So Much to See, So Little Time: How the Superior Colliculus (SC) Suppresses Unwanted Saccades. Focus on “Inputs to Inhibitory Burst Neurons From the Rostral and Caudal Superior Colliculus”

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The brain of frontal eyed animals is confronted with a plethora of visual stimuli and must make a decision to turn both eyes to view but one stimulus. Once this decision is made it must be translated into a motor command to move the eyes. The superior colliculus (SC) is one site in the brain stem where the transition from sensation to movement is carried out. The primate and feline SC are arranged topographically such that neurons at the rostral pole are activated by small-amplitude saccades, whereas neurons located in the caudal SC discharge before large saccades. Although the immediate premotor structures that control the eyes in the pons and medulla are known to receive projections from the SC (Harting 1977; Huerta and Harting 1984), understanding their physiological control by supranuclear structures has been plagued by a number of baffling observations. Pioneering experiments by Precht et al. (1974) carried out in anesthetized cats demonstrated that the abducens nucleus, where motor neurons that drive the eye outward are located, received primarily polysynaptic excitation from the contralateral SC. On the other hand, the experiments of Grantyn and Grantyn (1976) demonstrated disynaptic activation of abducens motoneurons via a single premotor neuron. Results from alert, behaving monkeys favored the concept of polysynaptic activation from the contralateral SC (Raybourn and Keller 1977) and showed no direct projections from the SC onto the pontine medium lead burst neurons that provide the direct excitatory drive to the abducens motoneurons (Keller et al. 2000; Strassman et al. 1986). At the same time, Raybourn and Keller (1977) demonstrated that the omnipause neurons, which must be inhibited in order for a saccade to occur, actually received rapid, direct, monosynaptic excitation after SC stimulation. Inhibition arrived later via indirect polysynaptic connections. These observations have raised a number of questions about how saccades are generated. How do supranuclear regions such as the SC excite the abducens motoneurons on one side while simultaneously suppressing their counterparts on the other? Are descending connections to the abducens di- or polysynaptic? How can the SC provide excitation to the omnipause neurons while at the same time participating in saccade generation?

The answers to these questions are elegantly and succinctly addressed in a paper appearing in this issue (p. 697–712) by Sugiuichi et al. (2005). In an earlier paper, the current authors (Izawa et al. 1999) were unable to decide if the inhibitory activity in abducens nucleus arose from the SC proper (via commissural connections to the opposite SC), from inhibitory relay neurons in the midbrain or pons that then projected to the paramedian pontine reticular formation (PPRF), or indirectly via contralateral inhibitory burst neurons (IBNs) in the paramedian ponto-medullary reticular formation (PPMRF). Recent evidence that the SC has a “fixation zone” of neurons located at the rostral pole that pause for every saccade and display a tonic level of activity when the eye position is stable has added an additional wrinkle (Munoz and Wurtz 1995). A similar fixation zone has been documented in the FEF (Bizzi 1968; Bruce and Goldberg 1985; Suzuki and Azuma 1977). To sort out the question of supranuclear activation of the immediate premotor neurons, a fresh approach was needed.

The major hypothesis championed by the new data are that projections from the rostral and caudal portions of the SC are differentially routed via inhibitory interneurons located in the omnipause region of the pons and the burst regions of the PPMRF, respectively. The authors performed intracellular recordings from the inhibitory burst neurons in the PPMRF of the anesthetized cat while selectively stimulating the rostral and caudal portions of the SC using an electrode array. Two major inhibitory, tectofugal pathways are clearly demonstrated. Activation of the rostral SC on either side generated disynaptic inhibitory postsynaptic potentials (IPSPs) in the IBNs mediated by the omnipause neurons in the raphe interpositus. In contrast, caudal SC stimulation produced disynaptic IPSPs in the ipsilateral IBNs that could be abolished by midline sectioning at the level of the IBNs. Evidence that activation of the caudal SC produced monosynaptic excitatory postsynaptic potentials (EPSPs) in the contralateral IBNs (which have extensive reciprocal connections with the ipsilateral IBNs) provides the physiological underpinning for suppression of ipsilateral (unwanted) saccades at both the motor and premotor levels. These results also suggest that saccade triggering is the result of a balance between the inhibition of contralateral IBNs from the rostral SC mediated by omnipause neurons and the excitation of the same IBNs from the more caudal SC. Such a mechanism might also account for the conflicting results obtained from anesthetized and awake experiments in cats and primates (Grantyn and Grantyn 1976; Keller et al. 2000; Raybourn and Keller 1977). Finally, the current paper provides evidence for stronger projections to the IBNs from the caudal than the rostral portions of the SC. This finding may provide the missing link for the neural mechanism via which IBNs carry eye-velocity-coded signals (Cullen and Guitton 1997). In sum, these experiments open new avenues to a better understanding of how the brain stem synthesizes a selective motor control signal from the variety of possibilities presented by the visual system.
REFERENCES


