Force as the controlling muscle variable in limb movement

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The major problem with Stein's approach to the issue of movement control is a failure to identify levels within what must obviously be a hierarchical control system. The control of the everyday skilled movements that he uses as examples is a very different process from the control characteristics of reflexive activity in a single muscle of a decerebrate cat. To use evidence from the latter case in support of positions concerning the former leads to the kinds of difficulties Stein outlines.

It seems far more parsimonious to us to regard the central nervous system (CNS) as a controller of force and rate of change of force (Cheney & Fetz 1980) for each muscle in a group of muscles producing a movement. The temporal and spatial relationship programmed by the CNS for these various force vectors can produce the resultant desired movement, whether it is one of high velocity, a stiff supporting limb, or a slow forceful movement.

The arguments against force as the controlling variable are not convincing. The nonlinearity of the relationship between force generation and rate of motor impulses may in fact constitute useful information for the CNS. The argument that other factors affect muscle force may, as Stein himself points out, be taken into account in planning movement. That this would require a highly complex computational system is no reason to discount the probability, since, as Stein points out later in the paper, constraining the brain to a single mode of control makes the enormous computing power of 10^{10} cells available for exactly such refinements. The contention that evidence for low gain in Golgi tendon organ reflexes serves to discount force as a controlling variable is not valid and is an example of misapplying evidence from different levels of analysis. Low gain characteristics in a reflexive context do not necessarily indicate an absence of value of such feedback in the nonreflexive central projections, nor do we know whether additional gain may occur at higher levels, and we do not, in any case, know the sensitivity of the decoding system at those higher levels.

Since we know that force can be controlled and may suspect the evidence against it, what is the role of the other systems Stein identifies? We propose that these systems (length, velocity, stiffness, and viscosity) provide the feedback information, along with the force receptors, which enable movements to be controlled with such precision, just as joint and cutaneous receptors will also signal the overall appropriateness of the movement. The relative contributions of these systems will vary with the nature of the movement.

Are position-control systems active during leg movement of walking arthropods?

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As Stein suggests, it might be of interest to compare data and hypotheses obtained from vertebrates with those obtained from arthropods. The reflex in the femur–tibia joint of an insect

(*Carausius morosus*, Phasmids) has been investigated in detail, with the following results: in the quiet, *inactive animal* (standing free or fixed) the reflex operates with negative feedback and the gain varies from less than 1 up to 10. The response to a step stimulus is phasic and decays with a time constant of about 1 second for the flexor subsystem and several seconds for the extensor subsystem (for review see Bässler, in press).

In the walking animal there is still a reflex with negative feedback. However, the gain is considerably reduced (no dimensionless gain factors are known, but force measurements show that the maximum amplitude is reduced to about 30% compared to that in the inactive animal). In addition, the time constant is decreased. For the FETi motoneuron the time constant changes from ~ 0.5 sec in the standing animal to ~ 0.01 sec in the walking animal when calculated from electrophysiological recordings (Cruse 1981; Cruse & Pflüger 1981; Cruse & Schmitz, in preparation). This might be interpreted as a change from position to velocity control. However, the two parameters cannot be separated unequivocally because the phasic property of the reflex depends upon the speed of movement of the limb. With a given time constant of the order of 1 second the system can be regarded as position sensitive for frequencies >> 1 Hz and velocity sensitive for frequencies << 1 Hz.

In any case, reduction of amplitude and of time constant would decrease the damping properties of the putative servo system and so allow faster limb movements. In addition, it would improve the stability of the whole system, which might be necessary because the upper corner frequency for the muscle system might be increased as a result of the activity of the common inhibitor neuron (Ballantyne & Rathmayer 1981) and because of possible recruitment of "faster" motoneurons. When the animal produces very fast "struggling" movements the gain of the reflex is decreased to zero in the extensor subsystem and even changed to positive feedback in the flexor subsystem (Bässler 1974). This fits the hypothesis that this servo system shows adaptive control so that it adapts a high gain to produce strong resistance reflexes during posture (which, however, disappear within a few seconds; this is appropriate in a biological sense to avoid doing work against a long-maintained load). For fast, controlled movements during walking the gain falls to zero or becomes positive to produce very fast struggling movements.

Since all control experiments showed that the femoral chordotonal organ was responsible for the main part of these reflexes, one can assume that the controlled variables are position and velocity (see above). Ablation of position-sensitive hair fields in more proximal joints have shown that corresponding feedback systems are also active in other leg joints during walking (Wendler 1964).

Several experimental results obtained from crabs, crayfish, and lobsters fit very well with this hypothesis and show that crustacean limb movement is also controlled by a position-controlling servo mechanism during walking (Barnes, Spirito & Evoy 1972; Barnes 1977; Cruse, Clarac & Chasserat, in preparation). In contrast to mammalian systems, no servo-assisted control system as produced by α-γ linkage is necessary to describe the data obtained from crustaceans and insects. According to the present data on leg movements in arthropods, the assumption of a simple follow-up servo system is sufficient. However, anatomical and physiological results concerning the muscle-receptor organ and the myochordotonal organ might indicate the existence of servo-assisted control mechanisms in the walking legs of crustacea.

The hypothesis mentioned by Stein – that the overall effect of the different servo systems might help to overcome several nonlinearities existing in the system – can also be put forward for insects. Our results show that the mechanism controlling the distance between the body and the ground in walking animals, which uses several subsystems of the leg, acts as a simple spring system (Cruse & Braun, in preparation). This finding was unexpected, because open-loop experiments in fixed animals had revealed strong nonlinear properties in the different subsystems.

Finally, I should mention that the interpretation of the mammalian muscle-spindle system as a servomechanism was proposed by Wagner in several papers in 1925–27 (see review of Wagner 1960), a fact that is seldom referred to in the literature. Therefore, Wagner should be quoted as well as Merton (1953).