Variations of reflex parameters and their implications for the control of movements

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In this commentary we elaborate on the similarities and differences between the λ model, proposed by Feldman and his colleagues, and a classic position servosystem. We point out in particular some implicit assumptions and predictions of the λ model as well as some instances where the model may need to be modified.

A simple classic position servosystem is shown in block diagram form in Fig. 1. The reader should note the transformation of physical variables around the loop. If it is assumed that the input is voltage as a function of time (e.g., a series of nerve impulses) and that the transformations around the loop are linear, then the transformation of physical variables around the loop is as follows: The input voltage is transformed to a force (or torque in rotational systems), and the two variables are related by the constant of proportionality *KT* (e.g., *N* − *m*/*V*); the force or torque is then transformed into a position (a translation or a rotation), and the constant of proportionality between these two variables is *KP* (e.g., rads/*N*−*m*). Finally, for the purpose of measuring the error (difference between intended and actual position), the output position must be transformed back into the physical dimensions of the input, that is, into volts. The constant of proportionality in this case is *KF* (e.g., *V*/rad). In general these "constants" will all depend on the input frequency, but a consideration of the static or low-frequency limit should suffice for the present purpose. In the diagram the constant *Fp* is an external perturbation (i.e., a force or torque) acting on the system.

How is the output of a position servosystem (indeed, any closed-loop or open-loop system) changed? In all real control systems that we know of, the output is changed by changing the input to the system. The output is never changed by changing the stiffness *K* ($K = KF \times KT$ [check the dimensions!]) of the system. Changes in stiffness are only made to adapt the system to variations in external or internal conditions (e.g., changing load characteristics, changes in the proportionality constants

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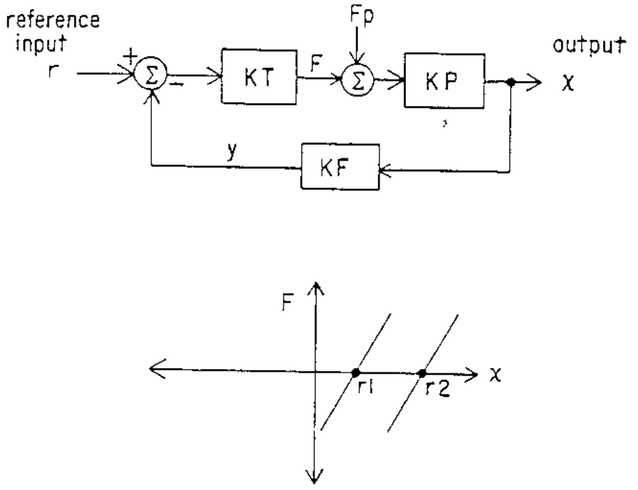

Figure 1. (Capaday and Stein). A classic position servosystem is shown in block-diagram form with an emphasis on the transformation of physical variables. The variable F represents force (or torque in rotational systems); Fp is an external perturbation acting on the system; X is the output or controlled variable and is in this case a position (either a translation or a rotation); finally, r the reference and y the feedback parameter must have the same physical dimensions. By changing the reference value from $r1$ to $r2$ the force-vs.-position (F vs. X) relation is shifted along the X axis.

due to wear), not to produce changes in the output. Berkinblit et al. clearly point out in the target article some of the problems with "stiffness control" as a way to produce changes in the equilibrium position of the muscle-load system. There are, however, at least two other reasons why control of stiffness alone is not an appropriate way to produce changes in equilibrium position. To move a large load over a short distance would require a large increase in stiffness, which may bring the muscle-load system beyond the limit of stability. Conversely, to move a small load over a long distance would require that the stiffness be significantly reduced, with the consequence that the response of the muscle-load system would be sluggish. These two points, as well as the ones made by Berkinblit et al. in the target article, make it unlikely that the body uses stiffness control as a mechanism for producing movements.

The input (r) to the classical position servosystem in Fig. 1 is related to the threshold λ of the stretch reflex[1] (s.r.) This can easily be shown by considering that:

$$F = KT(r - y) \qquad (1)$$

and because $y = XKF$, it follows that $F = KT(r - XKF)$. By letting $\lambda = r/KF$, then:

$$F = KTKF(\lambda - X) \qquad (2)$$

which has the same form as equation (2) in the target article. Changing the reference value from $r1$ to $r2$ is similar to changing the threshold λ of the s.r. (Fig. 1). Therefore, the s.r. in the λ model operates in the same way as a classic position servosystem. However, the vast majority[2] of position servosystems operate on loads whose characteristics are essentially constant; consequently, the input–output relation r vs. X is unique (i.e., for fixed system parameters). In contrast, it is obvious that humans and animals do not move against loads of constant characteristics. Therefore, the static input–output relation (λ vs. X, where λ is a central command) will depend on the characteristics of the particular load being manipulated (assuming for simplicity that the muscle parameters are constant). In particular, if the load is changed, the parameter KP in Fig. 1 will also change. The point is that the reference signal must be adapted to the characteristics of the load. In other words, the amount by which the stretch-reflex threshold λ must be changed in order to move to a given position, and in a given way (e.g., speed), depends on the particular characteristics of the load; there is no unique input–output relation (λ vs. X), and consequently the commands must be adapted to the load. Because there is no unique input–output relation, the CNS must determine the state of the muscle-load system before issuing appropriate motor commands. This operation can be referred to as "state-feedback." One of the strengths of the λ model is that it contains, albeit implicitly, the intuitive idea of "state-feedback."

Berkinblit et al. favor the idea that the motor commands act to change one parameter, the s.r. threshold λ but are there circumstances where the reflex stiffness is also changed? We briefly discussed that in practice changes in stiffness (other loop variables may be involved as well) are used to adapt the system to variations in external conditions such as variations of load characteristics. Indeed, two instances in which there may be a change in the reflex stiffness occur when the conditions of the motor task are changed, or the motor task itself is changed.

Akazawa, Milner, and Stein (1983) have shown that if subjects are required to maintain a constant position of the distal phalanx of the thumb against an unstable load (a torque motor with positive position feedback), the slope of the reflex responsiveness (mean electromyographic (EMG) level of the reflex response) against the tonic EMG level of the flexor was 40% larger in this task than in a task that required the control of the force exerted. They suggested that this finding implies that the stiffness of reflex origin is adaptively regulated; the stretch reflex stiffness was increased in order to stabilize an unstable load. In another instance, we have recently shown that during standing (a position-control task), the curve relating the soleus H-reflex amplitude to the tonic EMG activity in this muscle has a smaller slope and higher y-intercept (H-reflex amplitude at zero EMG) than during walking (Capaday & Stein 1985). The magnitudes of these two effects are substantial: up to a 5–6-fold difference in slope, and up to a 3–4-fold difference in threshold. The high values of the H-reflex during quiet standing (nearly zero EMG) imply that even a small amount of body sway will be strongly counteracted. However, during walking, high reflex amplitudes at EMG levels comparable to those of quiet standing would impede ankle dorsiflexion. Again, in this example the amplitude of the reflex response, and hence the reflex-evoked stiffness, is adapted to the task.

These changes in reflex sensitivity, and hence reflex-evoked stiffness, are not inconsistent with the λ model in its most general form. One of the conditions for a stable equilibrium point is that the stiffness of the stretch reflex must be greater than that of the load, which was appreciated by Feldman in his earlier papers on the λ model (Feldman 1974a,b). What is inconsistent with the above results is that the so-called invariant characteristic of the λ model (i.e., the constant form of the length-vs.-tension relation in the s.r.) is not invariant. A change in the slope of relfex response vs. background EMG reflects a change in the length-vs.-tension relation of the stretch reflex. This characteristic is therefore not invariant but is to some extent adapted to the task (e.g., walking vs. standing, stable loads vs. unstable or unpredictable loads.

In conclusion, because of a wide variation of possible load characteristics against which movements are made, both the threshold and the stiffness of the stretch reflex must be, and are, adaptively modified.

1. By stretch reflex, we refer, in the sense of the target article, to the overall effect of stretch. The intrinsic length–tension properties of muscle, plus the reflex force and stiffness produced by activating additional motoneurons, will contribute to the responses measured.

2. A particularly contemporary example of a position servosystem acting on loads of variable characteristics is the robot manipulator. The variations in load are mainly due to changes in the moment of inertia acting at each link as well as changes in the gravitational force acting on each link. However, in practice these variations in load are greatly minimized by large gear-reduction ratios between the load and the motor shaft.