MOTONEURONE TASK GROUPS: COPING WITH KINEMATIC HETEROGENEITY

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SUMMARY

Physiological principles of motor control have generally been based on linear servocontrol theories in which transducers of force, length and velocity are used to provide feedback to the motor actuators. Within the past few years, recordings of the activity of motoneurones and proprioceptors during normal motor behaviour have indicated a diversity that is not consistent with any one theory of motor control. This paper examines the heterogeneity of kinematic conditions under which muscles are called on to perform, and attempts to correlate this with the effects of various fusimotor states on the activity of the muscle spindle afferents, the major sensory signal source in most feedback control schemes. The concept of 'task groups' is proposed, in which functional groups of alpha and gamma motoneurones and spindle afferents are programmed to achieve optimal control over relatively restricted but more linear parts of their operating curves. Such a functional compartmentalization of the motor apparatus is thus consistent with several different theories of servocontrol, although it remains unclear whether such conceptual mechanisms are actually embodied in the highly complex neural circuitry present in the spinal cord and higher motor centres.

INTRODUCTION

Over the past three decades, neurophysiologists studying the neural circuitry responsible for control of skeletal muscles have developed several different general theories of sensorimotor control. These have usually invoked one or more of the sources of proprioceptive signals (e.g. muscle spindle and Golgi tendon organ afferents) in positive or negative feedback loops to the homonymous alpha motoneurones. Usually, the underlying control principle is one originally derived for machines employing linear servocontrol. For most of these theories, experimental conditions have been manipulated to ensure that the behaviour of the muscles is consistent with the theory. However, the goal of finding a universal control theory (and the implicit neural circuitry embodying that theory) remains elusive. As it has become possible to study the activity of the neural elements during a variety of normal motor behaviour, each theory has had to contend with situations in which its predictions seem to be at odds with the data.

Key words: Motoneurones, muscle spindles, motor control.

Rather than looking for new theories, it seems reasonable to ask whether the full range of motor behaviour is simply too heterogeneous to expect any single control principle to apply universally. Kinesiologists have long appreciated that the normal use of muscles includes very different kinematic conditions. They differentiate isometric, concentric and eccentric 'work' of muscles generating tension under conditions of zero, negative (shortening) and positive (lengthening) velocities, respectively. Because of the complex anatomical arrangements of uni- and multiarticular muscles and their tendons, any particular behavioural task or trajectory of limb motion is likely to require all three of these types of work in its production. I will here explore the notion that, to the extent that the highly distributed neural integrators of sensory and motor information can be said to embody *any* particular control theory, they do so only for certain well-defined working states of each muscle (or even parts of muscles).

KINEMATIC PROPERTIES OF THE SENSORIMOTOR APPARATUS

Because of the complex non-linearities of the muscle fibres and sense organs, the three states mentioned above – isometric, lengthening and shortening – represent quite different operating points.

The tension output of muscles at a given level of alpha motoneurone recruitment has been studied intensively under isometric condition; it is generally predictable because of the orderly size-ranked recruitment under most voluntary activation conditions (Milner-Brown, Stein & Yemm, 1973; Henneman, Clamman, Gillies & Skinner, 1974). Various time-dependent effects such as fatigue and potentiation are known, but it is not clear how significant these are for naturally occurring patterns and levels of activation. When active muscles are allowed to shorten at appreciable velocities, tension output falls rapidly, eventually to zero at V_{max} as originally described by A. V. Hill's equation (Hill, 1938). When active muscles are stretched by an external force, their tension output can rise dramatically for the same level of activation (Joyce, Rack & Westbury, 1969; Cavagna & Citterio, 1974). As the stretch proceeds past the backward excursion range of the cross-bridges, there may be a detectable yield, but tension generally stays high until the stretch begins to exceed the optimal overlap of the actin and myosin filaments (Rack & Westbury, 1969). The significance of a particular rate of muscle stretch or contraction depends on the internal fibre architecture, which in the case of pinnate muscles may substantially magnify the relative velocity at the sarcomere level (Gans, 1982). Relatively little information is available regarding the tension output of most muscles during active lengthening, despite its widespread occurrence as a *modus operandi* of normally behaving muscles (e.g. Walmsley, Hodgson & Burke, 1978).

Most models of motor feedback control loops have focused on the proprioceptive signal from the muscle spindles. In addition to the general utility of length and velocity transducers in control theory, there is a definite teleological appeal stemming from the amount of metabolic, developmental, phylogenetic and structural detail which Nature has lavished on this sense organ. The output of the muscle spindles,

particularly the velocity-dependent primary endings which have strong monosynaptic effects on the motoneurones, is even more highly state-dependent than that of the muscle fibres. In the absence of fusimotor drive, most spindle afferents have little or no spontaneous activity in a muscle under precisely isometric conditions. However, primary endings are exquisitely sensitive to tiny length fluctuations such as are likely to occur during voluntary attempts to maintain a constant limb position (Hasan & Houk, 1975). Once a stretch exceeds this short range of hypersensitivity, the afferent signal falls drastically to a condition in which it is proportional to muscle length times velocity raised to a fractional exponent of about 0·3 (Houk, Rymer & Crago, 1981). This makes the spindle capable of producing a monotonically rising output over a very broad dynamic range of lengths and stretch velocities, but makes it a relatively insensitive transducer of small changes in velocity. Under all shortening conditions, primary endings in de-efferented spindles (zero fusimotor drive) generally produce zero output; secondaries are also likely to be silenced at higher velocities of shortening. All of these tendencies can be greatly enhanced or reduced by the different kinds of fusimotor input to the mammalian muscle spindle as shown in Fig. 1B (for review, see Boyd, 1981).

ISOMETRIC CONTROL

If a subject is using muscles to maintain a steady limb position, he can take advantage of several possible strategies based on the above properties of the afferent and efferent components. Active muscle itself is a relatively stiff spring, particularly for small disturbances; co-contraction of antagonistic pairs, while perhaps tiring, works remarkably well. Bizzi and colleagues have examined the controllable levels of compliance which can be programmed into such systems of 'equilibrium spring pairs' using only degree of co-contraction without closed-loop feedback (Bizzi, Accornero, Chapple & Hogan, 1982). Positive feedback from the hypersensitive spindles could improve speed of return to equilibrium. Passive spindle afferents (with no fusimotor drive) may be used to provide a sensitive indication of deviations from the isometric state in otherwise relaxed ankle muscles during plantigrade standing (sway detection). When a single agonist muscle is used to hold a position against a load capable of applying large excursions of disturbance, the non-linear properties of active muscle can be damped and linearized by feedback from the muscle spindles and Golgi tendon organs. Houk (1979) has examined the properties of such systems for 'stiffness regulation'.

ACTIVE SHORTENING CONTROL

Use of a muscle to establish a particular trajectory of limb motion by means of muscular contractions requires special attention to the feedback signal. The muscle spindles are capable of generating non-zero output while rapidly shortening only if their intrafusal muscle fibres are simultaneously activated so as to shorten at a similar or faster rate and thereby maintain tension on the sensory apparatus. The co-

activation of the alpha and gamma (static) motoneurones has been proposed by Granit (1975) as a means by which the central nervous system can cause the muscle spindle afferents to act as the error signal for deviations from the desired trajectory of motion. If the rate of muscle shortening is lower than the rate of intrafusal contraction, the spindle afferents increase their discharge rate, which monosynaptically increases the level of excitation of the homonymous alpha motoneurone pool, accelerating the motion. If the rate of muscle shortening is too high, the spindle afferents will turn off, thereby disfacilitating the motor pool.
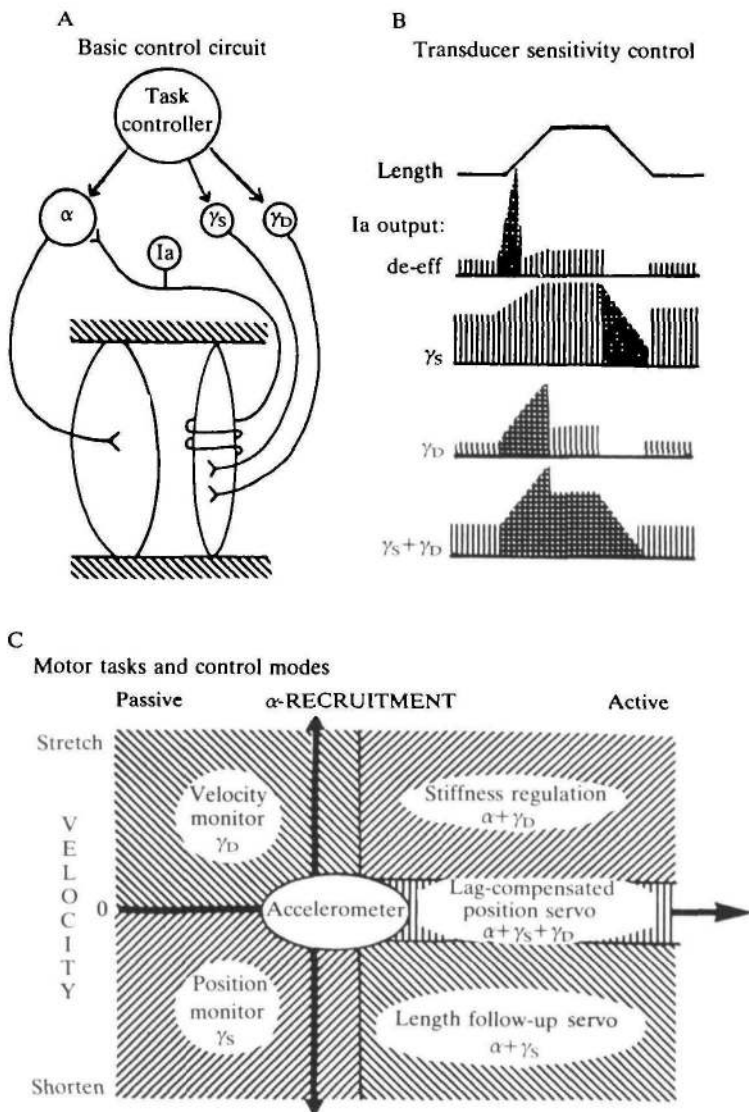

Fig. 1.

ACTIVE LENGTHENING CONTROL

The use of the force generating capabilities of muscle to control the rate of muscle lengthening is an important and much overlooked normal motor behaviour. Any rapidly alternating limb motion in which inertia is significant requires muscles to be activated to reverse the lengthening motion. However, movements such as shaking and scratching appear to be pre-programmed ballistic sequences whose trajectories and cycle times are more a function of the natural resonant frequencies of pendular motion of the limb segments than of feedback control. The most obvious examples of controlled lengthening arise in locomotion, when extensor muscles at the ankle and knee must absorb the gravitational load of the body weight in a moderately compliant manner to avoid excessive strain on joints and tendons.

The velocity of such controlled lengthening tends to be low but the excursions are large. Thus, a de-efferented spindle would generate some activity, but with the low sensitivity to velocity changes characteristic of its long range properties. Evidence from spindle recordings during active lengthening suggests that concurrent gamma dynamic activity enhances spindle primary afferent output under such conditions, providing a more sensitive feedback signal for motor control circuits (Hulliger & Prochazka, 1983; see also Fig. 2).

For all of the above kinematic conditions, the muscle spindle can, and generally does, provide an appropriately sensitive indicator of events, justifying its presumed relevance to motor control. However, it is apparent that the motor control system can and must programme several different kinds of fusimotor action to obtain the desired sensitivity from these transducers. Furthermore, the meaning (in control theory

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Fig. 1. (A) Archetypical servocontrol circuit employing excitatory feedback from muscle spindle primary afferents (Ia) onto alpha motoneurones (α). The absolute and relative sensitivity of the afferent to length and velocity perturbations is under the control of at least two types of fusimotor neurones, gamma static (γ_S) and gamma dynamic (γ_D). (B) Various states of the spindle Ia output in response to a ramp perturbation of length, shown with cross-hatched areas of maximal sensitivity (defined as largest change in output without saturating). In the de-efferented state (de-eff), the afferent is hypersensitive to the onset of a lengthening perturbation; under gamma static influence, activity is generally high except during muscle shortening which exceeds the rate of intrafusal muscle contraction; under gamma dynamic influence, activity is strongly dependent on velocity of stretch, with no activity during shortening; under combined static and dynamic influence, spindle afferent discharge can follow at least modest rates of lengthening and shortening. (C) The work of the muscles is divided into a two dimensional space whose axes are velocity (ordinate) and degree of recruitment (abscissa). Several different functions for spindle afferent feedback are indicated in the various domains of this space for which they are best suited, together with the general pattern of extrafusal (α) and intrafusal (γ_S and γ_D) recruitment needed to function optimally in these domains. During active lengthening (upper right), the enhanced stretch sensitivity provided by gamma dynamic activity would be used to improve the stiffness of the muscle when it is used as a spring; during active shortening (lower right), gamma static activity is needed to maintain spindle activity above zero to provide an error signal for a length follow-up servo. In the near-isometric active state between them, the modest velocity-dependency of the afferent provides a phase leading detector of small stretches which might help to compensate for the motor lag time; in the low recruitment, near isometric state at the centre, the hypersensitivity of the de-efferented spindle to small stretches provides the earliest indication of a small stretch of the resting muscle; in the passive (inactive) muscle at left, fusimotor activity could be used to optimize the spindle afferent signal during lengthening (upper left) and shortening (lower left), presumably for use in the control of active antagonist muscles or to provide general kinesthetic information to higher centres.

terms) of the spindle afferent activity under these varied conditions is not the same, nor is the desired response from the motor controller.

Fig. 1 summarizes some of these different domains. In the short range hypersensitive condition, the spindle acts somewhat like an accelerometer, having
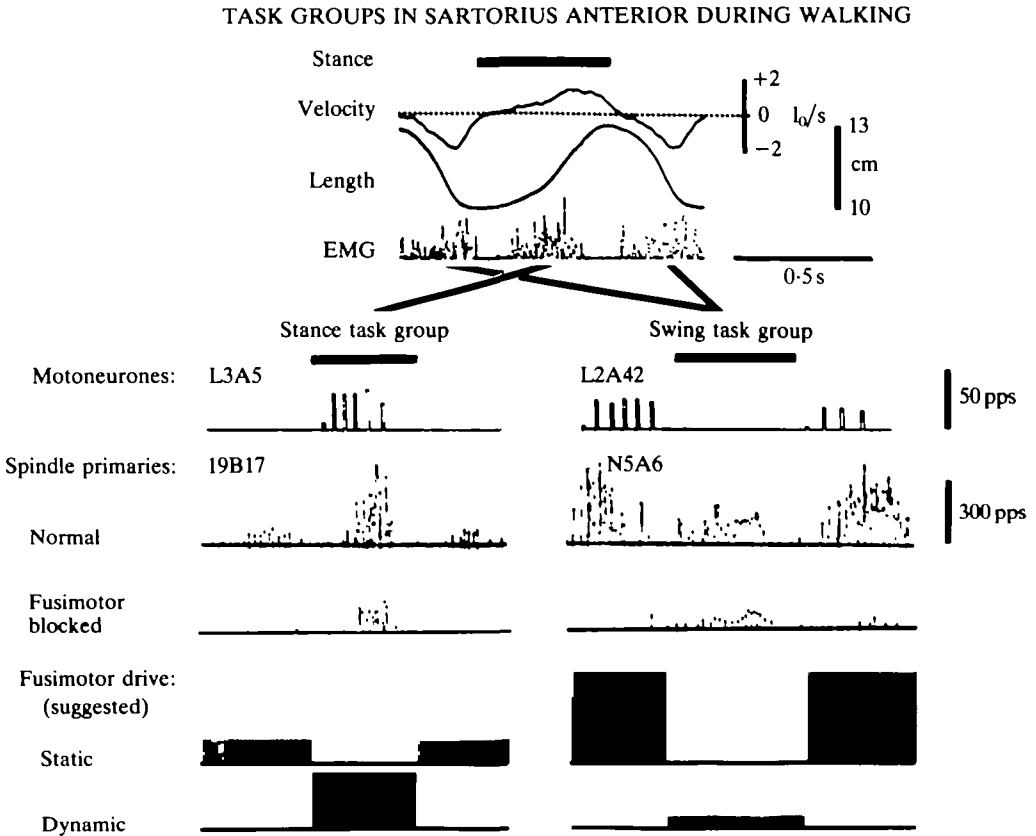

Fig. 2. A summary of unit activity of alpha motoneurones and spindle afferents recorded from the cat anterior sartorius muscle using chronically implanted electrodes and transducers in freely walking animals. Top centre traces present one and a half step cycles (stance phase in the middle flanked by two swing phases), showing that the two periods of recruitment of this muscle evident in its EMG (rectified and integrated into 2–ms bins) occur during lengthening (in stance phase; from implanted length gauge) and shortening (in swing phase), respectively. The activity of individual motoneurones projecting to this muscle is divided into two functional groups consisting of units recruited only during stance (e.g. L3A5) and units recruited only during swing (e.g. L2A42). Spindle primary afferents are less clearly divided, but some tend to have more highly modulated activity during stance (e.g. I9B17) and some are more active during swing (e.g. N5A6). When low concentrations of lidocaine were infused around the femoral nerve during walking to block small calibre fusimotor fibres (using a chronically implanted catheter leading to a cuff around the nerve), the activity of both types of primary afferents became much lower, more homogeneous and consistent with expectations from the properties of de-efferented spindles. The bottom two traces in each group suggest simple patterns of gamma dynamic and gamma static activity that might be responsible for the quantitatively different patterns of spindle activity occurring before fusimotor blockade. (Reprinted from Loeb, 1984, with permission from the publishers.)

maximal sensitivity to small, rapid stretches, and relative insensitivity to large and/or slow movements. Because of its highly non-linear behaviour, it probably functions best as a trigger of programmed responses (e.g. sway correction manoeuvres) rather than as part of a continuous feedback loop.

During muscle shortening, the spindle can be used to detect mismatches between the desired and the actual trajectory of shortening, but the necessary fusimotor static activity would seriously compromise the usefulness of both primary and secondary endings as a reference of absolute muscle length.

In lengthening muscle, the spindle secondaries (lacking any input from the intrafusal bag_1 type muscle fibre under gamma dynamic control) probably provide a good indicator of muscle length, perhaps contributing much of the kinesthetic sense of joint position. Spindle primaries probably have increased velocity sensitivity as a result of gamma dynamic action. It has been suggested that this first derivative information might compensate well for the activation lag of extrafusal muscle, which poses a serious instability problem in conventional control theory (Stein, 1974).

MOTOR CONTROL DURING LOCOMOTION

The above theoretical arguments constitute *post hoc* explanations for data which we and others have been gathering on the normal patterns of activity in muscle spindle afferents and alpha motoneurones recorded from chronically instrumented, unrestrained cats walking on a treadmill. Single unit activity is recorded by chronically implantable, fine wire microelectrodes which 'float' in spinal canal structures such as the dorsal root ganglia and ventral roots (Prochazka, Westerman & Ziccone, 1976; Loeb, Bak & Duysens, 1977; Hoffer, O'Donovan, Pratt & Loeb, 1981). Other chronically implanted transducers and electrodes permit definitive identification of efferents and afferents, their conduction velocities and modalities, and provide precise data on the length, tension and electromyographic activity of the parent muscles (Hoffer & Loeb, 1980). The body of data now available permits the following generalizations (for review, see Loeb, 1984).

(1) Antigravity, monarticular extensor muscles such as the soleus (ankle extensor) and vastus (knee extensor) have a single period of myoelectric activity which produces tension mostly during muscle lengthening. Spindle primary afferents in these muscles appear to have heightened sensitivity to small changes in this lengthening velocity as a result of dynamic fusimotor activity (Hulliger & Prochazka, 1983; G. E. Loeb, J. A. Hoffer & C. A. Pratt, in press).

(2) Monarticular flexor muscles have a single period of myoelectric activity which produces active shortening. During this period, muscle spindle activity is sustained, presumably by static fusimotor action (Loeb & Duysens, 1979).

(3) The biarticular anterior sartorius muscle (hip flexor and knee extensor) has two periods of electromyographic activity per step cycle. Activity during stance phase is caused by one group of motor units which generate tension under lengthening conditions. Activity during swing phase is caused by a completely independent group

of motor units which actively shorten (Hoffer, Loeb, O'Donovan & Pratt, 1980). Spindle afferent activity tends to be rather heterogeneous, with some units sensitive mostly to the velocity of stretch during stance and others generating most of their activity during the shortening phase in swing. Blockade of gamma motor axons with lidocaine during walking has confirmed that both patterns of activity are influenced by fusimotor activity, presumably static during shortening and dynamic during lengthening (see Fig. 2 and Hoffer & Loeb, 1983).

(4) Cutaneous stimulation during walking evokes a characteristic flexor reflex pattern consisting of excitation in flexor muscles and inhibition of extensor muscles. The bifunctional muscles such as anterior sartorius and rectus femoris participate as flexors during the reflex. However, the excitation includes both the motoneurones that are normally recruited as flexors (active shortening during swing phase) and those that are normally recruited as extensors (active lengthening during stance phase) (Loeb, Marks & Hoffer, 1983).

(5) The hamstrings include another group of biarticular muscles which also generate both swing phase and stance phase activity during locomotion. However, both electromyographical activity periods may result from the same group of motoneurones, according to temporal patterns of depolarization seen in a few motoneurones by intracellular recording during 'fictive' locomotion (activation of the neural step cycle generator in a paralysed, decerebrate preparation; see Perret & Cabelguen, 1975). Interestingly, both periods of active tension development tend to occur during kinematically similar muscle length excursions: brief periods in which the muscle acts as a stiffly elastic strut which first lengthens and then shortens.

TASK GROUPS

One way to account for all of these findings is to suggest that the motor system employs many different types of control principles (see Fig. 1), tailoring the recruitment of muscles and the information flow from their proprioceptors to the tasks at hand. When a muscle is required to perform more than one kinematic type of task (e.g. active lengthening vs active shortening), it may solve the control circuit problem by functionally dividing itself into two separate task-orientated groups. If the muscle's action is needed for a ballistic effort in which feedback control will not be used (e.g. escape or flexion reflex) such divisions may be temporarily ignored so that the entire motor pool is activated. Interestingly, only the alpha motoneurones appear to be recruited in this reflex; spindle gain remains unchanged (G. E. Loeb, J. A. Hoffer & W. B. Marks, in press). In the context of this meeting, it seems useful to pose the question of whether there may be structural or biochemical specializations in these different task groups of muscle fibres that may improve or otherwise change their performance under the particular kinematic conditions in which they tend to be active.

This notion of 'task groups' has the advantage of preserving traditional, linear servocontrol approaches to the use of proprioceptive feedback. It requires only that we recognize that different kinematic conditions require different servo mechanisms.

A corollary of this notion is that the fusimotor control of the muscle spindle should be concerned more with optimizing the sensitivity of the spindle under the kinematic conditions to be encountered than with adhering to any invariant principle such as alpha-gamma co-activation. Thus, the spindle efferents and afferents come to be a specialized part of the task group which includes the particular alpha motoneurones responsible for performing the task. For the kinematically limited conditions of the task, each element performs in a more nearly linear manner than is possible over the larger physiological range. Breaking a complex function into several approximately linear regions is a time-honoured engineering strategy.

However, it may be that this notion only temporarily papers over a larger problem in physiological motor control. It is becoming increasingly clear that the simple mono- and disynaptic pathways for conveying proprioceptive feedback onto motoneurones are not simple nor are they dominant among the pathways impinging on the motoneurones. Interneurones carrying such definitive names as 'the Ib inhibitory interneurone' and 'the Ia inhibitory interneurone' receive inputs from many homonymous and heteronymous receptors, descending pathways and other segmental interneurones, and project onto homonymous, synergistic and antagonistic motoneurones as well as other interneurones (Jankowska, 1983). Even monosynaptic transmission appears subject to complex gating mechanisms such as presynaptic inhibition derived from a variety of local and remote sources. Furthermore, the mechanical delay in the muscles makes the contribution of long interneuronal chains in both the spinal cord and many higher structures potentially much more important than that of the better known local circuits, which can often be severely disturbed experimentally without significant loss of performance.

It seems most unlikely that the proliferation of motor control circuitry now being described by anatomists and physiologists is going to organize itself into patterns as neat as the boxes and arrows of servocontrol theory. This is akin to the problem of sensory perception, which was once similarly 'clockwork' orientated: if you stubbed your toe, a bell rang in your brain. Sensory physiology has begun to cope with the theoretical problems of distributed computation in which the function of the whole is not evident from the structure of the parts. Motor physiology will have to accept similarly abstract concepts and theories and not wait for the circuitry to suggest the function. It will be important to keep in mind that the existing principles of servocontrol represent merely those that have so far been discovered by this actively evolving field of mathematics and control engineering. The existing concepts already have been found to be sorely wanting in the field of robotics and they are being rapidly augmented by new ones. In particular, most control engineering techniques are well known to be quite unsuited to control involving strongly non-linear motors and transducers, exactly what is found almost universally in living organisms. It remains to be seen whether any of the current control theories will survive as useful, if oversimplified, abstractions of real phenomena, or whether they will all be replaced by concepts whose sophistication better matches that of the physiological apparatus and its behavioural performance.

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