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Trajectory Interpretation by Supplementary Eye Field Neurons During Ocular Baseball

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Trajectory interpretation by supplementary eye field neurons during ocular baseball. *J Neurophysiol* 94: 1385–1391, 2005. First published May 11, 2005; doi:10.1152/jn.00109.2005. Good performance in the sport of baseball shows that humans can determine the trajectory of a moving object and act on it under the constraint of a rule. We report here on neuronal activity in the supplementary eye field (SEF) of monkeys performing an eye movement task inspired by baseball. In "ocular baseball," a pursuit eye movement to a target is executed or withheld based on the target's trajectory. We found that a subset of neurons in the SEF interpreted the trajectory according to the task rule. Other neurons specified at a later time the command to pursue the target with the eyes. The results suggest that the SEF can interpret sensory signals about target motion in the context of a rule to guide voluntary eye movement initiation.

INTRODUCTION

An object that moves in the environment could be predator or prey, a threatening projectile such as a tossed stone, or it might have no consequence at all. The odds of an animal's survival increase as its strategy to deal with moving objects becomes more sophisticated. Simple animals respond to moving objects reflexively. For example, the size of an object is sufficient for a toad to approach or to avoid it (Ewert 1980). However, the actions of primates are often guided by learned experience, as opposed to them being innate reflexes. Therefore to fully understand the neuronal control of primate behavior, it is critical to understand how the brain operates in the context of learned contingencies. This study was done to determine the role of the supplementary eye field (SEF), a structure involved in voluntary eye movement initiation, in interpreting a moving stimulus that signals an eye movement in the context of a rule.

Previous studies have shown that neurons in the SEF are active during saccadic (Schall 1991; Schlag and Schlag-Rey 1987) and smooth pursuit (Heinen 1995; Heinen and Liu 1997; Petit and Haxby 1999) eye movements. Stimulation here evokes saccades (Russo and Bruce 2000; Schlag and Schlag-Rey 1987; Tehovnik et al. 1999) and can facilitate pursuit initiation (Missal and Heinen 2001). These results suggest that the SEF participates in eye movement control. Other studies suggest a more specific role of the SEF in controlling voluntary eye movements. For example, it appears to participate in predictive and anticipatory smooth pursuit. Neuronal activity

during pursuit of predictable target motion has been observed here to peak before the predictable target events (Heinen and Liu 1997). A related result is that electrical microstimulation of the SEF can cause anticipatory smooth pursuit to begin earlier (Missal and Heinen 2004). It has also been shown that SEF neurons are more active for voluntary saccades directed opposite the target's location in the antisaccade task (Schlag-Rey et al. 1997).

Antisaccades, as well as predictive and anticipatory pursuit, are voluntary eye movements in the sense that they are executed without the direct guidance of a visual target and require learning. Because the SEF is involved in smooth pursuit, we wanted to know if this region might interpret the trajectory of a moving stimulus that may or may not become the target of an eye movement depending on a learned rule. The task we devised to test this is inspired by baseball, a sport that epitomizes interpreting a moving target in the context of a rule. A key feature of ocular baseball is the waiting period, during which the target moves and the animal must maintain fixation. A waiting period has been used before in laboratory go/nogo paradigms to study how eye or limb movements are planned in the SEF (Mann et al. 1988). In these paradigms, the animal plans the response while waiting and viewing a persistent stimulus. After the waiting period, a cue is given to move or not. In ocular baseball, the waiting period instead is imposed following the introduction of the cue, the moving target. Therefore neuronal activity related to interpreting the trajectory of that target can develop before activity related to the response occurs.

In ocular baseball, monkeys rotate their eyes and direct the fovea appropriately to "hit" and subsequently pursue with an eye movement a moving spot target (Fig. 1). Here, the animal must pursue the target if it crosses a visible strike zone ("strike" trials), and withhold eye movements if it does not ("ball" trials). Thus the trajectory of the target is a cue indicating whether the animal should make or withhold an oculomotor response. It was found that one population of neurons in the SEF reflected the state of the cue. At a later time, another population was activated before and during a movement on strike trials. The results suggest that the SEF can interpret a cue in the context of a rule to guide eye movement behavior.

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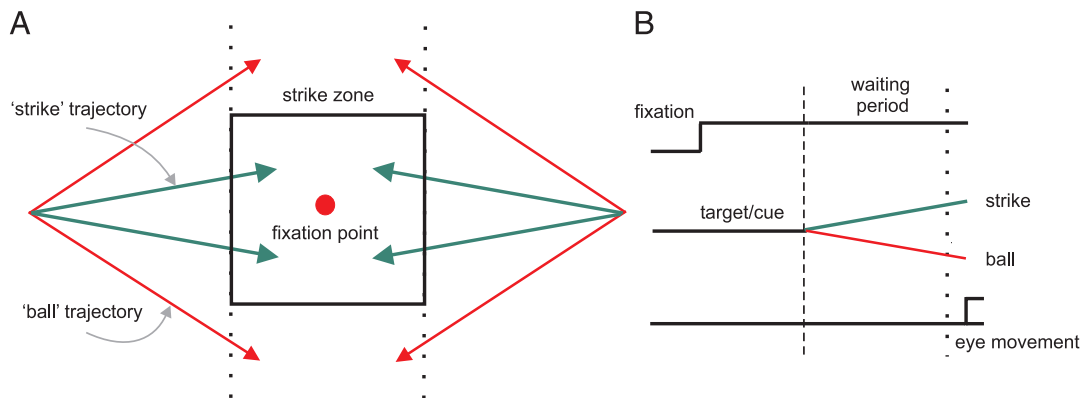
FIG. 1.   The ocular baseball paradigm. *A*: spatial layout. The animal fixates a red spot illuminated on the screen. Surrounding this spot is a visible, square "strike zone" that subtends 12°. An illuminated target begins to move from 1 of 2 20° eccentric positions in either the left or right periphery. If the target crosses the strike zone (strike trial, green), the animal must follow it with the eyes. If the target bypasses the strike zone (ball trial, red), the animal must withhold eye movements and maintain fixation. Order of presentation of trajectory angles was random in these experiments. The dotted line indicates in all plots when the target intersects the leading edge of the strike zone. *B*: sequence of events. Fixation point is illuminated and 500 ms after the monkey acquires it, the target appears and begins to move. Trajectory of the target is also the cue, specifying to the animal whether or not to follow it with the eyes. Waiting period overlaps time during which the cue evolves. Dashed and dotted lines define limits of the waiting period.

METHODS

Two male rhesus monkeys (*Macaca mulatta*; referred to as GU and SA) weighing between 5 and 7 kg were used in the study. All procedures were approved by the Institutional Animal Care and Use Committee and were in compliance with the guidelines set forth in the United States Public Health Service Guide for the Care and Use of Laboratory Animals. Monkeys had scleral coils, head restraint devices, and recording chambers implanted previously (Missal and Heinen 2001). Chambers were both located 24 mm anterior (Horsley-Clark coordinates), centered on the midline for GU and 5 mm right of the midline for SA. Monkeys were seated in a primate chair with head fixed 40 cm from a tangent screen in a dimly lit room. The baseball target was a 0.5° bluish-white spot of light (luminance = 2 cd/m²) projected by an oscilloscope onto the screen (luminance = 0.05 cd/m²). The fixation point was a 0.5° red spot generated by a projection LED. The strike zone was a clearly visible 12°-wide white square, displayed in the center of the screen with a slide projector for the entire trial.

Monkeys began the trial by fixating the red spot in the center of the screen. The baseball target appeared 20° eccentric, randomly on the left or right, and began to move toward the center of the screen. Possible angles were ±5, ±10, or ±15° (strike targets) and ±30, ±40, or ±45° (ball targets) with respect to horizontal. In an individual trial block, all strike angles had the same magnitude, as did all ball angles. Target speed was between 20 and 40°/s, and was also constant in a trial block. The waiting period was defined as the time between when the target began to move and when the target crossed the invisible vertical line defined by the leading edge of the plate (Fig. 1*A*). Hence the duration of the waiting period varied as a function of target angle and speed. Monkeys were required to maintain their gaze in a 3° electronic window centered on the fixation point during this time, or the trial was aborted. After the waiting period, in strike trials, the monkeys had to track the target and maintain eye position within a 5° window centered on the target. In ball trials, the animals had to maintain fixation within a 6° window. In either case, an error aborted the trial. On successful completion of the trial, monkeys received a few drops of liquid reward. Only data from correct trials are reported. The intertrial interval was 500 ms.

Eye movements were recorded with implanted scleral coils. Angular eye position was sampled at 1 KHz and stored on disk for off-line analysis. Eye velocity was obtained by off-line digital differentiation of the position records, and passed through a two-

pole Butterworth filter (cut-off = 50 Hz). Pursuit onset time was calculated from eye velocity using a linear regression method (modified from Kao and Morrow 1994). Saccades were not removed from the records. Single neurons were recorded from the SEF using tungsten microelectrodes (FHC) with an impedance of 1.0–1.5 MOhm, tested at 1,000 Hz. To obtain a continuous representation of the instantaneous neuronal activity in time, spike occurrences were convolved with a Gaussian function (sigma = 30 ms) to yield spike density.

To determine the time that neuronal activity became different for ball and strike trials (separation time), we applied a Wilcoxon rank-sum test to the instantaneous spike density values at each time-point in the interval of 500 ms before to 1,000 ms after target motion onset. Separation time was defined as when the P value of the ball/strike activity difference reached significance (0.05) and remained significant for ≥100 consecutive ms.

RESULTS

We recorded 55 neurons from two monkeys performing the ocular baseball task. Thirty-four of these fell into two distinct classes and are analyzed here. Neurons of the first type were active in strike trials, but not ball trials, and therefore will be referred to as "strike neurons." The results from a typical strike neuron are shown in Fig. 2*A*. Note that the activity in the strike trials was strong but that the neuron was virtually silent in the ball trials when the animal had to maintain fixation. For each neuron, mean activity in strike and ball trials was calculated over the interval from target motion onset until reward onset. The strike to ball activity ratios are plotted in Fig. 2*B*. Asterisks indicate significance (Wilcoxon rank-sum test, $P < 0.05$).

The other class of neurons responded specifically during the waiting period (Fig. 3). The neuron shown in Fig. 3*A* responded preferentially to ball targets. Other neurons preferred strikes. Because this differential activity was limited to the waiting period, it appeared related to the cue and not the motor response. Therefore these cells appeared to be interpreting the trajectory of the target in the framework of the rule governing ocular baseball. We refer to them as "cue neurons." As before, the strike to ball (if the
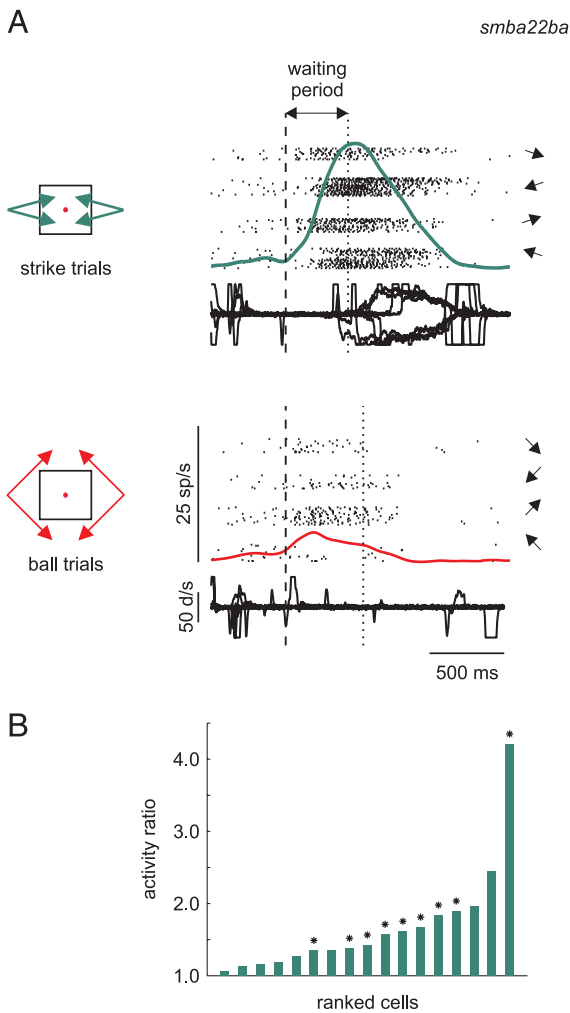
A

smba22ba

FIG. 2. Neuronal activity and ocular behavior during the task for strike neurons. *A*: rasters show the activity of a single neuron from multiple trials, grouped together here for each of the 4 strike trajectories (±5°; top) and each of the 4 ball trajectories tested (±30°; *bottom*). Icons on the *left* indicate the trial type (strike or ball), and arrows on the *right* show the angle of target motion used to obtain the rasters in each group. Solid, continuous line superimposed on rasters shows activity averaged over the entire block as a spike density function (green for strike trials, red for ball trials). Dashed line represents time that the target appeared, and dotted line represents time that it crossed the leading edge of the strike zone. Trials were aligned on target appearance. This neuron had higher activity in strike trials than in ball trials. Below the neuronal data are displayed the raw horizontal eye velocity traces from only the 1st 2 trials tested at each angle for clarity. Small spike-like incursions represent saccades, which have been clipped at 50°/s, and smoother traces pursuit eye movements. Note that small eye movements can occur before the target crosses the strike zone, provided that eye position remains within an electronic window set equal in size to the strike zone. *B*: ratio of mean strike to ball activity for all cells. Asterisks indicate significance.

izing activity for the different directions of motion during the waiting period. One concern with the cue cell data are that a significant difference between strikes and balls could arise merely if higher activity for a single direction of motion biased the mean activity in either the strike or ball trials to significance. However, this was not the case. Figure 4 shows examples of typical tuning curves for strike and ball cue neurons. These cells were not selective for a specific angle of target motion; rather, they signaled differentially whether the target would cross the plate or not. For all of the cue cells, we performed a Kruskal-Wallis ANOVA on the spike counts during the waiting interval, grouped by target direction. Ball and strike trials were analyzed separately. No significant activity difference was observed ($P < 0.05$) between strike directions in 14 of 17 cells and ball directions in 14 of 17 cells. The unique selectivity of the cue neurons for a rule-defined set of angles therefore distinguishes them from motion-selective neurons in the middle temporal (MT) (Albright 1984; Dubner and Zeki 1971; Maunsell and Van
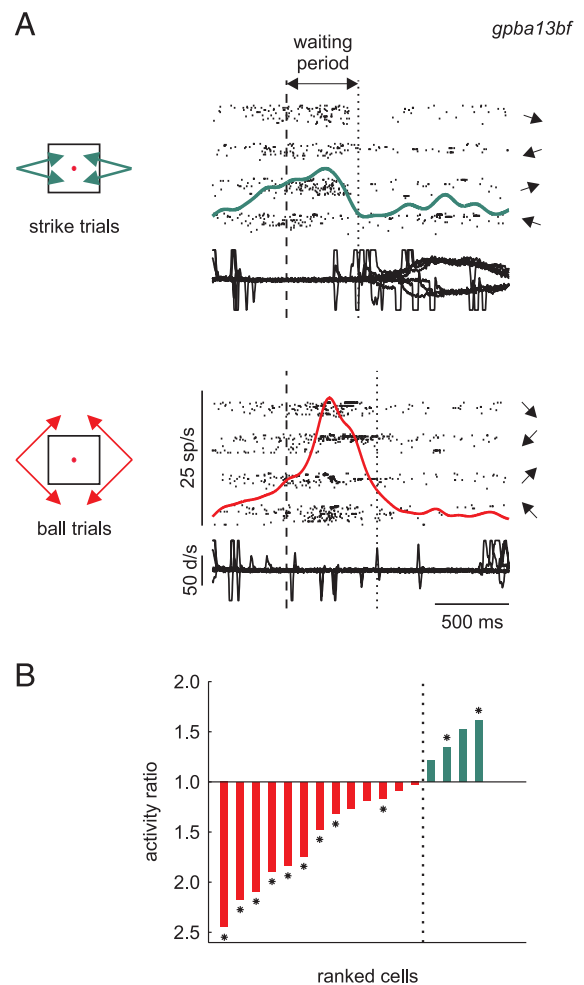
A

gpba13bf

FIG. 3. Cue neurons. *A*: activity of a single cue neuron and accompanying eye movements. Note that the activity of this cell was greater during the waiting period for balls (±40°) than for strikes (±15°). Other cue cells showed higher activity for strikes. Details as in Fig. 2. *B*: activity ratios for all cue cells. For strike-preferring cells, the strike to ball activity ratio was calculated and plotted on the upper axis (green bars). For ball-preferring cells, the ball to strike ratio was used, plotted on the lower axis (red). Asterisks indicate significance.

neuron preferred strikes) or ball to strike (ball preference) activity ratio for the waiting period was computed and is plotted in Fig. 3*B*. Again asterisks indicate significance (Wilcoxon rank-sum test, $P < 0.05$). There was no systematic topographical distribution of strike and cue neurons, although cells of the same type were often found in the same penetration.

In a visual area of the brain, the baseball task could be used to assess the receptive field of a neuron by character-
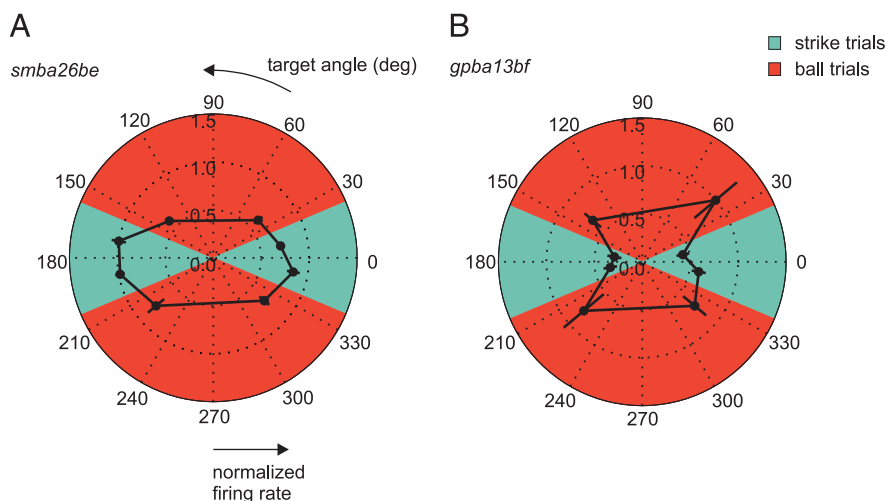
FIG. 4. Tuning functions of cue neurons. *A*: mean activity during the waiting period of a cell that preferred strike trajectories. Note overall higher activity for strikes, regardless of target approach angle. Strike angles are shaded in green, whereas ball angles are shaded in red. *B*: neuron that preferred ball angles. Details as in *A*. Error bars indicate SE.

Essen 1983) and the medial superior temporal (MST) (Zeki 1980) regions of the brain that process visual motion.

Given their respective responses, it is plausible that the cue cells signal to the strike cells whether to initiate a movement or not. If this is the case, the cue cells must interpret the trajectory of the target before the strike cells are differentially activated, and the strike cells in turn must respond before pursuit is initiated. To determine the time that a given neuron discriminated strikes from balls (separation time), we tested when the difference in neuronal activity for these conditions became significant with a rank-sum test applied at each time-point (Fig. 5*A*; see METHODS). The median separation time for cue cells was 142.5 ms (mean, 185.2 ms) after target motion onset, and the median separation time for strike cells was 400.5 ms (mean, 368.9 ms; Fig. 5*B*). To compare these neuronal latencies with movement initiation time, we also plotted pursuit onset as a cumulative probability function. Median pursuit latency was 463.0 ms (mean, 495.2 ms). These results suggest the sequence by which neuronal processing in the SEF unfolds over time during ocular baseball, with cue cells interpreting the trajectory of the target, and strike cells conveying a movement trigger.

The cue cell activity could be used to interpret the trajectory of the target, but is it? Because a rapid response to the target was not required, it could be that the animal was ignoring the cue and merely pursued the target if and when it entered the strike zone. To investigate this, pursuit latency was calculated with respect to when the target crossed the plate and plotted in Fig. 6. The distribution is not consistent with a reactive movement; rather, pursuit often begins well before the target crosses the plate, providing evidence that the target's trajectory was used by the monkey to guide its response.

DISCUSSION

We report here on the activity of single neurons recorded in the SEF of monkeys performing an ocular baseball task that was designed to investigate cognitive components of preparatory neuronal activity. In the sports of baseball (Bahill and Laritz 1984) and cricket (Land and McLeod 2000), the decision of whether to swing the bat at an approaching ball requires that the batter interpret the ball's trajectory in the context of a rule. During ocular baseball, cue neurons in the SEF were differentially active for strikes and balls. Another population of neurons, the strike neurons, was active for movement execution. The time that the cue cells differentiated the target motion preceded the time that strike cells became active, which in turn led the movement execution, suggesting the sequence of neural events from cue interpretation to behavior.

In a natural setting, after an animal has discriminated the trajectory of a moving object, it must decide whether or not to act on it. In primates, the decision is usually based on learned information regarding the potential benefits of avoiding or acquiring the object. Ocular baseball is designed to explore the neuronal substrate of this behavior. In the classic go/nogo task, where the waiting period occurs before the cue is given, the cue and movement activity are confounded.

In ocular baseball, the cue coincides with the waiting period. This allows cue-related activity and movement-related activity to be assessed independently. Ocular baseball imposes the added constraint over discrimination tasks that, not only must the animal discriminate a target's trajectory, it must then make or withhold an eye movement after evaluating that trajectory in the context of a rule.

In this task, the activity of strike cells preceded the eye movements and continued during them. This type of cell is likely from the class of SEF neurons previously reported to be involved in movement preparation and execution. Movement-related activity here has been observed to accompany simple, visually guided saccades (Lee and Tehovnik 1995; Schall 1991; Schlag and Schlag Rey 1987). When tested with a go/nogo paradigm, preparatory set activity preceding saccades has been observed (Schall 1991). Movement-related activity also been reported to accompany smooth pursuit (Heinen 1995). When tested with predictable target motion, some SEF neurons have been shown to exhibit activity that precedes, or anticipates, predictable target events during pursuit (Heinen and Liu 1997). The SEF projects to the superior colliculus (Huerta and Kaas 1990), which is involved in saccade (for a review, see Sparks and Hartwich-Young 1989) and smooth pursuit generation
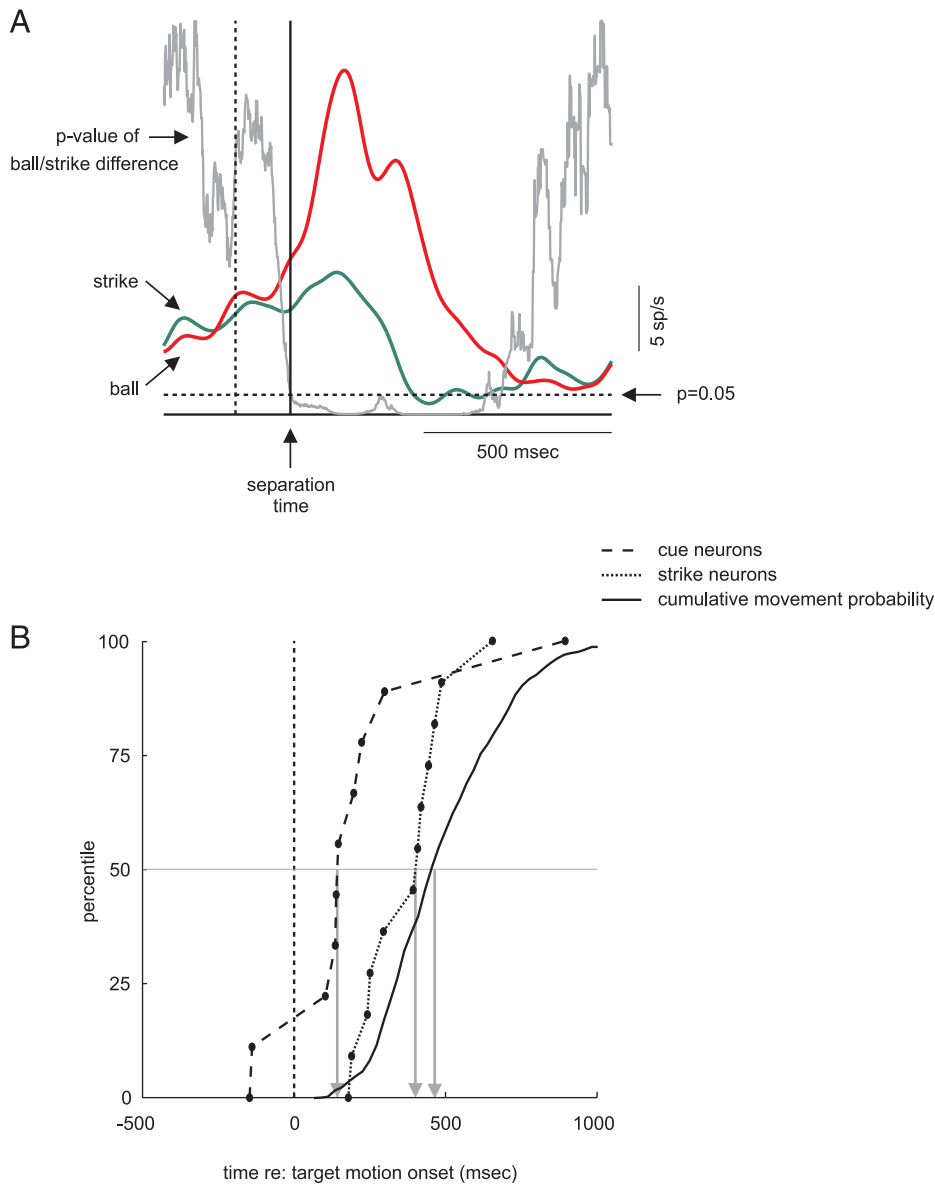
A

B

FIG. 5. Sequence of neuronal activation in the supplementary eye field (SEF) and behavior during ocular baseball. *A*: determining ball/strike separation time. Separation time was defined as when the instantaneous spike density values for strike and ball trials became significantly different and remained significantly different for 100 ms (see METHODS). Activity during ball trials (red line) separates and becomes significantly different from activity for strike trials (green line) when the *P* value (gray line) drops below 0.05. *B*: cumulative distributions of separation times for cue and strike neurons, as well as smooth pursuit latencies. Median separation time for cue cells (142.5 ms) preceded that of strike cells (400.5 ms), which in turn preceded median pursuit latency (463.0 ms). Dashed vertical line indicates beginning of waiting period. Cells that did not have a separation time within the analysis period do not appear in the cumulative plots ($n = 7$ cue cells and $n = 5$ strike cells).

(Krauzlis et al. 2000) and also projects to nucleus reticularis tegmenti pontis (NRTP) (Huerta and Kaas 1990), which plays a role in pursuit (Suzuki et al. 2003). Therefore movement planning and execution activity of the strike cells might trigger or modulate the movement command generated in these brain stem structures. Further evidence for this is that the strike cells became active on average 62.5 ms before the movement, similar to the latencies of saccades evoked from the SEF by microstimulation (Russo and Bruce 2000).

The cue cells that we recorded in this study were differentially active for strikes and balls and seem to be involved in interpreting target trajectory in a rule-governed framework for several reasons. Because the differential activity was limited to the waiting period, it was probably related to the cue and not the movement itself. Nor were these simply visual-motion neurons, because we found little evidence of selectivity for any specific direction of target motion (see Fig. 4), contrary to what is seen in motion processing areas

such as MT (Maunsell and Van Essen 1983; Zeki 1974). Neurons in MT can make fine discriminations about the direction of motion of random dot patterns (Britten et al. 1996) and are likely used in the earliest phase of baseball, when trajectory angle must be discriminated before the rule is applied. The tuning functions of cue neurons were very different from MT neurons and remarkable in that the highest activity accompanied four different directions of target motion, as opposed to one as is usually observed (Maunsell and Van Essen 1983; Zeki 1974). Furthermore, these neurons interpreted the trajectory on average 258 ms before the strike cells, a sufficient lead time for them to convey the decision to the strike cells to become active. To shed more light on whether the strike cells, and the animal, were "reading out" the decision of the cue cells, it is important to know if cue cell activity agreed with the behavior on error trials. Unfortunately, the relatively low error rate (~5%) precluded a meaningful analysis of this relationship.
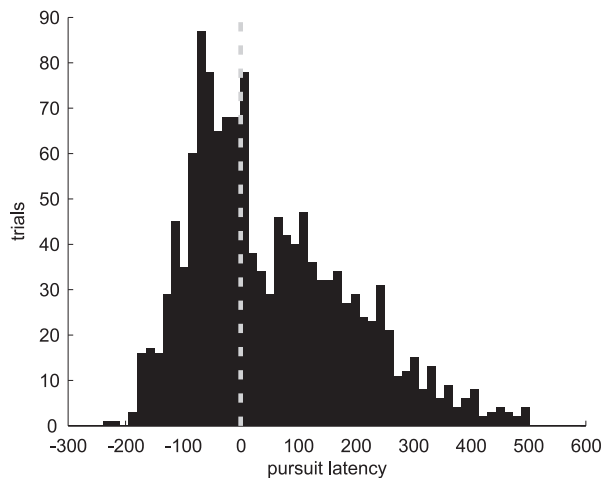
FIG. 6. Pursuit latencies aligned with respect to plate crossing. Distribution is consistent with the monkeys timing their eye movements to coincide with when the target crossed the plate (dashed line) rather than waiting for the target to cross and generating a reflexive movement.

There are other potential interpretations of our cue cell behavior in the context of activity recorded from the SEF in other studies. One study found that some SEF neurons were more involved in object-centered coding than in coding for rules (Olson and Gettner 1999). In this study, SEF activity was higher for saccades made to one end of a target, regardless of whether the "rule" of the task was to saccade to that end or to the other end of the target based on a color cue. The target trajectories in our experiment could be thought of as boundaries of a virtual object, and cue cells, which are active when the target starts to move at the periphery, might be coding the edge of the virtual object. However, our cue cells responded equally well for left and right target motion, evidence against this. Another interpretation is that the cue cells are fixation neurons (Bon and Lucchetti 1992; Lee and Tehovnik 1995; Schlag et al. 1992), because a majority of them are active during ball trials when the monkey must maintain fixation. This seems unlikely because the activity of cue cells during the waiting period is very different for strikes and balls, despite that the monkey is fixating in both cases. Furthermore, during the movement period in ball trials when the monkey continues to fixate, cue cells do not show a consistent pattern of activity, sometimes even decreasing to baseline levels (e.g., see Fig. 3).

The relative times of neuronal and behavioral events during ocular baseball hint at the sequence of processing that transpires during the task. Cue cell separation occurred before strike cell separation, suggesting that the cue cells might notify the strike cells that a movement was, or was not, needed. The difference in median separation time (258 ms) is quite large, and therefore the cue cells likely did not directly trigger the strike cells; rather, strike cell activity was delayed until the appropriate time. In future work, we plan to take advantage of this delay to test whether the cue cells take longer to interpret more difficult trajectories, resulting in a later median separation time. The difference in separation times for the strike cells and movement onset was

62.5 ms, suggesting that this is the time necessary for the strike activity to affect the response.

Two other regions, the prefrontal cortex (PFC) and a section of premotor cortex (PMC) located posterior to the arcuate sulcus, have been shown to be active during rule-guided behavior (Wallis and Miller 2003). In that study, monkeys performed in a matching and nonmatching sample task. In it, the monkey was shown a sample picture and was cued to select at a later time a picture that was either the same as or different from the sample. The monkey had to continue holding a lever if the picture did not conform to the same/different rule and release it if it did. Neurons were selective for various aspects of the task, but in both areas, cells were the most selective for one of the rules or one of the behaviors. Both areas are reciprocally connected with the SEF (Huerta and Kaas 1990). It is possible that the SEF could be reading out rule-related information from these prefrontal areas, or alternatively, be their functional analog in the control of eye movements. Whether in cooperation with prefrontal cortex or not, our results suggest that the SEF may provide a linkage between interpreting a rule and issuing a movement command.

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