Does the Velocity Sensitivity of Muscle Spindles Stabilize the Stretch Reflex?

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Abstract. A model of the stretch reflex based on detailed experimental studies of muscles, muscle receptors and reflex pathways has been analysed. Muscle receptors respond to the velocity and the acceleration of movement, as well as to muscle length. The effect of the velocity sensitivity on the stability of the stretch reflex is considered. It is concluded that the velocity sensitivity can compensate to some extent for the sluggishness of muscles and the delays introduced by reflex pathways. However, the value of velocity sensitivity found experimentally is greater than that required to stabilize the stretch reflex optimally. The velocity sensitivity will have some tendency to produce oscillation, and it is suggested that a small degree of oscillation may be beneficial to linearize muscle properties.

In recent years evidence has accumulated from experiments on behaving animals and man (Cody et al., 1975; Vallbo, 1971) that muscle spindle afferents are active not only during passive stretch, but also during active, voluntary contractions. Through their reflex connections they can assist in the production of voluntary movements (the servo-assisted hypothesis for the control of movement; Matthews, 1972; Stein, 1974). However, these reflex connections form a negative feedback loop (in which a stretch of a muscle leads to a contraction after some delay). Negative feedback loops with time delays can also give rise to damped oscillations, and if the gain is sufficiently high, to instability. Lippold (1970) presented evidence that physiological tremor arose from the tendency for instability in the stretch reflex, although this view has recently been challenged (Rietz and Stiles, 1974).

There are now extensive single unit studies on the dynamic properties of the nerve fibres and muscles involved, so a more quantitative analysis is possible of the factors involved in stabilizing and destabilizing neuromuscular systems. A preliminary analysis was included in a recent review article (Stein, 1974) and it may be useful to start from the conclusion based on Figure 1, which is reproduced from that article. The curves labelled A in Figure 1 represent the gain and phase of a feedback loop which consists merely of a time delay of 25 ms. The gain is constant and the phase of the output lags increasingly behind the input as

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Fig. 1. Computed gain and phase for a feedback loop with properties based on the stretch reflex from mammalian muscles. Further explanation of the curves is given in the text and in Stein (1974)
frequency increases. There will be a tendency for oscillation at the frequency at which 180° phase lag is shown (20 Hz). Muscles behave as low-pass filters, as indicated by the curves labelled B, so that the gain declines at high frequencies when the properties of muscle are included and extra phase lags are introduced. These dynamic properties of muscle tend to stabilize the system in that the gain, and hence the tendency, for instability is less at the frequency (7.5 Hz) at which 180° phase lag is observed.

Muscle spindle afferents behave as high-pass filters which respond to muscle length and its derivatives. The velocity sensitivity of the receptors, as shown by the curves labelled C, can compensate at low frequencies for the low-pass characteristics of muscle, and for the phase lags introduced by the time delays and muscle properties. This property of muscle receptors was first noted experimentally by Poppele and Terzuolo (1968) and has been confirmed by later studies (Rosenthal et al., 1970; Stein, 1974). A further theoretical possibility was suggested by Matthews (1964), namely that the velocity sensitivity of muscle receptors might be adjusted to optimally stabilize the system. This possibility did not seem to be supported by the calculations shown in Figure 1. When the velocity sensitivity of muscle spindle afferents is included (the curves labelled C in Fig. 1), the gain at the frequency where 180° phase lag is found (13.5 Hz) is considerably higher than at the corresponding frequency (7.5 Hz) in curve B. Thus, the velocity sensitivity of muscle spindles appears to destabilize or produce oscillations rather than stabilizing the system and preventing oscillations. This conclusion, which is contrary to Matthew’s suggestion, is subject to several objections:

1) In Figure 1 the gain has been noted at only one frequency (where 180° phase lag is observed), rather than solving the full equations and determining quantitatively the tendency for oscillations to occur.

2) Only isometric conditions of muscle were considered whereas normally, muscles will be contracting against the elasticity of their antagonists and the inertia of more distal portions of a limb and its external load. The tendency for stability might be quite different under more realistic loading conditions. Even under isometric conditions some internal shortening can take place against the tendons and other elastic elements in series with the contractile proteins. This internal shortening was neglected.

3) The muscle properties were those of plantaris muscle, a relatively fast muscle, not soleus muscle, as originally stated (Stein, 1974). Soleus muscle is considerably slower and the conditions for stabilizing slow, postural muscles may be quite different from those for fast muscles.

4) The time delay considered is the sum of all the delays involved in conduction, synaptic transmission, excitation-contraction coupling, etc. This delay will vary depending on the distance of the muscle from the spinal cord. In addition, there are pathways other than the monosynaptic reflex which need to be considered (Matthews, 1969), and during normal behaviour the “functional stretch reflex” (Melvill Jones and Watt, 1971) may involve higher centres, rather than merely spinal reflex pathways. Indeed, there is evidence for more than one supraspinal pathway (Murphy et al., 1974; Tatton et al., 1975; Milner-Brown et al., 1975), and the conditions for stability may vary with the time delay of the pathways involved.

5) Primary muscle spindle afferents respond with greater than 90° phase advances over a range of frequencies (Popple and Bowman, 1970), which implies that these fibres are sensitive to acceleration as well as length and velocity. This acceleration sensitivity was not considered in previous work.

We therefore thought it worthwhile to reconsider the role that the velocity sensitivity of muscle receptors plays in the control of movement. More general methods for quantitatively determining the tendency for oscillation are described in the Methods and these are used in the Results section to consider systematically the factors listed above on the stabilizing or destabilizing effect of the velocity sensitivity of muscle spindle afferents.

Methods

Figure 2 shows a block diagram of the system considered here. Experimental determination of the parameters and general properties of the system have been considered previously (Bawa et al., 1976a, b; Stein and Öğütöreli, 1976; Öğütöreli and Stein, 1975). Muscle is considered as a second-order system in which, under isometric conditions, there is a transfer function of the form

\[
G(s) = \frac{G_1}{(s + \alpha)(s + \beta)}
\]

where for a linear system

\[
\tilde{G}(s) = \int_{0}^{\infty} e^{-st}G(t)dt,
\]

in which \(G_1 = \frac{k_1 k_2 C}{B(k_1 + k_2)}\) in terms of the parameters of Figure 2 (Stein and Öğütöreli, 1976), one rate constant \(\alpha\) represents the decay of the active state following a muscle action potential and

\[
\alpha = \frac{1}{B(k_1 + k_2)}\left(k_1 + k_2\right)
\]

represents a visco-elastic constant. The transfer function is the Laplace transform of the impulse response of the system \(G(s) = \int_{0}^{\infty} e^{-st}g(t)dt\), where for a linear system \(g(t)\) would be the twitch response of the muscle. The values used as standard (Öğütöreli and Stein, 1975), based on experimental studies of plantaris muscle of the cat (Bawa et al., 1976b), are: \(B = 40 N·s/m\); \(C = 2.9 N\); \(D = 0.5 N·s/m\); \(M = 0.3 kg\); \(k_2 = 647 N/m\); \(k_1 = 2200 N/m\); \(k_5 = 880 N/m\); \(t_n = 0.025 s\); \(\beta = 30 s^{-1}\). Plantaris is a relatively fast muscle and the corresponding rate constants \(\alpha\) and \(\beta\) for a slow muscle such as soleus are about a fifth as great. We have therefore set \(\beta = 6s^{-1}\) and \(B = 8 N·s/m\) in modelling a slow muscle. When the external loads are considered, which themselves constitute as second-