

Movement selection in advance of action in the superior colliculus

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THE primate superior colliculus contains a map of saccadic eye movements^{1,2}. Saccades are high-velocity eye movements to selected targets in the visual field, but little is known about the neural mechanisms responsible for target selection or the related problem of choosing a particular movement from the oculomotor repertoire. Two classes of neurons have been described in the superior colliculus which show bursts of activity before the saccade: discrete bursters display a vigorous pre-saccadic burst and prelude bursters³ show low-frequency activity as a prelude to burst onset. We have designed experiments to test whether prelude activity is related to saccade selection. Our tasks use a cue to specify which of two physically identical visual stimuli is the goal of an impending saccade. This cue is spatially and temporally isolated from the potential targets as well as from visual cues signalling movement initiation. Our results show that prelude activity occurs shortly after information is available for correct saccade selection and, more importantly, the activity is predictive of saccade choice. The results thus suggest that the superior colliculus participates in the process of saccade selection.

Only two of our seven trial types are described. In trial type one (Fig. 1a), the animal was required to maintain fixation of a light-emitting diode (LED) illuminated red or green for 300 to 600 ms. Then, two additional eccentric yellow LEDs were illuminated (one above and one below the horizontal meridian) for 1,000 to 7,000 ms while fixation was maintained. When all three LEDs were extinguished, a saccade to the location of one

of the eccentric targets within 300 ms produced a reward. A red fixation stimulus indicated that the upper LED (or T1) served as a rewarded target and the lower LED (T2) served as a distractor. Conversely, a green fixation stimulus signalled that T2 was the target and T1 was the distractor. (Ottens *et al.*^{4,5} used a similar task for different purposes.) The precise target locations and the colour of the fixation target were varied randomly from trial to trial. For this reason, the (to be) rewarded movement could not be determined until all three LEDs had been illuminated.

During recording sessions, we first plotted the response field of an isolated neuron. Next, two conditions in which an LED was centred in the unit's response field were compared: trials in which that LED served as a target or as a distractor. Because the trials being compared differed only in the colour of the fixation LED (which was always outside the unit's response field), differences in activity occurring before the movement initiation cue can be attributed specifically to whether or not the stimulus was selected as a saccadic goal.

Figure 2a depicts the activity of a prelude burster on a single type one trial. As determined on single target trials, the neuron responded vigorously before movements to the upper target but was silent before movements to the lower target (Fig. 1a). On this trial, the red fixation stimulus signalled that an upward movement would be rewarded. The unit began to discharge shortly after the metrics of the required movement were specified by target onset, 5.5 s before the cue to initiate the saccade.

As illustrated in Fig. 2b, this cell was relatively silent throughout trials in which a green fixation LED signalled that a movement to T2 would be rewarded. The animal responded correctly, as predicted by the prelude activity.

Figure 2c depicts a trial in which the animal made a rare error. As in Fig. 2b, the green fixation light signalled that a movement to T2 would be rewarded. The prelude burster, however, fired vigorously and the animal looked incorrectly to

T1. The metrics of the upcoming saccade, not the colour of the fixation LED, were accurately predicted by the activity of the prelude burster. This pattern of results has been observed in all 22 prelude bursters studied.

We plotted the response fields of prelude bursters to determine how completely these neurons discriminate between targets and distractors. In this analysis, the location of one potential target (for example T2) was fixed where it elicited no response; the other (T1) was moved randomly throughout the response field. On a given trial T1 was either the distractor or the target, permitting us to map the unit's target-movement fields and distractor non-movement fields. Target-movement fields are plots of the horizontal and vertical amplitude of a rewarded movement against either the burst or prelude activity of the unit. Distractor non-movement fields are plots of the x and y position

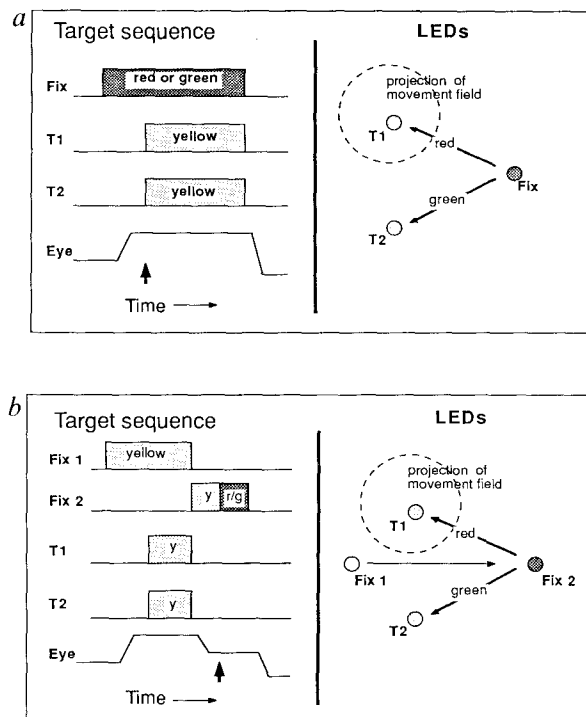


FIG. 1 Trial types used to separate the effects of movement selection and visual stimulation on prelude burster activity. *a*, Trial type 1. Animals first fixated a central red or green LED. After 500 ms, two yellow LEDs were illuminated at eccentric locations. The colour of the fixation LED signalled which of these would be the end-point of a rewarded saccade (the target) and which served as a distractor. After a variable interval of between 1,000 and 7,000 ms, the potential targets and the fixation LED were extinguished and the animal made a saccade to the target's location. This temporally isolated target specification from response initiation. Arrow, onset of the potential targets; this was the point in time at which the animal had sufficient information to select the correct response. *b*, Trial type 2. This identified the coordinate framework used by the prelude bursters. A fixation LED was illuminated yellow (300 to 600 ms); the two potential targets (yellow) were then presented for between 1,000 and 1,500 ms and all three LEDs were extinguished. The animal then made a saccade to a second yellow fixation LED. After 300 to 500 ms this second fixation LED turned red or green, specifying which remembered potential target would serve as the target and which was the distractor. After between 700 and 2,000 ms, the fixation LED was extinguished, releasing the movement. At the beginning of this final interval the animal has sufficient information to select accurately a response. The rewarded saccade to the remembered target is not identical to the retinal eccentricity of the visual target because a saccade has intervened. Activity during this final interval indicates that the response being represented in the prelude burster is independent of the retinal locus of visual stimulation. The arrow indicates the time at which the second fixation LED changed colour, providing the animal with sufficient information to select the correct response.

of the distractor against burst or prelude activity. As shown in Fig. 3*a*, prelude activity decreases as the selected movement deviates from the unit's best movement. Figure 3*c* is a target-movement burst field for this same unit. Note that whereas burst rate is double or triple that of the prelude, the spatial tuning of the response is quite similar.

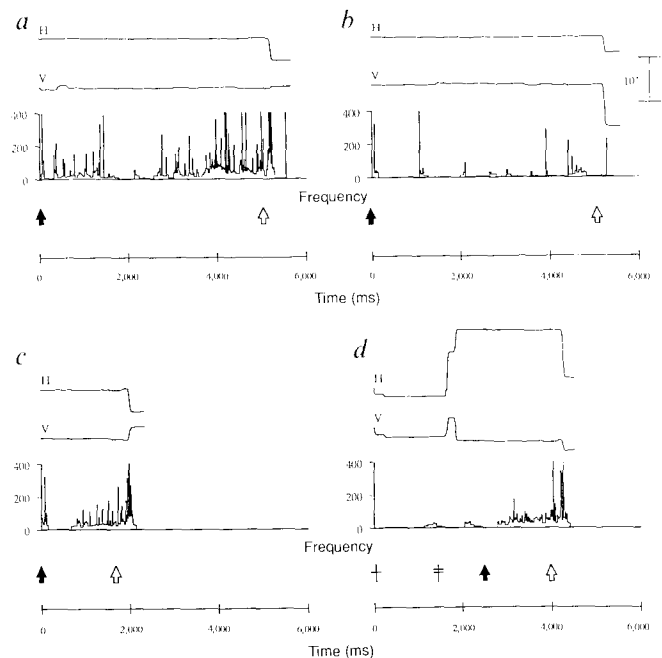


FIG. 2 We used standard electrophysiological methods¹¹ for recording single unit activity and monitoring eye position^{12,13}. Two monkeys (*Macaca mulatta*) were placed on a weekly regimen of water restriction and were trained to perform oculomotor tasks for a water reward. Correct eye movements were reinforced on a variable ratio schedule (VR 2); a 750-ms noise burst served as a secondary reinforcer on all correct trials. Experimental sessions lasted for 2–3 h under dim illumination. Recordings were performed in three colliculi. Four single trial records demonstrate the behaviour of prelude bursters during trial types 1 and 2. For each trial, H and V plot horizontal and vertical eye position respectively. Frequency plots the instantaneous frequency (reciprocal of interspike interval) for a single unit on a single trial. The filled arrow indicates, for each trial type, the time at which sufficient information is available to the animal for correct response selection. *a*, The behaviour of unit rh515a during a type 1 trial. Two targets were presented: one placed to specify a movement to $(-6, 0)$, in the centre of the unit's target-movement field (MF), and the other at $(-6, -14)$, outside the unit's MF. The red fixation LED signalled that a movement to $(-6, 0)$ would be rewarded. The unit became active and stayed active for 5.5 s, until movement onset. The open arrow indicates the offset of all LEDs, cueing movement initiation. The movement that occurred was correctly directed to $(-6, 0)$. *b*, This trial differed from *a* only in the colour of the fixation LED. Here a green LED signalled that a movement out of rh0515a's MF would be rewarded. The unit was relatively silent during the 5.5-s interval preceding the movement to $(-6, -12)$. *c*, On this trial the fixation light (green) signalled that a movement to $(-6, -12)$ would again be rewarded. On this occasion unit rh0515a became active and produced a burst of activity, accurately predicting an erroneous (unrewarded) movement to $(-6, 0)$. *d*, A type-two trial is presented for unit rh0515b (adjacent to rh0515a). Firing accurately encoded the impending movement to a remembered target at $(-6, -4)$ only after enough information was available to specify the rewarded movement (filled arrow). Note that information about which stimulus serves as the target and which serves as the distractor is provided by a change in the colour of the second fixation LED. This occurs after both potential targets have been extinguished and an intervening eye movement has occurred. Cross, onset of the potential targets; double cross, time at which both potential targets were extinguished. (Although this unit showed no decrement in response amplitude to remembered targets, for other cells, prelude activity to remembered targets was often reduced when compared with prelude activity to visual targets. The level of reduction varies tremendously from unit to unit; some respond as vigorously to remembered targets as to visual ones, others are nearly inactive before movements to remembered targets.)

How completely does the response of a prelude burster select between a target and distractor? Figure 3*b* plots the prelude activity as a function of the location of the distractor. Figure 3*d* plots the peri-movement burst against the location of the distractor (*x* and *y* coordinates of the potential target to which a movement was not directed). A comparison of Fig. 3*a* with *b* and Fig. 3*c* with *d* reveals that prelude bursters carry a signal from which the response to the distractor is largely, but not entirely, filtered.

Prelude bursters respond differentially to distractors and targets presented at the same location in their response field. A ratio of prelude activity observed with targets at the centre of the target-movement field, with that observed when the same LED serves as the distractor, provides an index of the unit's target/distractor selectivity. Figure 4 is a histogram of this selectivity ratio ($N = 22$). Similar selectivity occurs during the burst period, as can be seen in Fig 3*c* and *d*.

In a second trial type (Fig. 1*b*), after animals fixated a yellow LED for 300 to 600 ms, two yellow potential target LEDs were illuminated simultaneously for 1,000 to 1,500 ms. All three yellow LEDs were extinguished and a second yellow fixation light was illuminated at a new location. After fixation of this second

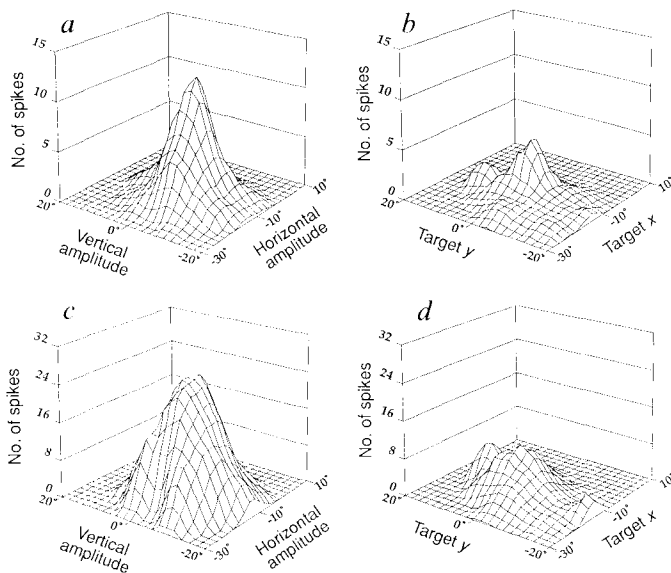


FIG. 3 Four hundred movement trials were used to construct these plots of unit rh0611's target-movement and distractor non-movement sensitivities. *a*, Target-movement prelude field. For each of the 400 trials the number of spikes in the 200 ms before the movement initiation cue is plotted against the horizontal and vertical amplitude of the movement. Prelude activity occurring well in advance of the movement is spatially tuned. *b*, Distractor non-movement prelude field. Here the same unit activity for each of the 400 trials is plotted against the *x*, *y* coordinates of the distractor. *c*, Target-movement burst field. This target-movement field plots the number of spikes occurring from 100 ms before to 100 ms after movement onset against the horizontal and vertical amplitude of the movement. *d*, The same peri-movement activity measured in *d* is plotted against the *x*, *y* coordinates of the distractor. (Note the differences between the ordinate and abscissa pairs on the left and right panels of Fig. 3. The left panels plot actual movements against spike counts. The right panels plot distractor location against spike counts. All movements terminated within 3 degrees of the target and were rewarded.) A target-movement field is defined as a plot of the number of spikes in the burst or prelude interval as a function of the horizontal and vertical components of a movement directed towards the (rewarded) target. The term 'target-movement field' is used to identify movement fields constructed of the rewarded movements to one of two potential targets. This terminology is intended to differentiate these rewarded movements, or target movements, from erroneous movements to the distractor. Conventional movement fields use a single target to which all accurate movements are directed.

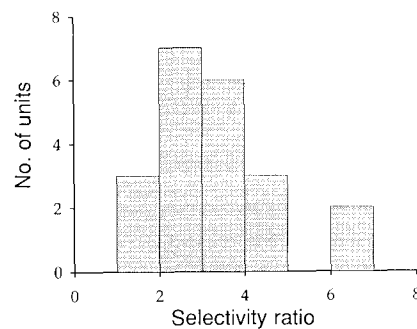


FIG. 4 Prelude selectivity ratio for each unit examined. This measure quantifies the ability of a unit to reject distractors and represent only the selected response. Selectivity ratios were computed from the spike counts of type 1 trials in which one LED was outside the target-movement field of the unit (as determined on single target trials) and the other LED was near the centre of the unit's target-movement field. These rewarded type 1 trials were separated into those directed into the response field of the unit (target trials), and those directed out of the response field of the unit (distractor trials). For each unit, average spike counts on target trials were divided by average spike counts on distractor trials to compute the selectivity ratios. The modal unit showed a selectivity ratio of 3.14:1. Twenty-one units are plotted here. An additional unit with a selectivity ratio of 30 is not plotted.

fixation LED for 300 to 500 ms, the colour changed to red or green, specifying one of the (now absent) potential targets as the saccadic goal. After 500 to 2,500 ms this LED was extinguished. Reward was contingent upon a saccade to the remembered target location within 500 ms. This task allowed us to determine whether the response field of a prelude burster was referenced to the retinal location of the target stimulus or to the metrics of the movement required to fixate the target. This was accomplished by requiring the additional eye movement that intervened between the retinal presentation and the movement to the target.

Figure 2*d* plots a single type-two trial. Prelude activity occurs after the change in colour of the second fixation LED specifies which movement will be rewarded. As with type-one trials, prelude onset is tightly coupled with information about the metrics of the selected movement. On type-two trials, however, that information is not available until after the intervening saccade, at which time the second fixation stimulus changes to red or green.

Examining prelude bursters during these tasks yielded several novel observations. The first is that prelude onset can precede burst onset by at least 7 s. Second, this early responding occurs only after sufficient information is available to permit accurate response selection. Finally, prelude bursters respond differentially to targets and distractors, even if they are identical stimuli. These data are consistent with the hypothesis that the low-frequency activity of the prelude burst cells reflects the output of the covert process of response selection.

Previous studies have identified neurons in the superior colliculus^{6,7}, and other brain areas⁸⁻¹⁰, that become active long before movement onset. It is not known if the activity of these cells qualifies them for identification as target or response selection output elements. Response selection output elements must be differentially sensitive to target and distractor stimuli and changes in their activity must be linked to the time at which sufficient information is available for response selection, as is the case for prelude bursters. Neural signals related to the metrics of a movement, or to the onset of potential targets, are readily observed, but, isolating neural signals related to the process of movement selection is difficult because selection occurs without a behavioral manifestation. Tasks like those in this experiment, which temporally and spatially isolate selection cues, should facilitate an analysis of response selection at the neuronal level. □

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