors that shared a different color) under three interleaved conditions designed to test the effect of a luminance- versus a color-manipulation (see Fig. 1a-c). For the luminance-easy (Lum-easy) and isoluminance-easy (Iso-easy) conditions the target chromaticity (“pink”, 330 degrees on the azimuth of the isoluminant color plane, CIE x = .329, and y = .248) was easily discriminable from the distractor chromaticity (“yellow”, 45 degrees on the azimuth of the isoluminant color plane, CIE x = .403, and y = .397). The only difference was that for the Iso-easy condition the stimuli were isoluminant with the background at 20.5 cd/m², whereas in the Lum-easy condition -36% luminance contrast was added to the stimuli (producing 5.5 cd/m² difference from the background). In the third isoluminance-difficult (Iso-diff) condition all stimuli were isoluminant with the background as in the Iso-easy condition but the distractor chromaticity was shifted closer to the target chromaticity. This distractor chromaticity was moderately different for each animal (5 and 0 degrees on the azimuth of the isoluminant color plane for monkey Y and Q respectively), and was set after a period of training in which we
observed a robust increase in saccadic reaction time while maintaining saccadic direction error rates below chance levels. Cell recording began only after behavior was stabilized. After several weeks of neural recording, stimulus colors were then swapped such that the target was now “yellow” and distractors “pink”. Once monkeys learned the new configuration, neural recording began once again. No differences were found with either configuration (see supplementary Fig. S3), so the data were collapsed in the main manuscript.

**Procedure**

Monkeys were seated in a primate chair (Crist Instruments Co., Inc., MD, USA), head-restrained facing the video monitor. Once an SC neuron was isolated, its visual response field was mapped using a rapid visual stimulation procedure (see for details). Monkeys then performed the visual search task. Each trial started with fixation of a central black fixation spot for 500-800ms followed by its removal and the simultaneous onset of one of the color-singleton search arrays shown in Fig. 1, which were randomly interleaved on a trial-by-trial basis. Monkeys simply looked to the target for a juice reward. Direction errors were not rewarded.

**Analyses and neuron classification**

Individual spikes were sorted offline using Plexon Offline Sorting Software (Plexon Inc., Dallas, Texas, USA) to remove artifacts and verify single units. Target-aligned spike density functions were created by convolving individual spikes with a function that resembles a postsynaptic potential, with a time constant of 1ms for the growth phase, and 20ms for the decay phase. Saccade-
aligned spike density functions were created by convolving individual spikes with a Gaussian kernel ($\sigma = 5\text{ms}$).

A delayed saccade task was used to classify each neuron under the same scheme as described in a previous paper (a similar classification scheme has been used by others). Briefly, neurons were classified as transient-visual, sustained-visual, transient-visuomotor, sustained-visuomotor, or motor-only (see Fig. S4). Only sustained-visuomotor SC neurons were reported in the main manuscript because these are thought to be the primary neurons associated with visual target selection in the SC. We did not find SC neurons with the biphasic pattern of visual activity described by McPeek. Transient-visual neurons were not sampled because they do not respond significantly to isoluminant colors. Consistent with earlier reports, the sample of sustained-visual neurons (N=17) did show significant color-related responses that were significantly delayed relative to luminance (see Fig. S5a), but these neurons poorly discriminated the target from distractors (see Fig. S4a-c), and did so too late to play an important role in target selection (Fig. S5b). The sample of transient-visuomotor neurons (N=7) showed small, unreliable visual responses to isoluminant color stimuli (Fig. S4g-i), and were therefore not included in the main manuscript. Motor-only neurons (N=17) lack visual activity altogether and were therefore also not included in the main manuscript (Fig. S4j-l).

A neuron was defined as visuomotor if the average firing rate right around the time of saccade onset (-25 to +25 ms) was greater than 3 standard deviations above a pre-saccadic epoch (defined as the average firing rate from -150 to -50
ms before saccade onset). Saccadic reaction time (SRT) was the time from target onset to saccade onset. Visual response onset latency (ROL) was the time from target onset to the point at which neural activity first exceeded 4 standard deviations above a baseline and remained so for >= 40ms. The baseline firing rate was the average activity from -70ms to +30ms relative to target stimulus onset. Peak visual response was the maximum response within 150 ms of target onset. Neural discrimination time (DT) was derived for each neuron within each stimulus condition using ROC analysis (receiver-operating-characteristic) similar to what has been detailed in previous studies\textsuperscript{2,17}, and was defined as the time in which discrimination probability reached a threshold of 0.7 and remained above this point for >= 20ms. Repeated measures ANOVAs were always performed across stimulus conditions, and F-statistics were always significant at p < .05 or better. Thus, for brevity, only t-statistics for simple effects were reported in the manuscript. Alpha levels were adjusted for multiple comparisons using the Bonferroni correction.
Figure 1. (a-c) Schematic of stimulus conditions and color space used to derive stimuli (see Methods). Luminance-easy (black), Isoluminance-easy (red), Isoluminance-difficult (blue). (d-e) Selection process illustrating predictions. D=distractors, T=target, BG=background, SRT=saccadic reaction time, ROL=visual response onset latency, DT=neural discrimination time.
Figure 2. Behavioral results across stimulus conditions. (a) Cumulative SRT distributions for correctly directed saccades (thick lines) and saccade direction errors (thin lines) across conditions. (b) Mean saccadic reaction time (SRT) across the 44 sessions for each stimulus condition. Mean proportion direction errors (PDE) across the 44 sessions for each stimulus condition (symbols in (c) represent PDE for each session). Dotted line in (c) represents chance error level. Errorbars represent ±1 SEM. * = $p < .00001$, Bonferroni corrected.
Figure 3. (a-b) Rasters and (c-d) spike density functions for an example sustained-visuomotor neuron across stimulus conditions (illustrated on the left). (e-f) Population spike density functions for N=44 neurons across conditions (shading = ±1 SEM). Dots in a-b represent spikes. Dotted lines in c-d represent the cumulative SRT distributions for trials associated with the target-related spike density function. Grey shaded region in c-d represents an epoch from 100-180ms from target onset for the comparison of distractor-related activity across conditions. RF=response field, illustrated by the circle around the search item in a-b, and the arrow represents the correct saccade direction. T=target, D=distractor, ROL=response onset latency, DT=discrimination time.
Figure 4. The relation between ROL, DT and SRT for (a) the luminance manipulation, and (b) the color manipulation. (c-e) Cumulative distributions summarizing the results with means in the inset. * = $p < .00001$, Bonferroni corrected.
References


