

Roles of Proprioceptive Input in the Programming of Arm Trajectories

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It has been known for more than 100 years that loss or impairment of sensation in our limbs may produce severe disorders of movement and that sensory input plays a critical role in controlling movement. Indeed, the skin, muscles, and joints of our limbs are richly innervated by a variety of sensory receptors that convey proprioceptive information to all levels of the nervous system. What role this input plays in movement control has been a question of recurring interest but remains incompletely understood. In 1895, Mott and Sherrington demonstrated that surgical deafferentation of a monkey's limb produces severe disorders of movement and an unwillingness to use the limb in purposeful action. They therefore concluded that movement initiation requires the support of afferent information and proposed that coordinated movement results from the concatenation of reflex responses. Subsequently, however, it was established that deafferentation does not abolish the capacity to make purposeful movements and that motor performance may be substantially preserved when deafferentation is bilateral or when specific training procedures are used (Munk 1909; Knapp et al. 1963; Taub and Berman 1963; Polit and Bizzi 1979). This indicated that sensory input from the limbs is required neither to initiate movement nor to perform complex motor acts, as originally believed by Sherrington. Rather, the central nervous system makes use of motor programs to direct movements (Keele 1968). Nevertheless, the movements of deafferented monkeys have been repeatedly described as clumsy, inaccurate, and poorly coordinated (Munk 1909; Bosson 1974). Thus, although not necessary for the production of movement, sensory information, particularly from muscle receptors, clearly plays an important role in its control.

To examine the role of proprioceptive input in the control of limb movement, several investigators (Forget and Lamarre 1982, 1983, 1987; Rothwell et al. 1982; Sanes et al. 1985) have examined control of single-joint arm movements in patients with large-fiber sensory neuropathies. In this rare condition, there is degeneration of large afferent fibers, notably those conveying proprioceptive information, with little or no effect on motor fibers. These investigations have shown that such patients have major deficits in the feedback control of movement, i.e., in the ability to correct errors based on information from the moving limb. Thus, patients are neither able to maintain the limb in a

fixed position nor to maintain their force at a constant level without visually monitoring the position of the limb or the force applied. They also cannot compensate for unexpected changes in loads encountered during the course of limb movements (Rothwell et al. 1982; Sanes et al. 1985). Errors are reduced, however, when patients are able to watch the limb during movement, so that visual feedback is apparently able to compensate, at least in part, for the loss of proprioceptive information. Lack of cutaneous feedback also readily explains the loss of dexterity in fine movements, such as buttoning clothes or grasping small objects, in which tactile cues are used to guide movement.

In contrast, the mechanisms involved in programming the trajectories of movements before they begin, a process referred to as feedforward control, have appeared largely normal in the deafferented patients of these studies. However, several considerations suggest that, in addition to deficits in feedback control, impairments of feedforward control might also contribute to the motor impairments that occur in these patients. First, Rothwell and colleagues (1982) reported that the learning of new and complex tasks, such as driving an unfamiliar automobile, was impaired in their deafferented patient. Second, the increased variability and lack of precision in the patterning of muscle contraction in isotonic (Forget and Lamarre 1983, 1987) and isometric tasks (Gordon et al. 1987) suggests an impairment in feedforward control. Third, the apparent absence of deficits in programming trajectories could have resulted from the relative simplicity of the processing required to specify the direction and extent of single-joint as opposed to multijoint movements (Flash 1987; Soechting 1989). The accurate performance of multijoint movements requires the nervous system to transform the spatial coordinates of the target, represented in extrinsic or retinotopic coordinates, into a complex set of commands specified in terms of an intrinsic coordinate system based on the controlled biomechanical variables of the limb (Atkeson 1989; Soechting 1989). In the case of even simple pointing and reaching movements, in which two or more limb segments must be rotated by multiple muscle groups acting in different ways, the task is biomechanically quite complicated. Therefore, it is reasonable to assume that specification of movement parameters requires precise information about the state of the limb prior to movement (Polit and Bizzi 1979; Hasan and Stuart 1988).

