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# Population coding of saccadic eye movements by neurons in the superior colliculus

**Choongkil Lee*, William H. Rohrer* & David L. Sparks†**

Neurobiology Research Center, Department of Physiology and Biophysics, University of Alabama, Birmingham, Alabama 35294, USA

**The deeper layers of the superior colliculus are involved in the initiation and execution of saccadic (high velocity) eye movements[1]. A large population of coarsely tuned collicular neurons is active before each saccade. The mechanisms by which the signals that precisely control the direction and amplitude of a saccade are extracted from the activity of the population are unknown. It has been assumed[2–6] that the exact trajectory of a saccade is determined by the activity of the entire population and that information is not extracted from only the most active cells in the population at a subsequent stage of neural processing. The trajectory of a saccade could be based on vector summation of the movement tendencies provided by each member of the population of active neurons[4] or be determined by a weighted average of the vector contributions of each neuron in the active population[2]. Here we present the results of experiments in which a small subset of the active population was reversibly deactivated with lidocaine. These results are consistent with the predictions of the latter population-averaging hypothesis and support the general idea that the direction, amplitude and velocity of saccadic eye movements are based on the responses of the entire population of cells active before a saccadic eye movement.**

* Present addresses: Department of Psychology, Seoul National University, Seoul, Korea (C.L.); Department of Anatomy, University of Medicine and Dentistry of New Jersey, PO Box 55, Piscataway, New Jersey 08854, USA (W.H.R.).
† To whom correspondence should be addressed.

Neurons in the superior colliculus displaying saccade-related spike activity have movement fields, that is, each cell discharges in association with saccades having a particular range of directions and amplitudes[2,7,8]. These neurons form a map of motor (saccadic) space as they are topographically organized on the basis of their movement fields[2,7,9]. The high-frequency burst of spike activity generated by collicular neurons is tightly coupled temporally to saccade onset[10], but spatially the movement fields are large and coarsely tuned[2]. Consequently a large population of cells is active before each saccade. Here we reversibly deactivated a small subset of the active population with lidocaine. Figure 1 outlines the rationale of the experiment and illustrates the main predictions of the population-averaging hypothesis. It is assumed that the population of neurons discharging before a saccade occupies a symmetrical area[3]. For example, the hypothetical region of neurons active before a 5° rightward saccade is shown schematically by the stippled region in panel *a*. Neurons in the middle of this active population (*A*) discharge maximally before the intended saccade (a straight right saccade 5° in amplitude). Referring to the motor map, neurons located at point *B* discharge maximally before upward (20° angle) saccades 4° in amplitude and neurons at point *C* discharge maximally before downward (−20° angle) saccades 9° in amplitude. The population-averaging hypothesis suggests that for each subset of active neurons (*B*) tending to produce movements other than the programmed saccade, there will be another subset

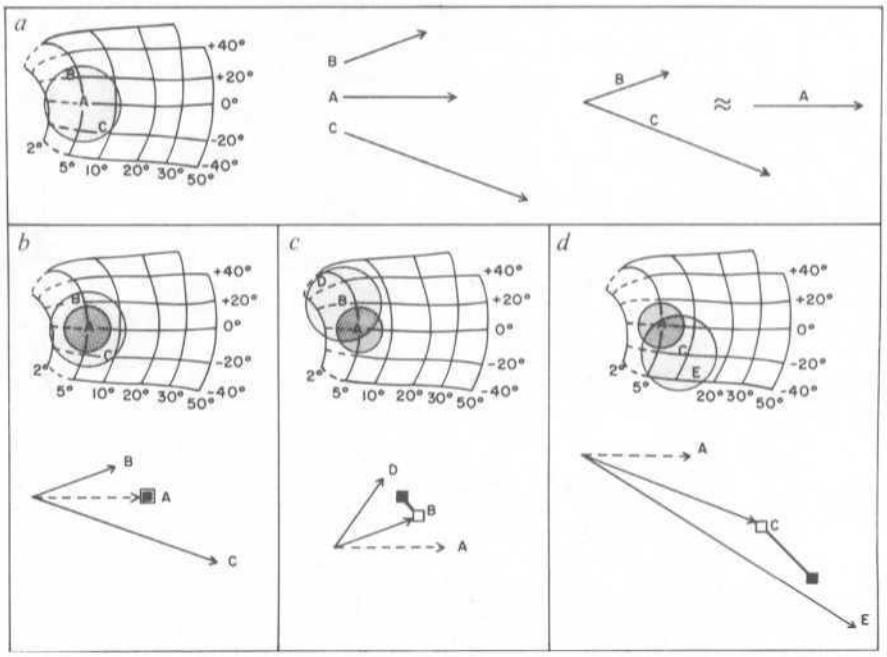


**Fig. 1** *a*, The population-averaging scheme of Sparks *et al.*[2]. Left: the motor map of the left superior colliculus based on Robinson's[9] microstimulation study. Isoamplitude lines (2° to 50°) run from the lateral edge to the medial aspect of the superior colliculus. Isodirection lines (−40° to 40°) run from the rostro-lateral edge to the caudo-medial border of the colliculus. The stippled area represents the hypothetical extent of cells active before saccades to a target located 5° to the right of the fixation stimulus. The active population is assumed to be symmetrical in shape[3]. Moreover, it is known[2] that neurons in the middle of the active population fire most vigorously and that, for other cells, the peak firing rate descreases as a function of distance from the centre of the active region. Middle: cells at locations *A*, *B* and *C* fire most vigorously for the movements shown. Right: weighted averaging of activity at points *B* and *C* yields the same movement as activity at the centre of the active population (*A*). Note that a true average of vectors **B** and **C** does not yield vector **A** because of the non-linearity of the amplitude scale in the motor map. If one assumes a homogeneous distribution of cells and a symmetrical spatial distribution of firing rates (see above), a non-linear synaptic weighting of the contribution of cells at different locations to brainstem oculomotor nuclei is required by this scheme. *b–d*, The predicted effect of deactivating a subset of cells in the active population. The site of deactivation (darkly stippled circle) remains the same in each panel, but the location of the active population (lightly stippled area) is different in each panel because saccades to three different targets are required. Beneath each map are the saccade vectors associated with neural activity at each of the locations illustrated. The open square represents the vector of the intended, or programmed, saccade associated with activity in the lightly stippled area. The dashed line represents the vector of the movement tendency produced by neurons at the deactivated site. These neurons will not contribute to the metrics of the saccade, and a saccade to the approximate location of the filled square is predicted.

**Methods.** Three monkeys (*Macaca mulatta*) were trained to look to visual targets for a liquid reward. A laboratory computer controlled the experiments and compared eye and target positions. Eye position was monitored by the scleral search-coil technique[15]. On each trial, the animal fixated a centrally located visual stimulus for a variable period. Then the fixation stimulus was extinguished and an eccentric target appeared simultaneously. Reward was contingent on the occurrence of a saccade that directed gaze toward the eccentric stimulus. An insulated silver-coated glass pipette[14] filled with 2% lidocaine hydrochloride was used for extracellular recording of unit activity, for the reversible inactivation of neural elements near the tip of the probe, and for electrical stimulation (stimulation trains 50 ms in duration at a rate of 500 Hz; each pulse was 0.2 ms; current ranged from 25–40 μA). The location of the pipette tip in the collicular motor map was determined from movement field plots and measurements of the direction and amplitude of stimulation-induced saccades. The behavioural effects of lidocaine injections were assessed by comparing saccades to a selected set of targets before and after deactivation of collicular neurons.

of equally active neurons ($C$) tending to produce a movement such that the weighted average effect of neural activity at points $B$ and $C$ will result in a saccade with the programmed direction and amplitude (panel *a*, right). According to this hypothesis, each member of the active population contributes to the ensuing saccade. Detection of the locus of the most active elements in the population is unnecessary.

Suppose that a small region of collicular neurons (the darkly stippled area in Fig. 1, panel *b*), normally discharging maximally before straight right saccades 5° in amplitude, were deactivated with lidocaine. If the animal were required to make a 5° rightward movement, according to the population-averaging hypothesis, saccadic direction and amplitude would be unaffected (panel *b*). The weighted vector average of the movement tendencies produced by the unaffected active cells (the lightly stippled area) will result in a saccade having the correct direction and amplitude. For example, the weighted average of the movements produced by neurons near points $B$ and $C$ outside the deactivated region is still a 5° rightward movement. Referring to panel *c*, with the same region of neurons deactivated, if the animal is now required to make an upward (20° angle) saccade 4° in amplitude, the active population shifts to a location centred around point $B$. The deactivated neurons (normally discharging maximally before saccades that are larger and have less of an upward component than the programmed movement) will not counterbalance the effect of other cells (location $D$) firing maximally before saccades that are smaller and have more of an upward component than the intended movement. Consequently, the animal should make a hypometric saccade that has too much of an upward component (filled square). Similarly, with the same region of neurons deactivated, if the animal attempts to make a downward (−20° angle) 9° amplitude saccade, the resulting movement should be hypermetric and have too much of a downward component (panel *d*). Thus, with neurons in a single region of the colliculus deactivated, a predictable pattern of errors should be observed for attempted saccades within the movement fields of the deactivated cells.

The predictions of the vector summation model[4] differ from those illustrated in Fig. 1. Inactivation of a subset of the active population should always produce hypometric saccades (regardless of the location of the inactivated cells within the population) because the amplitude of a saccade is determined by summing the movement contributions of each cell in the active population.

We found that the trajectory of saccades to visual targets was modified for 5–20 min after injections of 50–200 nl 2% lidocaine hydrochloride. Results typical of those obtained from three monkeys and a total of 17 injection sites in the rostral superior colliculus are shown in Fig. 2. Effects of deactivating a region of the deeper layers of the superior colliculus upon the direction and amplitude of visually guided saccades are illustrated. The plots show the position of the initial fixation (+) and the endpoint (the tip of the arrow) of the 'best saccade,' defined as the movement produced by stimulation at the injection site. Each

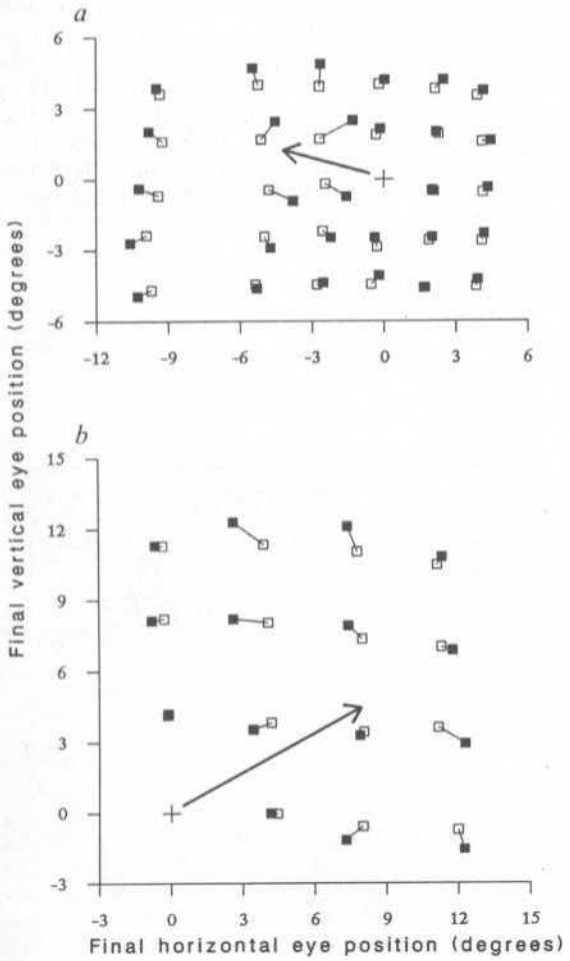


**Fig. 2** Effects of a single 200 nl injection of lidocaine on the amplitude and direction of saccades to visual targets. The axes represent the horizontal and vertical end points of visually guided saccades. The location of the fixation target is indicated by the +. Electrical stimulation of the superior colliculus drove the eyes to the location marked by the tip of the arrow. Each open square represents the average of the end points of visually guided saccadic eye movements to one target before deactivation; filled squares represent the average end points of saccades to the same targets after deactivation. Lines connecting the squares represent the average error introduced by deactivation of part of the active population. *a*, Results from an injection site where the 'best saccade' was up and leftward. *b*, Results from an injection site in the left superior colliculus with an up and rightward 'best saccade'.

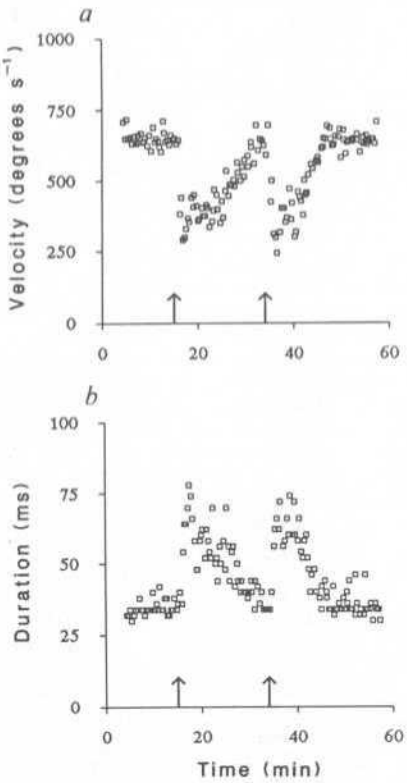


**Fig. 3** The effects of two injections (each 100 nl 2% lidocaine) on visually guided saccades similar in direction and amplitude to the 'best saccade'. (The time of the injection is indicated by the arrows.) Each plotted point represents data from a single trial. For the data plotted, the saccade target was presented at the same location (6° to the right of and 10° above fixation). The reduction in vectorial velocity of ~250° $s^{-1}$ (*a*) was compensated for by an increase in saccadic duration (*b*).

symbol represents the average endpoint of 3 to 5 visually guided saccades. Unfilled symbols represent movements occurring before the injections; filled symbols represent post-injection trials for matching targets. Referring to Fig. 2*a*, note that, as predicted by the population-averaging hypothesis, saccades to targets requiring more of an upward component than the 'best saccade' had too much of an upward component, and saccades to targets requiring movements with more of a downward component than the 'best saccade' had too much of a downward component. Also as predicted, movements to targets requiring a saccade smaller in amplitude than the 'best saccade' were hypometric; saccades to targets requiring a movement larger than the 'best saccade' were hypermetric. For the injection site represented in Fig. 2*a*, saccades to targets in the opposite half of the visual field were unaffected. The range of movements affected varied with the volume of the lidocaine injection.

For most injection sites, the direction and amplitude of movements similar to the 'best saccade' were not altered noticeably after the injection. Note that in Fig. 2*b*, saccades to targets requiring movements with a direction and amplitude similar to the 'best saccade' were quite accurate. But the velocity of movements similar to the 'best saccade' was dramatically reduced (Fig. 3*a*), although, unlike earlier reports[11,12], we found these reductions were accompanied by increases in duration (Fig. 3*b*), such that saccadic amplitude remained relatively constant.

The prediction of vector-summation models[4] that inactivation of any subset of the active population invariably produces hypometric saccades was not confirmed. Instead, the pattern of errors in the amplitude (hypometria or hypermetria) and direction of visually guided saccades after deactivation of a localized region of collicular neurons was that predicted by the population-averaging hypothesis. In agreement with the suggestion that the amount of activity of the active population is a determinant of saccadic velocity (ref. 13; D. P. Munoz and D. Guitton, personal communication; W.H.R., J. White and D.L.S., unpublished observations), inactivation of a subset of the active population produced reductions in saccadic velocity.

The population-averaging hypothesis holds that computation of the metrics of saccadic eye movements is based on a weighted average of the saccade-related discharges of the entire active population. According to the hypothesis, small changes in the direction and/or amplitude of saccadic movements are produced by slight shifts in the locus of the active population in the superior colliculus. The effects of variability or 'noise' in the discharge frequency of a particular neuron are minimized as the contribution of each neuron to the direction and amplitude of the movement is relatively small. In this manner, broadly tuned movement fields (resulting in a large population of neurons being active during a specific movement) may contribute to, rather than detract from saccadic accuracy.

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