

Investigating the role of the superior colliculus in active vision with the visual search paradigm

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Abstract

We review here both the evidence that the functional visuomotor organization of the optic tectum is conserved in the primate superior colliculus (SC) and the evidence for the linking proposition that SC discriminating activity instantiates saccade target selection. We also present new data in response to questions that arose from recent SC visual search studies. First, we observed that SC discriminating activity predicts saccade initiation when monkeys perform an unconstrained search for a target defined by either a single visual feature or a conjunction of two features. Quantitative differences between the results in these two search tasks suggest, however, that SC discriminating activity does not only reflect saccade programming. This finding concurs with visual search studies conducted in posterior parietal cortex and the idea that, during natural active vision, visual attention is shifted concomitantly with saccade programming. Second, the analysis of a large neuronal sample recorded during feature search revealed that visual neurons in the superficial layers do possess discriminating activity. In addition, the hypotheses that there are distinct types of SC neurons in the deeper layers and that they are differently involved in saccade target selection were not substantiated. Third, we found that the discriminating quality of single-neuron activity substantially surpasses the ability of the monkeys to discriminate the target from distracters, raising the possibility that saccade target selection is a noisy process. We discuss these new findings in light of the visual search literature and the view that the SC is a visual salience map for orienting eye movements.

Introduction

The optic tectum is a sensory–motor structure located on the roof of the midbrain; it is highly conserved in the brains of vertebrates, and referred to as the superior colliculus (SC) in mammals (Butler & Hodos, 2005). It is organized into several dorsoventral layers, with neurons in the superficial layers receiving their major inputs from the retina and neurons in its deeper layers projecting outputs to orienting motor systems. Its sensory inputs are not limited to one modality, as many neurons in the SC deeper layers have multisensory (visual, auditory, somatosensory) responses. These sensory representations are well organized and form topographical maps of the external space and body, which are in register with each other and with the motor representations that produce body, head and ocular orienting responses. Based on a large body of anatomical and physiological evidence, the SC can be conceptualized as an integrated circuit for the processing of spatial sensory information and orienting responses.

In this paper we contend that the optic tectum's integrated circuit for the processing of spatial sensory information and orienting responses is conserved in the primate SC. In this view, the seemingly automatic visuomotor function of the optic tectum is integral to, and not distinct from, the voluntary control of orienting behavior. Additional flexibility in control may be offered by cortical innovations, whereby newer cortical areas in primates with projections to the SC exert modulatory influences to regulate the exploratory eye movements associated with active vision. We argue that the role of the primate SC in visual search is best understood within the construct of the visual salience map, and we present new data that cast light on the neural basis of saccade target selection in SC during visual search.

A vision-for-saccade interface

Primates are foveate animals and, accordingly, detailed analysis of the visual scene requires the precise orienting of their visual axis. The distinctive visual ability of catarrhine primates, which include old world monkeys and hominoids, rests on a sophisticated oculomotor system and is reflected in a large ocular motility. Despite the evolutionarily recent emergence of cortical control of eye movements,

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the SC remains a crucial structure in the regulation of visual behavior in these primates. The removal of the SC leads to prolonged deficits in the production of visually guided saccades (Schiller *et al.*, 1980), including the complete elimination of short-latency 'express' saccades (Schiller *et al.*, 1987). Furthermore, the cortical control of saccades by the frontal eye fields (FEF) within the prefrontal cortex (PFC) seems dependent on the integrity of the SC (Hanes & Wurtz, 2001). Within the SC deeper layers, the vast proportion of neurons display bursts of action potentials time-locked to the initiation of saccadic eye movements with restricted amplitudes and directions, which define the neuron's movement field (Wurtz & Goldberg, 1971; Schiller & Stryker, 1972; Sparks *et al.*, 1976; Sparks, 1978; see for review Sparks, 1986). The spatially organized distribution of these saccade-related neurons forms a topographic map of saccade vectors, which can also be revealed by delivering short trains of low-current electrical pulses (Robinson, 1972). Many of these saccade-related neurons also send axons to the premotor saccade-generating circuit (Keller, 1979; Gandhi & Keller, 1997; Rodgers *et al.*, 2006; see also Moschovakis *et al.*, 1988; Scudder *et al.*, 1996). That the saccade-related bursts of SC neurons instantiate motor commands to move the eyes has been demonstrated by the predictive relationship between this activity and saccade occurrence. SC neurons change their activity before saccades are executed instead of countermanded, and this change in activity occurs before saccades are canceled and within the minimal conduction time needed for SC signals to reach the eye muscles (Paré & Hanes, 2003).

The retinotopic organization of the primate SC is unique among mammals, as its superficial layers contain an exclusive representation of the contralateral visual field (see for review Kaas & Huerta, 1988). This diagnostic organization extends to the deeper layers, where only contraversive saccade vectors are represented (Robinson, 1972). The SC layered organization resembles that of cortex, with its two main sites of integration in supra- and infragranular pyramidal neurons (see for review Douglas & Martin, 2004; see also Larkum *et al.*, 2009). In contrast to cortex, wherein interlaminar processing is well established, the interplay between the SC superficial and deeper layers has long been debated. There is now a large body of evidence from several mammalian species for direct anatomical and functional connections between neurons in the superficial layers and neurons in the deeper layers (see for review Isa & Hall, 2009). In primates, evidence has come from anatomical reconstructions of SC neurons in a platyrrhine (genus *Saimiri*, old world monkey) species, which showed that axons of superficial layer neurons project to the deeper layers and that dendrites of movement neurons within the deeper layer reach the superficial layers (Moschovakis *et al.*, 1988). Also relevant is the physiological evidence of excitatory connections between the superficial and deeper layers in species belonging together with primates to the *Euarchontoglires* super-order – *Scandentia* (genus *Tupaia* – Lee *et al.*, 1997) and *Rodentia* (genus *Rattus* – Isa *et al.*, 1998; genus *Mus* – Phongphanphane *et al.*, 2008).

The registration of the visual and motor maps and their direct linkages suggest a substrate for the visual grasp reflex, i.e. the inflexible orienting to a salient visual stimulus (Hess *et al.*, 1946; Theeuwes *et al.*, 1998), as posited by the foveation hypothesis (Schiller & Stryker, 1972). This is consistent with the general observation in various vertebrate species that microstimulation of the optic tectum elicits predictable and species-specific orienting responses toward the receptive fields of the stimulated neurons. The basic circuit underlying this orienting function in the optic tectum of vertebrate brains thus appears to be conserved in the primate SC, notwithstanding the fact that saccade production does not require visual stimulation (e.g., Mays & Sparks, 1980) and the SC deeper

layers receive visual inputs from sources other than the superficial layers (e.g., Lui *et al.*, 1995; Paré & Wurtz, 1997; Sommer & Wurtz, 2000; see also Fries, 1984; Baizer *et al.*, 1993; Lock *et al.*, 2003; see for review May, 2006). The primate SC therefore cannot be viewed only as a motor map that can be completely dissociated from visual processing on either anatomical or physiological grounds. Case in point, even the SC saccade-related neurons that project to the brainstem saccade-generating circuit possess visually evoked responses (Rodgers *et al.*, 2006).

With respect to current models of visual search behavior, the integrated visuomotor functions of the primate SC suggests that it instantiates the theoretical construct of the visual salience map, on which featureless representations shaped by stimulus-driven and goal-directed signals compete for selection as saccade targets (see Discussion). Considering its phylogenetic antiquity, its highly conserved circuitry and its well-established role in orienting behavior (Ingle, 1973), the optic tectum may well be the primordial salience map regulating orienting behavior. Given the conservative nature of the evolution of neural circuits (e.g., Katz & Harris-Warrick, 1999), it is unlikely that such function was entirely replaced by cortical areas in mammals, including primates. It can easily be argued that the primate SC is ideally suited to investigation of the process of saccade target selection because its neuronal activity more closely impacts this process than cortical activity by virtue of its direct outputs to the saccade-generating system.

Saccade target selection

The gathering of visual information is an active process involving sequences of gaze fixations interrupted by saccadic eye movements that redirect the line of gaze to the next item selected for processing. This process is referred to as active vision. Two distinct processing stages are thought to take place during each gaze fixation: (i) the selection of the next saccade target from alternatives through visual/attentional analysis; and (ii) the programming of the saccade response that eventually brings the target image onto the fovea (see for review Schall & Thompson, 1999).

The first evidence linking SC neuronal activity with the process of saccade target selection can be found in early studies of the primate SC (Goldberg & Wurtz, 1972; Wurtz & Mohler, 1976). Wurtz and colleagues recorded visually responsive neurons in superficial layers while monkeys made saccades to one of two visual stimuli presented simultaneously, one located in the neuron's receptive field, the other outside. They found enhanced activity on trials in which saccades were made to the stimuli located in the neuron's receptive field compared to trials in which saccades were made to the other stimulus. This enhancement was not observed when monkeys were required to withhold the saccade response. This finding was replicated (Ottes *et al.*, 1987; see also Gattass & Desimone, 1996) and extended to neurons with both visually evoked responses and saccade-related activity within the SC deeper layers (Ottes *et al.*, 1987), hereafter referred to as visuomovement neurons. Discriminating activity of neurons within the deeper layers has since been reported in several subsequent studies using a variety of saccade selection tasks (Glimcher & Sparks, 1992; Basso & Wurtz, 1998; Horwitz & Newsome, 2001a,b; Krauzlis & Dill, 2002; Port & Wurtz, 2009).

It is difficult to interpret the exact role of the SC in saccade target selection from these earlier studies because of the limited complexity of the visual displays (in which only one distracter is presented and often has the same visual features as the saccade target), advance instruction about the saccade target, or the imposed delay period

between the stimulus presentation and the response. For instance, advance instruction and imposed delays may promote early selection so that saccade programming is initiated well in advance of the response. Such experimental conditions have poorly replicated those of naturalistic active vision. These studies also limited their recording exclusively to a subset of SC saccade-related neurons, those showing a low-frequency 'buildup' or 'prelude' in activity well in advance of saccade initiation in delayed saccade tasks (Glimcher & Sparks, 1992; Munoz & Wurtz, 1995). This sampling bias necessarily excludes neurons that lack low-frequency activity in delayed saccade tasks but nonetheless might be involved in saccade target selection during naturalistic active vision; the increased fixation control required in withholding saccades during a delay period probably suppresses such activity.

Thus far, only two studies have adopted the visual search paradigm to investigate the role of the SC in saccade target selection during active vision. In the first study McPeck & Keller (2002a) trained monkeys to perform a visual feature search task, in which a display of four stimuli contained a target defined by color that the monkeys had to foveate strictly after a single saccade. In contrast to the early studies, this study reported that the activity of visually responsive neurons within the superficial layers did not differ according to whether a target or a distracter was in their receptive fields. Discriminating activity was observed in all saccade-related neurons recorded within the intermediate layers, regardless of whether these showed visually evoked responses, delay period activity or only saccade-related activity. McPeck & Keller (2002a) also examined the temporal relationship between SC discriminating activity and saccade initiation to cast light on the nature of this activity, as has been done previously in FEF (Thompson *et al.*, 1996). One prediction is that SC discriminating activity signals both where and when to make a saccade, in which case it would be closely related to the programming of the saccade and thus correlated with saccade initiation, i.e., the time at which a neuron discriminates the target from distracters predicts saccade initiation (i.e., predictive discrimination time). Alternatively, it could strictly signal where (but not when) to make a saccade, in which case it would occur irrespective of saccade initiation (i.e., invariant discrimination time) and reflect the selection of the search target. Saccade-related neurons lacking visually evoked responses were found to follow the first prediction, whereas visuomovement neurons followed either prediction in approximately the same proportion. This duality has also been observed in FEF (Sato & Schall, 2003), and interpreted as evidence that the selection of the search target and the programming of the targeting saccade are instantiated by distinct neuronal populations within each brain region.

In the second study, Shen & Paré (2007) recorded visuomovement neurons while monkeys performed a visual conjunction search task, in which a display of eight stimuli contained a target defined by a unique combination of color and shape that the monkeys had to foveate but not strictly after a single saccade. All visuomovement neurons had discriminating activity, but about one-third were found to signal to some extent the presence of the search target in their receptive fields regardless of the saccade goal. This difference in responses may again be evidence that saccade target selection and saccade programming are instantiated by distinct neuronal populations. Nevertheless, a neuron's response in visual search was predicted neither by its position along the visuomovement axis nor its discharge characteristics, such as magnitude of visually evoked responses or saccade-related activity. This study showed that SC neuronal activity reflects not only saccade programming (i.e., the selection of saccade goals, as in McPeck &

Keller, 2002a), but also stimulus representations whose magnitude is predictive of which stimulus will be selected as a saccade target (Shen & Paré, 2007).

From this review of the evidence linking SC activity with the process of saccade target selection we identify three outstanding questions, for which we sought answers experimentally.

What process is instantiated by SC discriminating activity?

Visual search studies in SC suggest a mixture of signals probably reflecting saccade target selection and saccade programming (McPeck & Keller, 2002a; Shen & Paré, 2007), which is consistent with results obtained in FEF (Thompson *et al.*, 1996; Sato & Schall, 2003). However, recent studies in posterior parietal cortex (PPC) of monkeys performing more unconstrained visual search tasks (i.e., with less emphasis on accuracy) have reported that visually responsive neurons within the lateral intraparietal (LIP) area discriminate the search target at a fixed time in advance of saccade initiation (Ipata *et al.*, 2006a; Thomas & Paré, 2007). This finding suggests that LIP discriminating activity signals saccade programming. This is a surprising finding given that area LIP provides inputs to FEF and SC, wherein a duality of processing has been observed. Could the apparent difference in processing in PPC vs. FEF and SC only be related to task constraints? In this study we examined whether the PPC observations also apply for SC neurons recorded during unconstrained search.

Are different types of SC neurons involved in the selection process?

In light of contradicting findings (Goldberg & Wurtz, 1972; Wurtz & Mohler, 1976; Ottes *et al.*, 1987; Gattass & Desimone, 1996; McPeck & Keller, 2002a), it remains unclear whether visual neurons in the SC superficial layers participate in saccade target selection. In addition, the arbitrary classification of SC neurons and the focus on neurons with low-frequency activity in delayed saccade tasks in previous studies restrict our understanding of the link between SC activity and saccade target selection as well as the integrated visuomotor functions of the SC. To address this gap in our knowledge, we examined the relationship between the discharge properties of a large sample of neurons ($n = 189$) across the SC layers and the quality of their discriminating activity in visual feature search.

Is visual search performance fully predicted by the SC discriminating activity?

Shen & Paré (2007) demonstrated that the quality of the discriminating activity of SC visuomovement neurons just prior to saccades correctly directed to the search target was near perfect and generally exceeded the overall accuracy in the visual conjunction search task observed in each corresponding session. Because this analysis only considered correct trials, such a high discrimination is expected from neurons whose activity is thought to reflect the process of selecting the search target and play a critical role in guiding behavioral choice (Schall, 2003). FEF visuomovement neurons have also been found to approximate or outperform behavior (Thompson *et al.*, 2005; Trageser *et al.*, 2008). However, a similar analysis conducted by Kim & Basso (2008) suggested that the activity of several simultaneously-recorded neurons poorly predicts behavioral performance.

The application of signal detection theory in neurophysiology has helped establish a direct link between neural activity and visual discrimination using directly comparable physiological and psycho-

physical variables (Parker & Newsome, 1998). In contrast to the analyses conducted in previous visual search studies, this approach considers all behavioral outcomes (correct and incorrect trials) and determines the degree to which neural activity can predict performance. We sought to address the discrepancy of results highlighted above by extending the previous analysis of Shen & Paré (2007) to neurons recorded in conjunction search as well as feature search and by considering data from correct and incorrect trials.

Materials and methods

We collected data from two female rhesus monkeys (*Macaca mulatta*, 4.5–6.0 kg, 8–10 years) cared for under experimental protocols approved by the Queen's University Animal Care Committee and in accordance with the Canadian Council on Animal Care guidelines. The surgical procedure, stimulus presentation and data acquisition have been described previously (Shen & Paré, 2006, 2007; Thomas & Paré, 2007). Monkeys received both antibiotics and analgesic medications during the post-surgery recovery period, after which they were trained with operant conditioning and positive reinforcement to perform fixation and saccade tasks for a liquid reward until satiation. The extracellular activity of single SC neurons was recorded using previously described methods (Paré & Wurtz, 2001), and spike occurrences were sampled at 1 kHz. This report includes data obtained from neurons that were the focus of the study of Shen & Paré (2007).

Behavioral paradigms

Monkeys first performed a delayed saccade task to characterize the discharge properties of the neurons and delimit their response fields (Paré & Wurtz, 2001). This task temporally dissociated visual stimulation from saccade execution by introducing a delay of 500–1000 ms between the presentation of a visual stimulus and the disappearance of the fixation stimulus, which acted as the signal for the monkeys to make a saccade to that stimulus. In visually guided trials the visual stimulus remained on during the delay period, while in memory-guided trials the visual stimulus was extinguished after 100 ms and the monkey had to make a saccade to its remembered location. These trial types were randomly interleaved, and the saccade stimulus was presented either in the center of the neuron's response field or in the diametrically opposite location relative to the fixation stimulus position.

Following the delayed saccade task, monkeys performed unconstrained visual search in a feature (color) search task and, in some sessions, a conjunction (color–shape) search task. For sessions in which both the feature and conjunction search tasks were run, the task order was counterbalanced across days. Details of the feature (Shen & Paré, 2006; Thomas & Paré, 2007) and conjunction (Shen & Paré, 2006, 2007) search tasks have been reported previously. Briefly, each search trial began with monkeys fixating a central stimulus. This fixation stimulus disappeared with the simultaneous appearance of a concentric array of one target and seven distracters. On each trial, either the target or a distracter stimulus appeared randomly in the center of the neuron's receptive field, and all other stimuli were randomly positioned equidistant from the central stimulus position and from each neighboring stimulus. Monkeys were rewarded maximally for fixating the location of the target stimulus within 500 ms of the display presentation, and were partially rewarded (< 0.33 of the maximum amount along with the reinforcement tone) for locating it with multiple saccades within 2000 ms of the initial eye movement. In the feature search task, the target could be a green or red circle presented with red

or green circle distracters, respectively. The target therefore changed randomly from trial to trial and was defined as the 'oddball' stimulus. In the conjunction search task, the target was a unique combination of a color (red or green) and a shape (circle or square), and the distracter stimuli were other combinations of those features. The conjunction target remained the same throughout an entire session but changed between sessions. Trials were deemed correct if the monkey successfully foveated the target after a single saccade.

Data analysis

We took two measures of visual search performance. Response accuracy was taken as the probability that the first saccade landed on the search target in a session. Response time (RT) was taken as the time between the onset of the search display and the initiation of the first saccade for each trial in a session.

Details of the neuronal data analyses have been described previously (Thompson *et al.*, 1996; Shen & Paré, 2007; Thomas & Paré, 2007). Neuronal activity in visual search tasks was quantified as continuously varying spike density functions aligned on the onset of either the visual stimulus presentation (stimulus aligned) or the first saccade (saccade aligned) from a minimum of 10 trials. Spike density functions were constructed by convolving spike trains with a combination of growth (1-ms time constant) and decay (20-ms time constant) exponential functions that resembled a postsynaptic potential (Thompson *et al.*, 1996). Neuronal activity in delayed saccade trials was quantified using spike density functions constructed with a Gaussian ($\sigma = 10$ ms) substituting for each spike (Paré & Wurtz, 2001).

We used the now common method (Thompson *et al.*, 1996; Shen & Paré, 2007; Thomas & Paré, 2007) derived from signal detection theory to quantify the separation between a neuron's activity associated with the search target and that associated with distracter stimuli. Receiver operating characteristic (ROC) curves were built for successive 5-ms intervals by plotting the probability that the rate of target-related activity is greater than a criterion rate as a function of the probability that the rate of distracter-related activity is greater than that same criterion. The area under each of these curves (auROC) was plotted as a function of time, and the time course of neuronal discrimination was captured by the Weibull function that fit best with the data. Best-fit functions were calculated only with activity occurring before the initiation of saccades landing correctly on target, and they were terminated when there were fewer than five target or distracter trials; distracter trials were trials in which the target was at one of the three most distant positions from the response field. The ranges of response latencies in target and distracter trials were matched across all conditions. The discrimination magnitude (DM) of each neuron was defined as the upper limit of the best-fit functions, and the point at which these functions reached a criterion value of 0.75 was taken as the neuron's discrimination time (DT).

We used the data collected in the delayed saccade task to segregate neurons into putative groups: (i) those with visually evoked responses and movement-related activity (visuomovement neurons); (ii) those with movement-related activity but without visually evoked responses (putative movement neurons); (iii) those with visually evoked responses but without movement-related activity (putative visual neurons); and (iv) those with delay period activity (see Tables 1 and 3). This grouping was arbitrary, as there were no distinct breaks along the continuum of discharge properties of our large sample (see Figs 3 and 5), and carried out only to more explicitly test the hypothesis that different types of SC neurons are involved in the process of selection during visual search. Neurons with movement-related activity were all

TABLE 1. Neuronal discharge properties of the putative groups of neurons having different visual and saccade activity characteristics

Neuronal activity characteristics	Sample size	Baseline activity (sp/s)	Visual response (sp/s)	Saccade activity (sp/s)	VMI
Without movement activity	39	10 ± 2 (0 – 33)	93 ± 6 (23 – 202)	50 ± 6 (0 – 139)	0.40 ± 0.05 (–0.09 to 1)
With movement activity	150	5 ± 0.6 (0 – 38)	62 ± 4 (0 – 262)	240 ± 12 (28 – 665)	–0.54 ± 0.03 (–1 to 0.39)
Visuomovement activity	137	5 ± 0.6 (0 – 38)	68 ± 4 (10 – 262)	244 ± 12 (28 – 665)	–0.50 ± 0.03 (–0.93 to 0.39)
Without visual activity	13	1 ± 0.4 (0 – 6)	4 ± 1 (0 – 9)	195 ± 43 (54 – 618)	–0.94 ± 0.02 (–1 to –0.82)

Visual responses were the mean discharge rates calculated in the first 100 ms following stimulus onset. Peak saccade activity within ±25 ms of saccade onset is reported for neurons having significant movement activity, while saccade activity for neurons without movement activity was taken as the discharge rate at saccade onset. Visuomovement index, VMI (see Materials and Methods). Mean values are ±SEM and values in parentheses are range.

TABLE 2. Feature search discrimination parameters for the putative groups of neurons having different visual and saccade activity characteristics

Neuronal activity characteristics	Proportion of discriminating neurons (%)	Stimulus-aligned DM	Stimulus-aligned DT (ms)	Saccade-aligned DT (ms)
Without movement activity	27/39 (69)	0.80 ± 0.03 (0.26 – 1)	114 ± 4 (66 – 154)	–34 ± 5 (–80 to –1)
With movement activity	149/150 (99)	0.97 ± 0.004 (0.69 – 1)	109 ± 1 (69 – 160)	–45 ± 1 (–94 to –1)
Visuomovement activity	136/137 (99)	0.97 ± 0.004 (0.69 – 1)	108 ± 1 (69 – 155)	–46 ± 2 (–92 to –1)
Without visual activity	13/13 (100)	0.94 ± 0.03 (0.76 – 1)	125 ± 5 (98 – 160)	–35 ± 7 (–94 to –3)

DM values were calculated from all neurons, while DTs included only those neurons that reliably discriminated the target from distracters (auROC ≥ 0.75). Mean values are ±SEM and values in parentheses are range except where indicated as %.

TABLE 3. Neuronal discharge properties during the delay period of delayed saccade tasks for the three groups of neurons having different visual and saccade activity characteristics

Neuronal activity characteristics	Proportion of delay-responsive neurons (%)	Visual delay activity (sp/s)	Memory delay activity (sp/s)	VIS-MEM separation index
Without movement activity	36/39 (92)	48 ± 6 (2 – 132)	18 ± 2 (0 – 53)	0.79 ± 0.04 (0.10 – 1)
With movement activity	139/150 (93)	31 ± 2 (0.2 – 160)	18 ± 1 (0.5 – 80)	0.67 ± 0.02 (0 – 1)
Visuomovement activity	127/137 (91)	33 ± 2 (1 – 160)	19 ± 1 (1 – 80)	0.67 ± 0.02 (0 – 1)
Without visual activity	12/13 (92)	8 ± 2 (0.2 – 21)	11 ± 3 (0.5 – 34)	0.59 ± 0.06 (0.19 – 0.84)

Delay activities and separation index values are reported for only those neurons with significant delay activity in at least one of the two delayed saccade tasks (rank-sum test, $P < 0.05$). Mean values are ±SEM and values in parentheses are range except where indicated as %. The proportions of delay-responsive visual neurons in the visually- and memory-guided delayed saccade tasks were 33/39 (84%) and 11/39 (28%), respectively. These figures were 127/150 (85%) and 102/150 (68%) for neurons with movement-related activity.

located within the SC deeper layers, as they were recorded 1–3 mm below the SC dorsal surface. The putative visual neurons were recorded within the top 1 mm of the SC dorsal surface and presumed to be located within the superficial layers, although their exact lower boundary can be difficult to distinguish physiologically. As both visually evoked responses and saccade-related activity are transient events, we used different criteria from that used to determine the longer lasting delay period activity (see below). Neurons were identified as having visually evoked responses if their activity during the first 100 ms following stimulus presentation was at least 10 spikes per second (sp/s) greater than their mean baseline activity (100-ms interval ending with stimulus onset) in the visually guided trials of the delayed saccade task. These neurons consistently discharged at least a single spike above baseline per trial, time-locked to the onset of the visual stimulus. This arbitrary criterion was preferred to a statistically significant increase from baseline activity because baseline activity is very low in SC neurons (Table 1), especially in neurons with movement-related activity (median, 2.0 sp/s). Neurons were identified as having movement-related activity if their activity within 25 ms of saccade initiation in the visually guided trials of the delayed saccade task exceeded the mean activity during the last 300 ms of the delay

period by 2 SD. For these neurons with movement-related activity ($n = 150$), the peak activity occurred 0.06 ± 0.72 ms from saccade onset. From these data, we also quantified the relative magnitude of visually evoked and saccade-related activity of each neuron with a visuomovement index (Shen & Paré, 2007): $VMI = (vis - mov)/(vis + mov)$, where vis is the mean discharge rate over the first 100 ms following stimulus presentation, and mov is the peak discharge rate within 25 ms of saccade onset (or the discharge rate at the time of saccade onset for neurons without movement-related activity). Neurons with stronger visually evoked activity have VMIs closer to +1.0 and those with stronger saccade-related activity have VMIs closer to –1.0. The VMI of our sample of 189 SC neurons spanned the whole range (–1.0 to +1.0) and averaged -0.34 ± 0.04 . We also identified delay-responsive neurons as those which had activity over the last 300 ms of the delay period (in either the visually or memory guided trials) of the delayed saccade task that was significantly greater (rank-sum tests, $P < 0.05$) than their baseline activity (100-ms interval ending with stimulus onset). For these neurons, we also calculated a VIS/MEM separation index to quantify the relative magnitude of visually guided and memory-guided delay period activity for each neuron (Paré & Wurtz, 2001). This index was the area under ROC

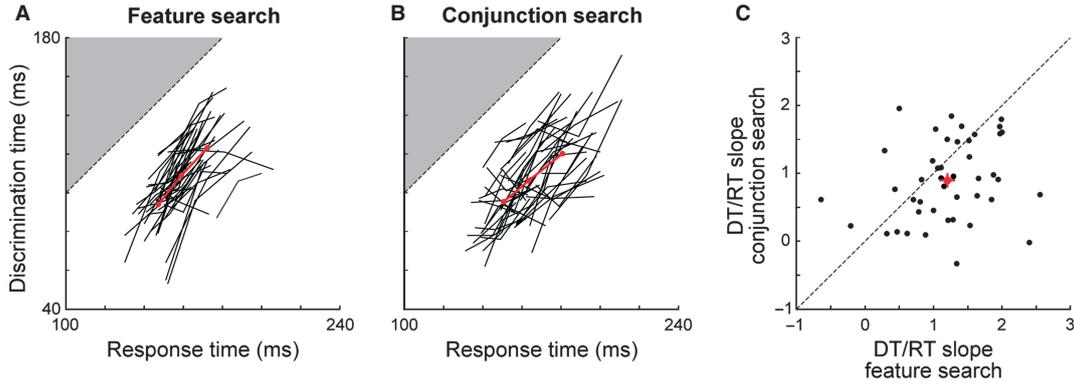


FIG. 1. Temporal relationship between discrimination time (DT) and response time (RT) for neurons recorded in both (A) the feature and (B) the conjunction searches. For each of the 44 neurons in this sample, the RT distribution was divided into three groups (short, medium and long) and DT determined for each group separately. These consecutive triplets of DT/RT data points for individual neurons are linked with two black lines, and the red line indicates the average across neurons. (C) The mean slope of each neuron's lines in conjunction search is plotted against those obtained in feature search. Average \pm SEM is shown in red.

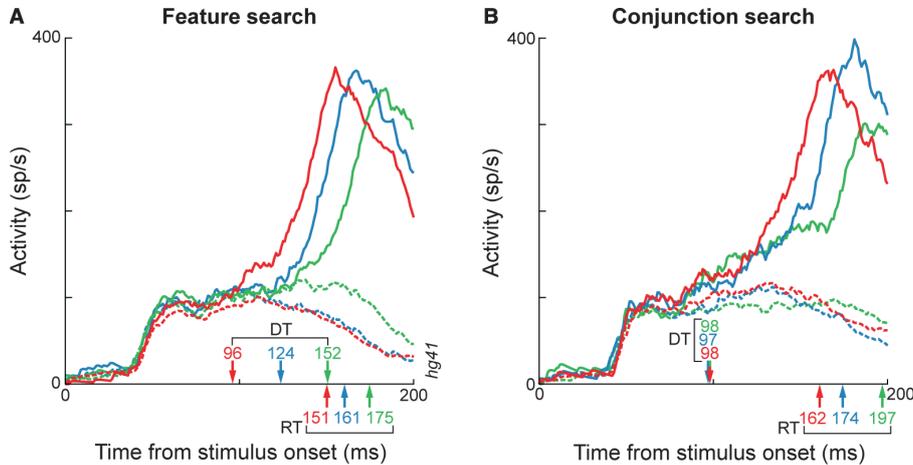


FIG. 2. SC neuronal activity associated with the target and distracters during (A) feature and (B) conjunction searches exemplified by a neuron with both visual responses and movement-related activity. Neuronal activity is shown for trials in which the target (solid lines) or a distracter (dashed line) appeared in the neuron's receptive field as well as for each group of response time (RT: short, red; medium, blue; long, green). Mean RT for each group and corresponding discrimination time (DT) are displayed for each task. A large difference in the DT-RT relationship between feature and conjunction searches was observed in this neuron; mean DT/RT slopes were 2.4 and -0.02 , respectively.

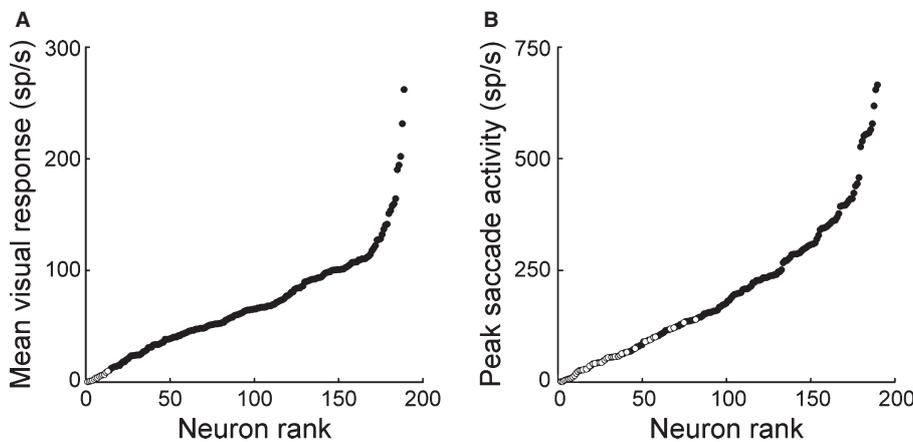


FIG. 3. (A) Distribution of visually evoked responses (mean activity 0–100 ms following stimulus onset) for the sample of 189 SC neurons. Neurons were classified as having visual activity if they met the arbitrary minimum criterion of 10 sp/s (filled circles). (B) Distribution of saccade-related activity (peak discharge rate within ± 25 ms of saccade onset) for the same sample. Neurons were classified as having saccade activity if their peak discharge rate was significantly greater than their delay period activity (filled circles; see Materials and Methods).

curves quantifying the probability that the visual delay activity is greater than and distinct from the memory delay activity. Indices > 0.5 indicate a more visually dependent neuron while indices < 0.5 indicate a more visually independent neuron.

All values are reported as mean \pm SEM unless otherwise noted.

Results

What process is instantiated by SC discriminating activity?

To determine the process that is instantiated by SC discriminating activity, we examined the relationship of DT and RT in a sample of neurons recorded in both feature and conjunction search. There were sufficient data in 44 neurons for this analysis. All 44 neurons had both visually evoked responses and saccade-related activity (see Materials and Methods). In these sessions, response accuracy was greater in feature than in conjunction search (0.84 ± 0.016 vs. 0.68 ± 0.016 , paired *t*-test, $P < 0.0001$) and RT was shorter in feature than in conjunction search (156 ± 1 vs. 164 ± 2 ms, $P < 0.001$), suggesting that the conjunction search task was more difficult than feature search. Nevertheless, DT was not different between feature and conjunction search tasks (107 ± 2 vs. 107 ± 3 ms; $P = 0.89$). For each neuron and task, we divided the trials into short, medium and long RT groups and determined DT for each group. We then determined the slope of the relationship between DT and RT. A slope of 1 would indicate that DT is predictive of saccade initiation, suggesting that SC discriminating activity is involved in saccade programming. Alternatively, a slope of 0 would indicate that DT is independent of saccade initiation, suggesting that SC discriminating activity signals only saccade target selection (see Thompson *et al.*, 1996).

In feature search, the DT/RT slope averaged 1.20 ± 0.10 (Fig. 1A). This was significantly different from 0 (*t*-test, $P < 0.001$) and its difference from 1 just reached significance ($P = 0.04$). In conjunction search (Fig. 1B), the DT/RT slope for those same neurons averaged 0.90 ± 0.09 , which was also significantly greater than 0 ($P < 0.001$) but not significantly different from 1 ($P = 0.25$). Consistent with this finding, the distribution of DT/RT slopes with activity aligned on saccade initiation was near 0 (feature, -0.26 ± 0.12 , $P = 0.03$; conjunction, 0.04 ± 0.12 , $P = 0.77$) and significantly different from -1 ($P < 0.0001$).

We found no evidence for two distinct processing stages as the distributions of the DT/RT slopes were unimodal (dip test, $P = 0.78$ and 0.99 for feature and conjunction search, respectively). Our results suggest that SC neuronal discrimination generally predicts saccade initiation. If the relationship between DT and RT were the same across the two tasks, the longer RT in conjunction search would be accounted for by a shift in DT. This, however, was not the case. First, DT led saccade initiation significantly earlier in conjunction search (-55 ± 2 vs. -48 ± 2 ms; paired *t*-test, $P < 0.01$). Second, the DT/RT slopes in conjunction search were significantly shallower than in feature search (Fig. 1C; paired *t*-test, $P < 0.05$), and about two-thirds of neurons (31/44, 70%) had shallower slopes in the conjunction search task. Figure 2 illustrates the large, seemingly qualitative, differences in the responses of some individual neurons.

The results from this neuronal sample are representative of the general population, as very similar results were obtained with a larger sample. Considering every neuron with sufficient data in feature search ($n = 150$), the DT/RT slope averaged 1.11 ± 0.05 , which was significantly different from 0 (*t*-test, $P < 0.001$) and near 1 ($P = 0.04$). In conjunction search, the DT/RT slope for a sample of 73 neurons averaged 0.93 ± 0.07 , which was also significantly greater than 0 ($P < 0.001$) but not significantly different from 1 ($P = 0.35$).

Altogether, these observations suggest that SC discriminating activity signals saccade goal selection when monkeys perform an unconstrained search for a target defined by a single visual feature or a conjunction of two features. Nevertheless, the differences observed between search tasks suggest that the SC discriminating activity is somewhat distinct from a saccade programming, i.e., there may be a shift away from a saccade goal selection process and towards a process of saccade target selection in conjunction search when task demands increase.

Are different types of SC neurons involved in the selection process?

To determine whether different types of SC neurons are involved in the selection process during visual search, we determined both DM and DT during a feature search task for our sample of 189 SC neurons. In this diverse sample there was a continuous unimodal distribution of both visually evoked responses (Fig. 3A; dip test, $P = 0.56$) and saccade-related activity (Fig. 3B; $P = 0.95$) measured in the visually guided delayed saccade task. Table 1 describes the discharge properties of this neuronal sample and of the putative neuronal groups, which primarily distinguish neurons located in superficial and deeper layers (see Materials and Methods). All but one neuron with movement activity discriminated the target from distracters before saccades (see Table 2). Considering only those movement-related neurons that had reliable discriminating activity before saccades ($n = 149$), this occurred 109 ± 2 ms following stimulus onset and 45 ± 2 ms before saccades. The average DM for these neurons was near perfect (0.97 ± 0.005). Notably, when data were aligned on saccades, DT occurred 11 ms earlier for visuo-movement neurons than for movement neurons (*t*-test, $P < 0.05$; see Table 2). This difference did not hold, however, if a 20 sp/s criterion was used to classify a neuron as having reliable visually evoked-responses ($P = 0.18$), suggesting that the difference above is deceptive. Interestingly, we also found reliable discriminating activity in over half (27/40, 68%) of our sample of neurons without movement activity. For those putative superficial-layer 'visual' neurons that had reliable discriminating activity, DM was on average 0.91 ± 0.01 (see Table 2). Unlike what has been previously reported (McPeck & Keller, 2002a), the activity of a large proportion of neurons from the superficial layers of SC is modulated during a feature search task.

To determine whether a neuron's discharge characteristics predict its ability to participate in the selection process during visual search, we related each neuron's DM and DT to its visually evoked responses, saccade-related activity and position along the visuo-movement axis (VMI). Each of these discharge parameters was found to predict a neuron's DM to some extent (Fig. 4A, D and G; Spearman correlation, $P < 0.05$), especially saccade activity. DT was similarly correlated with saccade-related activity (Fig. 4E and F). A neuron's DT was not (or not consistently) predicted by its visually evoked responses (Fig. 4B and C) and VMI (Fig. 4H and I). Overall, this analysis suggests that the stronger the saccade activity the better the discrimination (i.e., the larger the DM and the earlier the DT).

Most previous studies of saccade selection in SC have limited their investigations to a subset of SC neurons displaying sustained activity during the delay period of delayed saccade tasks. It is, however, unknown whether this activity pattern is indicative of a neuron's participation in the selection process. Across our sample, we found little evidence for a distinct group of delay-responsive

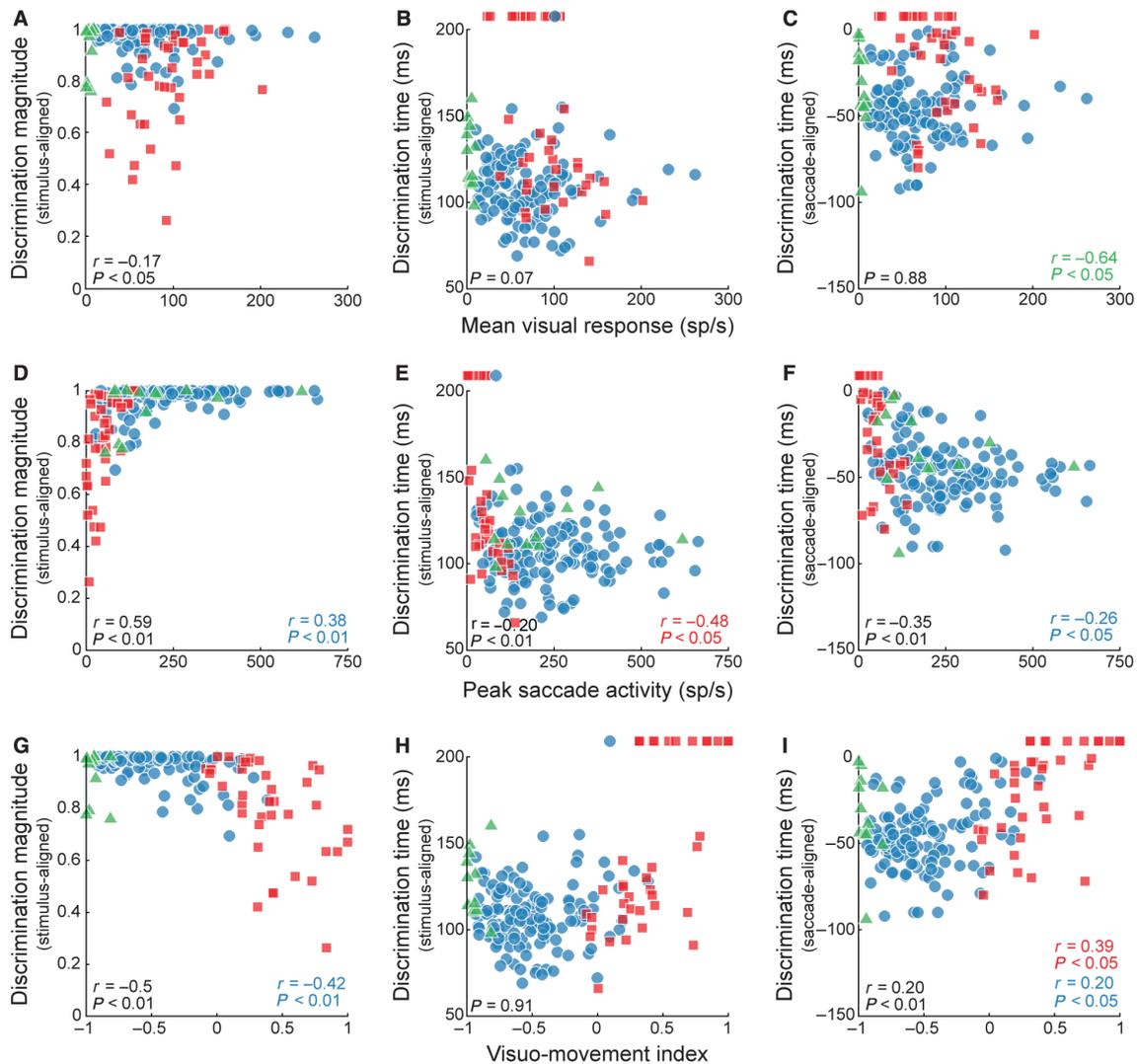


FIG. 4. Saccade target selection parameters (DM and DT) plotted as a function of each neuron's (A–C) visually evoked responses, (D–F) saccade-related activity and (G–I) position on the visuomovement axis. Red squares, putative visual neurons; blue circles, visuomovement neurons; green triangles, putative movement neurons. Data points outside the vertical axes are those neurons that did not reliably discriminate the target from distracters before saccades (DM < 0.75). Statistical values in black are from Spearman correlation tests across all neuronal types. Individual correlations within neuronal groups were also performed. Those that were significant ($P < 0.05$) are denoted in their corresponding colors.

neurons in either the visually- or memory-guided delayed saccade tasks (dip test, $P = 0.97$ and $P = 0.95$, respectively). Figure 5 illustrates the continuum in this activity pattern and Table 3 summarizes the relevant statistics for the putative neuronal groups. Most important, the correlation analyses shown in Figure 6 reveal that a neuron's DT and DM were generally not related to its delay period activity in either the visually guided (Fig. 6A–C) or memory-guided (Fig. 6D–F) saccade tasks. A neuron's position along the VIS-MEM Separation Index was only weakly correlated to its DM (Fig. 6G). Of those putative visual neurons with discriminating activity, the relationship between delay period activity and DT was neither consistent (Fig. 6B–C and E–F), nor generalized to the entire group of visual neurons – of those that did not have reliable discriminating activity, the majority also had significant delay activity (see Fig. 6). A similar analysis of the DT/RT slopes reported in the previous section (see Fig. 1) also revealed no relationship between a neuron's slope and its discharge characteristics in either feature or conjunction search (Spearman correlation, all $P > 0.17$).

Altogether, these observations suggest that all types of SC neurons participate in the selection process during visual search and that the quality of a neuron's discrimination is generally not related to its discharge properties, with the notable exception of the strength of its saccade activity. This last correlation, albeit weak and perhaps due in part to the inclusion of visual neurons, somewhat echoes the results of Thomas & Paré (2007), who reported that the saccade activity of an LIP neuron predicted its DM. A large DM is, however, a logical consequence of a high discharge rate reached before a targeting saccade, compared to a saturated or declining rate that is associated with distracters (see Fig. 2).

Is visual search performance fully predicted by the SC discriminating activity?

We tested the degree to which SC discriminating activity predicts visual search performance by comparing the saccade-aligned DM to response accuracy. Similar to our previous report (Shen & Paré, 2007), DM as determined from only correct trials was significantly

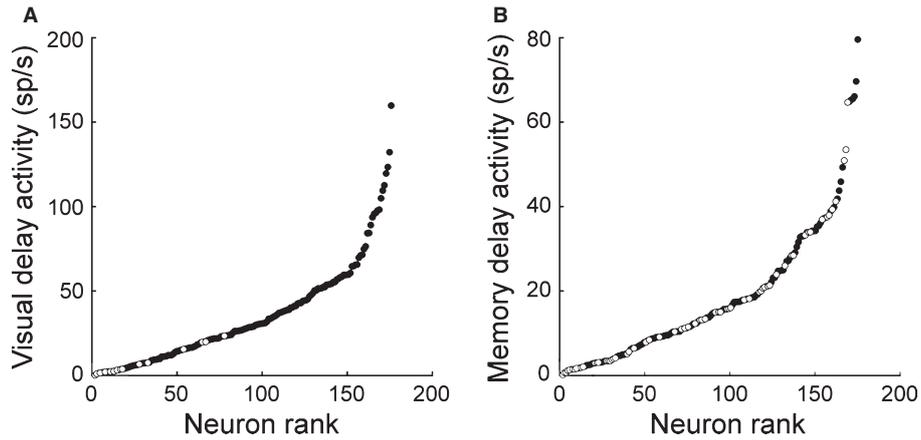


FIG. 5. Distribution of delay period activity (mean discharge rate during the last 300 ms of the delay period) during (A) visually guided and (B) memory-guided trials for the sample of 189 SC neurons. Neurons that have significant delay period activity (rank-sum test, $P < 0.05$) are denoted by the filled circles.

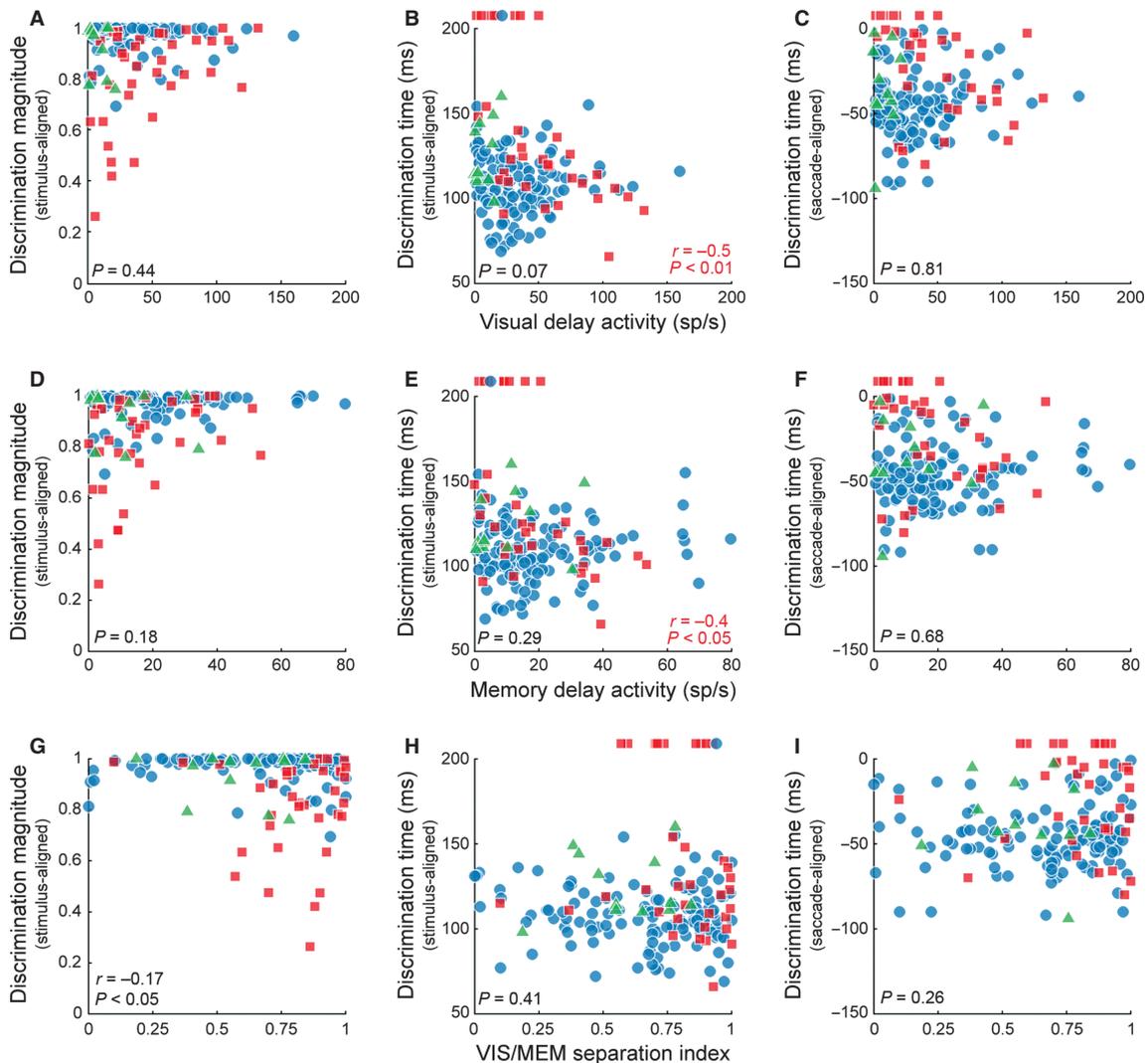


FIG. 6. Saccade target selection parameters (DM and DT) plotted as a function of each neuron's (A–C) visual delay activity, (D–F) memory delay activity, and (G–I) position on the visual/memory separation index. Red squares, putative visual neurons; blue circles, visuomovement neurons; green triangles, putative movement neurons. Data points outside the vertical axes are those neurons that did not reliably discriminate the target from distracters before saccades ($DM < 0.75$). Statistical values provided as in Fig. 4.

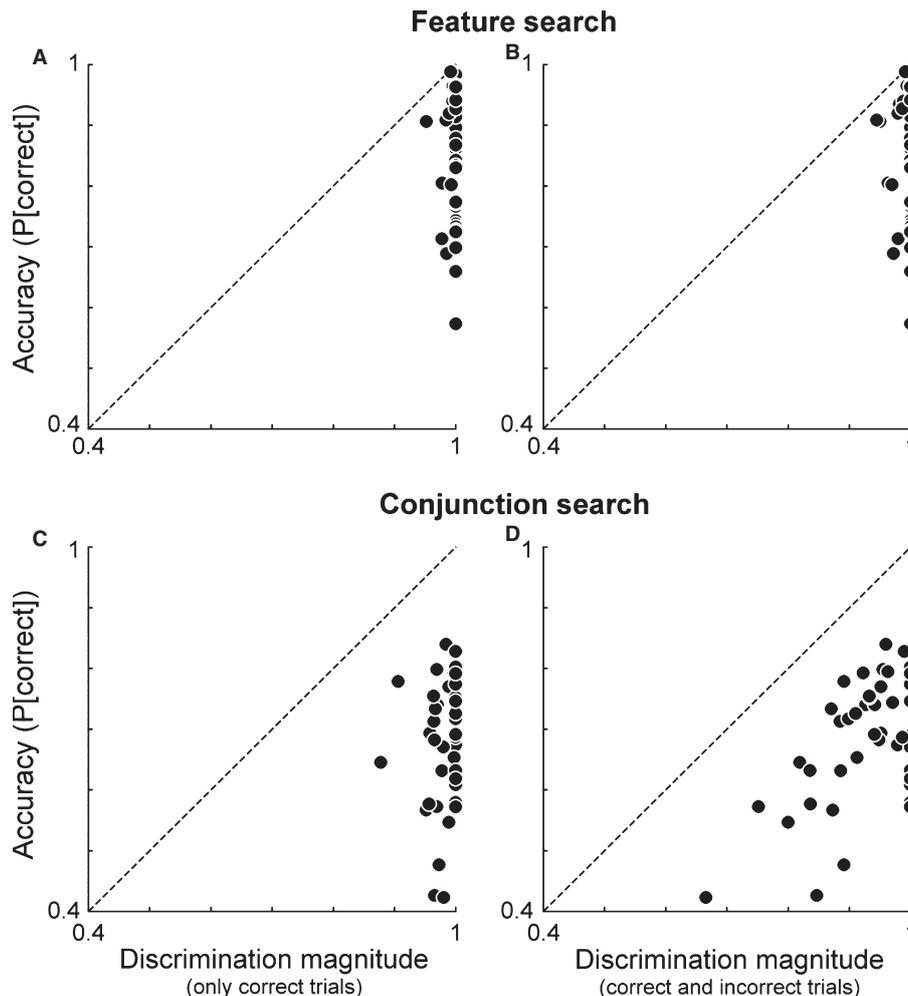


FIG. 7. SC discriminating activity surpasses in quality the search performance of the monkeys. Response accuracy is plotted as a function of discrimination magnitude (DM) as determined from (A and C) only correct trials or from (B and D) both correct and incorrect trials. This analysis includes the same subset of 44 neurons recorded in both feature and conjunction search tasks as depicted in Fig. 1.

greater than the monkeys' response accuracy in feature search (Fig. 7A; 1.00 ± 0.001 vs. 0.84 ± 0.016 ; paired *t*-test, $P < 0.001$) as well as in conjunction search (Fig. 7C; 0.98 ± 0.004 vs. 0.68 ± 0.016 ; $P < 0.001$). When considering all trial outcomes (correct and incorrect trials), a perfect match between DM and response accuracy would indicate that the SC discriminating activity fully predicts search performance. We found, however, that DM remained significantly greater than response accuracy in both feature (Fig. 7B; 0.99 ± 0.002 ; $P < 0.001$) and conjunction search (Fig. 7D; 0.93 ± 0.011 ; $P < 0.001$). Even if we were to consider the auROC value 10 ms prior to saccades, after which SC activity may be considered 'committed' to a certain saccade program (see Pare & Hanes, 2003), SC discriminating activity was still significantly better than response accuracy in both feature (auROC for correct trials: 0.96 ± 0.008 ; $P < 0.001$; all trials: 0.94 ± 0.013 ; $P < 0.001$) and conjunction search (correct trials: 0.91 ± 0.011 ; $P < 0.001$; all trials: 0.88 ± 0.012 ; $P < 0.001$). In fact, while the auROC values do decrease with time before saccade onset, they are still significantly greater than accuracy even 20 ms before saccade onset for both feature (Fig. 8A) and conjunction (Fig. 8B) search tasks. That SC activity discriminates the search target much better than the monkeys suggests that there is substantial noise between the SC saccade selection process and saccade programming, or that signals

from less discriminating neurons are added to this neuronal population (Parker & Newsome, 1998).

Discussion

In our review of the existing visual search literature, we identified three outstanding questions regarding the linking proposition that SC discriminating activity instantiates saccade target selection, for which we sought answers experimentally. First, we compared the activity displayed by SC visuomotor neurons recorded in both feature and conjunction search to determine what process is instantiated by SC discriminating activity. We found quantitative differences that suggest that this activity predicts saccade initiation but does not simply instantiate saccade programming. This finding helps reconcile previous PPC, FEF and SC studies of the saccade target selection process that takes place during visual search as well as support the view that the SC is not simply a motor map. Second, we analyzed a large sample of SC neurons recorded during feature search to determine whether different types of SC neurons participate in the saccade target selection process. We found that visual neurons in the superficial layers do possess discriminating activity and that the process of saccade target selection is not limited to any specific type of SC neurons. These data

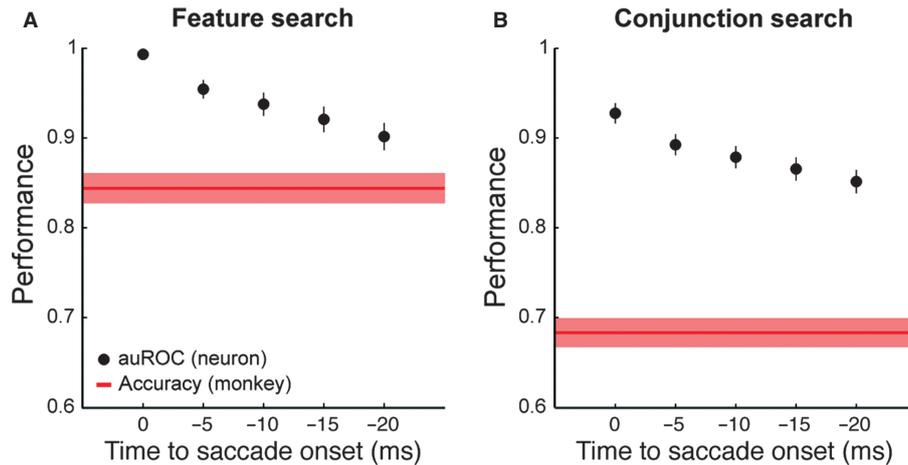


FIG. 8. Neuronal discrimination ability (auROC \pm SEM) determined from both correct and incorrect trials as a function of time before saccade onset in (A) feature and (B) conjunction search tasks. This analysis includes the same subset of 44 neurons (as in Fig. 1 and Fig. 7). Mean performance accuracy (\pm SEM) is denoted by the red curve.

also provide additional evidence against the hypothesis there are distinct functional types of SC neurons in the deeper layers. Third, we investigated whether the SC discriminating activity accounts for visual search performance. Our results revealed that it surpasses in quality the performance of monkeys in both feature and conjunction searches. This finding is important as it informs us about potential noise in the neural process of saccade target selection. We discuss these new findings in light of the framework that the SC is a highly conserved visuomotor map.

The SC as a salience map

The guidance of covert attention during visual search or of gaze fixations during active vision has been formalized by models that postulate the existence of a visual salience map (Treisman, 1988; Cave & Wolfe, 1990; Olshausen *et al.*, 1993; Wolfe, 1994; Logan, 1996; Findlay & Walker, 1999; Hamker, 2006; Cutsuridis, 2008). The salience map contains representations of objects whose magnitudes dictate the probability of selecting that item for further processing and, in the case of overt visual search, the probability of selecting that item as the next saccade target. These topographically organized representations are featureless and shaped by both stimulus-driven inputs from feature maps and goal-directed signals. The competition between the multiple visual representations is usually modeled as being resolved through a winner-take-all mechanism, which then provides a single output signal specifying the next target of interest and a single representation to a downstream motor map (e.g., Glimcher *et al.*, 2005; Beck *et al.*, 2008; Cutsuridis, 2008; see also Hamker, 2006). The feature maps might be instantiated by feature-selective neurons in extrastriate cortex (e.g., Chelazzi *et al.*, 1998; Bichot *et al.*, 2005). Goal-directed signals, such as knowledge of target identity and prior history, could be instantiated by neuronal activity within the prefrontal cortex (e.g., Rossi *et al.*, 2007; see for review Miller & Cohen, 2001).

Neuronal activity in cortical visuomotor areas, in particular the FEF and area LIP, are thought to form the salience map itself. The responses of FEF and LIP neurons are generally not feature-selective and their activity evolves to signal the saccade target before saccade initiation (FEF – Thompson *et al.*, 1996; Bichot & Schall, 1999; LIP – Ipata *et al.*, 2006a; Thomas & Paré, 2007), and independently of a

targeting saccade (FEF – Thompson *et al.*, 1997; Sato & Schall, 2003; LIP – Ipata *et al.*, 2009). In addition, the activity associated with a stimulus predicts the probability that it is selected as a saccade target (FEF – Thompson *et al.*, 2005; LIP – Ipata *et al.*, 2006b) and this activity is modulated by goal-directed signals (Bichot & Schall, 1999). The instantiation of the salience map in this frontoparietal circuit has been reviewed elsewhere (Thompson & Bichot, 2005; Bisley & Goldberg, 2010; see also Johnston & Everling, 2008; Paré & Dorris, 2011). The FEF is only common to primates (Preuss, 2007a; Kaas, 2008), and the PPC involvement in regulating eye movements appears even more evolutionarily recent (Paré & Dorris, 2011). Together with the superior temporal sulcus cortex, the PFC and PPC are generally described as a ‘higher-order’ network. This network, however, is evolutionarily recent, as it has no clear homologue in nonprimate mammals and is fully defined only in catarrhine primates (Preuss, 2007a,b), which include old world monkeys and hominoids. This primate ‘high-order’ network is heavily interconnected with the dorsal pulvinar and the SC. As reviewed above, the latter’s homologue, the optic tectum, is common to all vertebrates, including those with limited cortex. Neurons in the primate SC have visually evoked responses that are not feature-selective (Marrocco & Li, 1977; Ottes *et al.*, 1987; McPeck & Keller, 2002a; Shen & Paré, 2007), and their activity evolves to signal the saccade target before saccade initiation and independently of a targeting saccade (McPeck & Keller, 2002a,b; Shen & Paré, 2007). In addition, the magnitude of these representations predicts which stimulus will be selected as a saccade target (Shen & Paré, 2007), and the modulation of SC activity by reward information can be taken as reflecting goal-directed influences (Dorris & Munoz, 1998; Ikeda & Hikosaka, 2003). Such evidence supports the hypothesis that the SC also instantiates the visual salience map and perhaps its first instance, as we have argued above, which is further elaborated with inputs from cortical innovations to enhance behavioral flexibility.

Contrary to certain models of visual search (e.g., Cave & Wolfe, 1990; Itti & Koch, 2000; Hamker, 2006; Cutsuridis, 2008), there may be no separate motor map from the visual salience map as the deeper layers of SC seem to serve both functions, with integrated inputs from superficial-layer visual neurons. This visuomotor structure should instead be considered as a visual salience map for eye movements, in which the outcome of a competition between

multiple representations within SC provides a single motor output via its direct connections to the brainstem saccade-generating circuit once the saccade trigger threshold is reached (see also Findlay & Walker, 1999).

Does the SC neuronal activity signal saccade target selection?

Our analysis of the temporal relationship between SC discriminating activity and saccade initiation indicated that the former occurred at a fixed instant ahead of the latter. This finding would appear to lend support to the hypothesis that the SC discriminating activity signals only the selection of saccade goal, but the quantitative differences in this relationship between feature and conjunction searches suggest that the SC discriminating activity is probably distinct from saccade programming.

The unimodal distributions in DT/RT slopes observed in this study seem inconsistent with that of McPeck & Keller (2002a) as well as Shen & Paré (2007), who reported a subset of visuomotor neurons whose activity signaled the search target in incorrect trials (see, however, Kim & Basso, 2008; Port & Wurtz, 2009). To address this, we conducted the same slope analysis on the neurons from our previous report and found that the distribution of DT/RT slopes was also unimodal (dip test, $P = 0.87$) and not significantly different from 1 (mean 0.85 ± 0.12 ; t -test, $P = 0.20$). The discrepant results obtained from these two analyses may be explained by the unconstrained nature of the visual search task used in our studies, compared to other studies of SC and FEF neurons. Our search tasks do not emphasize accuracy, as reward is not exclusively associated with a single correct saccade to the search target. In line with our results, studies of LIP neurons recorded in unconstrained search tasks have also reported unimodal distributions in DT/RT slopes centered on 1 (Ipata *et al.*, 2006a; Thomas & Paré, 2007). Based on the evidence of some visual processing occurring up until saccade initiation, Thomas & Paré (2007) have argued that LIP discriminating activity reflects the simultaneous selection of the saccade target and goal. This interpretation is in keeping with the idea that, in natural situations, the selection of the next saccade target, or the associated deployment of visual attention, is usually not distinct from the selection of the next saccade itself (see for review Findlay & Gilchrist, 2003; Paré *et al.*, 2009).

The varying DT-RT relationship observed in this study suggests the same conclusion for SC neurons and helps to reconcile our results with the several findings that SC neuronal activity discriminates visual stimuli well in advance of saccade initiation in instructed, delayed saccade selection tasks (Glimcher & Sparks, 1992; Basso & Wurtz, 1998; Horwitz & Newsome, 2001a,b). The different results between feature and conjunction searches may be related to the demands in visual processing of the respective search displays. With the increased difficulty in discriminating the target during conjunction search (as reflected in lower response accuracy and longer RT), neurons could be recruited more for the process of target selection, ultimately resulting in substantial changes in neuronal activity patterns, such as those illustrated in Fig. 2.

Integrated SC neuronal population

We found discriminating activity in a large sample of SC neurons with discharge properties spanning a wide and clearly continuous range along single discharge dimensions: (i) visually evoked responses; (ii) saccade-related activity; and (iii) visual and memory delay activity. These results concur with our previous two-dimensional analysis (Paré & Wurtz, 2001; see also Munoz & Wurtz, 1995) as well as the

broad range of discharge properties observed in SC neurons projecting to the brainstem saccade-generating circuit (Rodgers *et al.*, 2006). They contrast, however, with the frequently held view that SC neurons form distinct types or classes beyond that prescribed by their locations within superficial and deeper layers (e.g., Mohler & Wurtz, 1976; Sparks *et al.*, 1976; Mays & Sparks, 1980; Guitton, 1991; Munoz & Wurtz, 1995; Ignashchenkova *et al.*, 2004). Any difference we observed, especially within neurons with movement-related activity, was quantitative rather than qualitative. Simple arbitrary criteria therefore provide little predictability as to a neuron's contribution to the process of saccade target selection. Multidimensional analyses may perhaps provide a basis for SC neuronal classification, but it appears judicious to extend the already accepted concept of population coding for saccade production (Lee *et al.*, 1988) to saccade target selection. As such, the emphasis on SC neuronal classes is currently tenuous, and there is little justification for considering only an arbitrarily defined subset of SC neurons when investigating saccade target selection.

High quality of SC discriminating activity

Signal detection theory has long been used by psychophysicists to measure the ability of subjects to detect or discriminate sensory stimuli and has been adopted by neurophysiologists to quantify the discriminating activity of neurons (see for review Parker & Newsome, 1998). Using this approach, we found that the ability of our monkeys to discriminate a target from distracters was surpassed by the discriminating activity of single SC neurons. One explanation for this finding is that signals from less discriminating neurons are added to this neuronal population (Parker & Newsome, 1998). In support of this hypothesis is the finding that one-fourth (15/61) of the SC output neurons identified by Rodgers *et al.* (2006) had neither visually evoked responses nor saccade-related activity. Alternatively, there could be substantial noise between the SC selection process and saccade production, such that behavioral errors are made despite correct target discrimination. We have previously reported that the great majority of erroneous responses made in our feature search task are saccades directed to distracters adjacent to the target (Shen & Paré, 2006). The proportion of these errors in this study was, on average, 0.72 ± 0.01 , and counting these as correct responses increased accuracy from 0.84 to 0.96. The difference with SC discrimination magnitude (0.99) is then significantly reduced, but it is still statistically significant (t -test, $P < 0.01$). If we considered the auROC just before the system is committed to a particular saccade program (i.e., 10 ms before saccades; 0.94), neuronal performance was no longer different from that of the monkeys in feature search ($P = 0.10$). However, this was not the case for conjunction search, for which there is no adjustment to performance accuracy. These mislocalization errors are certainly due to stimulus crowding in our search display and this could easily be reduced by using a display so that a neuron's receptive field would not encompass adjacent stimuli.

Another consideration is that single-neuron analyses may overestimate the quality of neural processing. In these analyses, an assumption is made whereby the population is represented by a neuron whose receptive field contains the target and an 'anti-neuron' of identical discharge properties whose receptive field contains a distracter. Such idealized representations are probably oversimplifications given the wide variety of activity patterns within a neuronal population. Kim & Basso (2008) attempted to address this limitation by simultaneously recording the activity of several SC neurons during a feature search task. In opposition to our findings, they reported that the discriminating ability measured from two SC neurons in only

correct trials was considerably surpassed by the overall response accuracy of the monkey. A comparative analysis of the activity of two simultaneously recorded neurons must take into account any large difference in discharge properties. It is unclear whether the analysis conducted by Kim & Basso (2008) normalized neuronal activity or replicated our previous results (Shen & Paré, 2007) when considering single neurons and the neuron/anti-neuron assumption. Comparison of results between studies are challenging when behavioral tasks and data analyses are significantly different. We feel confident that the analysis in our study is valid but we also acknowledge its obvious limitations. Thus far, the comparison between neuronal and behavioral performance in visual search studies has considered only one or two conditions of target discriminability, e.g., feature and conjunction searches, when the signal detection theory approach consists of comparing full psychometric and neurometric functions. Further research is necessary to address this gap.

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Abbreviations

auROC, area under the ROC curve; DM, discrimination magnitude; DT, discrimination time; FEF, frontal eye field; LIP, lateral intraparietal area; PFC, prefrontal cortex; PPC, posterior parietal cortex; ROC, receiver operating characteristic; RT, response time; SC, superior colliculus; sp/s, spikes per second; VMI, visuomovement index.

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