Are gaze shifts controlled by a 'moving hill' of activity in the superior colliculus?

In his recent *TINS* article, Guitton[1] proposes that during the course of a saccadic gaze shift a neural image of gaze motor error moves across the superior colliculus (SC) of the head-free cat. Gaze motor error is a term used to describe the difference between the current direction of gaze and the desired direction of gaze. Guitton and colleagues claim[1–3] that during a large gaze shift (e.g. 50°), a population of neurons in the caudal colliculus with activity related to movements of the eyes and head and coding a 50° motor error will discharge first. As the eyes and/or head move (reducing gaze motor error), the site of neural activity migrates rostrally in the SC until, finally, neurons at the rostral pole of the colliculus encoding a motor error of zero become active. If the distribution of activity within the SC is represented as a relief map, the nested contours of increasing activity can be thought of as a 'hill', which, according to Guitton's hypothesis, migrates rostrally during the course of the gaze shift. According to this hypothesis, gaze motor error is mapped dynamically by the location of active cells within the motor map found in the deeper layers of the SC. This is a novel view of the role of collicular neurons in the control of orienting movements. If true, it has important implications for experiments concerned with the question of how collicular signals are transformed into those required by motoneurons innervating extraocular and neck muscles.

General issues

Before examining the observations offered in support of the hypothesis, it is useful to point out several issues that the evidence must address. First, it is necessary to establish that the locus of neural activity moves continuously across the colliculus in association with a single movement, not in sequential steps that are correlated with separate components (eye and head) of the gaze shift. Second, the 'moving hill' is viewed as a command signal that initiates and dynamically controls the timecourse of the change in gaze. Thus, collicular activity must be sufficiently advanced in time with respect to the onset of movement to allow for intervening neural processes that mediate the gaze shift. Third, extraneous causes of activity, such as sensory responses of the cell, must be excluded. Fourth, the movement fields of the cells must have properties consistent with the model. Finally, if the 'moving hill' is to be the only mechanism for controlling gaze shifts, changes in gaze should not occur in the absence of activity in the collicular output neurons.

Evaluation of the evidence

The experimental observations on which the 'moving hill' hypothesis is based[2,3] do not exclude the possibility that activity in the SC steps discontinuously from caudal to rostral as the head and eye components of the gaze shift are executed. Munoz, Guitton and Pélisson[2] recorded the activity of tectoreticular and tectoreticulospinal neurons [TR(S)Ns] in cats trained to generate orienting movements with either the head free or immobilized. They report, for example, that a cell that discharges maximally before a 12–13° eye movement when the head is fixed also discharges during head-free gaze shifts of 40–50°. This is presented as evidence for the 'moving hill' hypothesis – evidence that rostral cells discharge during large gaze shifts. This interpretation of the data must be evaluated in the context of the characteristics of gaze shifts in cats. Cats have a limited range of eye movements and the contribution of the eye component to large gaze shifts is similar over a large range of orienting movements[4]. Gaze shifts ranging from 15–60° usually include an eye movement of 12–15° (see Fig. 5 of Ref. 4). Thus, it is not surprising that cells discharging before 12° saccades also discharge during gaze shifts of up to 60°. All large gaze shifts include an eye movement of about 12–15°. Almost all of the cells used to argue for a rostral migration of activity[2] discharged maximally for movements of 13° amplitude or greater, movements near the oculomotor limit of the cat. These are cells that would be expected to discharge for all gaze shifts larger than 15° in amplitude. Even if cells in the rostral SC that are active before very small eye movements were observed to also discharge during large gaze shifts, this observation would not necessarily support the 'moving hill' hypothesis. Relatively smooth gaze shifts often contain multiple eye movements[5], and small (less than 5°) eye saccades often occur near the end of a large gaze shift. The activity observed in the rostral colliculus during large gaze shifts could occur because many large gaze shifts are generated, in part, by sequential commands for eye saccades.

The timing of the activity of neurons used as evidence for the 'moving hill' hypothesis is not that required by the model. Consider, for example, the activity of a TR(S)N cell that discharged maximally before a 15° gaze shift (Fig. 7 in Ref. 2). The authors argue that the peak of spike activity of this cell occurs near the onset of small gaze shifts but, as the amplitude of the gaze shift increases, the peak of activity is increasingly delayed with respect to movement onset. This is presented as evidence for the 'moving hill' hypothesis. Note, however, that 'the peak discharge occurred synchronously with and shortly after' the start of the optimal (15°) gaze shift. Thus, the peak discharge of this cell cannot be driving dynamic motor error because, even for optimal movements, the peak of activity begins after the motoneurons have sent their command to the extraocular muscles. To argue that activity occurring before the measured peak of activity is responsible for the activity of motoneurons would be logically inconsistent. The measures of activity used to build a case for a 'moving hill' must be ones that are believed to be critical at the level of premotor and motoneurons.

It has not been established that the neural activity presumed to represent dynamic motor error did not reflect sensory responses

of the neurons. TR(S)N cells, whose discharges purportedly encode motor error, are known to carry three types of signals: sensory responses modulated by the influences of attention, fixation and orientation; sustained discharges, related to either attentive fixation and/or the preparation of an orienting gaze shift to a target of interest; and activity related to the metrics of eye and/or head movements[2]. It follows that activity of TR(S)Ns observed during a gaze shift can be related to sensory stimulation (98% of these cells are responsive to visual stimuli[6]), preparation of an impending orienting movement or to movement metrics. In order to show that the activity occurring during a gaze shift is due to a 'moving hill' of neural activity related to dynamic motor error, controls must indicate that the observed activity is not sensory in origin or related to an impending movement. These controls were not performed by Munoz and colleagues. They analysed visually responsive cells, but tested them under conditions that do not permit a distinction between visual and motor responses. In their experiments 'the entire room was dimly lit, so that both edges of the barrier and the laboratory surroundings were visible[4]'. They did use trials in which the animal 'predicted' the future location of a food object to eliminate the food object as a visual stimulus. However, the edge of the barrier, a visual stimulus that had particular significance for the subjects being tested, was still visible. Thus, the late responses during large gaze shifts could be visual responses evoked by the image of the edge of the barrier entering or reaching more sensitive regions of the receptive field of the cell. This would explain why response latency depends upon the amplitude of the gaze shift. For large gaze shifts, a longer interval occurs before visual stimuli activate the cell. The fact that some TR(S)N cells discharge during gaze shifts in total darkness[3] does not rule out the possibility that visual responses account for the apparent migration of activity across the colliculus during gaze shifts to visible targets.

The 'moving hill' hypothesis assumes that the zone of neural activity always moves continuously toward the rostral pole of the SC. Accordingly, the movement fields of cells in the rostral colliculus should be bounded only at their central edges. Otherwise they would not discharge during all large gaze shifts. This is not a characteristic of movement fields of cells in the rostral SC in the monkey. The critical data are missing in the cat.

Finally, Munoz and Guitton[7] reported that TR(S)Ns 'were never observed to discharge, either tonically or phasically, during spontaneous gaze shifts made in the light or dark. Thus, cats can make saccadic gaze shifts even when their [TR(S)Ns] pathway is silent'. In a later paper[2], some TR(S)Ns were observed to be 'phasically active, albeit weakly, for some spontaneous movements made in the dark'. Generally, the SC is assumed to play a major role in the generation of spontaneous saccades because most frontal eye-field neurons are silent during spontaneous movements[8,9] and lesions of the SC produce a dramatic reduction in the number of spontaneous saccades[10]. If these findings in monkeys generalize to cats, the observation that TR(S)Ns are almost totally silent during spontaneous gaze shifts indicates that the spontaneous movements mediated by the SC occur in the absence of a 'moving hill' of TR(S)N activity. If so, there must be another collicular mechanism for producing saccades.

Concluding remarks

To summarize: the evidence offered in support of the 'moving hill' hypothesis is as consistent with a sequential pattern of activity as it is with a continuous migration of activity across the colliculus; the activity described occurs too late to provide the motor error signal to premotor circuits involved in the generation of eye and head movements; the evidence does not rule out visual responses as the cause of the apparent migration of activity; movement fields of cells in the rostral colliculus of primates are not unbounded peripherally, as is required by the model, and the essential observations have not been made for the cat; and spontaneous gaze shifts, presumably mediated by the SC, can occur in the virtual absence of activity in TR(S)N cells.

In conclusion, evidence offered in support of the 'moving hill' model is either inconsistent with this model or subject to plausible alternative explanations.

David L. Sparks
Dept of Psychology, University of Pennsylvania, 3815 Walnut St, Philadelphia, PA 19104, USA.

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