

MUSCLE RECEPTORS IN THE CONTROL OF VOLUNTARY MOVEMENT

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OUR only means of interacting with the outside world is via voluntary muscle contraction. The versatility, speed and precision of the control of our muscles is a source of constant inspiration to anyone studying their physiology. The initiation of the complex patterns of nervous activity representing the desired movements is the responsibility of the higher parts of the nervous system and study of this aspect of motor control is still at an early stage. However, knowledge of the segmental level of control, by which voluntary muscles convert these patterns into co-ordinated movements, has reached the point at which we can make some reasonably complete attempts at synthesis and quantitative modelling of its physiological

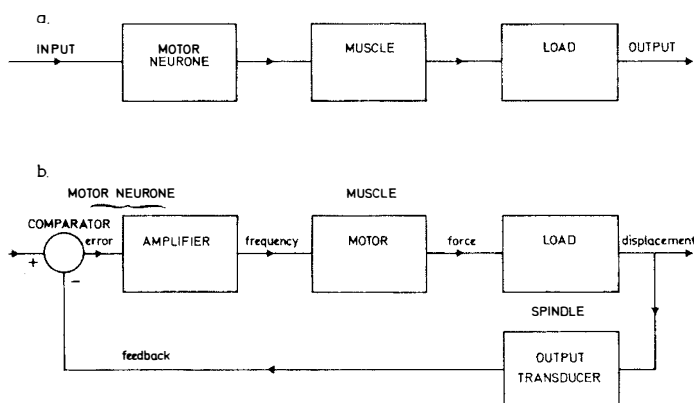


FIG. 1

a, System representation of muscle control without feedback. b, With feedback.

mechanisms. The basis for such attempts is an understanding of the significance of negative feedback in control. We start, therefore, with a statement of the useful properties of negative feedback systems in general.

In Figure 1, *a* is shown a representation of a 'control' system without feedback. Each box is a sub-system with an input and an output. For example, the first box could be a motor neurone pool, with the input representing the total frequency of excitatory synaptic drive. The output is the frequency of impulses leaving along the axons to the muscle. This output is in turn the input to the second subsystem, the muscle and things attached to it. In this instance, the output might be regarded as displacement. If everything were known about the properties of the motor neurone pool, the muscle and its load, then, in principle, it would be possible to know the right input to apply to achieve a particular output. In practice, all these properties may be so subject to change that the resulting displacement differs

widely from what was intended. This arrangement, as it stands, hardly deserves the name of a control system.

In Figure 1, *b* two more components have been added. A transducer measures the output and sends a corresponding signal to be compared with the input signal in the comparator. The difference between the original input signal and the feedback signal is often called the 'error' signal and is now the new input for the original system. Although a variety of physiological receptors can give some information about the displacement output of our muscle system, the one which measures displacement most precisely and sends its signal back most directly to the motor neurones is the muscle spindle. Two points should be noted here. First, the motor neurone is the obvious choice for comparator. Its discharge frequency (the error signal) depends on the instantaneous algebraic sum of excitatory and inhibitory inputs. Second, we know that the muscle spindle input to motor neurones is excitatory and this might suggest that the feedback would be positive instead of negative. However, a sign reversal occurs in the muscle in that an increase in the drive to the muscle causes a shortening, that is, a negative displacement and a reduction in spindle discharge. If instead of the variable input to the whole system there is a constant reference level then the arrangement becomes the myotatic or stretch reflex, which Sherrington recognised to be the basis of posture control. Engineers would refer to this as a regulator of muscle length, while the addition of the variable input makes it into a 'servo' control system.

What are the properties of this sort of arrangement? First, we must point out that it is the output detector or transducer which determines what variable is controlled. In the case of the muscle spindle this is displacement (and velocity). An input to the system leads to a contraction and shortening of the muscle and a reduction in spindle discharge. As the displacement continues the net error signal falls until, at a particular length, a balance is reached between the input signal and the negative feedback. In this event, the input signal clearly represents a particular defined displacement and the arrangement is a length servo. Anything which opposes the shortening reduces the negative feedback, increases the error signal and consequently the muscle force, so that, despite the load, the system will tend to produce the right displacement. Of course the load will have some effect, but less than in the absence of feedback control.

By the same principle, it can be seen that the servo will be relatively immune to disturbance by outside forces.

Furthermore, changes within the system, for example fatigue of the muscle, will tend to be compensated. The properties of the system become less dependent on those of the muscle and the load, provided the muscle spindle continues to work normally.

Another useful property is an improved linearity of response. Any departure from linear behaviour of the muscle or load (that is change in displacement proportional to input) will tend to change the error signal in such a way as to compensate for it, provided that the spindle behaviour is linear.

Finally, the speed of response can be improved by negative feedback. Suppose it is intended to cause and maintain a sudden displacement of a load. Without feedback, the correct force to maintain the displacement would have to be estimated and applied as rapidly as possible. In general, because of viscous and inertial properties of real loads, the desired displacement will not be achieved instantaneously but will lag behind the force. However, in the feedback system the

difference between the desired position and that achieved at any instant will be fed back so as to reduce this difference. Consequently, in the early stages of the movement, more force will be applied than is needed for the maintained displacement and movement is more rapid.

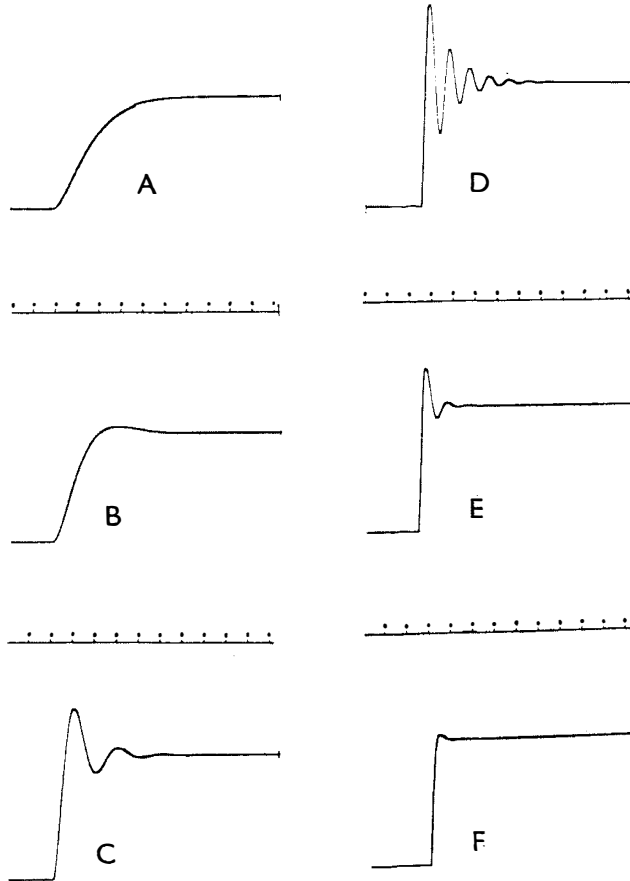


FIG. 2

Computer simulated movement of mechanical load by a sudden step of force, (A) without feedback, (B), (C) and (D) with increasing negative displacement feedback. (E) and (F) the effects of damping by negative velocity feedback.

These properties, relative immunity to outside disturbance and changes of load or of internal characteristics, linearity and good speed of response will be enjoyed by the biological feedback system, just as by the engineer's feedback controller (see Millhorn, 1966), but there are certain hazards. Consider the speed of response of a displacement servo system. Suppose the load to be moved is a sluggish (overdamped) combination of spring, and viscous element (the muscle itself behaves like this). Then in the absence of feedback, an input suddenly applied (fig. 2, A) causes a relatively slowly achieved displacement. The application of negative displacement feedback speeds this response (B), but if we seek to

improve things by applying more and more feedback then eventually the output overshoots (C and D) and in the extreme case oscillates indefinitely. This can be overcome by adding more mechanical damping, but this is wasteful of energy and the same effect is better achieved by adding negative velocity feedback (E). In the muscle servo this is also provided by the muscle spindles which give a frequency of nerve impulses depending not only on stretch, but also on rate of stretch. Now, in the presence of strong negative displacement feedback more velocity feedback can be applied (F) and will lead to a fast response without oscillation. There are definite limits to the improvement in response which can be obtained. If the force required to maintain the final displacement is half the maximum available, then no more than twice this force can be exerted at any time to speed up the movement, which is in any case limited by the contraction time of the muscle. Another important factor is the time delay around the control loop. At a certain frequency such a delay causes the negative feedback to become positive. If the reflex sensitivity is high enough, oscillations will occur, and can only be dealt with to a limited extent by velocity feedback.

The marvellous thing about the muscle servo is the facility, not generally available to the engineer, of modifying the strength of the displacement and velocity sensitivity separately from moment to moment to suit the particular load being moved. This adjustment is, of course, effected by the fusimotor system of small nerve factors supplying the intrafusal muscle fibres. The work of Matthews and his colleagues in recent years has shown the existence of separate static and dynamic fusimotor systems (see *e.g.* Matthews, 1964) acting in this way.

Soon after World War II, workers with some knowledge of these principles started to analyse muscle control in such terms, and they were very much impressed by the advantages conferred by feedback on postural muscles acting as regulators. Eldred, Granit and Merton (1953) were particularly concerned in this. However, there arose some confusion about the significance of the fusimotor system. The very effectiveness of the stretch reflex in resisting deformation was seen as an impediment to voluntary movements. Merton (1953) stated that 'during shortening, the resistance offered by the servo must be either overcome or removed'. Consequently, the demonstration that spindle activation could occur by way of fusimotor drive was welcomed as showing a way by which muscle control could be extended from regulator to servo action. Attempts to confirm this mechanism as a normal means of muscle control have been a dominant theme in this aspect of neurophysiology. Merton went so far as to say 'Excitation, applied to the main motor neurones is seen to be wrong in principle because it is just the sort of interference a feedback loop is designed to neutralise. The loop is best activated by altering the bias in its null detector.' This statement was made before the role of the fusimotor nerve in setting the static and dynamic sensitivities of the spindles was recognised. Merton's concept was that fusimotor drive merely increased the 'bias' or firing rate at a particular spindle length, and that the spindle acted as the comparator of the drive signal commanding a length change and the resulting reflex shortening. However it can be shown that if the sole function of fusimotor action was to inject an input in the form of a bias signal, this could just as well be achieved by direct excitatory input to the alpha motor neurone, and without the delays of the fusimotor pathway.

This being so, is there any significance in the fusimotor drive accompanying direct drive to the α motor neurone other than to set length and velocity sensitivity?

The answer to this seems to lie in the fact that without fusimotor input to the spindle, afferent discharge tends to be completely silenced during shortening of the muscle (fig. 3, A). If the spindle is silenced, negative feedback ceases to exist and control must deteriorate. The possibility of fusimotor drive maintaining spindle afferent activity during active shortening was demonstrated by Kuffler and Hunt in 1951 and has since been emphasised by Granit (1966), who refers to it as α - γ linkage. The occurrence of simultaneous activation of the alpha and fusimotor routes has been demonstrated for vestibular reflexes by Eldred *et al.* (1953), for respiratory muscle by Critchlow and von Euler (1963) and by Sears (1963) and for cat jaw muscle (fig. 3, B) by Taylor and Davey (1967).

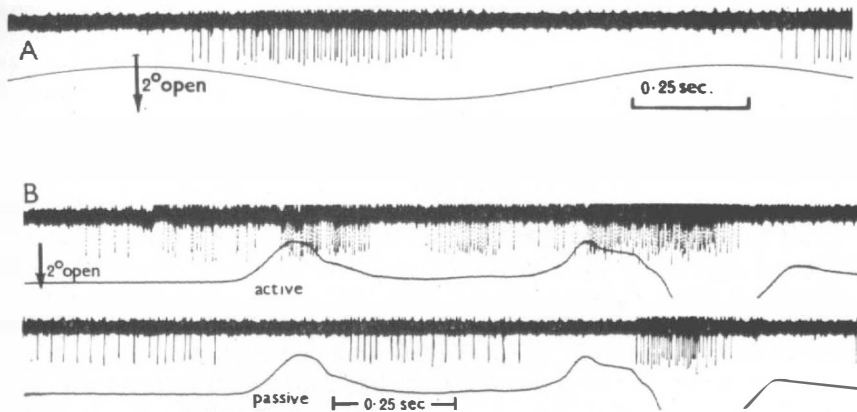


FIG. 3

A, The response of a cat temporalis muscle spindle to sinusoidal stretch, showing silencing during passive shortening. B, Contrasting the response of the above spindle to active (upper) and passive (lower) jaw movements.

The question remains as to how much fusimotor bias accompanies normal motor activity in unanaesthetised animals. We would like to know whether it is just sufficient to prevent the spindles being silenced, or enough to speed up the spindles in the way visualised by Merton, or just enough to tend to maintain constant output. This is a question which can only be answered by techniques of chronic recording from spindle afferents in normal movements. Some steps towards this have recently been taken by Hagbarth and Vallbo (1969) who have inserted microelectrodes into human nerve trunks. It could well be that the strength of fusimotor drive may be modified during the learning of a movement so that the distribution between the two routes may be optimised at the point where no change in spindle output occurs if the movement is correctly executed. Then a change in the load would not only result in the servo acting to correct this, but higher parts of the nervous system being made aware of the change by the fluctuation in afferent input, so that subsequent attempts might make allowance for the change.

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