Behavioral/Systems/Cognitive

Color-Related Signals in the Primate Superior Colliculus

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Color is important for segmenting objects from backgrounds, which can in turn facilitate visual search in complex scenes. However, brain areas involved in orienting the eyes toward colored stimuli in our environment are not believed to have access to color information. Here, we show that neurons in the intermediate layers of the monkey superior colliculus (SC), a critical structure for the production of saccadic eye movements, can respond to isoluminant color stimuli with the same magnitude as a maximum contrast luminance stimulus. In contrast, neurons from the superficial SC layers showed little color-related activity. Crucially, visual onset latencies were 30–35 ms longer for color, implying that luminance and chrominance information reach the SC through distinct pathways and that the observed color-related activity is not the result of residual luminance signals. Furthermore, these differences in visual onset latency translated directly into differences in saccadic reaction time. The results demonstrate that the saccadic system can signal the presence of chromatic stimuli only one stage from the brainstem premotor circuitry that drives the eyes.

Introduction

Human and nonhuman primates are the only mammals with trichromatic color vision (Jacobs, 1993), and it is generally believed that this system was driven by the nutritional advantage of discriminating ripe fruit from foliage (Mollon, 1989; Regan et al., 2001) and edible leaves (Dominy and Lucas, 2001). Color therefore plays an important role in segmenting objects from backgrounds, which can in turn facilitate visual search (D'Zmura et al., 1997) and the recognition of natural scenes (Gegenfurtner and Rieger, 2000). However, the neural representation of color is widely believed to be absent in brain areas that control saccadic eye movements (Marrocco and Li, 1977; Schiller and Malpeli, 1977; Schiller et al., 1979; Ottes et al., 1987), which serve to direct gaze toward colored objects in our environment. Instead, the saccadic system is thought to be essentially color-blind and predominantly driven by the achromatic "broadband" or luminance system (Schiller et al., 1979), which is relayed through the magnocellular layers of the lateral geniculate nucleus (LGN) to visual cortex. There is, however, a large network of direct and indirect projections from visual cortex (including areas involved in color processing) to saccadic substrates, in particular the superior colliculus (SC) (Fries, 1984; Lui et al., 1995; Lock et al., 2003), a critical structure in the control of overt and covert visual orienting (Kustov and Robinson, 1996; Ignashchenkova et al., 2004; Fecteau and Munoz, 2006; Dorris et al., 2007). Furthermore, behavioral observations are in sharp contrast with the assumption that the saccadic system is color-blind: human observers have no difficulty in detecting and rapidly orienting toward chromatic stimuli that are isoluminant with the background (White et al., 2006), implying that some information about stimulus location is propagated to the saccadic system.

Here, we sought to test for a direct neural correlate of color information in the saccadic system using stimuli derived from the Derrington–Krauskopf–Lennie (DKL) color space (Krauskopf et al., 1982; Derrington et al., 1984), and visible primarily through a chromatic difference from the background (i.e., visible primarily to color-sensitive mechanisms). We report the first evidence that neurons in the primate SC can respond vigorously to such stimuli, and although they tend to show limited color specificity, these color-related signals appear to involve different pathways than luminance as evidenced by differences in visual onset latency, and the recruitment of primarily neurons with a sustained visual response from the intermediate SC layers.

Materials and Methods

Data were collected from two rhesus monkeys (*Macaca mulatta*; 11 and 12 kg). Extracellular recording techniques as well as surgical procedures have been described previously (Marino et al., 2008).

Stimuli and equipment. Stimuli were presented on a cathode ray tube monitor at a screen resolution of 1024 × 768 pixels (75 Hz noninterlaced), subtending a viewing angle of 54 × 44°. The voltage-to-luminance relationship (gamma) for each of the phosphors of the monitor was linearized using the UDT Instruments S471 optometer with a model 265 photopic filter. The color properties of the monitor were measured using the PR-655 (Photoresearch), and corrections were made for the Judd–Vos modified luminosity function (Judd, 1951; Vos, 1978). Stimulus presentation and data acquisition were controlled by a UNIX-based real-time data control system (REX) (Hays et al., 1982). Spikes, eye position data, and event data were sampled at 40 kHz and recorded in a multichannel data acquisition system (Plexon).

Target stimuli were Gaussian windowed spots (SD, 0.7°) whose color properties were derived from the DKL color space (Krauskopf et al., 1982; Derrington et al., 1984) (see Fig. 1*b*). This color space corresponds closely to the type of segregation that exists along the geniculostriate pathway in early vision (Derrington et al., 1984). One pathway sums the inputs of the long- and middle-wavelength cones (L + M), producing a

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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 magnocellular, parvocellular, and koniocellular layers of the LGN, respectively.

The target color stimuli were chosen from 30° steps around the azimuth in the isoluminant DKL color plane (illustrated by the small circles superimposed around the plane) (see Fig. 1*b*) and were presented against an isoluminant (20.5 cd/m^2) neutral gray background illustrated by the very center point of the DKL space. Background illumination was well above scotopic, rod-dominated, light levels (typically <1 cd/m^2) (Hess et al., 1990). *Post hoc* measurements of the luminosity of each color stimulus showed negligible deviations (<0.3 cd/m^2 for all colors) from the background luminance (see supplemental Fig. S1*a*, available at www.jneurosci.org as supplemental material). The achromatic control stimulus was presented at 100% luminance contrast (black) and corresponds to the very most bottom point in the DKL space (see Fig. 1*b*). Along the cardinal color axes, the maximum achievable cone contrasts for our stimuli were ~7% for L-cones, 13% for M-cones, and 87% for S-cones. It is important to note that the maximum achievable cone contrast in the L − M (red–green) direction is naturally only approximately one-tenth of the cone contrast of the L + M (black–white) direction because of the overlap in the spectral sensitivities of the L- and M-cones.

Procedure. Monkeys were seated in a primate chair (Crist Instrument), head-restrained facing the video monitor. Once an SC neuron was isolated, its visual response field was mapped using a rapid visual stimulation procedure. On a given trial, a rapid series of 14 stimuli were flashed (100 ms duration and 150 ms interstimulus intervals) at random locations across the visual field. There were 182 possible stimulus locations evenly dispersed across the visual field, and all locations were stimulated once after 13 consecutive trials. Spikes were collected over a small epoch from 60 to 90 ms after each stimulus onset and averaged on a trial-by-trial basis using a real-time mapping program written in Matlab (MathWorks). Activity was interpolated between stimulus locations to produce a smooth map denoting the "hot spot" of the neuron, usually within ~40–50 trials.

Once the visual response field was mapped, monkeys performed a delayed saccade task (see Fig. 1*a*). Each trial started with fixation of a black fixation spot for 500–800 ms, and then a target stimulus appeared in the response field of the neuron. After a delay (500–800 ms), the fixation spot was removed and a saccade was generated toward the target stimulus for a liquid reward. The monkey first performed the task using the luminance-based target stimulus, and then using randomly selected DKL color stimuli (previously described).

For the behavioral "gap" task, the fixation point was removed 200 ms before the onset of the target stimulus to facilitate the disengagement of visual fixation while measuring the visual triggering capability of the isoluminant color stimuli relative to the maximum contrast luminance stimulus. Here, isoluminant color stimuli were chosen from the cardinal color axes only (red, green, blue, and yellow). Stimuli were presented randomly left or right of fixation at 12° eccentricity.

Analyses and neuron classification. Individual spikes were sorted off-line using Plexon Off-line Sorting software (Plexon) to remove artifacts and verify single units. Spike density functions were created by convolving individual spikes with a function that resembles a postsynaptic potential (Thompson et al., 1996) described by the following equation: $R(t) = (1 - \exp(-t/\tau_g)) \times (\exp(-t/\tau_d))$, where firing rate R, as a function of time t, varies according a time constant for a growth phase τ_g, and a time constant for a decay phase τ_d. Consistent with Thompson et al. (1996), we chose time constants of 1 and 20 for the growth and decay phases, respectively.

SC neurons have fairly characteristic responses ranging from pure visual to pure motor and have been well described (Mays and Sparks, 1980; Munoz and Wurtz, 1995; McPeek and Keller, 2002). The terms "phasic" versus "tonic" have been used to describe the visual characteristics of SC neurons (McPeek and Keller, 2002; Li and Basso, 2008), phasic referring to a short visual burst and tonic referring to an initial visual burst followed by an extended period of lower frequency activity. SC neurons are often categorized as one or the other. However, in the intermediate layers, visual responses more often fall along a continuum between these two extremes. In the current study, stimuli were designed to target the luminance or color-opponent divisions of the geniculostriate pathway in early vision, whose neurons characteristically show a "transient" versus "sustained" visual response profile, respectively (Kaplan et al., 1990). We therefore adopted this terminology for SC visual responses in the current paper.

Note that what we refer to as "sustained-visual" SC neurons correspond to what has been termed "tonic-visual" neurons by others (McPeek and Keller, 2002; Li and Basso, 2008). These are also thought to be similar to the so-called "quasivisual" neurons first described by Mays and Sparks (1980). However, the double-saccade test was not performed to confirm this. Our "sustained-visuomotor" neurons likely correspond to "visuo-movement prelude" neurons (McPeek and Keller, 2002) and "build-up" neurons (Munoz and Wurtz, 1995; Dorris and Munoz, 1998), but we did not formally test for prelude or build-up activity.

We derived a transient index similar to that of Schiller and Malpeli (1977) to classify neurons as either visually transient or sustained using the following equation: Transient index = $(I/(I + D)) \times 100$, which defines a ratio between I, the maximum activity within an initial period of the visual response, and D, the average activity during a delay period of the visual response (note that classifications were made using the maximum contrast luminance stimulus). The initial period was chosen between 50 and 100 ms from target onset because most peak responses for our luminance stimulus occurred within this range. The delay epoch started where the initial epoch ended, extending from 100 to 500 ms after target onset. The main advantage of the large delay epoch was to insure that we obtained a reliable sample of the sustained profile while avoiding sparse periods of inactivity that are not reflective of the overall sustained profile of the neuron. Transient indices could range from 50 to 100, and neurons with an index ≥95 were considered transient, but otherwise were considered sustained. We chose a transient criterion of 95 to bias against misclassifying neurons as transient unless they were very transient.

Neurons from the superficial SC are invariably visual (Marrocco and Li, 1977) and correspond to the "transient-visual" type described here. They were clearly sampled from the uppermost region of the superficial SC so we can state with confidence that they were located in the superficial SC. Our sample of sustained-visual neurons were sampled well below this (typically deeper than 1 mm) and appear to correspond to the tonic-visual neurons described by McPeek and Keller (2002), which are believed to be located around the junction between the superficial and intermediate SC. Thus, it is not absolutely clear whether they belong to the lower region of the superficial SC or the upper region of the intermediate SC. Visuomotor neurons with transient or sustained visual responses were invariably found below both transient- and sustained-visual neurons. A neuron was defined as visuomotor if the average firing rate right around the time of saccade onset (−25 to +25 ms) was >3 SDs above a presaccadic epoch (defined as the average firing rate from −150 to −50 ms before saccade onset).

A color sensitivity index, described by Johnson et al. (2008), was computed for correlations with the visual transient index. This was simply a ratio of the peak response for the optimal color over the peak response for our maximum luminance contrast stimulus: Color sensitivity index = peak (optimal color)/peak (100% lum contrast).

It is important to note that this color sensitivity index will vary dramatically depending on the contrast used to measure the responses to isoluminant versus luminant stimuli. Therefore, indices obtained here are not directly comparable with those obtained in other studies.

For statistical analyses, visual onset latencies were defined as the time relative to target stimulus onset in which visual activity first exceeded 3 SDs above a baseline (defined as the average activity of a 100 ms epoch before target stimulus onset) and remained so for a reasonable period of time (>35 ms). Peak visual response was the maximum response within

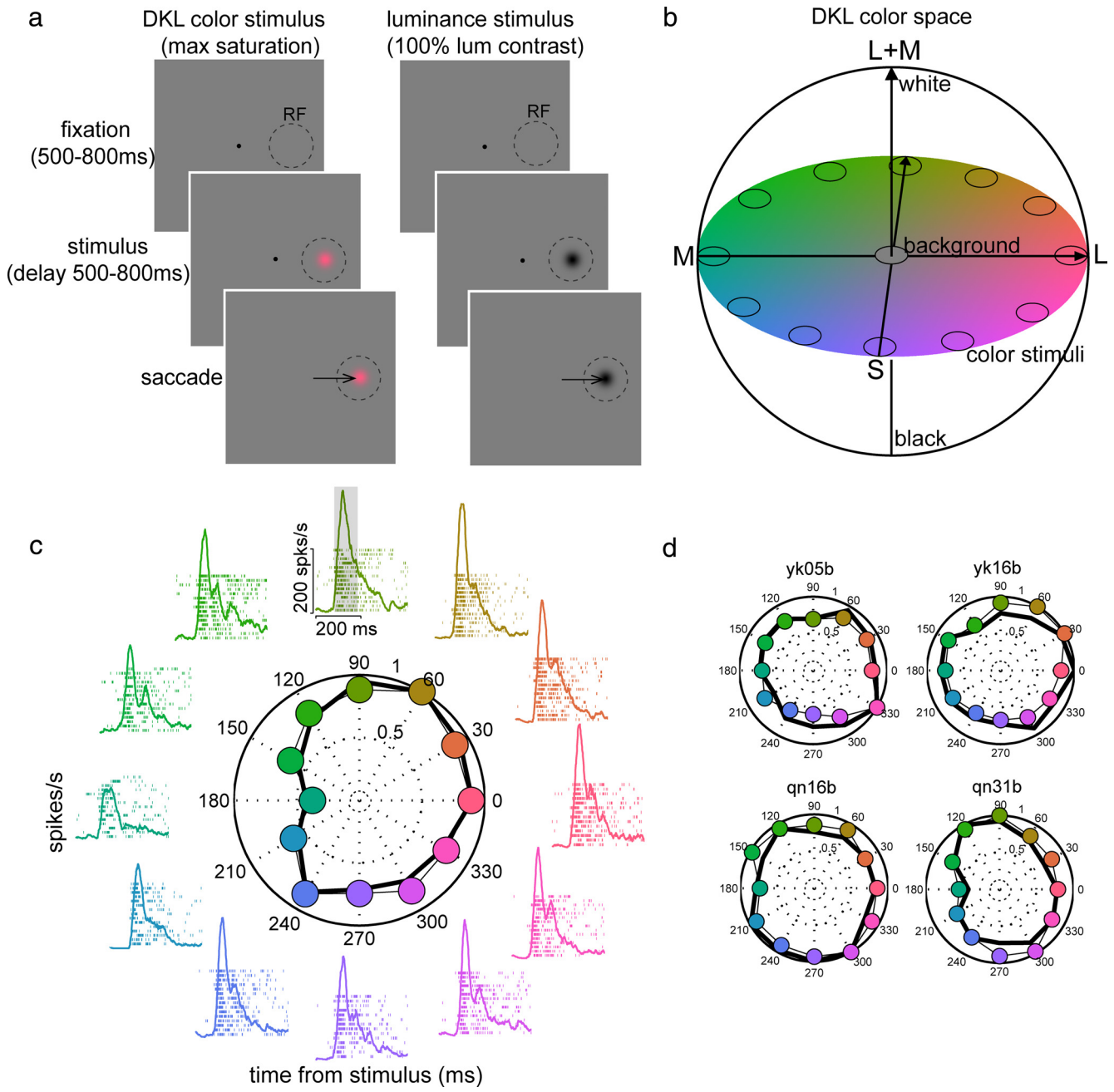

Figure 1. ***a***, Delayed saccade task. The monkey fixated a central black spot for 500–800 ms, and then a randomly chosen isoluminant color stimulus (Gaussian windowed; SD, 0.7°) appeared in the response field (RF) of the neuron. After a delay (500–800 ms), the fixation spot was removed, serving as a go-signal for a saccade toward the color stimulus. Comparisons were made with an achromatic black stimulus presented at 100% luminance contrast. ***b***, DKL color space (Krauskopf et al., 1982; Derrington et al., 1984) (see Materials and Methods). Color stimuli were chosen from 30° steps around the azimuth of the isoluminant plane at maximum saturation (illustrated by the circles superimposed on the color plane). The stimuli were presented against an isoluminant neutral gray background (20.5 cd/m^2) illustrated by the center point in the color plane. The achromatic black control stimulus corresponds to the very most bottom point in this space. ***c***, Rasters and spike density functions of a single sustained-visual SC neuron to each of the color stimuli (aligned on stimulus onset). At the center is a polar plot of the normalized peak responses for each color (colored symbols linked by the thin line). The thicker line shows the responses averaged over a short epoch (80–180 ms) defined by the gray shaded region. ***d***, Color tuning profiles for four additional sustained-visual neurons.

150 ms of target onset. For statistical comparisons, delay activity was defined as the average activity from 150 to 500 ms after target stimulus onset for our maximum contrast luminance stimuli, and 180 to 530 for our isoluminant color stimuli. The slight difference in the timing of these epochs was to account for the color-related delay in visual onset latency (see Fig. 2).

Results

We recorded the activity of 68 visually responsive neurons from the superficial (within 1 mm of SC surface) and intermediate layers (1–3 mm from SC surface) of the SC in two rhesus monkeys (*Macaca mulatta*) trained to perform a delayed saccade task using color stimuli presented against an isoluminant background (Fig. 1*a*) (for details, see Materials and Methods).

Neurons were categorized into two general visual classes (transient vs sustained) and whether or not they had motor activity (see Materials and Methods). Figure 1*c* shows rasters and spike density functions for a single sustained-visual neuron to the various colors chosen from 30° steps around the azimuth in the

DKL color plane (Fig. 1*b*). At the center is a polar plot showing the normalized peak response of the neuron for each color. This neuron showed a remarkably large response (161–432 spikes/s) to all isoluminant colors with a fairly broad color preference. Most of our sustained-visual/visuomotor neurons showed similarly strong responses (Fig. 1*d*), 36% (21 of 59) of which were moderately, although significantly, tuned [$p < 0.01$, r^2 from 0.65 to 0.93, planar-fit regression-based test for directional tuning (Kurtzer et al., 2005)], indicating the presence of at least some broad color preferences.

A critical question is whether these are true color-related signals (i.e., signals originating from the color-opponent system in early vision) or simply residual luminance signals. Residual luminance could render a photometrically isoluminant stimulus detectable from its background via luminance-sensitive mechanisms. This may arise from (1) less than perfect stimulus calibration, (2) variation in individual observer's isoluminant point, or (3) variation in the isoluminance balance of the individual neuron (Logothetis et al., 1990; Dobkins and Albright, 1994; Gegenfurtner et al., 1994) (see supplemental data, available at www.jneurosci.org as supplemental material). We would nonetheless expect the effect of residual luminance to be relatively small, at least compared with the magnitude of the responses observed here [e.g., somewhere in the range of 25% of the maximum response (Gegenfurtner et al., 1994)]. Given the size of the observed color-related response, we took a conservative approach to this issue by making comparisons between the optimal color of each neuron and an achromatic stimulus of 100% luminance contrast (Fig. 1*a*). This represents the maximum degree of separation possible between test and control stimuli within this color space, such that if residual luminance is responsible for the observed response to our color stimuli, it should be at least smaller than the response to an achromatic stimulus of maximum luminance contrast.

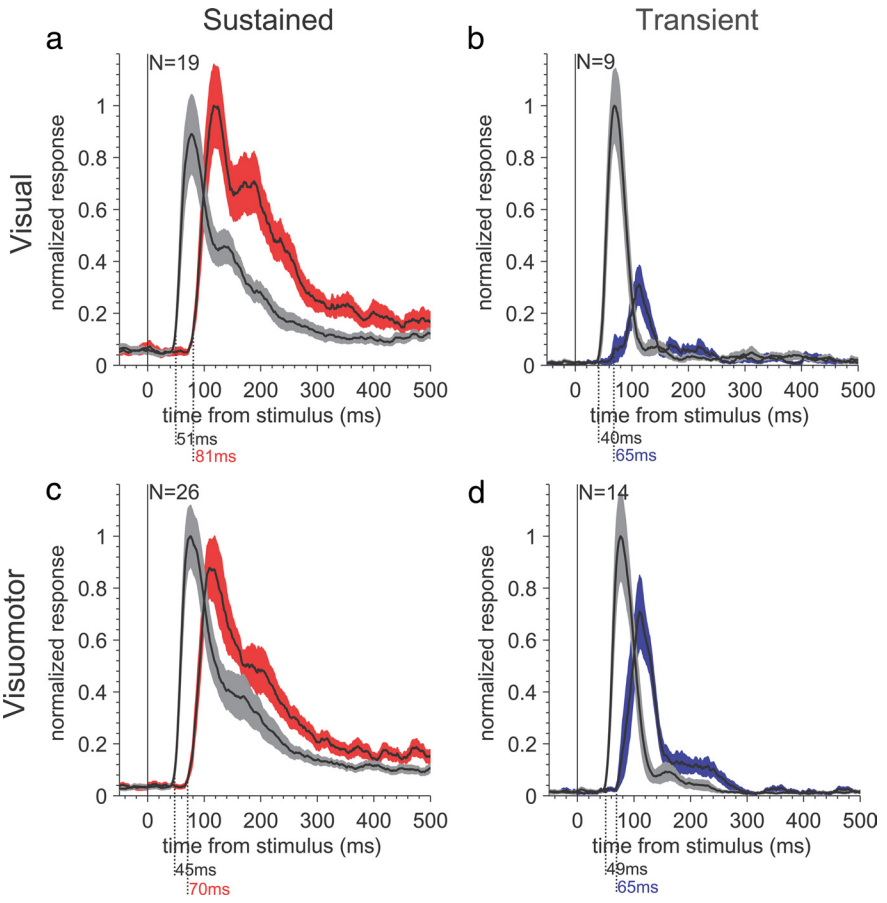

Figure 2. Comparison of the visual responses for the optimal color stimuli (colored traces) and maximum contrast luminance stimulus (black traces) across SC cell types. The top two panels show average normalized spike density functions for sustained-visual neurons to their optimal color stimulus (red traces) and the maximum contrast luminance stimulus (black traces) (***a***), and transient-visual neurons to their optimal color stimulus (blue traces) and the maximum contrast luminance stimulus (black traces) (***b***). ***c*** and ***d*** show averages for our sample of visuomotor neurons for the same two visual classifications. Note that transient-visual neurons (***b***) originated from the superficial SC layers (<1 mm from SC surface). Below each panel is the visual onset latency for each response profile. The shaded regions represent ±1 SEM.

Figure 2 shows the average visual responses (normalized to the maximum) for the four cell types. The top two panels show average responses for the maximum contrast luminance stimulus (black traces) and the optimal color stimulus (colored traces) for our sample of sustained-visual (Fig. 2*a*) and transient-visual (Fig. 2*b*) neurons. The bottom two panels (Fig. 2*c*,*d*) show average responses for visuomotor neurons with sustained and transient visual responses. For our sample of sustained-visual (Fig. 2*a*) and sustained-visuomotor (Fig. 2*c*) neurons, the average optimal color-related response (red traces) was remarkably high compared with luminance (black traces), with approximately equal peak activity (sustained-visual, $t_{(18)} = 1.43$, $p > 0.1$; sustained-visuomotor, $t_{(25)} = -0.02$, $p > 0.9$) and even slightly greater delay activity for color (sustained-visual, $t_{(18)} = 3.24$, $p = 0.005$; sustained-visuomotor, $t_{(25)} = 3.17$, $p = 0.004$) (for derivations of peak and delay activity and visual onset latency, see Materials and Methods). However, visual onset latencies were on average 25–30 ms longer for color for these two classes of neurons (sustained-visual, $t_{(18)} = 6.25$, $p < 0.00001$; sustained-visuomotor, $t_{(25)} = 4.48$, $p < 0.001$). In contrast, for our sample of transient-visual neurons (Fig. 2*b*), the best color-related response (blue traces) was reduced to approximately one-quarter of the magnitude of the 100% contrast luminance response ($t_{(8)} = -5.75$; $p < 0.001$). This result is consistent with previous reports that the superficial SC layers do not receive color-opponent inputs (Marrocco and Li, 1977; Schiller and Malpeli, 1977). The size of the color-related response for transient-visual neurons (Fig. 2*b*, blue traces) is also in close agreement with the degree of residual luminance expected from variations in the isoluminant balance of the individual neuron [e.g., as reported in the magnocellular division of the LGN (Logothetis et al., 1990), and middle temporal area (MT) (Dobkins and Albright, 1994; Gegenfurtner et al., 1994), which projects directly to the superficial SC layers (Lock et al., 2003)]. Visuomotor neurons with a transient visual response (Fig. 2*d*), which are located below the superficial SC layers, also showed fairly strong responses to color (blue traces). Key to all of these observations is that, if the color-related response seen in the SC was simply attributable to residual luminance, we would expect at best a weak response (at least smaller than our maximum contrast luminance stimulus) (Logothetis et al., 1990; Dobkins and Albright, 1994; Gegenfurtner et al., 1994), accompanied by a delay

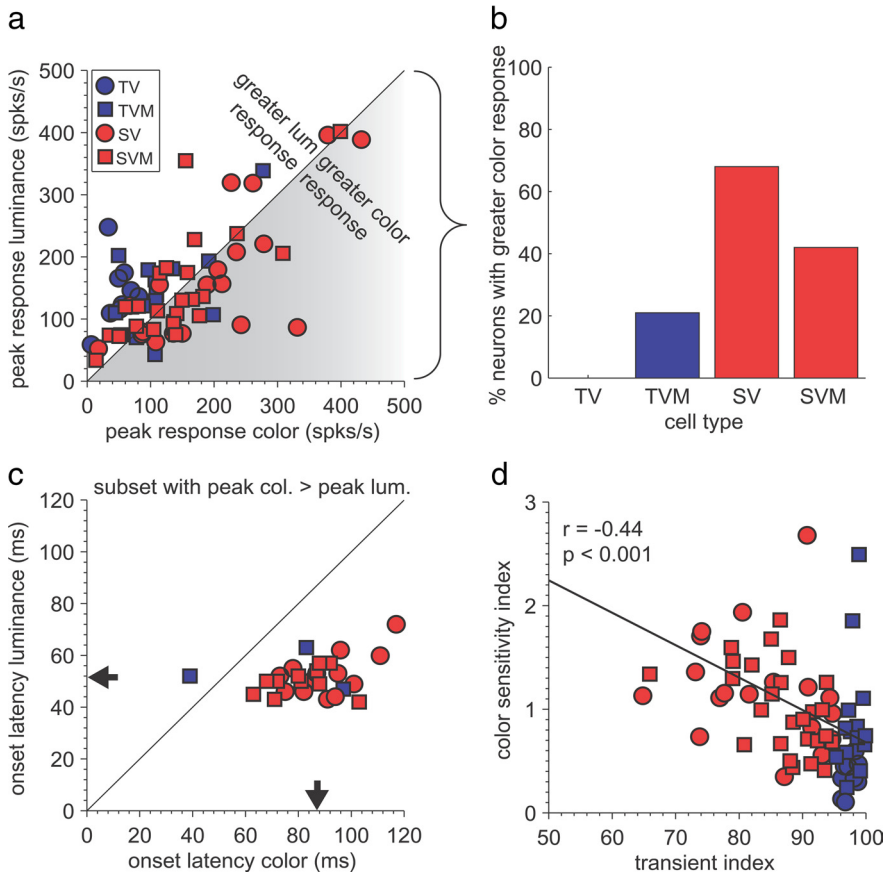

Figure 3. Summary of the peak visual responses and visual onset latencies for our sample of 68 neurons. ***a***, Peak visual responses. ***b***, Percentage neurons with greater color response. ***c***, Visual onset latencies. ***d***, A correlation between the color sensitivity index (Johnson et al., 2008) and transient index (Schiller and Malpeli, 1977) of each neuron (see Materials and Methods). TV, Transient-visual; TVM, transient-visuomotor; SV, sustained-visual; SVM, sustained-visuomotor. ***b*** and ***c*** represent a subset of the total sample of neurons whose peak visual response was greater for the optimal color than the maximum-contrast luminance stimulus. The arrows on the axes in ***c*** denote the median visual onset latency for the sample of neurons for color versus luminance.

in onset latency (Bell et al., 2006; Li and Basso, 2008). This is in sharp contrast to our observation of a strong response, yet accompanied by a significant delay in onset latency, particularly in terms of sustained-visual/visuomotor neurons (Fig. 2*a*,*c*; supplemental Fig. S1*e*,*f*, available at www.jneurosci.org as supplemental material).

Figure 3 summarizes the peak responses and visual onset latencies between color and luminance for each neuron across the cell types. A substantial percentage (41% or 28 of 68) of the total sample responded better to their optimal color than the maximum contrast luminance stimulus (Fig. 3*a*, shaded region), and Figure 3*b* shows the percentages across cell types. If we consider only those neurons with the better color-related response, the majority of these show longer visual onset latencies to color (Fig. 3*c*) and tend to have a sustained visual response profile (red symbols). In fact, there was a significant negative correlation between color sensitivity and the transient index of the neuron (Fig. 3*d*) ($r = -0.44$; $p < 0.001$) (for derivations of color sensitivity and transient indices, see Materials and Methods), indicating that neurons most sensitive to color tended to be the least transient (i.e., those with a more sustained response profile).

These differences in visual onset latency between color and luminance in the SC should correspond closely to differences in saccadic reaction time (SRT). To test this hypothesis, we had monkeys perform a gap saccade task (200 ms gap duration) (see Materials and Methods) to compare SRTs between color and luminance stimuli (these data were not available from the delayed saccade task because saccades were not triggered by the appearance of the target stimulus). The stimuli were randomly interleaved and appeared 12° left or right of fixation. Figure 4 confirms that the observed visual onset latency differences between luminance and color (medians of 36 and 38 ms collapsed across the cardinal DKL colors for monkeys Y and Q, respectively) translated very closely into SRT differences (medians of 32 and 38 ms for monkeys Y and Q, respectively). That is, SRTs were mostly determined by the relative arrival times of these stimuli, even with relation to differences between colors (see supplemental data, available at www.jneurosci.org as supplemental material). This is also remarkably close to human SRT differences between luminance and color using DKL-derived stimuli [36 ms for stimuli collapsed across various eccentricities and colors (White et al., 2006)].

Discussion

These results provide strong evidence that the primate SC has access to visual signals originating in not only magnocellular (Schiller et al., 1979) but also the color-opponent divisions of the geniculostriate pathway. This implies that the saccadic system has the capability of signaling the presence of chromatic stimuli, which is in agreement with the fact that human observers have no difficulty in orienting toward such stimuli overtly (White et al., 2006). However, the broad color-tuning profiles (Fig. 1*c*,*d*) suggest that information about color specificity may be limited in the SC. That is, these neurons appear to show strong "sensitivity," but only moderate "selectivity," for color. This almost certainly means that they receive inputs from multiple neurons tuned to different directions in color space (Sato et al., 1994).

The color-related responses we describe are unlikely because of residual luminance for several reasons: (1) The optimal color-related responses were often equal to or greater than maximum contrast luminance responses (Fig. 3). Even if our color stimuli carried a small residual luminance signal, they should have been at best only moderately "visible" to the SC if it were in fact color-blind. The magnitude of the color-related responses are especially remarkable given that the maximum achievable cone contrast for isoluminant stimuli (along the L–M direction) is naturally constrained to approximately one-tenth of the maximum cone contrast for luminance (see Materials and Methods). (2) The color-related responses were delayed by ~30–35 ms relative to luminance, independent of response magnitude. The most likely explanation for the delay is that the color-related signals traversed different pathways than luminance before finally converging on SC neurons. In other words, our chromatic stimuli were not simply acting like low-contrast luminance stimuli, as would be predicted if our results were primarily attributable to residual luminance (see supplemental data and Fig. S1*e*,*f*, available at www.jneurosci.org

as supplemental material). A delayed color response without a corresponding attenuated peak response implies that these signals involve intrinsically different mechanisms than luminance. This is consistent with the idea that the observed color-related response in the SC is the result of visual signals originating from the color-opponent divisions of the geniculostriate pathway. However, this latency difference vastly exceeds the conduction time differences through LGN (Maunsell et al., 1999), suggesting a transcortical contribution as well. Furthermore, the observed differences in visual onset latency between color and luminance coincided closely with differences in SRT (Fig. 4), which were remarkably close to what has been previously reported in humans using similar DKL-derived stimuli (White et al., 2006). Finally, (3) the color-related activity was associated with neurons from the intermediate SC layers (Figs. 2, 3). The same was not true for transient-visual neurons from the superficial SC layers, which is consistent with previous reports (Marrocco and Li, 1977; Schiller and Malpeli, 1977).

We also confirmed that the color-related SC activity is indeed mostly visual and is unlikely because of activity related to motor planning or target selection (see supplemental data, available at www.jneurosci.org as supplemental material). This is particularly true for our sample of sustained visual neurons ($N = 19$), which showed the most robust color-related responses (Fig. 2*a*) and, by definition, do not have motor-related activity (see supplemental data and Fig. S2*a*, available at www.jneurosci.org as supplemental material) and do not typically show target selection activity (McPeek and Keller, 2002).

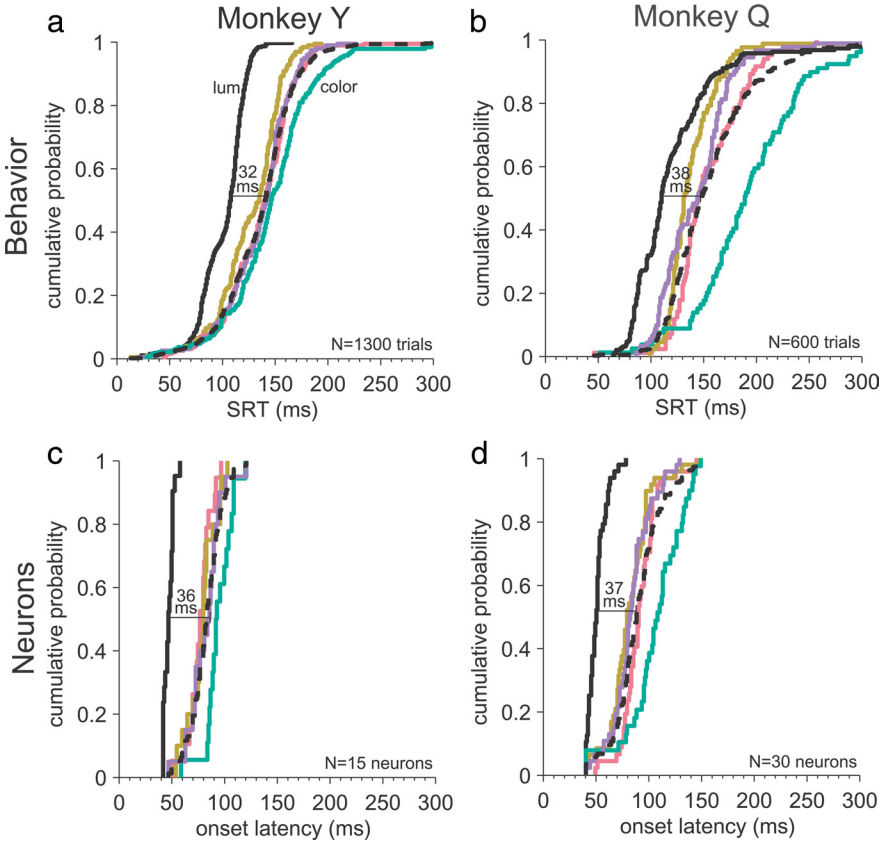

Figure 4. Cumulative SRT distributions for luminance versus color for monkey Y (***a***) and monkey Q (***b***) during a gap task (200 ms gap) [cumulative onset latency distributions (***c***, ***d***) from neural data obtained during the delay task were plotted for comparison]. The black solid traces represent the maximum-contrast luminance stimulus, and the colored traces represent the isoluminant DKL stimuli from the four cardinal color directions (red–green; blue–yellow). The black dashed line represents the average across the colors.

These results appear to be at odds with a previous study by Schiller et al. (1979), who examined the composition of the geniculostriate input into the SC by reversibly inactivating either the magnocellular (luminance) or parvocellular (color) layers of the LGN of anesthetized monkeys. They reported that the inactivation of the magnocellular layers eliminated visual activity in the SC, whereas the inactivation of the parvocellular layers did not. The authors concluded that the SC must be driven primarily by the achromatic broadband system. The fact that we do see a robust response to chromatic stimuli in the SC in awake monkeys implies that color-related activity in the SC might rely on the active engagement of the animal toward behaviorally relevant stimuli (Toth and Assad, 2002). For example, although the overt visual orienting system may have direct, bottom–up access to luminance, color may instead be transmitted to the SC via the same pathways that carry top–down, goal-related signals [e.g., via prefrontal cortex (Schall et al., 1995)]. The neurons carrying such signals might be either disrupted directly by the anesthesia itself or might only be active when awake animals perform goal-related tasks.

How might the SC gain access to color information? Dominant theories of perception and action have argued that visual pathways carrying signals for motor control ("dorsal stream") are mostly separate from visual pathways driving perception ("ventral stream") (Ungerleider and Mishkin, 1982; Goodale and Milner, 1992). Color was thought to belong exclusively to the latter (Livingstone and Hubel, 1988), but unlike the segregation that exists early in visual processing, color and luminance signals are not strictly segregated in the cortex (Sincich and Horton, 2005). Furthermore, the saccadic system receives projections from cortical areas belonging to both streams (Schall et al., 1995; Lock et al., 2003). The fact that we see such a dramatic difference between the response of transient-visual and sustained-visual/visuomotor neurons to color is consistent with the different visual inputs into the superficial versus intermediate SC layers (Lock et al., 2003). Incidentally, neurons from the parvocellular (color) layers of the LGN are characteristically sustained and tend to have slightly longer visual onset latencies than neurons from the magnocellular (luminance) layers of the LGN, which are characteristically transient (Kaplan et al., 1990). At least some of the difference we see in visual onset latency between color and luminance may be attributable to differences originating from these early visual pathways (15–20 ms) (Schmolesky et al., 1998; Maunsell et al., 1999; McAlonan et al., 2008), but the remaining difference must arise elsewhere (i.e., transcortically).

The distribution of visual corticotectal projections is extensive (Fries, 1984; Lui et al., 1995; Lock et al., 2003), so it is difficult to determine the precise nature of the inputs driving the differences seen here. In addition to the direct retinotectal input, the superficial SC layers receive direct projections from visual areas V1, V2,

V3, and MT (Fries, 1984; Lock et al., 2003), but the signals from these areas are not believed to be color-opponent (Marrocco and Li, 1977; Schiller and Malpeli, 1977; Schiller et al., 1979; Lia and Olavarria, 1996; Abel et al., 1997), and the results from our sample of transient-visual neurons support this (Fig. 2*b*). In contrast, the cortical projections to the intermediate SC layers are more complex, with direct inputs from frontal cortex (Leichnetz and Goldberg, 1988), plus extrastriate visual areas, some of which are traditionally associated with the ventral stream (Fries, 1984; Lock et al., 2003) (e.g., color-sensitive area V4). We do not yet have evidence that V4 neurons that project to the SC (Fries, 1984; Lock et al., 2003) are color-sensitive/selective, but given the color-related delay observed in the SC, this relatively later route (Schmolesky et al., 1998) is a possibility. Alternatively, the color-related signals might arise via an indirect route from V4 through the frontal eye field to the SC (Schall et al., 1995).

Our results also have important implications for the role of cone-specific signals in visual orienting. For example, Sumner et al. (2002, 2004) reported that stimuli invisible to the retinotectal and magnocellular pathways (S-cone isolating stimuli) can produce covert (as measured with manual reaction times), but not overt (as measured with saccades) orienting effects commonly associated with luminance-based stimuli [e.g., inhibition of return (Sumner et al., 2004)]. This was based on the premise that the superficial SC layers in particular do not receive inputs from S-cones (Marrocco and Li, 1977; Schiller and Malpeli, 1977), but until now it was not known whether neurons in the intermediate SC layers respond to color. In fact, ~14% (8 of 59) of the color-responsive neurons showed equal or greater responses in the S-cone direction than the maximum contrast luminance stimulus. Although we did not rigorously determine the optimal S-cone direction like Sumner et al. (2002, 2004), one would nonetheless predict at least some evidence of reduced visual activity around the S-cone direction if there were no such signals present in the SC. This was not the case (see supplemental Fig. S1*b*, available at www.jneurosci.org as supplemental material).

In sum, intermediate layer SC neurons are highly sensitive to isoluminant-color stimuli, and the color-related delay provides strong evidence that these signals traverse different pathways than luminance before converging on SC neurons. In natural visual environments, objects and the borders that define them are often isoluminant with the background (Hansen and Gegenfurtner, 2009). The intrinsic circuitry of the SC itself may use this information to make a better decision about saccade targeting.

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SUPPLEMENTAL DATA

Color-related Signals in the Primate Superior Colliculus

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Dealing with variation around individual isoluminance

One of the difficulties in isolating chromatic pathways is the natural variation that exists in individual isoluminance. Researchers have attempted to deal with this in different ways (for a detailed discussion see (White et al., 2006)), but the primary issue is that the various methods for determining isoluminance (e.g., heterochromatic flicker photometry or the method of minimum motion) tap neural pathways with different spectral sensitivities (Webster and Mollon, 1993), such that the optimal isoluminant point with one method is not optimal with another. One solution has been to assess isoluminance under the same conditions as the task of interest, i.e., to measure the effect of small luminance variations around the presumed isoluminant point (see for example (White et al., 2006; Braun et al., 2008)). Here this was achieved by varying luminance contrast around one of our photometrically isoluminant color stimuli (L-cone "red" stimulus, **Fig. S1d**) within the same delayed saccade task used to measure SC visual activity in the original experiment (**Fig. S1a**). Under this logic the luminance-contrast value that produces the weakest visual response can be thought of as the optimal isoluminant point. As a control, a second experiment was run on N=33 visual and

visuomotor neurons from the intermediate SC layers while varying luminance contrast (from -32 to +32 %) of a photometrically isoluminant "red" stimulus from the L-cone direction in the color space (**Fig. S1d**). Chromatic contrast was reduced to 70% here, from the maximum in the main experiment, to allow for luminance variation without exceeding the boundaries of the monitor gamut (see inset in **Fig. S1d**). Note that *transient-visual* neurons were excluded from this experiment because they did not show significant color-related activity (**Fig. 2b**).

(Supplementary Figure S1 here)

Figure S1 shows the results of the control experiment as well as the population average peak response across azimuth from the main experiment for comparison. Also plotted are the luminance measurements of our stimuli for both experiments (**Fig. S1a**, **d**). In **Figure S1a**, the luminance of each of the stimuli for the main experiment closely matched the background luminance of 20.5 cd/m^2 (with negligible deviations < 0.3 cd/m^2). **Figure S1b** shows the average peak response at each color. Given that this plot represents the average of many neurons with different optimal colors, we predicted an equal average response across azimuth (i.e., any unique tuning should cancel-out over the grand average). In general this was true, but there was a striking anisotropy in the M-cone "green" direction (180 deg) in which average peak activity was lower. This was also reflected in visual onset latencies (**Fig. S1c**) and behavior (SRTs in **Fig. 4** of main manuscript). There are several reasons to expect differences between DKL colors: 1) The maximum achievable cone-contrast is naturally different in different color directions in DKL space (typically ~80% in the S direction, ~7% in the L direction, and ~13% in the M direction (Gegenfurtner, 2003)). 2) Photometric isoluminance is based on foveal

vision, and visual sensitivity is known to vary with eccentricity differently for different colors (Mullen and Kingdom, 2002). 3) There are differences in L:M cone ratios for different observers (Roorda and Williams, 1999) and between human and non-human primates (Dobkins et al., 2000). 4) SRT differences across isoluminant DKL colors have been previously reported in humans (White et al., 2006).

For the main experiment, luminance deviations around the background were negligible (< 0.3 cd/m^2**, Fig. S1a**), so if we consider the effect of luminance-contrast on peak responses (control experiment, **Fig. S1e**), much larger differences than 0.3 cd/m^2 would be necessary to produce a significant effect. For example, there was little effect on the peak responses at up to +/- 8% luminance-contrast (**Fig. S1e**), which amounted to almost 4 cd/m^2 luminance deviation from the background (**Fig. S1d**). Furthermore, visual activity was never abolished at any luminance-contrast (there was no null point), but the smallest responses did fall around the photometrically isoluminant 0 point (**Fig. S1e;** solid gray lines show the results for each monkey separately). This indicates that our stimuli were reasonably isoluminant with the background for these animals.

Moreover, while these neurons (N=33) responded as well to their optimal colors (**Fig. S1e**, black square) as +/-32% luminance-contrast stimuli ($t(32)=1.1$, $p>.05$), visual onset latencies for the optimal isoluminant colors (**Fig. S1f**, black square) were far longer than expected from +/-32% luminance-contrast stimuli (**Fig. S1f** shaded region, $t(32)=2.6$, $p<.05$). Thus, our ~isoluminant color stimuli were not simply acting like low contrast luminance stimuli (as would be the case if residual luminance were driving the responses). This again indicates that the signals from these stimuli recruit largely different pathways before converging on SC neurons.

Also note that the stimuli in the control experiment (**Fig. S1d**) carried a chromatic component as well (i.e., chromatic contrast was only reduced to 70%, but not absent). The difference in peak visual response (**Fig. S1e**) between the optimal colors (black symbol, representing photometrically isoluminant stimuli at 100% chromatic contrast) and the 0% luminance-contrast stimulus (pink symbol centered at 0% lum. contrast, representing a photometrically isoluminant stimulus at 70% chromatic contrast) must be in part due to the reduced chromatic contrast for the latter.

Color-related visual signal versus motor-planning or target-selection signal

We explored the possibility that the color-related activity observed in the intermediate SC layers is not visual per se, but is instead 1) *motor-planning activity*, or 2) *target-selection activity*. There are at least two reasons why neither provides an adequate description of the color-related activity we observed:

1) For all intents and purposes, the color-related spike density functions (**Fig 2**) are identical to the luminance-based profiles (see also **Fig. S2**), the latter of which is indisputably visual. The primary difference between the two profiles is that the color-related response is delayed. While some of the low frequency activity following the initial visual volley might be related to target selection or motor preparation, this does not adequately explain the magnitude and frequency of the initial burst of activity following the onset of the target stimulus. This burst does not resemble what one would expect from a motor planning signal, which would presumably have a more accumulative “ramping-up” profile. Furthermore, this cannot adequately explain the activity of our sustained

visual-only cells (Fig. 2a), which by definition have no *motor-related activity* (see **Fig. S2a**), and do not typically show *target-selection activity* (McPeek and Keller, 2002).

2) If one observes the data aligned on the removal of the fixation point (the GO-signal), for sustained visuomotor neurons in particular (**Fig. S2b**), it can be seen that the delay activity shows the asymptotic minimum (represented by the gray shaded area) starting at around 160ms before the removal of the fixation spot. At least part of the low frequency activity during this epoch represents some baseline of the motor-planning signal, which is much weaker than the volleys of activity that precede it. Furthermore, these consecutive volleys of activity from about -800 to -300 ms (**Fig. S2a and b**) are locked to the different random delay periods between target stimulus on and fixation stimulus off, and again are virtually indistinguishable between color (red profiles) and luminance (gray profiles), with the exception that the former are delayed. Moreover, if the color-related activity for sustained visual-only neurons in particular (**Fig. S2a**) was predominantly target-selection activity, one might expect the largest response just after the removal of the fixation spot (GO-signal) around the time the target is selected for a saccade, which was not the case. These early volleys of activity are therefore most likely visual and are largely unrelated to target selection or motor-planning.

(Supplementary Figure S2 here)

FIGURE LEGENDS

Figure S1. A comparison of population average peak visual responses (panels b and e), and visual onset latencies (panels c and f) between stimuli as a function of azimuth in the isoluminant DKL plane (main experiment, panel a), and as a function of +/- luminance-contrast (control experiment, panel d). The illustrated insets in panels a and d depict the DKL coordinates of the stimuli. Note that for the control experiment (panels d-f), a single chromaticity was chosen (from the L-cone "red" direction), and chromatic contrast was reduced from maximum saturation in the main experiment to 70% in the control to allow for variation along the L+M luminance-axis without exceeding the limits of the monitor gamut (illustrated in inset in panel d). The black square symbol in panels e and f represent the average peak response and onset latency, respectively, for the optimal color stimuli (at 100% chromatic contrast) for the same set of N=33 visual and visuomotor neurons. Errorbars in panels e and f represent +/-1 SEM.

Figure S2. Population spike density functions aligned on the removal of the fixation point for our sample of *sustained visual* (a) and *sustained visuomotor* neurons (b), for the optimal isoluminant color stimuli (red) versus the maximum contrast luminance stimulus (gray). The consecutive volleys of activity from -800 to -300 ms are the initial visual bursts locked to the various random delay periods before the removal of the fixation spot. The *sustained visual* neurons (a) showed no significant motor-related activity. Gray shaded region in b (*sustained visuomotor* neurons) represents the asymptotic minimum delay activity, part of which is the baseline firing rate for the motor-planning signal. Line shading represents +/-1 SEM.

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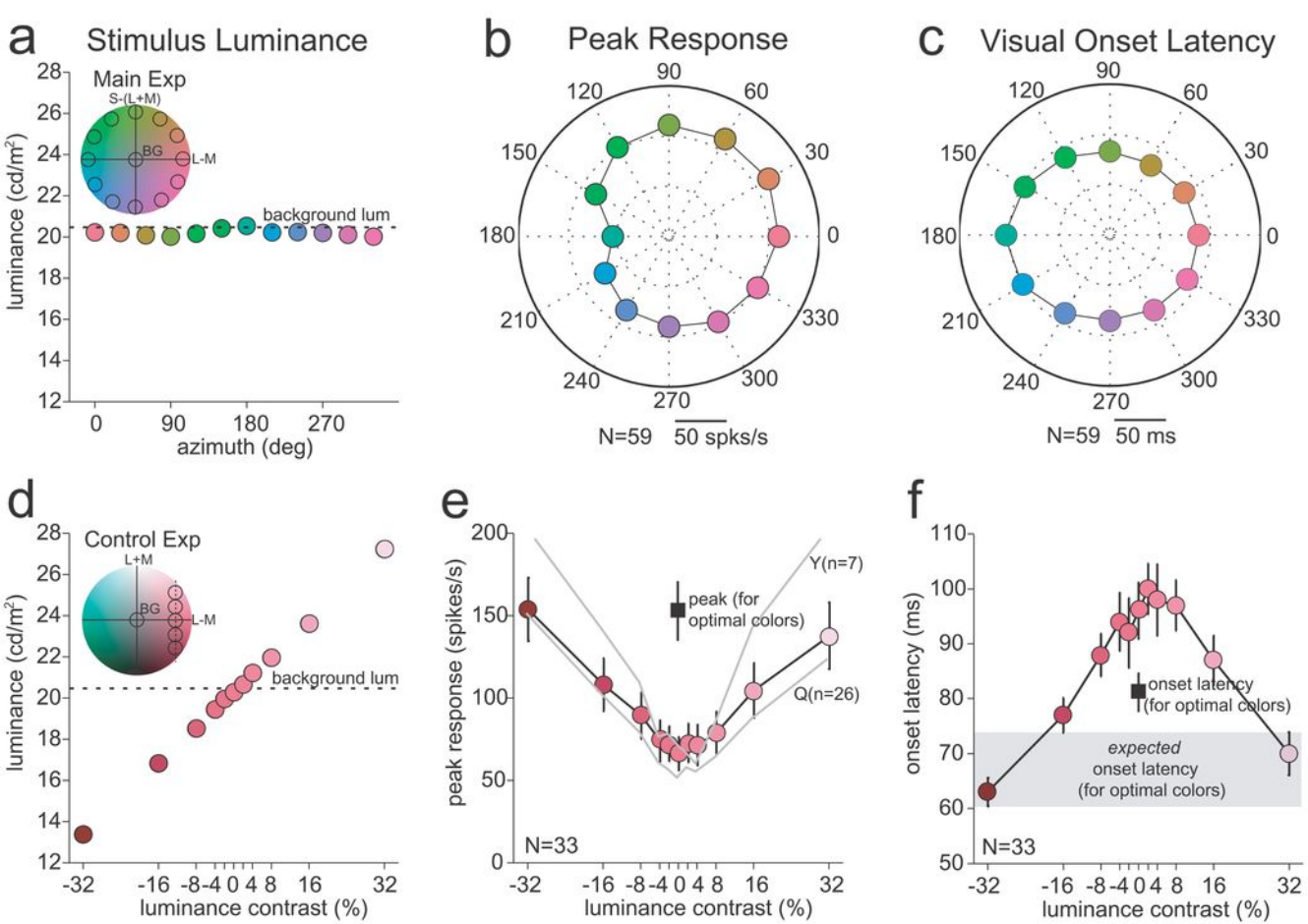
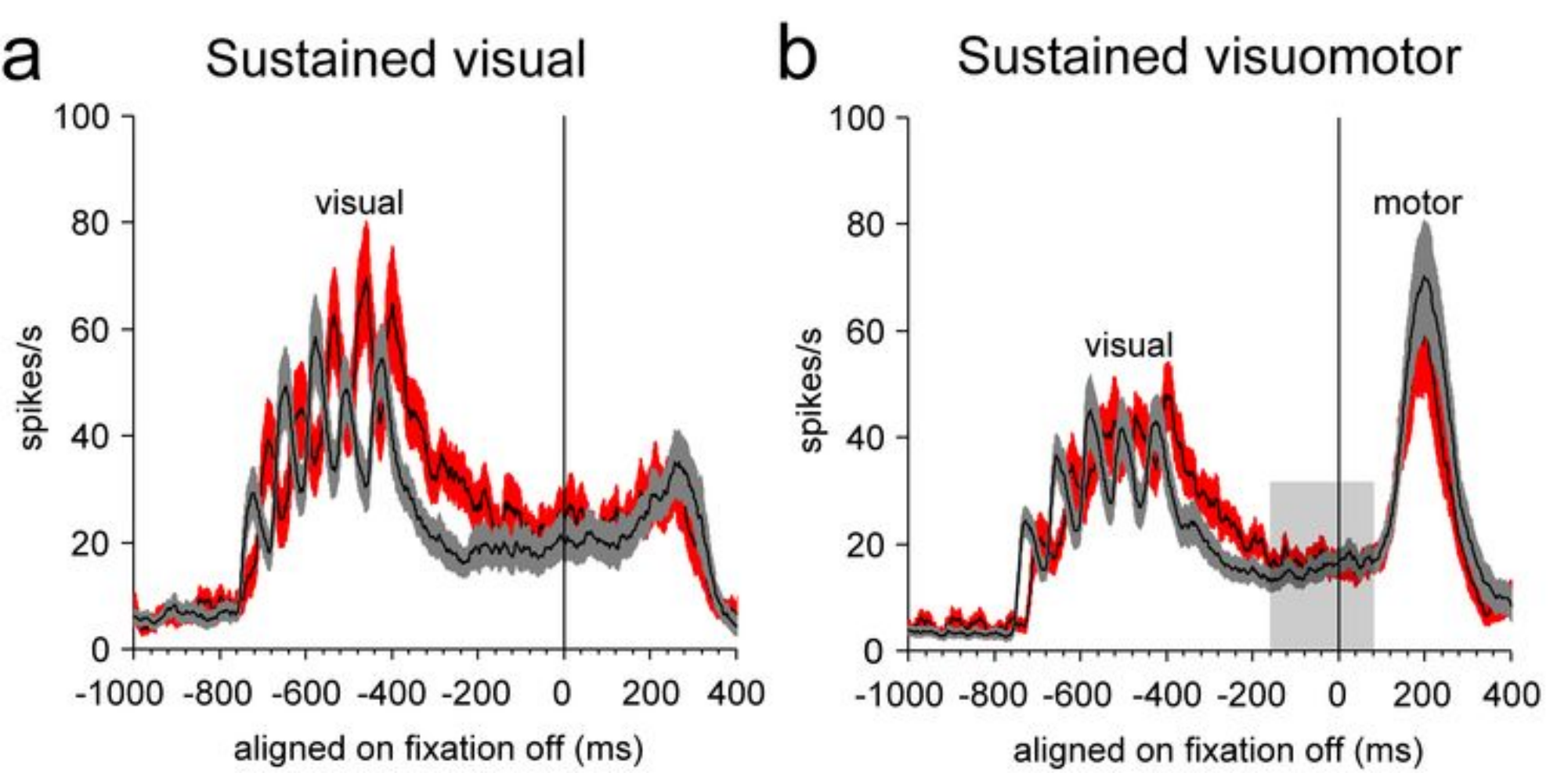

a
Stimulus Luminance
Main Exp
S-(L+M)
BG
L-M
background lum
luminance (cd/m²)
azimuth (deg)
b
Peak Response
N=59
50 spks/s
c
Visual Onset Latency
N=59
50 ms
d
Control Exp
L+M
BG
L-M
background lum
luminance (cd/m²)
luminance contrast (%)
e
peak (for optimal colors)
Y(n=7)
Q(n=26)
peak response (spikes/s)
N=33
luminance contrast (%)
f
onset latency (for optimal colors)
expected onset latency (for optimal colors)
onset latency (ms)
N=33
luminance contrast (%)


a
Sustained visual
b
Sustained visuomotor
100
80
60
40
20
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spikes/s
visual
motor
-1000 -800 -600 -400 -200 0 200 400
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