

control concepts have evolved. At our current primitive state of understanding this system, we do not yet know the best tools to use in its study, nor can we even be sure we have adequate ones. We had best, therefore, carefully formulate our questions and use such theoretical tools as we have with great caution and greater precision.

Do force-measuring sense organs contribute to the reflex control of motor output in insects?

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Stein suggests that some direct measurement of force may be an essential component of reflex motor control in the vertebrates. In the insect there is evidence that force-detecting elements do not contribute to reflex control in resting animals, although they may change motor output during certain active movements (Pearson 1972). A muscle system in the stick insect that has been examined in some detail is that which controls the protraction and retraction of the leg (Graham & Wendler 1981).

In a resting animal, if the leg is moved forward and backward relative to the body a typical resistance reflex is observed. Individual axons can be identified, and faster neurons are recruited as a function of the velocity of movement. The sensory contribution to this reflex can be examined by cutting away parts of the neuromuscular system. The reflex is unchanged after the cutting away of all of the leg except for the lower articulation connecting the base of the leg to the body and of all nerves but one sensory branch as well as the severing of the muscle tendons.

These results indicate that the primary input to the system is from a group of sense organs clustered around the lower joint. Cutting the tendons removes stress from the system and shows that force-detecting elements that might exist in parallel with the muscles, the tendons, or the lower leg joint produce no significant contribution to the reflex. Thus the premotor control system appears to use only position or velocity feedback when the animal is not spontaneously active. During active movements the reflex properties are significantly altered, and the properties of the active system are being explored. Under these conditions, force-detecting elements may contribute to the sensory input.

One might argue that insect movements are relatively crude compared to those of vertebrates, but this is not justified. Activities such as transfer of a spermatophore (in any orientation of the partners with respect to gravity), movements of the head and body during feeding, and walking behavior itself all show a manipulative ability and differential control of muscles that are comparable in complexity with "threading a needle." Insects have precise muscular-control capability with the advantage that the feedback system can sometimes be separated readily into its component parts.

Multiple roles of muscular afferents

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Stein has brought up such a large number of questions that it is necessary to make a choice in deciding what to comment upon. I shall restrict myself to some points of view concerning afferent feedback. The need for such feedback was well established by the end of the last century in experiments on deafferentation

(see, e.g., Mott & Sherrington 1895, on monkeys). The point I want to raise is that muscle spindles acting alone or in combination with skin and joint organs are not there merely to produce what is vaguely called servo assistance but also to feed back to the CNS (control nervous system) information that is of great importance for complicated motor acts.

Consider error detection, for instance. To begin with, an "error" has no existence in midair, as a thing in itself. An error detector can act sensibly only if it is related to the purpose of the movement in which it operates. The purpose will be consciously defined in voluntary movement but can also be enclosed within a programmed act that was at one time elaborated in response to a need but has later become automatized. Clearly the concept of *error* is tied to the concept of a *goal*. More often than not, the nervous structure incorporating the goal will be cortical.

In the first instance this general conclusion, translated into specific terms, means that there are as many roles for sensory feedback as there are goals for the motor marionette to achieve. Second, the sensitivity of the sense organs subserving error detection will ultimately be subordinated to the sensitivity to errors of the cortical structure representing the goal. If this structure is highly error-sensitive, then a slight change of spike frequency in the message suffices for a corrective cortical response. In this case the significance of the absolute firing rate of the acting sensory ending may be virtually nil. Its threshold, however, can never be neglected. With muscle spindles the gamma fibres will determine the sensory threshold, provided that alpha-gamma linkage has brought about the necessary amount of coactivation of both motor systems.

I have the impression that many writers think of coactivation merely in terms of motor effects through the spinal part of the gamma loop. Let me therefore refer to the early work by Kaada and myself (Granit & Kaada 1952), which showed that stimulating any site in the brain connected with motor activity also produced effects on the muscle spindles. At times these effects were large, even when the contractile state of the muscle in which the spindles were located was not changed. I thought that "unless stimulation in any one system is highly synchronized, it is likely to be rather ineffective without support from some other system" (Granit 1955). At the time it was commonly believed that spindles had no cortical representation and so it was impossible or, rather, unprofitable to discuss corticalized control in the way in which I have done now.

Even the gamma loop need not be restricted to just one motor function. In the experiments of Corda, Eklund, and v. Euler (1965), the role of spindles in the respiratory muscles of the chest in load compensation was definitely demonstrated. In the experiments of Marsden, Merton, and Morton (1972) on voluntary thumb flexion, sensory messages from muscle spindles and skin were found to provide the necessary information for eliciting the stronger contraction needed to overcome a greater resistance to the movement required. Two recent symposia (Granit & Pompeiano 1979; Pompeiano & Ajmone Marsan 1981) contain (among other papers) so much evidence for multiple roles of the gamma-spindle system that the advocates of simple explanations hardly need be taken seriously.

Force and stiffness: Further considerations

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We agree with Stein that a number of muscle variables are controlled by the nervous system. Our comments relate to the nature of force control and the reasons for stiffness control.

Control force derivatives. Stein selects Evarts (1968) as his sole representative of the view that force is a major control