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Representation of averaging saccades in the superior colliculus of the monkey

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Abstract. We tested the hypothesis that averaging saccades occur when two different saccades are prepared and executed simultaneously. The activity of saccade-related burst neurons (SRBNs) in the primate superior colliculus was recorded while monkeys made both non-averaging saccades to single targets and averaging saccades which directed the gaze between two simultaneously presented visual targets. For movements of comparable direction and amplitude, the activity measured during averaging and non-averaging saccades was statistically indistinguishable. These results are not consistent with the hypothesis that averaging saccades result from the simultaneous execution of two different saccades at the level of the collicular SRBNs. Instead, these findings indicate that averaging saccades are represented as single intermediate movements within the topographically organized map of these collicular cells.

Key words: Saccade – Oculomotor – Superior colliculus – Monkey

Introduction

Under most experimental conditions, saccadic eye movements direct gaze to particular visual targets. However, when two or more visual targets are presented, the saccade may direct gaze to a point intermediate between these targets (Becker and Jurgens 1979; Findlay 1982). The precise end points of these intermediate, or averaging, saccades have been shown to be influenced by target features (Findlay 1982) and the probability that a particular stimulus will serve as a saccadic goal (He and Kowler 1989). These data indicate that visual information from multiple targets and extra-visual information are both important in controlling the metrics of averaging saccades.

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Understanding the neural implementation of these intermediate saccades requires an examination of averaging and non-averaging saccades at different levels of the oculomotor system. At a purely sensory level, both targets must be represented. At the level of the oculomotor nuclei, only a single movement, the averaging saccade, is represented. At what level does this transformation from two sensory representations, to a single motor command occur? We examined this problem by analyzing the representation of averaging saccades in the SRBNs of the superior colliculus (SC), a structure where movements of different directions and amplitudes are represented in different regions of an anatomically organized motor map.

We used an experimental rationale different from that employed in the only previous examination of this issue (Van Opstal and Van Gisbergen 1990). Our examination of averaging saccades in the SRBNs of the SC is outlined in Fig. 1. Figure 1a refers to saccades directed to a single target. The left panel plots four movements (M1, M2, M3 and M4) to four different targets. The middle panel depicts the locations of the populations of neurons active before movements M1, M2 and M3. The right panel plots a section through the movement field of Cell 1, the neuron identified in the middle panel. The activity of the cell is plotted for a family of movements of the same amplitude, but of many different directions. Note that Cell 1 is highly active before movement M1 and less active before movement M2. Movements M3 and M4 do not involve the activation of cell 1, as illustrated in the center panel, and the cell is silent during these movements.

Figure 1b illustrates the pattern of SRBN activity predicted by the hypothesis that an averaging saccade is represented as a single movement to an intermediate goal. The left panel illustrates movements directed to each of the simultaneously presented targets (M1 and M4) and two intermediate averaging saccades (M2 and M3). The middle panel illustrates the locations of the populations of cells active before a movement to a visual target (M1) and before the two intermediate averaging

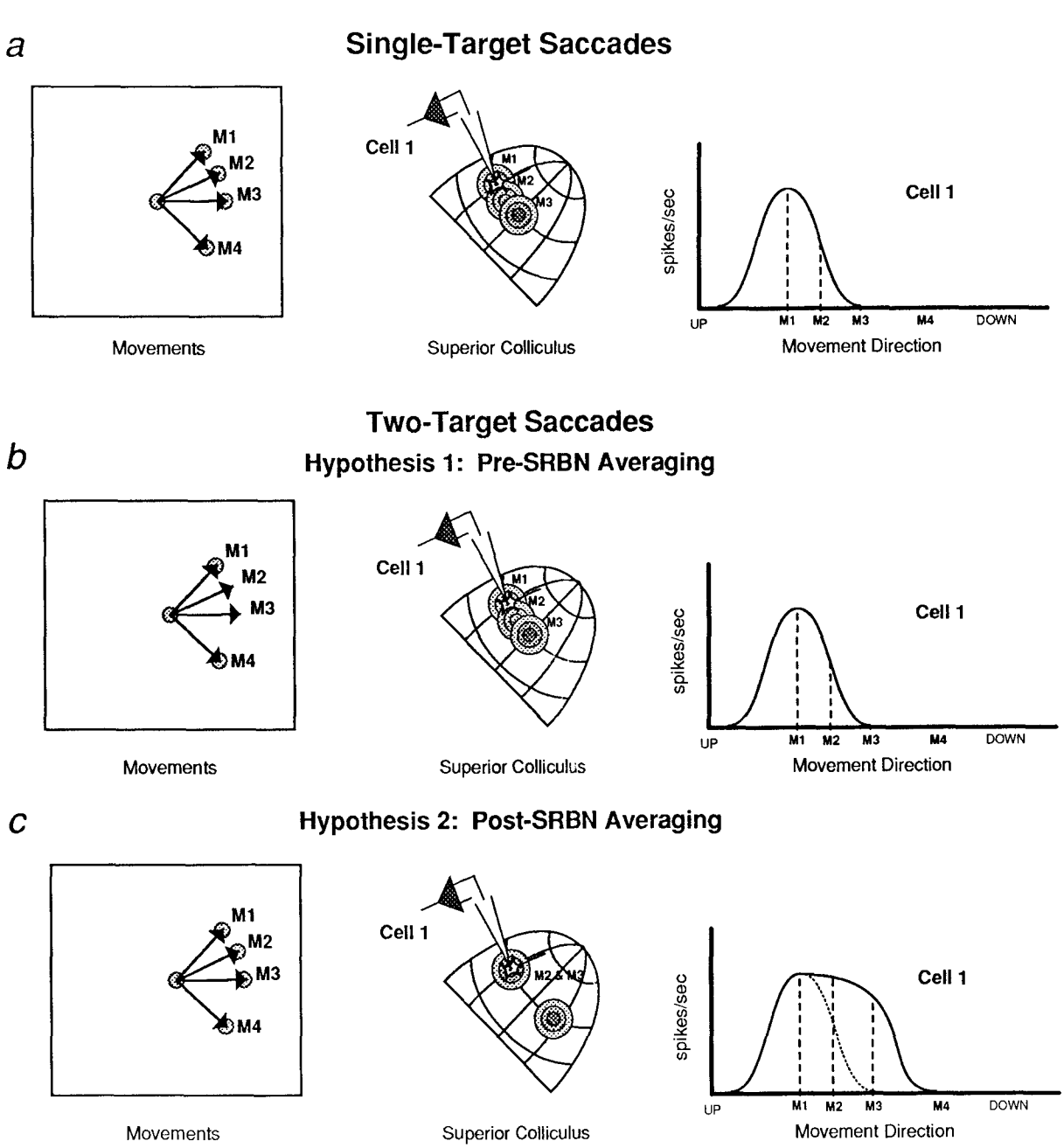

Fig. 1. a Four movements (M1, M2, M3 and M4) directed to four different targets on single-target trials *(left panel)*. The locations of the populations of neurons active before movements M1, M2 and M3 *(middle panel)*. A section through the movement field of Cell 1 measured under these single target conditions *(right panel)*. **b** Predictions of the hypothesis that an averaging saccade is represented, at the level of the collicular SRBNs, as a single movement to an intermediate goal. The activity of Cell 1 observed as a function of movement direction would be identical to the activity plot obtained on single-target trials, even though these movements are averaging saccades produced by two fixed targets. **c** Predictions of an alternative hypothesis suggesting that averaging saccades occur when multiple movements are initiated simultaneously at the level of the SC. Two separate populations are always active before averaging saccades, according to this hypothesis. Therefore, the movement field of Cell 1 observed under averaging conditions would differ from the movement field observed under non-averaging conditions

movements (M2 and M3). Note that this hypothesis requires that only a single population be active before each movement, just as is the case for single-target movements. Thus, as illustrated in the right panel, the frequency of firing for Cell 1 during averaging movements M2 and M3 is expected *to be the same* as the frequency of firing for these same movements during the visually-guided trials plotted in Fig. 1a.

Figure 1c presents an alternative hypothesis in which averaging saccades occur as a result of the simultaneous initiation of multiple movements by the collicular circuitry. According to this hypothesis, averaging saccades (M2 and M3) are produced by the SC when movements M1 and M4 are initiated simultaneously. Averaging saccades with different directions occur because the relative strength of the commands for movements M1 and M4

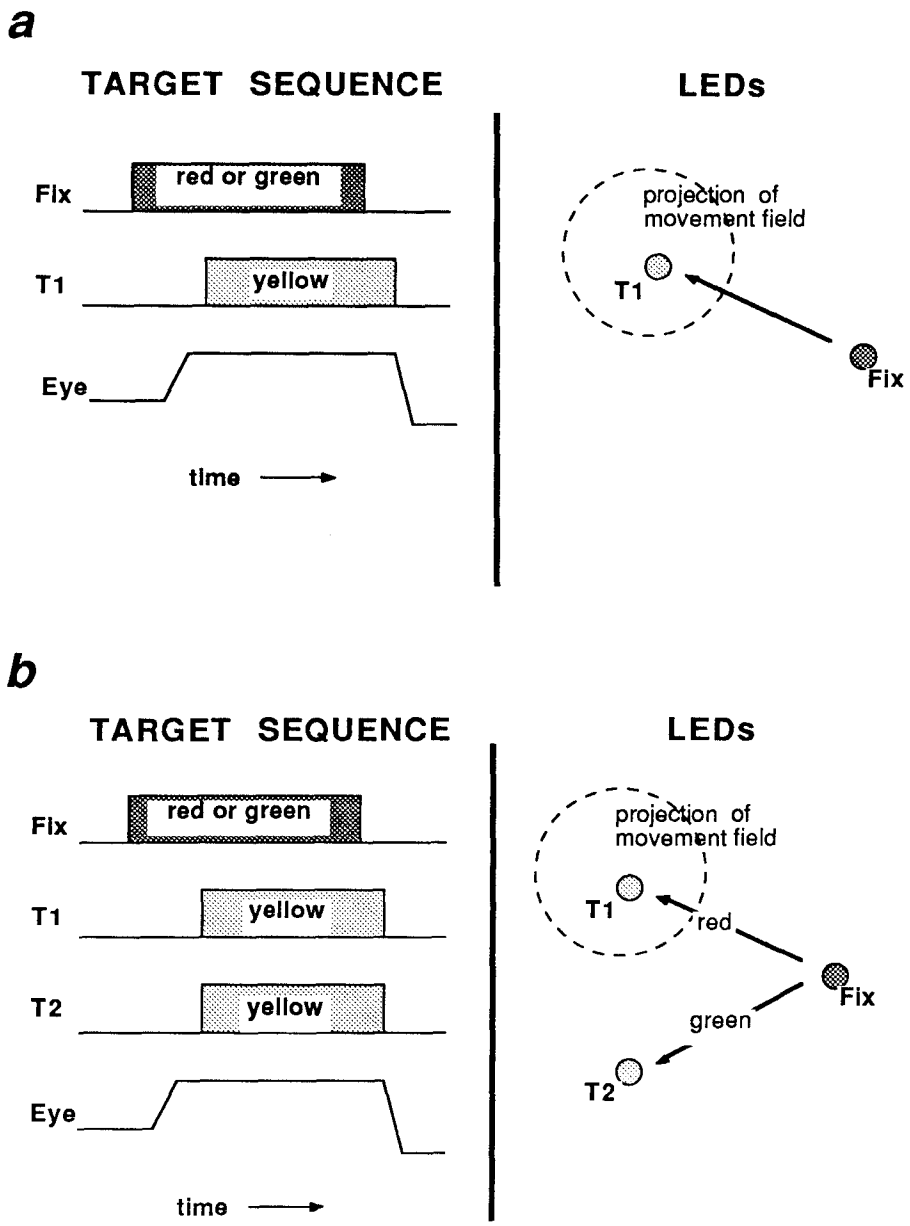

Fig. 2. a Single target trials. A central LED was illuminated red or green and animals were required to achieve fixation of this target (±3°) within 500 ms. After a delay of 50, 100, 150, 200, 300, 400 or 500 ms, a yellow eccentric LED was illuminated for 50 to 600 ms while the fixation target remained visible. The fixation target was then extinguished and a saccade to the eccentric target location (±5°) within 300 ms was rewarded. **b** Two-target trials. The central target was illuminated red or green. Animals made saccades to that location within 500 ms and after 50, 75, 100, 150, 200, 300, 400 or 500 ms, two eccentric yellow LEDs were illuminated. A green fixation target signaled that the lower of the two eccentric LEDs served as the saccadic target and the upper of the two LEDs served as an unreinforced distractor. A red fixation target signaled that the upper eccentric LED served as the target. After a delay of 50, 100, 150, 200, 300, 400 or 500 ms the fixation target was extinguished, and the animals received a reward for making a saccade to the identified eccentric target within 300 ms

vary from trial to trial. The locations of the two populations which, according to this hypothesis, are *always* active before averaging saccades like M2 and M3 are shown in the middle panel. Neurons between the two active populations that discharge maximally before movement M3 when it is elicited by a single target, may not discharge during movement M3 when it is elicited as an averaging saccade. Further, the movement field of Cell 1 would be predicted to change under these conditions, expanding to include averaging saccades. Cell 1 would be active before movements M1, M2 and M3 (right panel of Fig. 1c).

If averaging saccades are represented by collicular SRBNs as single saccades to an intermediate goal, the activity of a single neuron during a range of movements would be determined by the amplitude and direction of the movement, *not by the type of trial* (single- or two-target) used to elicit the movement. However, if averaging saccades occur when multiple movements are initiated simultaneously at the level of the SRBNs, then the activity of a single neuron during a range of averaging movements would be different from the same neuron's activity during a similar range of non-averaging movements. (The exact nature of this difference is not predicted by this general form of the hypothesis.) As the curve drawn in Fig. 1c indicates, this second hypothesis requires an extension of the movement field boundary toward the movement specified by the second target.

The responses of a single cell during movements to single targets were used to assemble a narrow section of the cell's movement field. Two-target trials were then used to obtain another sample of the movement field section under averaging conditions. We compared these two data sets to test the hypothesis that averaging saccades are represented in the SRBNs of the SC as two simultaneously initiated movements.

Materials and methods

Standard electrophysiological and oculomotor recording methods, described in detail elsewhere (Glimcher and Sparks 1993), were employed. All procedures used in this study were reviewed and approved by the University of Pennsylvania Institutional Animal Care and Use Committee and conform to all standards set forth in the National Institutes of Health's Guide for the Care and Use of Animals. The three female rhesus monkeys *(Macaca mulatta)* used in this study underwent two sterile surgical procedures under inhalant anesthesia. In the first procedure a scleral eye coil (Judge et al. 1980) and head restraint device were implanted. In the second, a 15-mm craniotomy was performed and a stainless steel receptacle for a hydraulic microdrive was mounted over the craniotomy. The receptacle was sealed with a sterile teflon plug. Nalbuphine was used to provide post-surgical analgesia.

A period of 2–3 months was allowed after the first surgery to permit complete osteo-integration of the surgical screws. The animals were then habituated to head restraint, placed on water restriction and trained to perform oculomotor tasks for a water or juice reward. When the animals had become proficient at these tasks, the second surgery was performed. A 1-week post-operative interval elapsed before the experimental sessions began.

During an experimental session, the animal's head was restrained and eye position was sampled at 500 Hz using the scleral search coil technique (Fuchs and Robinson 1966). Tri-color LEDS (red, green or yellow) located on a tangent board in front of the animal were used as visual targets. A hydraulic microdrive, affixed to the stainless steel receptacle, was used to lower parylene-coated tungsten electrodes (impedance: 0.5–1.2 MΩ) into the SC. The electrical signals encountered by the electrode tip were amplified and monitored. Electrodes were lowered until single SRBNs of the SC (as defined in Sparks 1978) were electrophysiologically isolated. Individual action potentials were discriminated from the electrode voltage waveform by time and amplitude criteria. In all, 12 SRBNs were studied for this experiment.

Two oculomotor tasks were used. In the single-target task (Fig. 2a) a central fixation LED was illuminated either red or green. Animals were required to fixate this target for 50–500 ms, after which an eccentric yellow LED was illuminated. Following a delay of 50–600 ms, the fixation LED was extinguished, cueing the animal to make a saccade to the eccentric target for a reward. This task was used to record the activity of SRBNs during a range of saccadic eye movements.

A second task (Fig. 2b) was used to examine the activity of cells during averaging saccades. In this two-target task, a central fixation LED was illuminated red or green, and the animal was required to fixate this LED for 50–300 ms. Two eccentric targets, T1 and T2, were then illuminated yellow for 50–300 ms while the fixation LED remained illuminated. The fixation LED was then extinguished, and saccades which brought the gaze to within 6° of the correct target within 300 ms were followed by a liquid reward. Thus, averaging saccades were typically unrewarded. T1 was selected to elicit a movement which was preceded by maximal or near-maximal activation of the SRBN under study. T2 was placed at the same horizontal eccentricity as T1, but at a vertical position which produced a movement that was not associated with activity of the cell under study. If the fixation LED was illuminated red, the upper of the two potential targets served as a saccadic goal. If the fixation target was illuminated green, the lower target served as a saccadic goal. The location of the saccadic goal varied randomly from trial to trial. (A similar task was employed by Ottes et al. 1985 in a series of behavioral studies.)

During an experimental session, a SRBN was isolated and single targets were presented in a range of horizontal and vertical positions in order to determine which movement was preceded by maximal activation of the cell under study. Then, 8–15 single targets, covering 20–30° vertically, but with the same horizontal eccentricity as the target eliciting the optimal movement, were used to obtain a vertical section through the movement field of the cell. This consisted of a plot of the number of spikes during the 100-ms interval centered on movement onset as a function of the vertical amplitude of the movement.

Two-target trials were then used to study the behavior of the cell during averaging movements. A large block (200–500) of two-target trials was presented with an intertrial interval of 500–1500 ms. Averaging saccades which directed the gaze to a point intermediate between the two targets occurred on less than 5% of these trials. The neural activity recorded during these averaging saccades provided another sample of a section through the movement field, a sample obtained during two-target trials and based upon averaging saccades.

Two animals were tested under dim illumination. The third animal was tested under conditions of total darkness.

Results

Figure 3 plots the trajectories of movements used in the analysis of one cell (rh0221a). Panel **a** plots the movements to single targets used to establish a baseline plot of movement-related activity. All movements occurring

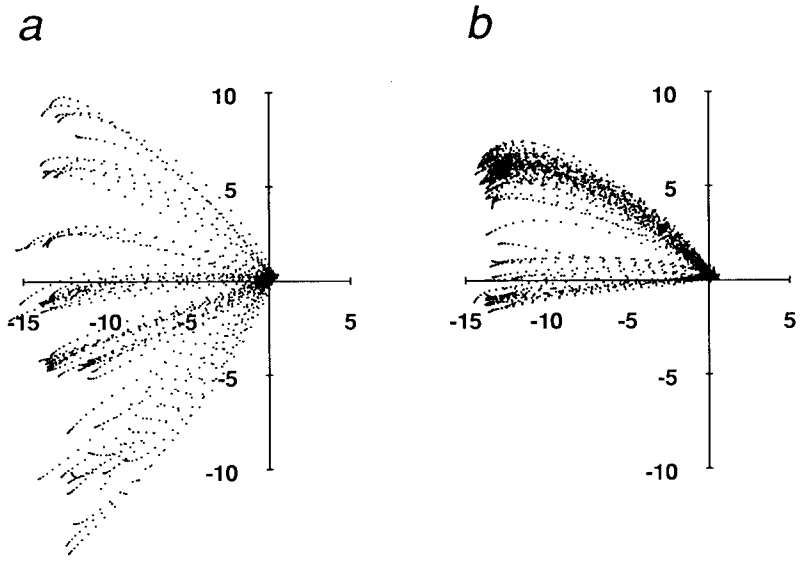

Fig. 3a, b. Movement trajectories for all single- and double-target trials used in the analysis of unit rh0221a. Points plot eye position sampled at 500 Hz. **a** Movements produced on single-target trials. **b** Movements produced on two-target trials. Targets were fixed at (−14, −2) and (−14, 8)

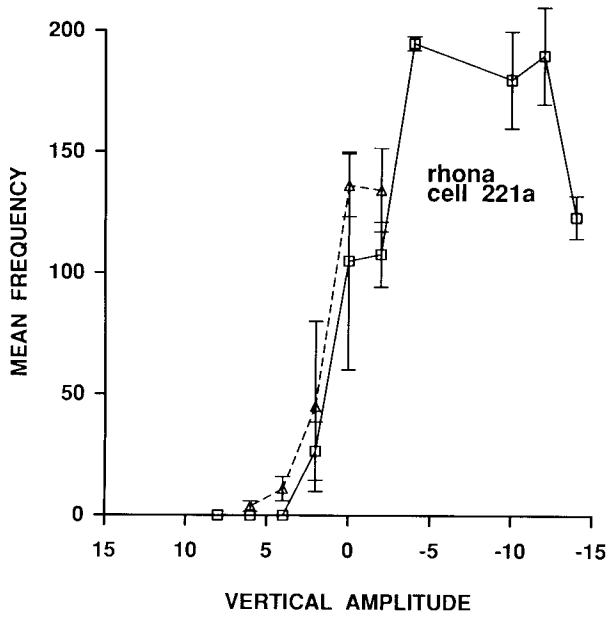

Fig. 4. The *solid line* plots the average spike frequency during the 100-ms peri-movement interval against vertical movement amplitude for a single cell (rh0221a) during single-target trials (average in 3 degree bins; the standard errors of the means are also indicated). The *dashed line* plots average spike frequency versus vertical movement amplitude for this same cell during two-target trials (average in 3 degree bins ±SEM)

on two-target trials, while the activity of the cell was recorded, are plotted in panel **b**. During the analysis of this cell, target T1 was fixed at 14° leftward and 2° downward (−14, −2) and target T2 was fixed at 14° leftward and 8° upward (−14,8). Many of the movements produced on these two-target trials were averaging saccades which brought gaze to a point between targets T1 and T2.

Figure 4 plots, for the same data set, the average spike frequency in the 100 ms peri-movement interval as a function of vertical saccadic amplitude. The solid line plots activity recorded during single-target trials. The cell fired vigorously for a movement of (−14, −2) and as the movements directed towards single targets shifted upwards from this movement, less activity was observed. The dashed line plots activity for movements of similar amplitude and direction recorded during two-target trials.

The hypothesis that averaging saccades are represented as two movements at the level of the collicular SRBNs predicts that the plot of spike activity versus movement direction measured under two-target conditions would be extended towards a movement to T2 (−14, 8) when compared to the same plot measured under single-target conditions. However, the plot of activity during actual averaging movements is not statistically distinguishable from the one obtained during non-averaging movements.

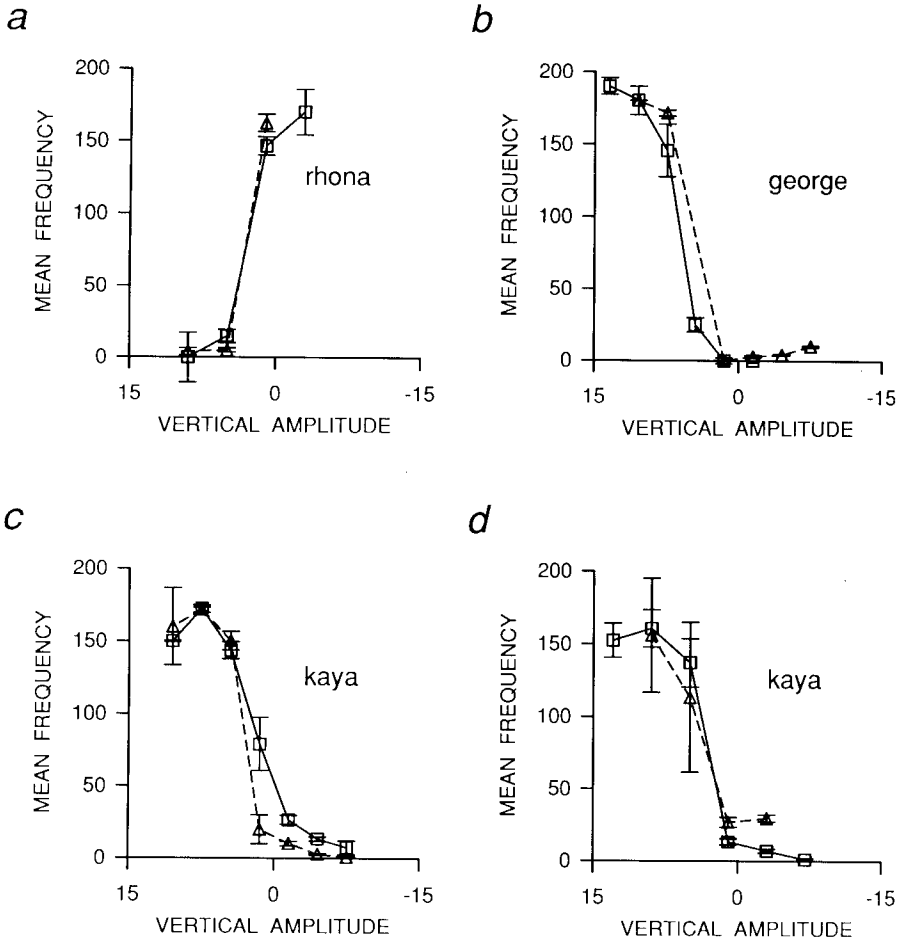

Fig. 5a–d. Average spike frequency during the 100-ms perimovement interval versus vertical movement amplitude for four additional units. *Solid lines* indicate activity during single-target trials, *dashed lines* indicate activity during two-target trials. All data were averaged in either 3 or 4 degree bins; standard errors of the means are indicated. Cells were studied in three different monkeys, as indicated by the animal name on each graph. Cells plotted are: a:rh0305 b:ge0328 c:ka1104 d:ka1105

Spike activity versus movement direction plots are shown for four additional cells in Fig. 5. Solid lines represent data obtained during movements to single targets. Dashed lines represent data for movements made during two-target trials. Thus, averaging saccades are preceded by a pattern of SRBN activation consistent with the prediction of the hypothesis that a single movement to an intermediate goal was prepared.

The similarity of the plots obtained on single target trials to those obtained on two-target trials suggests that there is no difference in the collicular representation of averaging and non-averaging saccades. The following analysis was performed to test this hypothesis. Averaging saccades were defined as movements occurring on two-target trials which terminated between the end points of movements to single targets T1 and T2. We computed the mean and standard deviation of the end points of movements directed to T1 or T2 on single target trials. Averaging saccades on two-target trials were then defined as those movements with end points lying between T1 and T2, movements with vertical components which were not within one standard deviation of the mean vertical end point of movements to T1 or T2 on single-target trials. Saccades to single targets with vertical end points in this same range were used for comparison.

The method of Ratkowsky (1983) was used to determine if these averaging and non-averaging data sets differed significantly. A third order polynomial was fit to each data set using a least squares algorithm. The two data sets, two-target averaging movements and single-target control movements, were combined, and a third order polynomial was fit to this pooled data set. The residual sum of squares and degrees of freedom associated with the two separate fits of averaging and non-averaging data were compared to the residual sum of squares and degrees of freedom associated with the fit of the pooled data. A computed F-ratio was used to determine the probability that the two data sets were derived from separate distributions. This test was performed by computing the F-ratio for the pooled versus separate comparison using the following formula:

$$F = \frac{(SS_{pool} - SS_{sep})/(df_{pool} - df_{sep})}{SS_{sep}/df_{sep}}$$

where:

SS_{pool} = Sum of Squares (SS) for pooled data set
SS_{sep} = Sum of Squares (SS) for averaging data set + SS for single-target data set.
df_{pool} = degrees of freedom (df) for pooled data set
df_{sep} = degrees of freedom (df) for averaging data set + df for single-target data set.

This F-value was converted to a P-value by entering a statistical table with $(df_{pool} - df_{sep})$ as the df of the numerator and df_{sep} as the degrees of freedom of the denominator.

All 12 units we examined were analyzed in this manner. In no case did the F-ratio yield a P-value less than 0.05. The data sets examined contained a minimum of 19 and a maximum of 82 averaging saccades (mean = 49). Thus, the hypothesis that averaging saccades are represented by the collicular SRBNs as two simultaneously initiated movements was not supported by this analysis.

Discussion

The population of collicular SRBNs represents impending movements as localized regions of activity on a topographically organized map of motor space (cf. Wurtz and Goldberg 1972; Robinson 1972; Sparks et al. 1976). Movements of different amplitudes or directions are represented by populations of SRBNs at different positions in the collicular motor map. Thus, identifying the collicular location or locations active before averaging saccades establishes the nature of the collicular representation of averaging saccades. The hypothesis that averaging saccades are produced, at the level of the collicular SRBNs, by two simultaneously initiated movements, requires that two separate loci of collicular units be active before averaging saccades. Our analysis of the SRBNs of the SC suggest that only one spatially defined population of these neurons is active before averaging movements. This observation indicates that the process by which an intermediate goal is computed from two visible targets is complete at the level of the collicular SRBNs.

Van Opstal and Van Gisbergen (1990) also examined the collicular representation of averaging saccades. They recorded the activity of single collicular cells during averaging movements produced by the rapid sequential presentation of two targets (a *double-step* task) and during non-averaging movements produced by the presentation of single targets. Gaussian functions that related spike activity during single target trials to movement amplitude or direction were compared to data obtained during two-target trials. Statistical analysis indicated that the functions derived from single-target trials only partially accounted for the spike activity observed on averaging trials. Including saccadic velocity as an additional free parameter increased the amount of variance accounted for by the single movement hypothesis, but only slightly.

Van Opstal and Van Gisbergen's examination attempted to test the null hypothesis that the activity of collicular cells associated with a single-target movement *did not differ* from the activity associated with an averaging saccade of the same direction and amplitude. Our strategy was to examine the behavior of a cell that discharged maximally for a movement to one of the two targets that were presented simultaneously during averaging trials. We tested a prediction of the hypothesis that averaging saccades are produced by the simultaneous initiation of two movements in the SRBNs of the SC, the prediction that the movement field of a cell under averaging conditions would appear to expand when compared to non-averaging conditions. As illustrated in Fig. 1C, the hypothesis that two movements are simultaneously represented at the level of the collicular SRBNs during averaging saccades predicts that the plot of spike activity versus vertical movement amplitude for averaging saccades will be extended when compared to the plot obtained on single-target trials. Differences in the shape

of the plots obtained by careful measurements of the edges of the movement field, would provide support for the hypothesis that averaging saccades occur when two movements are initiated simultaneously. If this hypothesis were correct, the form of the activity/movement-direction plot under two-target conditions would be a distorted version of the function observed under single-target conditions.

The alternative hypothesis, that averaging saccades are already represented as single movements to an intermediate location at the level of the collicular SRBNs, predicts that the functions described by the data would be identical under averaging and non-averaging conditions. The observed similarity between the plots for data obtained on single-target and two-target trials contradicts the prediction of the hypothesis that averaging saccades are produced by the simultaneous initiation of two movements at the level of the SRBNs. These findings are consistent with the predictions of the hypothesis that averaging saccades are initiated by collicular commands to initiate a single movement. Thus, these data suggest that averaging saccades occurring when *two targets are presented simultaneously* are represented by SRBNs as single movements to an intermediate goal.

The results presented here differ in one respect from the data presented by Van Opstal and Van Gisbergen (1990). They reported that, for movements associated with peak activity from the cell under study, discharge frequency was lower during averaging saccades than during non-averaging saccades. In contrast, the SRBNs presented here produced similar bursts for averaging and non-averaging saccades before which they fired most strongly. Our experiments differ from those of Van Opstal and Van Gisbergen in one important way which may account for this difference. In our experiments, averaging saccades were directed towards two targets that were presented simultaneously. Van Opstal and Van Gisbergen produced averaging saccades by presenting two targets sequentially. The discrepancy in our findings may be explained by recent evidence suggesting that under certain conditions, the location of SRBN activity within the collicular motor map may not accurately reflect the amplitude and direction of the saccade that is actually executed (Stanford et al. 1991; Schlag-Rey et al. 1992). This dissociation may occur under conditions in which the saccade goal is altered after a saccade has been initiated by the SC. When two targets are presented sequentially, the locus of SRBN activity may be more tightly coupled to the movement specified by the first target than to the amplitude and direction of the executed averaging saccade. If SRBN activity is related to the movement specified by the first of two targets, then the level of activity in the center of a movement field measured under these conditions would be reduced. This is the result observed by Van Opstal and Van Gisbergen (1990). Additional experiments are needed to describe the relationship between SRBN activity and the metrics of saccades occurring when two targets are presented sequentially.

Plots of spike activity versus saccade direction, like those obtained in this study, represent cross-sections of the movement fields of individual cells. However, when a single cell is part of a topographically organized population, the behavior of the population to which it belongs can be inferred from the single cell's activity. Thus, plots of the movement fields of single cells provide a powerful tool for the study of population responses during averaging saccades. In the application of this approach to the SRBNs of the SC, our data indicate that these cells represent averaging saccades as single movements directed between two simultaneously presented targets.

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