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The climbing fibre and mossy fibre systems supply afferent information to the cerebellum. To understand how these systems contribute to the control of movement, we must analyze the nature of the information that they transmit. The inferior olivary nucleus is a particularly attractive structure for such an analysis since it is the sole source of climbing fibres. Climbing fibres share many distinctive physiological properties and project to every part of the cerebellum. It seems likely that the functional significance of climbing fibre input will be similar for all parts of the cerebellum and of basic importance to cerebellar action.

Speculation on the function of the inferior olive stems largely from general models of the cerebellum rather than from consideration of olivary properties. The most widely held view is that the olive provides an error signal that is used to modify cerebellar output in order to correct motor performance. In this article we will argue that the inferior olive comprises a relatively limited somatosensory system that supplies information about disturbances to the body resulting from external events. The information does not depend upon active movement. In fact, somatosensory stimulation resulting from self-produced movements is ineffectual for activating olivary neurons. Such properties do not seem appropriate for providing error information about movements, and we will suggest an olivary function more consistent with its peculiar characteristics. The data that lead us to our conclusions are from results obtained with many coworkers including Farrel Robinson, Craig Weiss, John Alam and James Houk.

Our arguments rest on five main points: 1. The inferior olive is overwhelmingly concerned with transmitting somatosensory information. 2. An olivary neuron reports the occurrence of a particular somatosensory event rather than quantitative information about stimulus parameters. 3. The olive does not report information about self-produced movements. 4. Sensory information from the olive maintains a somatotopic alignment with the motor organization of the cerebellum. 5. Stimulation or natural activation of the olive has no direct motor consequences. Each of these properties has important implications for olivary function.

Somatosensory Responsiveness

Recordings of complex spikes from cerebellar cortex have repeatedly demonstrated that climbing fibres, and therefore olivary neurons, are acti-
vated by somatosensory stimuli (Thach, 1967; Oscarsson, 1968, 1969; Eccles et al., 1972), and direct recording studies of the inferior olive emphasize the overwhelming importance of somatosensory stimuli in activating olivary neurons (Gellman et al., 1983, 1985). Every major subdivision of the olive contains a majority of neurons which are responsive to cutaneous and proprioceptive stimuli.

Cells in rostral dorsal accessory olive (rDAO) demonstrate exquisite sensitivity to cutaneous stimuli even in the anaesthetized preparation (Gellman et al., 1983). Receptive field mapping in rDAO reveals well defined receptive fields which may represent areas as small as the pad on one toe. The organization of the receptive fields form a complete map of the entire contralateral body surface with a progression from face to forelimb to hindlimb moving medially to laterally in the nucleus. The somatotopy is well illustrated by a horizontal reconstruction of rDAO shown in Figure 1. Except for a slight increase in responsiveness to somatosensory stimuli (100% versus 96%) there is no change in the organization or sensory requirements of rDAO units when recording from an awake rather than an anaesthetized cat (Gellman et al., 1985). In either case, the rDAO unit signals the cerebellum that a particular part of the body has been touched.

Fig. 1. Somatotopic organization of DAO illustrated in a horizontal reconstruction. Each symbol represents the body location of receptive fields recorded on penetrations through that particular point. The inset provides a summary of the somatotopy. Approximately the rostral one half of the figure constitutes rDAO. (Gellman et al., 1983)