and why do cortical circuits contribute uniquely to adaptation? Is this a property of all cortical circuits? Is this form of adaptation a neural correlate of episodic memory? In addressing these questions, we are also provided with a new box of tools, including stimulation and response procedures imported from behavioral neuroscience.

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Going for the goal

Richard J. Krauzlis and Christopher D. Carello

A new study shows that activity in the superior colliculus encodes the distance to the goal of the orienting movement, not the particular saccade or saccades used to get there.

Long before air travelers experienced the indignity of being nearly strip-searched at the security checkpoint, they faced the routine inconvenience of extended layovers on the outskirts of unsolicited cities. Bravely, boarding passes in hand, air travelers have persevered through these idle hours by remaining focused on their final destination. Similarly, a new study in this issue shows that during the programming of orienting movements, a population of neurons monitors the progress toward the final goal of the movement, rather than the individual steps taken to get there.

The target of the study is the superior colliculus, which has long been known to be involved in the control of saccadic eye movements[1]. Stimulation at single sites in the colliculus produces saccades with a specific direction and amplitude. Adjacent sites in the colliculus produce saccades with slightly different directions and amplitudes, and together form a topographic map of possible saccade endpoints. Single-unit recordings in the colliculus have shown that saccade-related neurons are most active before and during saccades of a particular direction and amplitude, consistent with their placement within the topography of the motor map. These observations form the basis for the commonly accepted idea that activity at a given site in the superior colliculus promotes a particular saccade.

Bergeron and colleagues present data that challenge this idea[2]. Recording in

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the superior colliculus of cats, they evoked gaze saccades (saccades accomplished with a combination of eye and head movements) by presenting a small food target at one or the other end of an opaque barrier placed in front of the cat (**Fig. 1a**). Taking advantage of the natural recalcitrance of cats, the authors evoked gaze shifts that consisted of several small saccades of variable amplitude that were triggered in rapid succession, rather than a single large saccade that might have brought gaze to the target in one swoop. These multi-step gaze shifts made it possible to draw a distinction between the amplitudes of the individual saccades and the remaining distance to the goal, which the authors quantified as gaze position error (the difference between the current gaze position and the final target position).

Surprisingly, neuronal activity in the superior colliculus was highest, not at the sites matching the amplitudes of the individual saccades, but at the sites matching the amplitude of the current gaze position error (**Fig. 1c**). As the multi-step gaze shift proceeded, activity moved across the motor map of the colliculus as though monitoring the progress toward the ultimate goal of the movement. For the last saccade in the multi-step sequence, the saccade amplitude equaled the gaze position error, and thus when taken out of context, it is ambiguous in this case whether the active site in the colliculus represents the saccade amplitude or the goal of the movement. This last saccade suggests why this dissociation has not been observed in monkeys, who by either nature or training, tend to be more thrifty

in their movements and accomplish their gaze shifts in a single step.

These findings argue that the superior colliculus does not compose a map of saccade endpoints. Several previous studies have made related observations. For single-step saccades, there are natural circumstances that cause small but significant differences between the initial distance to the goal and the amplitude of the saccade that is made; in these cases, the active site in the colliculus matches the initial goal rather than the saccade amplitude[3,4]. It is also possible to artificially create multi-step saccades out of single-step saccades by electrically stimulating in brainstem regions that inhibit saccades. This stimulation truncates saccades in mid-flight, and at the end of stimulation, the gaze shift resumes with a second saccade that completes the movement to the target. During such interrupted saccades, the same saccade-related neurons that burst for the first saccade also burst for the second saccade, even though the second saccade would appear to be too short for that site in the motor map[5,6].

The multi-step gaze shifts studied by Bergeron and colleagues also demonstrate that the locus of activity does not specify the details of how the movement will be accomplished. Likewise, in studies of single-step saccades involving movements of both the eye and head, activity in the colliculus appears to represent the amplitude of the overall gaze shift, but not how the saccade will be apportioned into eye and head movement components[7,8]. For sites in the motor map representing small position errors, the goal can be acquired by very small saccades, but also by smooth pursuit eye movements or even by maintained fixation. Activity at these sites represents the distance to the target, regardless of which motor subsystem is used[9,10]. The interpretation of these results is far from settled, but the data suggest that the relationship between activity in the colliculus and the final motor commands is probabilistic, rather than one-to-one. This uncertainty may derive from
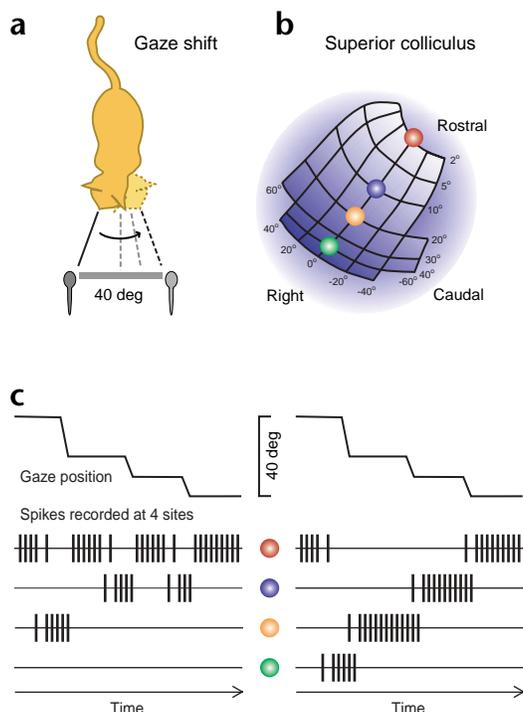
Fig. 1 . Experimental design and predictions. (**a**) Multi-step gaze shifts were elicited by presenting rewards at either side of an adjustable barrier. (**b**) Activity was sampled at a variety of sites across the motor map within the superior colliculus (SC). (**c**) During the multi-step gaze shift, the expected pattern of activity across the SC depends on whether each site represents the remaining distance to the goal (right) or a command for a particular saccade (left).

inspired but more achievable goal of fetching a cup of coffee, both of which seem to be under the purview of executive structures like the frontal cortex and the basal ganglia. Anatomy indicates that the colliculus may be informed of these goals, but its concerns appear to be more immediate. Then there are the nuts and bolts goals of accomplishing each movement with precision and grace, but as the current results point out, the activity in the colliculus appears to lie upstream of these important motor details, which are likely handled by the cerebellar cortex and associated nuclei. This suggests that motor control may involve a fairly elaborate hierarchy of goals, much like the extended hierarchy of feature extraction associated with sensory processing. At each stage of this motor hierarchy, the relevant details of the goal may be unpacked and delegated to lower levels, while feedback is provided back to the upper levels. It is interesting that within this motor corporation of goal setters and achievers, the superior colliculus has evidently secured a mid-level management position—it may not be part of the executive suite but it is not exactly blue collar either.

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the autonomy afforded the output pathways in the brainstem and cerebellum, which are probably in a better position to ensure that the final motor commands are properly tailored to the current sensorimotor context.

During the multi-step gaze shifts reported by Bergeron and colleagues[2], activity sweeps across the motor map. What is the function of this 'moving hill' of activity? According to the original hypothesis, elevated activity at an appropriate site in the motor map initiates the saccade; the sweep of activity across the colliculus actively controls the trajectory of the saccade, until at last the 'hill' reaches a so-called fixation zone at one end of the motor map, at which point the saccade is terminated[11,12]. In contrast, during the gaze shifts reported by Bergeron and colleagues, only the last saccade of the multi-step shifts ends with activity at the rostral colliculus. Thus, activation of the

rostral pole is not required to stop saccades. This finding complements other recent studies suggesting that the 'moving hill' cannot account for the trajectory of saccades[13,14]. Although there is still a consensus that elevated activity can initiate a saccade, the movement of activity across the colliculus does not appear to be responsible for actively steering the saccade, but instead represents a real-time estimate of the distance to the goal. We speculate that this information about the goal is an important resource, not just to the downstream structures charged with controlling the motor commands, but also to the upstream areas in the cerebral cortex that require updates about the status of ongoing movements.

One of the striking aspects of the work by Bergeron and colleagues is that it forces us to reconsider what a 'goal' means. There are broad goals such as the New Year's resolution to exercise more often, or the less