Editorial Focus

New Functions for an Old Structure: Superior Colliculus and Head-only Movements. Focus on “The role of primate superior colliculus in the control of head movements”

The superior colliculus (SC) is a multilayered structure in the mammalian midbrain. Even though the behavioral function of the SC has been studied for well over 30 years, it continues to be a source of surprising new findings. Traditionally it has been assumed that the primate SC selects and generates saccadic eye movements. However, more recent experiments in head-free monkeys suggested instead that the activity of SC neurons represent a command for a gaze shift (Freedman and Sparks 1997). Despite some evidence for this gaze hypothesis, it is still unclear what signal exactly is represented by SC neurons. One possibility is that the SC neurons form one unified map of gaze shift commands, which are divided into separate eye and head commands downstream of the SC. The other possibility is that the SC contains two populations of parallel active neurons that represent separate eye and head shift commands. One reason, why this question is surprisingly difficult to answer, is the synergy of eye and head movements during natural gaze shifts, which makes it difficult to separate the relationship of the different motor components to neural activity (Sparks 1999).

A new study of Walton and colleagues (Walton et al. 2007) appearing in this issue (p. ) addresses this problem heads-on. The authors of this study have trained monkeys in an elegant new task that requires the animal to perform head movements with and without gaze shifts. This allowed them to record SC neurons during head-only movements and during comparable gaze-shifts. In this way, they could separate the influence of head movements from gaze shifts and could study the influence of these two types of movements on neural activity. The authors report two major findings. First, they describe a new class of SC neurons that has not been described before. These ‘head-only’ neurons are active during head movement, even if these movements do not lead to any gaze shift. Second, the classically reported SC neurons that are active during gaze shifts involving a combination of eye and head movements are inactive during head movements that do not lead to gaze shifts.

The authors themselves are very careful in pointing out that we need to learn much more about the newly discovered head-only neurons, before we can be sure about their function, but we might sketch a few likely conclusions from this study. It seems clear that the superior colliculus is part of a pathway leading to the control of head movements. Anatomical studies have shown direct projections from the superior colliculus to centers in the brainstem and spinal cord that control neck muscles (Cowie et al. 1994; May and Porter 1992). Weak electrical stimulation of the superior colliculus evokes neck muscle activity and head movements without gaze shifts (Corneil et al. 2002, 2002). Taken by itself, the discovery of the head-only cells seems to argue against the notion that the SC represents a unified gaze shift command. However, this conclusion is directly contradicted by the second major finding of this study. Neurons associated with gaze shifts are not active during head-only movements. This indicates that these neurons represent specifically gaze shifts, but not the component movements. Thus, the study by
Walton and colleagues provides strong support for the unified gaze shift hypothesis, but how do the head-only movement cells fit into this picture?

It is possible that the head-only movement neurons represent a separate movement control system that can act independent of the gaze shifting system. Primates can and often do move their head without any gaze shifts, as anybody can attest to that has ever nodded in agreement while watching the expression of a conversation partner. It is already known that the SC of primates contains other non-gaze related motor neurons. In particular, arm movement related activity is clearly dissociable from saccades (Stuphorn et al. 2000; Werner et al. 1997; Werner et al. 1997). The activity of reach-related neurons is most strongly correlated with the activity of shoulder muscles and to a lesser degree with axial and more proximal muscles (Stuphorn et al. 1999). More recent findings in monkeys even suggest a role of superior colliculus in grasping and thus of hand conformation (Nagy et al. 2006). Primates are characterized by their high dependency on vision and on their highly flexible hand. Thus, it should not be too surprising to find that the primate SC controls the orientation of the head and arm, as well as gaze.

An additional function of the superior colliculus might be the coordination between different motor systems. Most orientation movements involve more than one effector system. For example, gaze shifts require the coordination of eye and head motor signals across two very different motor systems. The representations of intended eye and head movements require very different intrinsic reference frames. One important next step will be the simultaneous recording of the newly discovered head-only neurons and of neck muscle activity to get a fuller picture of the relationship between signals in the colliculus and kinematic and dynamic movement variables. In sum, the work of Walton and colleagues has opened up an exiting new avenue for studying the role of the superior colliculus in behavior.

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