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SENSORIMOTOR GAIN CONTROL: A BASIC STRATEGY OF MOTOR SYSTEMS?

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"The whole drama of the voluntary life hinges on the amount of attention, slightly more, or slightly less, which rival motor ideas may receive.... The sense organs and the bodily muscles which favour their exercise are adjusted most energetically in sensorial attention" . William James (1890)

"... the proprio-ceptors of the limb and body segments exhibit no germ of distance-reaction nor of projicience of sensation". (Sherrington, 1906)

"Improvements in the techniques of recording bioelectrical phenomena in nerves and muscles will make it possible to study these processes of set ... during the course of the entire motor act". (Bernstein, 1961).

1. INTRODUCTION

It is a matter of common observation that readiness, attention, intent and attitude can greatly affect motor responses to stimuli. Indeed psychologists have studied these interactions systematically for over a century (Gibson, 1941; Boring, 1957; Watson, 1963). Since the late 1940s, neurophysiologists have repeatedly encountered neural behaviour consistent with the pre-setting of motor systems: preparatory neural discharge has been described in various brain and brainstem areas (Evarts *et al.*, 1984) and preparatory changes in transmission have been extensively studied at the spinal cord level (Gurfinkel and Kots, 1966; Requin and Paillard,

1971) and the brainstem (Ghez and Pisa, 1972). In this review various examples of context- and task-dependent modulation of activity in sensorimotor pathways will be explored, with the aim of better defining the term set as applied to motor control. We will examine the related propositions that motor set is exhibited by nervous systems ranging from the simple to the most complex, and in mammals is mediated at all levels of the nervous system, ranging from the peripheral receptors to the association cortices.

2. SET

Evarts *et al.* (1984) reviewed the changing fortunes of the concept of set over the last few decades. Having come into widespread use after its introduction at the turn of the century (Ach, 1905; Watt, 1905), the term fell out of favour in the 1940s and 1950s. Among other pressures, the tenets of behaviourist psychology militated against unobservable mechanisms such as those hypothesised to 'hold' the excitation delivered by sensory conditioning inputs (Hebb, 1972). However, with the demonstration of 'hard' correlations between electroencephalographic activity, visual attention, and motor action, the concept of set was rehabilitated, ushering in a new phase of research. Information theory provided a conceptual framework, but perhaps more importantly, a major neurophysiological advance exploited by Evarts himself, the recording of the firing of single cortical neurones during voluntary movement (Jasper *et al.*, 1958; Evarts, 1964), soon provided the strongest evidence for task-dependent setting of neural activity.

For the sake of simplicity, Evarts *et al.* (1984) adopted the following truncated version of Woodworth's (1958) definition of set: *a state of readiness to receive a stimulus that has not yet arrived or a state of readiness to make a movement*. The two elements implicit in this definition, namely *perceptual set* and *motor set* were felt by Evarts and his colleagues to be inextricably linked. The definition is simple. Indeed it may be too simple to be particularly useful. For example, does set only exist prior to movement, or does it persist after movements have commenced, as Woodworth (1929) originally proposed? Are cyclical fluctuations in reflex transmission in say stepping, to be regarded as *changes* in set, or as the unfolding of a program of parameter changes which actually *comprises* set? Does "a state of readiness" imply the existence of executive neural centres other than those involved in moment-to-moment control? How is one to measure readiness independently of the changes in neural and muscular activity one supposes to be associated with it? How does the notion of set differ from that of gating? With neurophysiologists increasingly using the term set, it seems an appropriate time to try to pin down its meaning and scope in relation to known patterns of neuronal activity. It will be seen that this exercise reveals common links between certain neural elements not normally associated with one another.

2.1. ORIGINS IN PSYCHOLOGY

Though Wundt (1897) insisted that the science of psychology should only concern itself with mechanisms which could be directly measured, he did acknowledge that subjects' responses to stimuli in reaction time experiments depended upon attention, motivation and prior instruction. In the face of considerable opposition from Wundt, the term 'Einstellung' (attitude, set) was introduced in 1905 by his erstwhile assistant Külpe and the latter's colleagues in Würzburg, Ach and Watt (Gibson, 1941), to describe the internal state of subjects prepared by prior instruction to attend to particular aspects of stimuli about to be presented. The conscious task (Aufgabe) supposedly brought about an unconscious set in the subject, which determined the response to the stimulus. For example, when the instruction was to count objects, subjects were poor at recalling their different colours (Külpe, 1940). When instructed to add, subjects responded to numbers differently than when they were required to subtract (Ach, 1905). To some extent, these observations seem predictable, particularly in the latter case, and so the value of these experiments probably lies mainly in the concepts which led to their design. An interesting result was subsequently obtained which bears on how long a set may last. The question had arisen as to whether set caused irrelevant features to be eliminated at the perceptual stage, or whether they were eliminated from memory after stimulus presentation. Chapman (1932) adduced evidence that both processes occurred, irrelevant aspects which had survived the perceptual filter subsequently being forgotten faster than relevant ones.

The perceptual filter itself came to be associated in the 1950s with a mechanism for generalised arousal, centered on the reticular activating system (Hebb, 1955). The *difficulty* of a task was seen as a 'stressor' which produced measurable external manifestations such as palmar sweating and increased heart rate, and an hypothesised internal modulation of sensory transmission. The separate effect of the *importance* of the task to the subject was studied by Eysenck and his colleagues (1964), who described various types of improved sensorimotor performance in 'high-drive' subjects. It is a matter of common experience that excessive arousal or drive can lead to reduced motor performance, in particular because of the development of tremor, overshoot and other forms of unsteadiness (Kellog, 1932; Eysenck, 1964). At the other extreme, in undemanding situations when sensory input is repetitious and monotonous, arousal and vigilance tends to wane (Deese, 1955). Optimal performance has been postulated to occur at a median level of arousal (Hebb, 1955).

According to Gibson (1941), a difference developed between German and American psychologists in regard to the role of previous experience or habit in the formation of set. In America, set was thought to be the product of previous experience, whereas in Germany this factor was specifically excluded on both conceptual and empirical grounds. The split foreshadowed further serious difficulties. The problem was that set was being used in increasingly disparate situations, and began to mean very different things to different people. Gibson (1941) listed the following variants: mental set, motor set, neural set, voluntary set, unconscious set, postural set, organic set, preparatory set, task set (Aufgabe), situation set, goal set,

temporary set, permanent set, set to react, set to perceive, expectation (expectancy), hypothesis, anticipation, foresight, intention (aim, end, purpose, determination), attitude, directing tendency, determining tendency, tension, vector, need, attention, perseveration, preoccupation.

2.2. CONDITIONING: A FORM OF SET, OR VICE VERSA?

Pavlov (1917) wrote: "Such psychological expressions as the dog guessed, wished, desired, etc., were wholly withdrawn from our use (in our laboratory a fine was even imposed on their use)". Pavlov's stringent rejection of 'mentalist' concepts was taken over by the behaviourist school of psychology, which eschewed the introspective method and notions such as set. Yet, curiously, Pavlov's conditioning experiments were a logical extension of Sechenov's (1863) mentalist view that "when the stimulus is expected, the activity of another mechanism interferes in the phenomenon, restricting and retarding the reflex movement". As elaborated by Pavlov, the 'other mechanism' was in all cases a newly formed 'reflex' pathway. Nebulous terms such as expectation and readiness could be jettisoned, and replaced by the terminology of conditioned reflexes.

With this distance in time, the intensity of the philosophical and political debates surrounding these ideas seems quite odd: Sechenov was nearly brought to trial on the grounds that his theories of reflexes jeopardised criminal justice and social order. Pavlov's ban on anthropomorphic descriptors is less dated, as it had its parallels in behaviourism only two or three decades ago. However, as neurophysiology has advanced, many previously inaccessible processes have been pinpointed within nervous systems, and elucidated in remarkable detail. The perceived need to rigidly segregate psychological and physiological terminology has waned. The question thus arises: can a particular set be viewed simply as a conditioned reflex pathway? Or conversely, is a particular conditioned reflex the end result of an expectancy or setting process? Arguments have been adduced in favour of both points of view (Hull, 1929; Tolman, 1937). This issue is more important for neurophysiology than it may seem. Evarts (1966) and his colleagues were the first to use operant conditioning to study task-related firing of motor cortical neurons in monkeys. In the intervening two decades, the list of chronic single-unit studies involving conditioning techniques has steadily grown (e.g. Fetz and Finnochio, 1972; Porter *et al.*, 1971; Conrad *et al.*, 1974; Smith *et al.*, 1975; Wyler and Prim, 1976; Schmidt *et al.*, 1977, 1978; Thach, 1978; Matsunami and Hamada, 1981; Lemon, 1981; Martin and Ghez, 1985; Lecas *et al.*, 1986).

In line with the original interpretation of 'Einstellung', various psychologists have demonstrated a dissociation between *habit*, formed for example by operant conditioning, and *expectancy*, detected introspectively (Ach, 1905; Schilder, 1929; Schlosberg, 1932). The general finding was that subjects reported expectation of a stimulus, but could voluntarily suppress a conditioned response to it. This dichotomy between expectancy and task-intention was further demonstrated by Hilgard and Humphreys (1938). In the original sense of expectancy then, set clearly excluded conditioning effects. Yet, as pointed out by Gibson (1941), in the broader interpretation favoured by most American psychologists, and incidentally by present-day neurophysiologists, conditioned reflexes came to be viewed as being examples of set. In current psychological terminology, set now tends to be used to describe a more transient state than a conditioned reflex.

2.3. CELL ASSEMBLIES, PATHWAY ACTIVATION

Sechenov's (1863) notion of the formation of new brain reflexes in learning was soon followed by schemata of neuronal circuitry in which such pathways were formed by the hypothetical process of 'draining' (William James, 1890). Donald Hebb (1949, 1959) produced similar schemata of so-called 'cell assemblies', in one of which the *Einstellung* experiment of Ach (1905) was specifically represented. 'Draining' was supplanted by synaptic plasticity. The underlying theme, restated in the new terminology, was that learning, set and behaviour in general depended upon central mediating processes which altered the transmission of sensory information. Indeed this concept underlies much of present-day cognitive psychology (Posner, 1978). The point has now been reached where synaptic plasticity has been shown conclusively to underly various forms of sensitisation and habituation of primitive reflexes in specific species (Kandel, 1984). A newly learnt behaviour is thus associated with a functional change in transmission at specific synapses. The functional change is attributed to changes in the molecular structure of membrane channels.

As mentioned above, a problem with the term set is that it may have become too all-inclusive to be particularly useful. One option from a neurophysiological point of view, would be arbitrarily to limit its use to describing short-term neural states not involving structural changes at synapses. However, synaptic plasticity has been demonstrated in short-term as well as long-term sensitisation: a few exposures to a noxious stimulus produces sensitisation to a variety of other stimuli (Castelluci *et al.*, 1978) and this is associated with a modification of pre-existing macromolecules (Kandel and Schwartz, 1982). At this stage it is impossible to known how transient a behavioural state has to be *not* to be accompanied by structural changes at synapses, and so the above option for defining set has to be shelved, at least for the time being.

3. NOMENCLATURE: PARAMETERS vs VARIABLES

Control theory, information theory and cybernetics have provided some new analogies, new terminology and arguably, new insight. In a feedback loop, each element receives an input, and transmits it, generally in modified form, to the next element in the loop. The modification might be a simple amplification, but often dynamic changes are also involved. In a linear system, a *transfer function* describes each such modification. Generally the transfer function is a differential equation, often expressed as a Laplace

transform for ease of manipulation, relating an output variable to an input variable. The constants multiplying each differential coefficient are called parameters. For example, the equation relating the displacement $x(t)$ of a mass m due to a force $F(t)$ applied through a spring of stiffness k is:

$$F(t) = kx(t) + \frac{m\,\mathrm{d}^2x(t)}{\mathrm{d}t^2}.$$

$F(t)$ and $x(t)$ are variables (in this case functions of time t) and k and m are parameters. Taking the Laplace transforms and transposing, the transfer function, i.e. the ratio of output (displacement) to input (force), is:

$$\frac{x(s)}{F(s)} = \frac{1}{k + ms^2}$$

where s is the complex frequency. It is clear from this equation that variations in the parameters k and m will affect the gain and frequency response of the system.

In most man-made servo systems, the parameters are chosen and set so that the servo provides optimal control of the output variable, while remaining stable under all loading conditions. Parameters in physical systems can vary or 'drift' with time, and this can result in potentially catastrophic instability. There are therefore well established techniques for analysing the effect of parameter variation on closed-loop stability and performance (e.g. the root locus method, Nyquist diagrams etc.: Dorf, 1987). In advanced control mechanisms, additional flexibility is obtained by varying the parameters of the loop to optimise performance for particular tasks or loads. Programs controlling the time course of parametric variation are called 'parameter schedules'. For example, in a robot arm, stability criteria might dictate conservative parameter settings during load moving, but the loop gain can safely be increased once the arm becomes unloaded, so that speed and accuracy are improved. A further level of sophistication is introduced when parameters are changed so as to alter the relative weighting of two or more modalities of feedback. In robotics, control loops of this sort are referred to as hybrid systems. The analysis of such loops is sometimes easier in the time domain, with the selection of a number of state variables which allow the system's behaviour to be described in a set of simultaneous differential equations (Dorf, 1987). The parameters themselves may be treated as state variables, and the equations may be solved using digital or analog computers. Furthermore, linearity is not a prerequisite for this form of analysis, in contrast to classical frequency domain analysis.

Hybrid control with multiple feedback pathways is precisely what one is dealing with in mammalian neurophysiology. Taylor and Gottlieb (1985) suggested that in mastication, the control of jaw displacement and velocity is crucial until the moment of tooth contact, whereupon the control of force becomes more important. Taylor and Gottlieb made the important point that the nature of the controlled variable was determined by the nature of the feedback signal. Applying this to multivariate feedback, the weighting of the controlled (state) variables is determined by the relative magnitudes of the feedback parameters. In terms of neuronal circuitry in the above example, the parametric switching from movement to force control could be mediated by a mechanism as simple as presynaptic inhibition of spindle afferents by peridontal afferents or their interneurons.

In principle, the relative weighting of parameters could be continuously adjusted on the basis of information from a wide variety of sensors, and on hypotheses or predictions about the task at hand and its context. These ideas, which are commonplace in the field of robotics (Snyder, 1985), have much in common with Einstellung (attitude), Aufgabe (task) and set. It will be argued below that parameter control as a concept is useful in sharpening up the working definition of set, particularly from the viewpoint of neurophysiology.

4. STATE-DEPENDENCE OF MAMMALIAN REFLEXES

4.1. Changes Prior to Movement

William James (1890) and Sherrington (1906) both noted that muscle tone tends to increase in anticipation of movement. They explicitly rejected any change in sensitivity of peripheral receptors. Sherrington's view was that "distance receptors" (visual and auditory) "induce anticipatory or precurrent reactions", whereas the reflexes of certain non-distance receptors (e.g. lip and gustatory receptors) "stand in very close relation to consummatory events" (i.e. motor acts). The distance receptors "give the stimulus increased force.... not by altering the external stimulus, nor the receptor organ, but by, among other alterations, altering internal connections of the receptor arc".

Bassin and Serkova (1956) obtained electromyographic evidence of anticipatory muscle tone, which they dubbed the "ideomotor reaction". Bernstein (1961) maintained that the CNS achieves "anticipatory adaptations in terms of the tuning in advance of the arousal of all the sensory and motor elements which are employed". However, it was not until the mid-1960s that quantitative studies were performed of changes in tendon jerk and H-reflex responses prior to movement. Groups in the USSR (Gurfinkel, Kots and colleagues) and France (Paillard, Requin, Pierrot-Deseilligny, Coquery and others) systematically investigated the time course of adjustment of these presumed monosynaptic reflexes, and the effects of muscle task, choice (task complexity), training and other variables. Most experiments were of the following type: an auditory or visual warning signal was given, and after an interval of up to one second a 'go' signal instructed the subject to respond with a fast movement usually of the foot. In nearly all cases, tendon and H-reflexes altered significantly during the preparatory inter-signal interval. However, there were surprisingly large differences between the observations in the different laboratories. The Russian workers described sustained *increases* in both Hoffman (H) and tendon jerk (T) responses (Gurfinkel and Pal'tsev, 1965; Gurfinkel and Kots, 1966; Kots, 1977). The increases were larger if the muscle was an agonist in the up-coming movement (ca. 35–40% increase prior to 'go', rising to 80%

in the final 60 msec before contraction; c.f. antagonist: 15–20% increase which remained steady throughout the pre-contraction period). Other workers found similar H-response time courses in agonists, but decreases in the antagonists starting some 200 msec prior to agonist contraction (Coquery and Coulmance, 1971; Gottlieb *et al.*, 1970; Pierrot-Deseilligny *et al.*, 1971). Tanji and Taniguchi (1976) found that triceps surae H-responses in the preparatory period were inhibited by conditioning stimuli applied to antagonist afferents. To further complicate the picture, Requin and Paillard (1971) described small and transitory (ca. 200 msec) increases in H-responses after the warning signal followed by pronounced *decreases* until the go signal, whether in agonist or antagonist. Sustained increases were only seen in muscles in a limb not required to contract.

Brunia (1980) and Scheirs and Brunia (1985) have since carried out similar experiments, specifically to test for differences between muscles involved in the task and those not involved. H- and T-responses showed a sustained augmentation after the warning signal for up to four seconds prior to movement, irrespective of muscle involvement. These results were at odds with some of the authors' own earlier observations, and so Scheirs and Brunia (1985) speculated that increased task complexity might convert reflex time courses from the muscle-specific patterns seen by Requin and Paillard (1971) to the simpler diffuse increases described by Kots (1977). Another possibility was that in the earlier studies there might have been an undetected anticipatory tensing of involved versus non-involved muscles. Curiously, only Scheirs and Brunia (1985) were at pains specifically to control for this variable in their trials. Recently, Riedo and Rüegg (1988) confirmed that H-responses are facilitated in anticipation of movement even when the background EMG is maintained at a constant level.

Taken together, these results all point to modest changes in H- and T-responses commencing well before movement, with time courses which are quite task-dependent and variable between subjects. Despite the differences in experimental results, three very similar schemata, each dividing the preparatory period into three stages, emerged from these studies (Fig. 1). The stages were variously termed "pre-tuning, tuning and triggering" (Kots, 1977), "presetting, triggered processing and output processing" (Requin, 1985) and "stimulus bound generalised activation, response bound generalised activation and selective activation" (Brunia, 1980). In each case, the build up to movement was seen as proceeding from a diffuse increase in reflex transmission through a transitional stage, to a large focussed change starting 50–80 msec before muscle activation. The first stage, being stimulus-dependent, was interpreted in terms of perceptual set, whereas the final stage, being tightly linked to the task, was associated with motor set (Requin, 1985).

4.2. Instruction- and Task-Dependence of Human Long-Latency Reflexes

Prior instruction to subjects either to resist an imposed movement or to 'let go', has a large and functionally appropriate effect on the EMG responses observed (Hammond *et al.*, 1956). It is generally accepted that the short-latency components of response (15–25 msec in arm muscles) are much less instruction-dependent that the long-latency components (over 40 msec: Lee and Tatton, 1975; Evarts and Granit, 1976; Mortimer *et al.*, 1981; Marsden *et al.*, 1983). The short-latency components are therefore thought of as being more 'reflexive', that is to say they are more automatic and less subject to volitional change. Indeed the very use of the term 'reflex' to describe the long-latency responses has been questioned: "preprogrammed responses" (Dewhurst, 1967) and "triggered responses" (Crago *et al.*, 1976) have been suggested as being more fitting descriptors. There has also been much debate as to whether the long-latency responses are mediated segmentally (Matthews, 1984; Cody *et al.*, 1987), or via long-loop transcortical pathways (Lee *et al.*, 1983; Marsden *et al.*, 1983).

The issue is not just a semantic one. If the responses are mediated by the spinal cord, their modification by prior instruction could only occur by the setting of segmental transmission parameters in anticipation of the stimulus. The elucidation of the pathways and interneurons involved might just be within the grasp of existing neurophysiological techniques. If on the other hand the responses are mediated by complex and experimentally inaccessible supraspinal pathways, the task of identifying these and characterising transmission through them is probably beyond current methodology. In other words, even if instruction-dependence does result from a pre-setting of supraspinal transmission parameters, it is hard to see how this could be verified and unravelled in the foreseeable future.

On the other hand, irrespective of the CNS locus, by manipulating the relationship between sensory input and task, one can study whether or not the responses change with expectation in the way one would expect from adaptive transmission in sensorimotor pathways: is there a tight, albeit new transformation of stimulus to response (parameter variation), or is the relationship variable and better described as a non-specific triggering of a new motor program? Long-latency (120 msec) responses in human leg muscles elicited by rotational and translational movements of a supporting platform showed task-dependent adaptations consistent with parameter control (Nashner, 1976): responses which were 'inappropriate' in that they resulted in increased body sway were progressively attenuated in the course of four or five stimulus repetitions. Interestingly, subjects could not voluntarily hasten this process. Nashner argued that changes in the set underlying the responses, which, incidentally, he referred to as functional stretch reflexes, were "compelled by unexpected changes in the task, not by prior instructions". The necessity for a change in set could be realised only *after* experiencing an inappropriate response. In thumb positioning tasks, Akazawa *et al.* (1983) found that the amplitude of long-latency responses to stretch increased with three levels task difficulty. The responses themselves had a characteristic time course which commenced at a fixed latency after the stretch, and the changes were in size rather than shape, that is to say amplitude rather than time course. Again, it

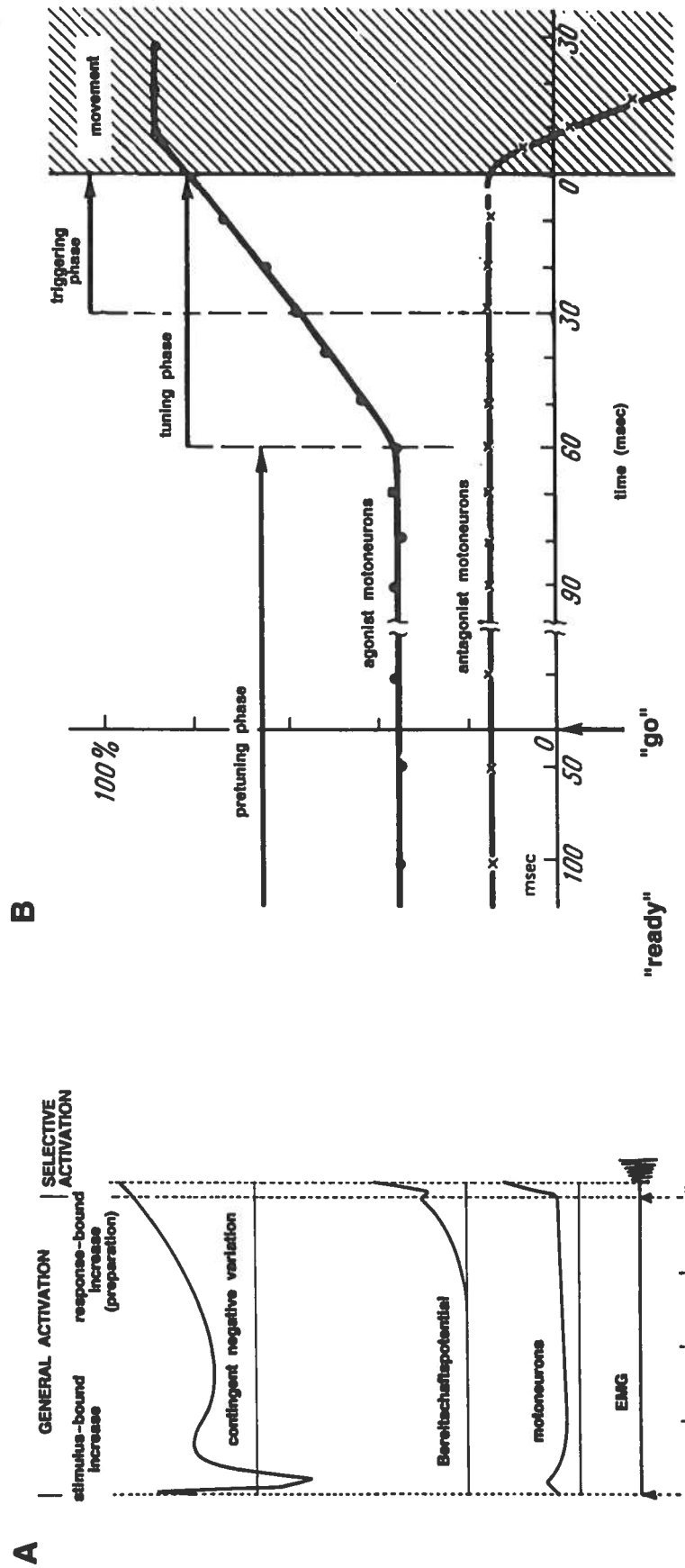

FIG. 1. Changes in cortical electroencephalographic potentials and spinal reflexes prior to voluntary movement. A: schematic time course of (1) contingent negative variation: the potential recorded over sensorimotor cortex in the fixed interval between a warning signal ("ready") and an imperative trigger signal ("go"); (2) Bereitschaftspotential (readiness potential): scalp potential recorded prior to self-paced movements (no "ready" signal); (3) Hoffmann (H) or tendon jerk (T) reflexes; (4) electromyogram (EMG). Reproduced with permission from Brunia (1980). B: schematic time course of H reflex amplitudes, showing the preparatory period divided into three stages: pre-tuning, tuning and triggering. The warning signal produces increases of 30–40% in homonymous reflexes (agonist) and 10–20% increases in the antagonist reflexes. Reproduced with permission from Kots (1977).

seems more sensible to view this as a graded change in transmission characteristics, rather than a triggering of three different motor programs.

In an intriguing recent study, Gielen *et al.* (1988) found dissociations of the short (25–50 msec) and long (50–75 msec) latency components of response in human arm muscles to imposed forearm perturbations. *M. triceps* and *m. brachialis* showed long-latency responses (increases and decreases respectively) to sudden forearm pronation, even though the muscles were not stretched. These responses, which occurred in combination with responses in *m. biceps* and *m. brachialis*, corresponded well to coordinated activation recorded separately in voluntary contractions against steady loads in the same directions as the perturbations. Again the question arises, were the long-latency responses triggered programs, or were they due to task-related re-routing of the afferent input? It should be noted that some subjects can produce voluntary biceps EMG within 60–70 msec of a tap applied to the contralateral hand within a second or so of a warning stimulus (personal observations, see also Evarts and Granit, 1976), so it is debatable that the 50–75 msec responses were purely 'reflexive'.

In spasticity, much is made of the increase in transmission in the monosynaptic reflex arc. However, after a little practice, some hemiparetic patients can set the level of muscle contraction and reflex responsiveness on their unaffected side so that EMG responses to biceps stretch are virtually indistinguishable from those on the affected side (personal observations, see also Powers *et al.*, 1989). The striking difference is that the responses on the affected side cannot be changed voluntarily. It is as though the lesion unilaterally disables task-dependent setting of transmission parameters, which instead remain fixed at 'default' values. After spasticity, the second most frequent motor control disorder is Parkinson's disease. In this condition too the long-latency responses to stretch tend to be relatively fixed, often at an inappropriately high level (Lee *et al.*, 1983). The setting of reflex gains to default values recalls Bernstein's (1940) description of motor learning: "when someone who is a novice at a sport, at playing a musical instrument or at an industrial process first attempts to master the new coordination, he is rigidly, spastically fixed and holds the limb involved, or even his whole body, in such a way as to reduce the number of kinematic degrees of freedom which he is required to control."

4.3. Modulation of Spinal Reflexes During Rhythmical Movements

The words Einstellung and set both imply a certain degree of stationarity. If something is set to a new state, it should remain that way for some time. On the other hand, if it continuously varies, then the only way in which set could legitimately be applied is in reference to the overall program or schedule which determines the modulated behaviour. Indeed Woodworth (1929) used set in precisely this latter sense, giving as an example a sequence of widely ranging intermediary actions necessary to achieve a particular goal.

During locomotion in cats, reflexes elicited by cutaneous stimuli are deeply modulated within each step cycle, producing net flexion in the swing phase and net extension in the stance phase (spinal cats: Forssberg *et al.*, 1975; thalamic cats: Duysens and Pearson, 1976; normal cats: Prochazka *et al.*, 1978; Wand *et al.*, 1980). H and T reflexes are also strongly modulated in the step cycle (mesencephalic cat: Akazawa *et al.*, 1982; normal human: Capaday and Stein, 1986; Llewellyn *et al.*, 1986) as are reflexes mediated by joint afferents (Andersson and Grillner, 1981). Phase dependent modulation of stretch reflexes has been observed in human arm muscles involved in sinusoidal tracking movements (Dufresne *et al.*, 1980). Phasic control of transmission has also been demonstrated in rhythmical masticatory movements in cats and monkeys (Lund and Olsson, 1983).

Clearly the modulation of reflex transmission during rhythmic movements is a well established and generalised phenomenon. Furthermore, it seems quite possible that the transmission of information ascending to and descending from the higher centres is also cyclically modulated. The key question in the present context is whether set is an appropriate term to use in relation to modulated transmission in a rhythmical movement.

In his review on locomotion, Grillner (1975) speculated on the interaction between reflexes and the central pattern generator. *Reflexes were "prepared to operate but (were) without any effect so long as the movement proceeds according to the set central program." They were "set to provide the appropriate compensation during locomotion" in such a way that their "effect would not perturb the locomotion."* In Grillner's view, supraspinal drive set the level of activity of spinal pattern generators to run stereotyped programs, of which phasic control of reflex transmission was an integral part.

Nashner (1980) used set in a similar way in describing the adaptive control of human gait. Figure 2 shows Nashner's schematic, in which the adaptive element "receives both the anticipated signals and the sensations correlated with the actual leg movements, detects specific discongruent features between these two complex patterns, and then transforms these discongruent features into the appropriate parametric commands." This scheme is in fact a slightly altered version of the reafference principle of von Holst and Mittelstaedt (1950). The use of the term parameter is related to, but different from that outlined in the discussion above on nomenclature: rather than being gain factors in differential equations of motion, parameters in Nashner's useage are peak amplitudes of variables such as joint displacement or velocity. In a linear system, peak amplitudes are proportional to gain factors. However, if the gain factors themselves vary, for example with time, their relationship to peak amplitudes can be complex, and the two meanings of 'parameter' diverge.

Nashner makes an interesting distinction between two kinds of input which in his model are summed to set the movement parameters: 'volitional' inputs, which are constant or slowly varied during the task, specify the rate and pattern of say stepping most appropriate to the expected terrain; 'postural' inputs, which may vary rapidly from one step to the next in

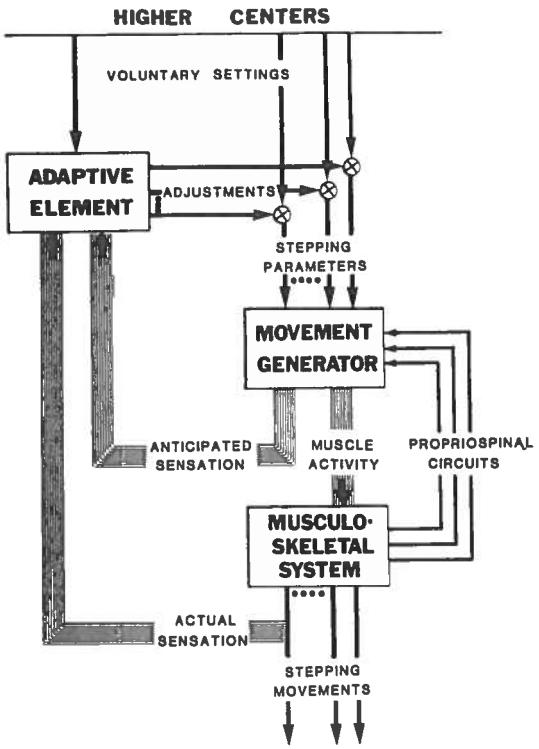

FIG. 2. Nashner's (1980) model of how stepping parameters of locomotor movements of the legs are adjusted by sensory responses to perturbations. Solid lines represent single-variable signals, parallel lines represent multivariate signals. Equivalent terms used by von Holst and Mittelstaedt (1950) were: efference copy (anticipated sensation); reafference (actual sensation); re-efference (adjustments). Reproduced with permission.

response to unexpected events, adjust the voluntarily set parameters. This view places somewhat more emphasis on sensory involvement than that of Grillner, but both echo Woodward's interpretation of a particular set as incorporating a detailed sequence, or subordinate program of action, tailored to meet a particular goal.

The problem with this interpretation is that it is rather open-ended. Where does the executive mechanism end and where does the subordinate program start? At what level of the CNS should the set commands be sought? Can criteria be defined to allow set commands to be differentiated from subordinate program commands? Locomotion provides a good testing ground for developing answers to these questions, and we shall return to this in the final section of this article.

5. STATE-DEPENDENCE OF INVERTEBRATE REFLEXES

Technically it is far easier to record from identified neurons mediating reflex responses in invertebrates than it is in the higher vertebrates. Consequently it has been possible to build up a fairly complete picture of the neuronal mechanisms underlying certain primitive behaviours and, as mentioned earlier, to elucidate in great detail the synaptic plasticity which underlies the sensitisation of these reflexes (Kandel, 1984).

There are some remarkable similarities in the neural mechanisms for motor control in certain invertebrates and in mammals, including humans. For example, the reflex phase reversals in mammalian locomotion referred to above are also seen in crustacea (DiCaprio and Clarac, 1981; Clarac, 1985) and insects (Bässler, 1983, 1986). Even in the periphery there are close parallels: the sensivitity of crustacean thoracico-coxal proprioceptors is under CNS control in a manner directly analogous to that in mammalian muscle spindles (Bush, 1981). At a conceptual level, the debate over the last few years about the autonomy of central pattern generators has centered around data obtained in invertebrates as well as vertebrates (Grillner, 1984). In terms of set, studies of the neural control of various motor behaviours in the stick insect (Bässler, 1983; Weiland and Koch, 1987) are of particular interest. Bässler and his colleagues systematically measured the gain of the femur–tibia stretch reflex in the resting animal and during walking, stimulus-evoked arousal and catalepsy (the slow return of a passively displaced limb) and rocking. At rest and in walking, stretch reflex gain was low. Gain was high in catalepsy or after the animal had been disturbed by a touch to the abdomen. In some species gain was also high in rocking behaviour, the reflexes evidently 'tuning' limb impedance to a minimum at the frequency of the centrally generated motor rhythm (Weiland *et al.*, 1986). Other state-dependent reflex adjustments have been described in crabs (DiCaprio and Clarac, 1981) and locusts (Zill, 1985), notably amongst them an increase in gain during exploratory movements. At least four conditions each with a characteristic reflex gain have thus been identified unequivocally: rest, arousal, stepping and active touch.

Bässler (1983) coined the term *program-dependent reactions* to describe these effects, the program being "a set of 'instructions' for directing basic motor neuron operations and/or appropriate responses to particular afferent input and/or to information from other parts of the CNS." The depression of stretch reflex gains in insect locomotion (Bässler, 1983) has also been observed in crustacea (Barnes, 1977). In the latter, it was noticed that during unexpected slips, stretch reflex gain was restored. It was hypothesised that the proprioceptive signals were compared to those "expected" from efference copy, and if the mismatch was large, stretch reflexes were disinhibited. This is strikingly similar to both Grillner's (1975) and Nashner's (1980) views quoted above, and again stems from von Holst's (1950, 1954) reafference principle. It also has some interesting parallels in other mammalian studies: Coulter (1974) suggested that in the dorsal column nuclei, incoming corollary discharge might be subtracted from movement-related sensory input before transmission to cortex; muscle spindle sensitivity adjusted via fusimotor neurons is low during gait in cats (Prochazka *et al.*, 1985), and increases in novel or difficult tasks (Prochazka *et al.*, 1988); in human calf muscles the gain of short-latency stretch reflexes is lower in walking than in standing (Capaday and Stein, 1986; Llewellyn *et al.*, 1986), and lower still in running (Capaday and Stein, 1987).

These striking similarities suggest that we may be dealing with a strategy of control which is very generalised across phyla: stereotyped movements performed in a familiar context are associated with low sensorimotor gains, whereas arousal, novelty, or the performance of demanding tasks are associated with higher gains. Further examples of state-dependent transmission will be described below, and in the final section of this paper we will examine the pros and cons of describing such strategies in terms of set.

6. DESCENDING CONTROL OF PROPRIOCEPTION IN MAMMALS

6.1. ALPHA–GAMMA INDEPENDENCE?

Until the late 1970s, most researchers felt that the role of the efferents innervating muscle spindles (fusimotor (γ-moto-) neurons) was to keep the spindles taut during active muscle shortening. On this view, fusimotor neurons were simply linked to, or co-activated with α-motoneurons, and were never separately activated (Granit, 1955, 1979; Matthews, 1972). Yet the early studies of fusimotor activation had in fact provided good evidence for independence: electrical stimulation of various CNS centres led to diffuse, tonic changes in fusimotor action, often unrelated to muscle contraction (Granit and Kaada, 1952; Granit *et al.*, 1955). Stimulation in the reticular formation was particularly effective, and this naturally led to speculation about a possible role for the fusimotor system in arousal and expectancy. However, such ideas soon fell out of favour and were replaced by the α–γ co-activation hypothesis.

Though co-activation soon became the expected norm, researchers continued to encounter tonic fusimotion during phasic α-activity. In the respiratory system, Sears (1964) and Corda *et al.* (1966) found that a component of fusimotor action was steady and independent of α-activation (recently corroborated by Greer and Stein, 1986). This was thought at the time to be related to a postural role of the intercostal muscles, rather than having anything to do with sensitivity-setting. Vestibular stimulation (Andersson and Gernandt, 1956; Poppele, 1967) in some cases evoked tonic fusimotor action independently of α-motoneuronal activation. Following the discovery that fusimotor action was of two distinct types, static and dynamic (Matthews, 1962), evidence was adduced that dynamic fusimotion, which greatly increases the stretch-sensitivity of spindle primary Ia endings, was less coupled to α-activation than static fusimotion, which increases spindle 'bias' (tonic firing) but reduces Ia stretch sensitivity (Bergmans and Grillner, 1969; Grillner *et al.*, 1969). A case was made for the existence of a region of the midbrain specialised for the selective activation of the dynamic fusimotor system (Appelberg, 1962, 1963, 1981; Taylor and Donga, 1989). Recently, the substantia nigra pars reticulata has been implicated in selective setting of static fusimotion (Schwartz *et al.*, 1984).

6.2. FUSIMOTOR SET

In the mid 1970s, techniques were developed which allowed the recording of spindle afferent discharge in cats and monkeys performing natural movements. It was immediately obvious that spindle afferents often fired as though they were signalling muscle length, albeit with dynamic, non-linear characteristics (Taylor and Cody, 1974; Goodwin and Luschei, 1975; Prochazka *et al.*, 1976, 1977, 1979; Loeb and Duysens, 1979). This was at odds with the expected outcome of α-coactivated fusimotion, namely that spindle discharge would be held more or less constant in the face of muscle length variations (Phillips, 1969). In fact the patterns of spindle afferent firing in the musculature involved in stepping and chewing were suggestive of steady fusimotor drive of the static type (Prochazka *et al.*, 1976; and in retrospect, Cody *et al.*, 1975). The anticipatory setting of such drive was evident hundreds of msec before movement (Prochazka *et al.*, 1975).

It was also noted that large increases in spindle primary sensitivity nearly always occurred when movements were imposed on an animal (Prochazka *et al.*, 1977; Prochazka and Wand, 1981). Yet such was the hold of the α–γ linkage concept, that the significance and reproducibility of this finding was only appreciated after many repeated observations. The need for a reappraisal of fusimotor control then gradually became clear and led to the formulation of the fusimotor set hypothesis (Prochazka, 1983; Prochazka and Hulliger, 1983; Prochazka *et al.*, 1988b). On this new view, fusimotor action is minimal in the resting animal; in routine, stereotyped movements it is set to low levels and is largely of the static type; as movement speed increases dynamic fusimotor action may also increase, but the full power of fusimotion is reserved for novel and/or difficult tasks, where strong dynamic action causes very large increases in spindle primary responses to muscle displacement. This is a major departure from previous ideas of proprioception. The role of the fusimotor system is not to compensate automatically for muscle shortening, but rather to allow state-dependent parametric adjustment of length and velocity feedback. Proprioceptive sensitivity is adjusted at its source by the CNS according to the overall sensorimotor requirements predicted for upcoming movements.

This view is by no means universally accepted. Alternative schemes propose partial α–γ independence, with only one type of γ linkage (Appenteng *et al.*, 1980; Gottlieb and Taylor, 1983: γ_s linked; Murphy *et al.*, 1984; Larson *et al.*, 1981, 1983: γ_d linked; Loeb *et al.*, 1985a, b, c: γ's linked to 'task group'). Most of the human neurography studies have provided continuing support for α–γ linkage (Hagbarth, 1981; Gandevia and Burke, 1985) though in recordings from presumed fusimotor fibres, firing increased independently of α-activity, and in relation to context and task (Ribot *et al.*, 1986). For technical reasons, there are severe restrictions on the freedom of movement of subjects in single fibre neurography. In fact the situations in which dramatic changes in fusimotor set have been detected in cats are probably out of the reach of current neurographic techniques in humans.

The controversy surrounding fusimotor control is partly due to the absence of recordings from convincingly identified fusimotor fibres during voluntary movement. The current theories are therefore based

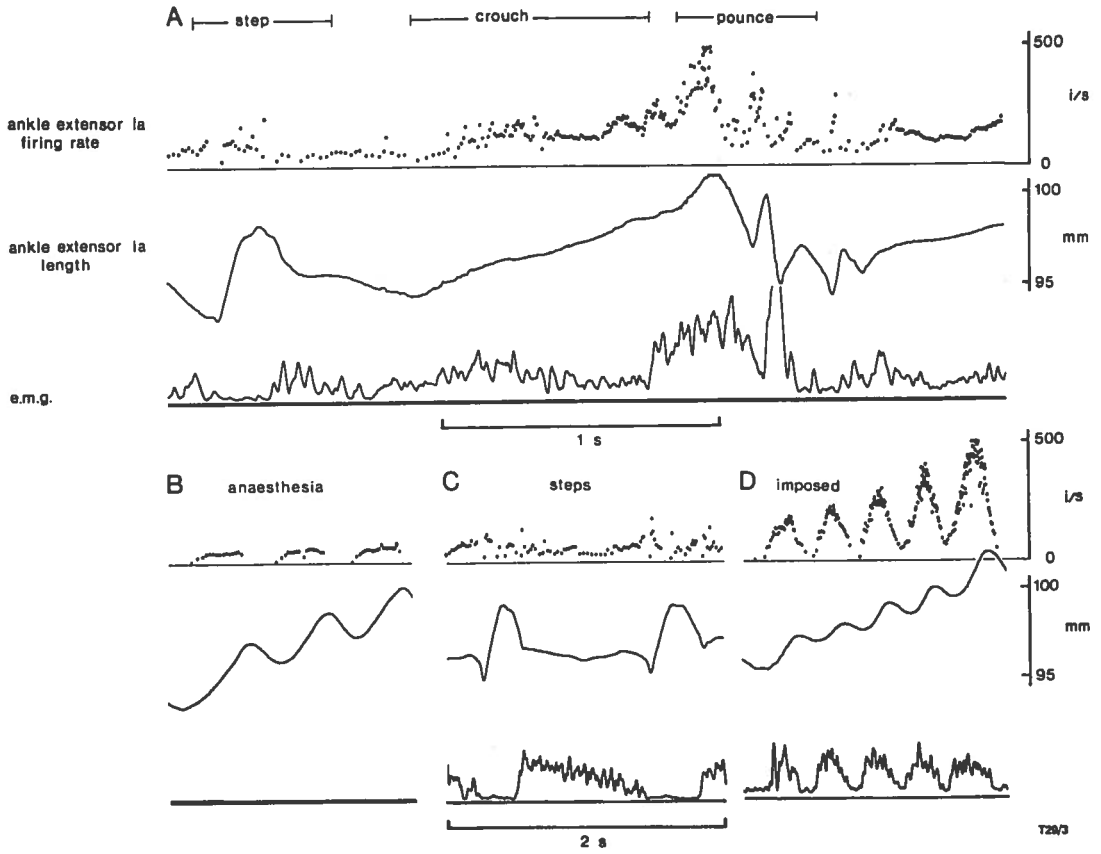

FIG. 3. Task-dependent responsiveness of a cat spindle primary ending. Top trace: instantaneous firing rate of the ending; middle: origin-to-insertion muscle length; bottom: EMG of receptor-bearing muscle. (A) Discharge during a normal step (left), then a crouch and pounce at a moving toy. Note the increased responsiveness of the spindle to muscle length variations during the crouch and pounce. (B) Stretch responses during deep anaesthesia (fusimotor action assumed abolished). (C) Firing during two normal steps, indicative of steady, low-level static fusimotor action. (D) Very high sensitivity to imposed stretches in the normal animal, indicating dynamic fusimotor action. Previously unpublished.

largely on inferences about fusimotion derived from spindle afferent firing recorded during voluntary movement. Even when these inferences are carefully verified in separate acute experiments (Hulliger *et al.*, 1987), there are limits to the resolution possible: in some cases a given pattern of afferent firing can be obtained by different admixtures of fusimotor activity; fusimotor stimulation can be altered over a certain range before causing clear and significant changes in spindle afferent firing; doubt lingers as to the error introduced by discrepancies between origin-to-insertion length and the length 'seen' by spindles (Griffiths and Hoffer, 1987; Hoffer *et al.*, 1989; Prochazka *et al.*, 1988a). However the situation is not as disadvantageous as it might be. Spindle afferents are innervated by up to 12 fusimotor fibres, whose action summates non-linearly. Access to the afferent firing patterns allows an assessment of net fusimotor action, which, paradoxically, would be difficult to estimate from the firing of random fusimotor fibres, even if their type (static or dynamic) could be ascertained. This is not to deny that recordings from fusimotor neurons would help in choosing between the current theories.

6.3. CONTEXT

When the changes in offset firing and stretch-sensitivity of identified spindle endings are large, there can be little doubt about the occurrence of state-dependent fusimotion. The previously unpublished record which in fact gave rise to the fusimotor set hypothesis is shown in Fig. 3A. The firing of one and the same ankle extensor spindle primary afferent in a cat is shown in a number of different situations: responses to imposed muscle stretch with the cat deeply anaesthetised (B) and awake (D); during normal stepping (A, first part, and C); and during the build-up to and execution of a pounce on a small moving toy. The afferent responded dynamically to muscle length in each segment. However its tonic firing was elevated in active steps compared to anaesthesia, suggesting static fusimotor drive; its stretch sensitivity was greatly elevated in imposed movements and during the crouch/pounce, suggesting increased dynamic fusimotor drive. The sustained large increases in Ia afferent sensitivity during imposed movements are very reproducible, and have always been something of a puzzle. Why should the cat 'choose' to increase

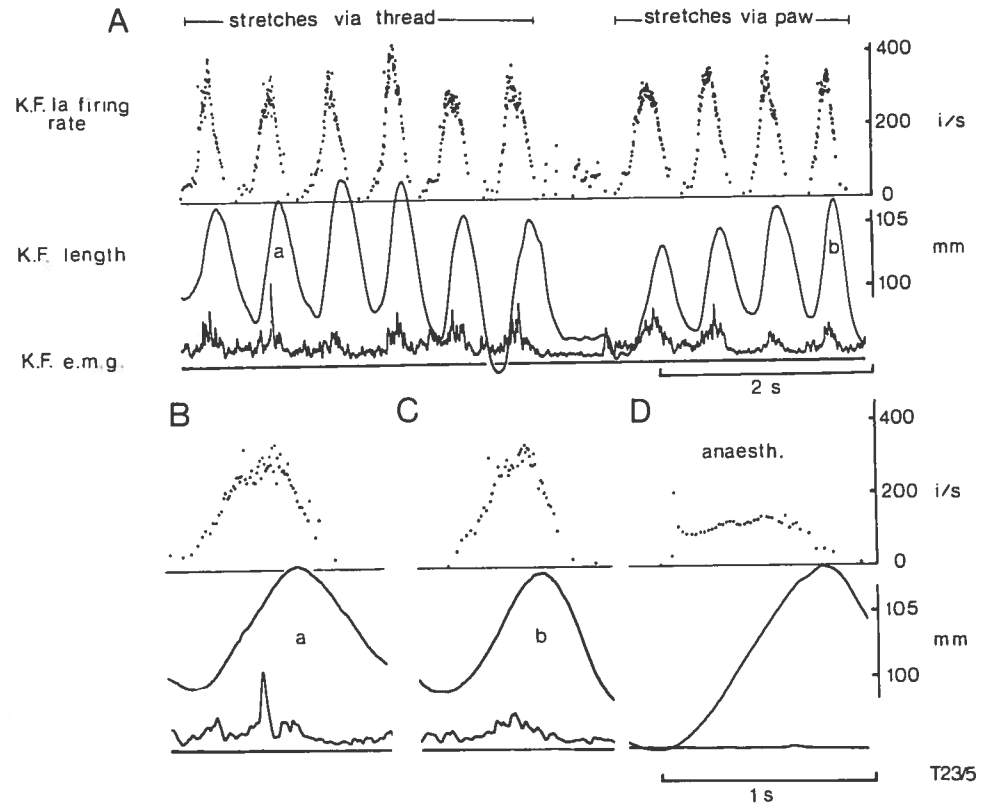

FIG. 4. Data indicating that the inferred dynamic fusimotor set in the context of imposed movements as illustrated in the previous figure is not just a reflex response to cutaneous stimulation. A: Movements were imposed by the experimenter (i) holding the cat's paw and (ii) pulling on a thread implanted percutaneously in the femoral epicondyle. The sensitivity of the knee flexor Ia ending was identical in these two situations (cf. B, C: which show cycles (a) and (b) from panel A), and elevated above that in anaesthesia (D: fusimotor action assumed abolished). Previously unpublished.

proprioceptive sensitivity in this seemingly innocuous situation? The answer may be that a cat unused to handling reacts warily. Though it may not be evident in its behaviour, sensory transmission has been increased 'just in case'. Wall (1975) suggested something similar for the dorsal column/medial lemniscal system, such that in stereotyped movements, sensory information is heavily attenuated, but that the attenuation is withdrawn in novel situations. Increased neuronal firing when an animal is handled or even approached by a human hand is well documented for parietal cortex (Mountcastle *et al.*, 1975; MacKay and Crammond, 1987).

An alternative explanation could be proposed for the sensitisation of spindle primaries in imposed movements: dynamic fusimotor action may simply be due to a reflex response to the associated cutaneous stimuli. However observations such as those in Fig. 4 refute this idea. Movements in this experiment were imposed in two quite different ways: one by holding the paw in the usual way, and the other by pulling on a percutaneous thread implanted in the lateral femoral epicondyle, so that there was little if any cutaneous stimulation at the point of application of force. The sensitivity of the spindle primary ending was indistinguishable in these two situations, and elevated far above that in the absence of fusimotor drive. This speaks strongly for a diffuse fusimotor activation in response to the overall situation the animal found itself in. Three levels of fusimotor action are thus portrayed in Figs 3 and 4: (1) negligible fusimotion during anaesthesia (also seen in resting, awake cats); (2) moderate static fusimotion during slow stepping; (3) greatly elevated dynamic fusimotion during imposed movements and vigilance. Enhanced dynamic fusimotor action has also been implicated in landing from falls and in the paw-shake response (Prochazka *et al.*, 1989a).

6.4. FUSIMOTOR MODULATION OF STRETCH REFLEX GAIN

Does the build-up of fusimotion hundreds of msec prior to movements parallel and contribute to anticipatory changes in H-responses and tendon jerks (T-responses)? Put another way, are the increases in T-responses (or even the H-responses) attributable to fusimotor sensitisation of spindles? Unfortunately, the time courses of fusimotor action and reflex amplitude have not been studied under identical or even similar conditions, so there is no direct evidence in this regard. Furthermore, fusimotor action does not alter spindle responses to tendon taps nearly as much as previously supposed (Gregory *et al.*, 1977): the pulsatile stretches involved probably saturate the spike generating mechanism. Therefore even very

large anticipatory increases in dynamic or static fusimotion would not of themselves increase T-responses significantly.

On the other hand, responses to longer-lasting stretches would certainly be expected to change. This in turn should show up in alterations to the so-called long-latency reflex responses (e.g. Hallett *et al.*, 1981). Gottlieb and Agarwal (1980) imposed rapid maintained perturbations at different times prior to and during phasic voluntary ankle movements in human subjects. Though there were preparatory increases in the long-latency reflexes, they were smaller than the changes in the short-latency reflexes. Furthermore, the interpretation is complex, in that the stretches were generally fast, and probably caused segmentation of spindle response (Hagbarth *et al.*, 1981; Prochazka and Wand, 1981). The way in which fusimotion affects segmentation is unknown: it may increase or decrease the transient responses and the depth of modulation between them. The issue is further complicated by the known instruction-dependence of longer-latency reflexes. Gottlieb and Agarwal (1980) favoured a central modulation of reflex gain rather than preparatory changes in fusimotion to explain their results. Dufresne *et al.* (1980) on the other hand interpreted modulations in the velocity component of myotatic reflexes of biceps brachii during voluntary movements in terms of task-related fusimotor action. The uncertainties pointed out above also apply to this latter study, but were specifically addressed by fitting the responses to a model incorporating position, velocity and acceleration terms, each with its own weighting function (parameter) and time delay. Fits were optimised iteratively, leading to a choice of delays and, importantly, time courses of the parameters. The conclusion was that prior to a voluntary movement, velocity feedback is increased by dynamic fusimotor action. The approach is certainly interesting, but without separate verification that dynamic fusimotor action would indeed cause the modelled changes in spindle velocity response, it is difficult to assess this evidence. Verification could in fact be carried out in acute experiments with a duplication of the length changes and muscle contractions which occurred (e.g. Hullinger *et al.*, 1987). It is worth noting that a pre-setting of dynamic fusimotor action had been suggested by Hagbarth (1967) to explain instruction-dependent increases in both short and long-latency stretch reflexes in the absence of background EMG changes.

On balance, there is now good evidence, mainly from chronic afferent recordings, for task-dependence of fusimotion in real-life voluntary movement. Many questions remain open. If a task involves only one limb, is fusimotion changed only in that limb (in other words, is fusimotion diffuse or focussed)? To what extent does fusimotion vary during a given task? Does the CNS normally use certain preferred combinations of static and dynamic fusimotor action? Finally, at a very general level, what advantage is conferred by adjusting the sensitivity of spindle transduction: does increased sensitivity mean increased resolution (larger ensemble firing rates, therefore more resolvable levels) or is the ensemble response large enough without fusimotion to exceed what can be resolved centrally anyway? If the latter is true, the advantage must be sought elsewhere. For example, flexibility may be improved by being able to adjust the relative gain of length feedback over other inputs and thereby switch from one mode of control to another. This might apply not only at the reflex level, where it could result in stiffness control (Crago *et al.*, 1976), but also at higher levels, where switches from feedback-dominated control to centrally-dominated control have been hypothesised (Evarts *et al.*, 1984; see Section 7.2). Alternatively, it may be desirable to adjust the sensitivity to match the expected amplitude of movements (operating range adaptation, e.g. visual and auditory systems). Whatever the answer, the observed changes in spindle firing are impressive: for identical stretches, the ensemble Ia input from a cat gastrocnemius muscle to the spinal cord might peak at 5 kilo-impulses/sec (Kips) in the resting animal, at 10 Kips during stepping (Prochazka *et al.*, 1989b), and at 50 Kips during imposed stretch (assuming 100 Ia afferents peaking at 50, 100 and 500 ips respectively, as illustrated in Fig. 3).

7. MODULATION OF SENSORY TRANSMISSION TO SUPRASPINAL AREAS

7.1. BEREITSCHAFT (READINESS)

The first evidence for preparatory activity in the brain preceding movement came from recordings from single cortical neurons in monkeys (Jasper *et al.*, 1958, 1960). The extent of this activation was then revealed in averaged electroencephalographic recordings in humans (contingent negative variation: Walter *et al.*, 1964; Bereitschaftspotential (readiness potential): Kornhuber and Deecke, 1965). Figure 1B illustrates schematically the temporal relationship between these potentials and the preparatory increases in reflexes discussed above. The contingent negative variation shows a long and maintained change between the warning signal and the go signal. The Bereitschaftspotential appears prior to self-paced movements generated without warning signals, and has a shorter time course. The two phenomena are clearly related, and it has been argued that the contingent negative variation is made up of an initial stimulus-bound component with which the response-bound Bereitschaftspotential summates (Brunia, 1980). The contingent negative variation and Bereitschaftspotential are generally understood to reflect preparatory neuronal activity, notably in the supplementary motor area, premotor cortex and sensorimotor cortex. This has been corroborated in single unit studies and recently, by regional blood flow measurements (Roland *et al.*, 1980).

7.2. SET AND THE SINGLE UNIT

There is a large literature on preparatory activity of single neurons in the sensorimotor cortex and cerebellum (reviews: Fromm, 1983; Evarts *et al.*, 1984; Brooks, 1984; Martin and Ghez, 1985). Other supraspinal areas in which single-cell firing has been associated with attention and preparation for movement are: posterior parietal cortex (Leinonen, 1980; Mountcastle *et al.*, 1975; MacKay and Crammond,

1987), supplementary motor area (Brinkman and Porter, 1983; Tanji and Kurata, 1983), premotor cortex (Mauritz and Wise, 1986; MacKay and Crammond, 1987), thalamus and basal ganglia (Jasper and Bertrand, 1966; Delong and Strick, 1974; Strick, 1976; Neafsey *et al.*, 1978; Macpherson *et al.*, 1980).

Evarts *et al.* (1984) made the useful distinction between central 'set cells' with *tonic* preparatory activity in the interval between a warning signal (instruction stimulus) and a go signal (trigger stimulus) and neurons which fired in close temporal association with movement, and in which the effects of preparation could only be observed in *transient* responsiveness to perturbations ('gain control'). The significance of this was discussed in terms of Allen and Tsukahara's (1974) proposal that in preparation for a centrally programmed movement, there may be a switching from feedback-dominated control mediated by the cerebellar interpositus nucleus, to open-loop predictive control involving the dentate nucleus. In the motor cortex, the tonic task-related neurons were hypothesised to set the activity of interneurons to favour the transmission either of dentate or of interpositus inputs to pyramidal tract neurons according to whether central or feedback control was required. Neurons with task-dependent transient responses were downstream of the gating or routing process. Though the terms 'gating' and 'switching' were used, in fact the proposed mechanism could equally well be described as parametric gain control.

7.3. Cutaneous and Proprioceptive Transmission: Biassing

Until recently, there was a consensus that neurons in the post-central somatosensory area 1, which receive mainly cutaneous input, but also some proprioceptive input, did not show pre-movement activation (Bioulac and Lamarre, 1979; Fromm and Evarts, 1982; MacKay and Crammond, 1987). However, Nelson (1988) found that biassing in area 1 was quite common, especially if the warning signal was vibrotactile rather than visual. A significant proportion of neurons in premotor area 6, primary motor area 4, 'intermediate' area 3a, and posterior parietal areas 5, 7 and junctional area 2/5 showed firing "anticipating environmental events of motor significance" (MacKay and Crammond, 1987). Some of these areas, notably 3a, 4 and 2/5 receive substantial proprioceptive inputs (Soso and Fetz, 1980). Indeed it has been suggested that area 3a pyramidal tract neurons, which show tonic preparatory behaviour, are responsible for controlling anticipatory fusimotor action (Fromm, 1983). Non-pyramidal tract neurons of the same area behaved primarily like sensory receiving neurons, showing transient sensory behaviour but no task-related biassing (Fromm and Evarts, 1982). This distinction incidentally highlights the poor resolution of indicators such as evoked potentials or regional blood flow, which reflect the general 'busy-ness' of large ensembles of neurons, but fail to differentiate between sub-populations which may have very different functions.

7.4. Cutaneous Transmission: Gain Control

As pointed out above, preparatory activation or biassing is one thing, but gain control in the transmission of transient inputs may be another. It is generally agreed that the early components of the cortical potentials evoked by cutaneous stimulation in humans are reduced by 40–60% prior to and during movement (Giblin, 1964; Coquery *et al.*, 1972; Papakostopoulos *et al.*, 1975; Rushton *et al.*, 1981; Cohen and Starr, 1987). There is some disagreement regarding the later components (Lee and White, 1974; Rushton *et al.*, 1981). In the pathway from spinal cord to cortex, 20–30% reductions have been observed in evoked potentials recorded in the medial lemniscus just prior to voluntary movement (Ghez and Lenzi, 1971; Ghez and Pisa, 1972; Coulter, 1974; Dyhre-Poulsen, 1978; Chapman *et al.*, 1988).

At first it was concluded from these data that cutaneous sensory transmission is reduced during movement, perhaps reflecting corollary suppression resulting from efference copy (Coulter, 1974). The issue however is far from simple. Psychophysical studies in humans have shown that though the ability to *detect* cutaneous stimuli is indeed decreased during movement (Coquery, 1978; Dyhre-Poulsen, 1978), tactile discriminative ability is maintained (Lamb, 1983; Chapman *et al.*, 1987). Even more telling, there can be large changes in evoked potentials without corresponding changes in perception (Coquery, 1978).

But the major puzzle in what used to be considered a simple pathway transmitting the bulk of mechanoreceptive input to cortex is that perceptual thresholds and two-point discrimination are virtually unaffected by dorsal column lesions (Wall, 1970, 1975); tactile size-discrimination of small surfaces on the other hand is clearly impaired (Vierck, 1978). Many sources of descending control of transmission through the dorsal column nuclei have been documented (Towe and Jabbur, 1961; Towe, 1973), but their functional roles remain unclear. To explain the unexpected lesion findings, it has been hypothesised that the dorsal column–lemniscal system does not mediate simple sensory information, but rather that it is involved in higher order sensory processing, particularly in relation to exploratory movement ('active touch': Wall, 1970, 1975; Vierck, 1978). On this basis, the changes in transmission detected in the evoked potential experiments might reflect a task-related switch from say cutaneous to proprioceptive input as implicitly suggested by Dyhre-Poulsen (1978) or a suppression of re-afferent signals by efference copy Coulter (1974). Though the *reason* for parameter control in this system is a matter of conjecture, its *existence* seems beyond doubt.

In keeping with the observations of reduced evoked potentials during movement described above, Chapin and Woodward (1982a) found in a sample of somatosensory cortex neurons which responded to pawprods in the gently restrained rat, that 48% responded only weakly or not at all to foot contact during normal locomotion; the remaining 52% responded similarly in the two conditions. Interestingly, the responsiveness of cells depressed in gait was restored or even augmented during exploratory

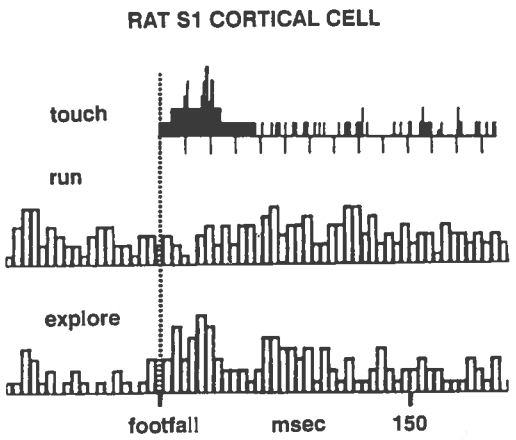

FIG. 5. Task-dependent responsiveness of a rat somatosensory cortical neuron. Top: response histogram of the cell to paw-prods in the gently-restrained animal; middle: peri-stimulus histogram aligned to the moment of foot-fall during running (note the absence of a response); bottom: restored responsiveness to foot-fall during exploratory movements. The middle and bottom histograms were generated from the same number of foot-falls. Reproduced with permission from Chapin and Woodward (1982a).

movements or locomotion over irregular surfaces (Fig. 5). This suggests that sensory transmission might be increased in situations where it is required for adaptive responses to the environment. Palmer *et al.* (1985) compared responses of cat motor cortical neurons to electrical stimuli applied to the footpad in three situations: rest, locomotion and during landing from falls. Responses of most cells were elevated compared to rest in the falls, particularly in the waiting period prior to the drop. During gait, transmission was elevated above rest levels during the swing phase, but reduced below rest levels just prior to and during the stance phase. A similar phase-dependent modulation was demonstrated for the 48% of rat somatosensory cortex neurons referred to earlier (Chapin and Woodward, 1982a, b).

In related studies, Poranen and Hyvärinen (1982) presented monkeys with vibrotactile stimuli and visual cues indicating whether a motor response would be rewarded or not. Neurons in area 4 and the secondary somatosensory area showed increased responsiveness to vibration when the monkey expected a reward. Neurons in the thalamic ventro-posterolateral nucleus (VPL) and in somatosensory areas 3b, 1 and 2 were unaffected by such expectation. In similar experiments, Nelson (1984, 1987) found many area 1 neurons which also showed sensitisation to relevant stimuli, though he confirmed the negative finding of Poranen and Hyvärinen (1982) for area 3b neurons (see also Kurata and Tanji, 1985). Nelson also stressed that some area 1 and 3a neurons responded to cutaneous vibration with *reductions* in firing. These reductions were augmented in rewarded trials. This finding highlights an inadequacy of the evoked potential method similar to that discussed above: in a cluster of neurons in which some neurons are excited and some inhibited, changes in transmission might not correspond in a simple way to changes in the net evoked potential. It is worth noting the relationship between responsiveness and relevance in the visual system for neurons in all premotor areas so far studied: in the frontal eye fields, substantia nigra and superior colliculus neurons responded to stimuli better if they were targets for saccades (Wurtz *et al.*, 1980; Wurtz, 1984).

In summary, there is now good evidence that cutaneous sensory transmission to cerebral cortex tends to be reduced from resting levels during stereotyped motor tasks, but is elevated above resting levels in novel situations or during exploratory tasks. This is in accord with Wall's (1975) hypothesis that for predictable movements "the setting of filters would limit the total amount of information transmitted but would select particular types of information. For novel movements, somatosensory transmission delivers 'uncensored, unanalysed' information to the cortex". There is clearly much in common between this, the state-dependence of reflexes and the hypothesised mechanism of 'fusimotor set' discussed earlier. We will return to these ideas in due course.

7.5. Proprioceptive Transmission: Gain Control

Evarts *et al.* (1984) viewed kinesthetic inputs as having a 'special' relationship with movements. Area 4 pyramidal tract neurons were found to respond more sensitively to limb perturbations if the task for which the animal was prepared involved activation of those neurons (Evarts and Tanji, 1976). The responses consisted of an early and a late component, the latter being more instruction-dependent than the former. This difference is of interest because it had been shown in a similar paradigm that cooling of the cerebellar dentate nucleus selectively reduced the late component of response (Conrad *et al.*, 1974, 1975). Motor cortex neurons responsive to perturbations during a precise positioning task were unresponsive during ballistic movements (Fromm and Evarts, 1977; Evarts and Fromm, 1977; see also Muir and Lemon, 1983), though there was doubt as to the constancy of the afferent input evoked by torque pulses in the two conditions. As might be expected of the cerebral cortex, neurons in pre- and post-central areas showed a range of response properties, but there did seem to be a correlation between conduction velocity and dynamic responsiveness in pyramidal tract neurons (Fromm *et al.*, 1984). Tanji (1976) reported an increased sensitivity of area 3a neurons to perturbations applied during a precise positioning task compared to a non-hold period, even when the involved muscles were less active. Tanji argued in terms of a peripheral mechanism involving fusimotor action, rather than a central control of transmission. Wolpaw (1980a, b) found that responses of area 2 and 4 neurons were increased with increasing voluntary contraction of the involved muscles (corroborated by Fromm *et al.*, 1984). Some of the change in bias and responsiveness of the neurons was attributed to central 'gating' (i.e. central gain control) and some to contraction-coupled fusimotor action on spindle endings, though again there was uncertainty as to the constancy of the afferent inputs elicited at the different forces.

In contrast with these interpretations, Soso and Fetz (1980) found that cortical somatosensory

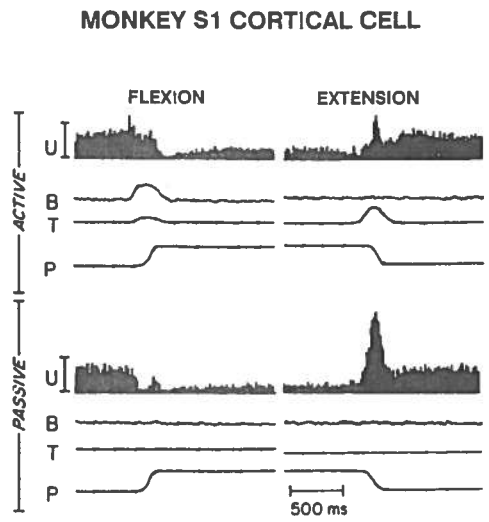

FIG. 6. Task-dependent responsiveness of a monkey somatosensory cortical neuron. U: unit discharge histogram; B, T: averaged biceps and triceps brachii EMG; P: elbow position (flexion upward). *Active* movements were self-generated between mechanical stops, with no special requirements of accuracy; *Passive* movements were imposed by the experimenter to mimic the active ones. The movement-related modulation of firing was greater in the *passive* imposed movements. It is argued in this review that the latter situation is in fact associated with elevated vigilance or arousal. Reproduced with permission from Soso and Fetz (1980).

neurons in post-central area 2/5 in monkey became *less* sensitive to peripheral input during voluntary movement (Fig. 6). The modalities affected seemed to be largely proprioceptive; cutaneous transmission apparently remained unchanged. The comparison was between responses to comparable active (voluntary) and 'passive' movements, the latter being imposed on the animal. As it happens, the situation in which an investigator manually imposes limb movements usually leads to greatly increased dynamic fusimotor action, at least in the cat (see Section 6.2). Soso and Fetz (1980) assumed that the observed reduction of control neuronal sensitivity during active movements reflected a reduction of gain in CNS pathways. However, in view of the cat data it seems quite possible that the muscle spindles in the 'passive' imposed movements were in fact under strong dynamic fusimotor action, and therefore responded at near-maximal sensitivity, even though the animals had been trained to accept the imposition of movements without resisting them. During the relatively uncomplicated, well-rehearsed voluntary movements, fusimotor action and spindle sensitivity were very likely at low levels. Looked at this way, there is an alternative interpretation of the data: during stereotyped movements proprioceptive gain at the peripheral level was low; it was elevated during the imposition of movements upon the animal; the central changes were therefore due to the fusimotor modulation, either exclusively, or in conjunction with additional central modulation of the ascending signals. Interestingly, some 'proprioceptive' area 3a neurons recorded by Yumiya *et al.* (1974: Fig. 2) also showed higher dynamic sensitivities to imposed movements compared to voluntarily produced movements. The authors overlooked this difference, but in the light of what has just been discussed, it could well be another example of gain control of proprioceptive input to cortex.

In summary, recordings from cerebral cortical neurons receiving proprioceptive input have indicated convincingly that there is a task- or context-related modulation of sensitivity to limb movement. The modulation seems to be in the same direction as might be expected at the muscle spindle level in response to task-related fusimotor action, and so at this stage it is not possible to decide whether additional gain control occurs in pathways leading from the periphery to the cortex.

8. CEREBELLUM

8.1. TASK-RELATED RESPONSIVENESS

The cerebellum has been called the "head ganglion of the proprioceptive system" (Sherrington, 1906). There is little doubt that its primary role is in the control and learning of skilled movement. Similarly to cerebral cortical neurons, cerebellar nuclear cells and Purkinje cells in cerebellar paravermal cortex have been reported to respond less to cutaneous and proprioceptive inputs if these are applied during active, self-generated movements rather than during rest (Harvey *et al.*, 1977, 1979). In these experiments, some of the stimuli were applied reproducibly by an actuator-controlled manipulandum, but the majority were applied manually as taps applied to skin and muscle. These latter stimuli were probably quite variable, so further confirmation and quantification of the finding is needed, and again it should be pointed out that the imposition of movements on an animal "at rest" is quite likely associated with a heightened state of vigilance or arousal. Related experiments have indicated that just as in the cerebral cortex, during stereotyped movements, somatosensory transmission to cerebellum is reduced, and in novel tasks or after unexpected stimuli it is restored or even elevated (Gilbert and Thach, 1977; Andersson and Armstrong, 1987). These studies were mainly concerned with climbing fibre input, the modulation of which might well have occurred at the olivary level, given the compelling evidence of task-related control of transmission in this region (Gellman *et al.*, 1985; Chapman *et al.*, 1986).

In general, neuronal encoding and transmission involves dynamic filtering of the input signal, whether it be differentiation, integration or both. At the Purkinje cell level, high-pass filtering of somatosensory inputs mediated by mossy fibres has been reported by a number of workers (MacKay and Murphy, 1974; Harvey *et al.*, 1977; Bourbonnais *et al.*, 1986). It is not known whether this filtering is invariant, whether it depends on motor task, or indeed to what extent it dominates over the wide-band transmission which has also been documented for these cells (Rubia and Kolb, 1978; see also Fromm *et al.*, 1984). The issue is not a trivial one, because in control systems operating at high loop gain, net phase shifts around the loop are quite

crucial to stability and dynamic performance (e.g. Stein and Oguztöreli, 1976).

Strick (1983) investigated the responses of cerebellar interpositus and dentate cells in monkey experiments similar in design to those of Evarts and Tanji (1976). Interpositus neurons discharged as though they were faithfully signalling the mechanical effects of the applied torque pulses, whereas dentate cells responded in a much more task-dependent manner. Strick's interpretation was that interpositus activity was linked in some way to the early component of motor cortical response described by Evarts and Tanji (1976), and dentate activity was linked to the set-dependent late component. It was argued that the dentate discharge, but not that of interpositus, might generate the late motor cortex responses as evidenced by their attenuation during dentate cooling (Conrad *et al.*, 1975), and the appropriateness of response latencies along the cerebello-thalamo-cortical pathway (but cf. MacKay and Murphy, 1979a). Strick proposed that the pre-programming of the response of dentate neurons to kinesthetic inputs was an integral part of developing a motor set to move in a particular direction.

8.2. 'METASYSTEMIC' CONTROL BY CEREBELLUM

MacKay and Murphy (1979b) extensively reviewed the literature in relation to the idea that the cerebellum exerts 'metasystemic' control over motor reflexes: "the function of the cerebellum is the control of the feed-back nervous mechanisms involved in purposeful motor activity" (Rosenblueth *et al.*, 1943). In fact the notion of the cerebellum as being separate from motor pathways, but controlling transmission in them, is a very old one (Holmes, 1917; Lorente de No, 1924). Furthermore, it is an important concept within the framework of this review article, for in a sense it ascribes to the cerebellum the mechanics of producing set-related combinations of transmission parameters in sensorimotor pathways.

A compelling example of the cerebellar modulation of gain in an extra-cerebellar reflex pathway is found in the short-term visual suppression of the vestibulo-ocular reflex. This suppression serves to maintain visual fixation on a moving target during concomitant head movement (Ito, 1976) and is not to be confused with the long-term adaptation evoked for example by the chronic wearing of reversing prisms (Miles, 1987). The suppression has been hypothesised to result from inhibitory control of the vestibular nuclei by flocculo-nodular Purkinje cells (MacKay and Murphy, 1979b). However there is no firm proof that the cerebellum is entirely responsible for this control. The vestibulo-ocular reflex is in fact a prime example of task- or context-dependent transmission in a sensorimotor pathway: if subjects being rotated with their eyes closed imagine a target stationary in the external environment, this enhances the reflex, whereas if they imagine the target moving with them, this suppresses it (Barr *et al.*, 1976). Because of these attentional effects, it is common practice to distract subjects with simple arithmetical tasks in order that the vestibulo-ocular reflex can manifest itself 'freely'.

In relation to limb movements, the dentate nucleus has been implicated in the control of spinal reflexes in two quite separate ways, one involving the fusimotor system, and the other the synaptic transmission to motoneurons. Gilman (1974) showed that in monkeys, lesions of the dentate or its output pathways in the superior cerebellar peduncle and ventrolateral nucleus of the thalamus, all reduced the static stretch sensitivity of gastrocnemius spindle Ia afferents. Because the cerebellar lesions were ineffective if the pyramids had previously been sectioned, Gilman concluded that the dentate nucleus probably augmented spindle sensitivity by activating the fusimotor system via the motor cortex. Bantli and Bloedel (1976) stimulated the dentate nucleus in the monkey after cortical ablation, and detected changes in synaptic transmission in hindlimb Ib, but not Ia reflex pathways to motoneurons. This indicated that the dentate could influence segmental reflex transmission via extrapyramidal pathways, possibly the reticulospinal system.

MacKay and Murphy (1979a,b) were at pains to distinguish between the view that the cerebellum is in the pathway of principal motor control loops, forming part of them, and the view that it is a parametric controller of transmission in extracerebellar loops. The former notion underlies the hypothesis of 'feedback or central program set', where motor cortex receives either kinesthetic feedback mediated by interpositus or programmed commands from dentate (Allen and Tsukahara, 1974; Evarts *et al.*, 1984; see also Fig. 7A). The latter notion (see Fig. 7B) is exemplified by the presumed cerebellar setting of the fusimotor system (Gilman, 1969).

In fact there is now considerable doubt that interpositus is in the short-latency feedback pathway to motor cortex as suggested by Murphy *et al.* (1975). First, reversible cooling of interpositus was rarely found to change the short-latency response of cells in motor cortex to limb perturbations (Vilis *et al.*, 1976). Second, in the pathway from interpositus to motor cortex, though ventrolateral thalamic neurons were observed to fire in relation to arm movements, they did not respond early enough to torque pulses to mediate the earliest responses in motor cortex (Strick, 1976; Macpherson *et al.*, 1980). Third, MacKay and Murphy (1979a) showed that in any case cat motor cortex cells had a lower threshold to muscle stretch than did interpositus neurons.

At first sight the interpositus cooling experiments also weaken the 'metasystemic' parametric control hypothesis insofar as they indicate that proprioceptive transmission to motor cortex is unrelated to interpositus outflow. However, there was an interesting discrepancy between the effects of cerebellar cooling on responses to imposed and self-generated arm movements in monkeys. Imposed torque pulses produced stretch-related short-latency EMG responses which were only slightly increased by cerebellar cooling (Vilis and Hore, 1977), but in prompt voluntary elbow movements, stretch-related EMG and motor cortical responses were significantly enhanced by cerebellar cooling (Hore and Flament, 1988). It was argued that the torque pulses may have been so fast as to produce a saturated neural discharge which could not be significantly influenced by

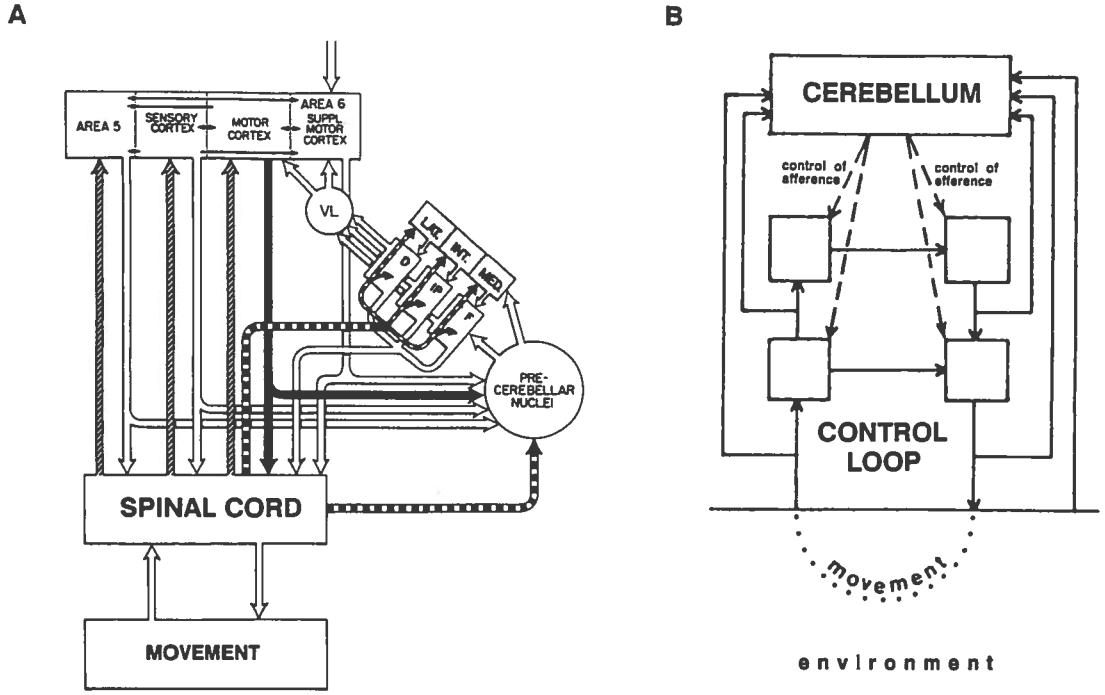

FIG. 7. A *feedback* versus a '*metasystemic*' role for the cerebellum. A: The cerebellum processes commands descending from the cerebral cortex along with feedback from the spinal cord, and sends the resulting output to cerebral motor areas and spinal cord. Reproduced with permission from Brooks and Thach (1981). B: The cerebellum exerts parametric gain control over extracerebellar sensorimotor pathways. The dentate nucleus is hypothesised to control the afferent limb of such pathways, while the interpositus tends to control the efferent limb. Reproduced with permission from MacKay and Murphy (1979).

the cerebellum, whereas in the slower voluntary movements cerebellar gain control could manifest itself.

The sites of action of putative cerebellar gain control are a matter of speculation. Flament and Hore (1986) and Hore and Flament (1988) suggested that in cerebellar dysfunction there might be inappropriate levels of fusimotor activity, which would result in increased firing in antagonist spindles during agonist shortening contractions. This is an important point which needs clarification, ideally in experiments in which both spindle and EMG responses to stretches of widely ranging velocity are recorded with and without cerebellar cooling. However, as indicated for example by the fact that cerebellar tremor can persist after deafferentation (Liu and Chambers, 1971), it is clear that there are control mechanisms other than fusimotion which depend upon the cerebellum.

Of course it is by no means agreed that the main function of the cerebellum is to control transmission elsewhere in the CNS. Houk (1987), for example, argued against this concept, proposing instead that the cerebellum be viewed as an array of adjustable pattern generators, producing motor command sequences for transmission to spinal alpha-motoneurons via the red nucleus. Between these extreme positions there are various theories of cerebellar function which incorporate both command and regulatory functions (reviewed exhaustively by Brooks and Thach, 1981). Whatever the answer, there can be little doubt that an important function of the cerebellum is to contribute to the processing of sensory input on its way to influencing motor output. Furthermore, such processing is evidently highly adaptive, that is to say task- and context-dependent. The cerebellum, red nucleus and surrounding regions are definitely implicated in fusimotor control, which itself seems to be highly adaptive, so the description of these structures as "the head ganglia of the proprioceptive system" is entirely appropriate. Finally, there is good evidence that the learning of skilled movements depends at least in part on gradual adaptive changes in transmission within the cerebellum (Gilbert and Thach, 1977) and in structures influenced by the cerebellum (Brooks, 1984).

9. SYNTHESIS

9.1. CONTROL OF TRANSMISSION IN SENSORIMOTOR PATHWAYS

The aim of this review has been to bring together some widely ranging observations, on the suspicion that they all derive from an identifiable general strategy of sensorimotor control in nervous systems. Let us consider the following possibility: *sensorimotor transmission is controlled such that 'gain' and 'offset' are increased prior to and during all movements*. Does this hypothesis cover the data discussed above? The answer is no, because although some results point this way (e.g. increases in human H-reflexes and increased firing of motor cortex and other supraspinal neurons in monkeys prior to move-

ment), there are numerous examples in which gain seemed to be *reduced* when stereotyped movements were compared to the 'rest' condition (e.g. invertebrate as well as human stretch reflexes during locomotion; cutaneous transmission to somatosensory cortex during locomotion in rats).

Let us modify the hypothesis: *sensorimotor transmission is controlled according to motor task in a particular way: gain and offset are increased prior to and during movements which are novel, difficult or performed in unfamiliar contexts.* This formulation fits some of the observed phenomena, notably fusimotor set and the increased responsiveness of motor cortex neurons in precision tasks. However, it does not cover the observations of specific gain changes in certain classes of stereotyped movement (e.g. invertebrate reflexes in walking, catalepsy and rocking; human H-reflexes in standing, walking and running; rat somatosensory cortical responses in walking vs standing). To include these, let us try the following: *sensorimotor transmission is controlled in certain characteristic ways: gain and offset are low in the resting animal and in routine motor tasks; they are increased (1) in movements involving novelty, difficulty, exploration and/or learning; (2) in contexts evoking generalised vigilance and arousal; (3) in certain motor disorders. Finally, they are cyclically modulated in stereotyped tasks such as locomotion and breathing.* This hypothesis seems to cover most of the observations discussed previously, though it does tend to gloss over the evidence that for a particular task, gain in one sensorimotor pathway may change differently from that in another (e.g. Marsden *et al.*, 1983; see Section 9.4).

Let us now recall some of the key hypotheses cited in this review.

Set is "a state of readiness to receive a stimulus that has not yet arrived or a state of readiness to make a movement" (Evarts *et al.*, 1984).

Prior to a movement there are three stages of preparation variously called: "pre-tuning, tuning and triggering" (Kots, 1977); "pre-setting, triggered processing and output processing" (Requin, 1985); "stimulus-bound activation, response-bound activation and selective activation" (Brunia, 1980).

For predictable movements the setting of neuronal filters limits the total amount of information transmitted but selects particular types of information. For novel movements, somatosensory transmission delivers 'uncensored, unanalysed' information to the cortex (Wall, 1975).

Reflexes are prepared to operate but have no effect if the movement proceeds according to the set central program (Grillner, 1975). Proprioceptive signals are compared to those 'expected' from efference copy, and if the mismatch is large, stretch reflexes are disinhibited (Barnes, 1977).

The modification of responses to successive perturbations involves the detection and transformation of specific discongruent features between anticipated signals and sensations correlated with the actual movements into the appropriate parametric commands (Nashner, 1980).

There is a logical progression in these hypotheses from neuronal preparation prior to movement (the setting or tuning of filters for particular tasks), through to automatic error correction and adaptive control based upon mismatches between sensory input and efference copy. It is worth noting that the hypotheses were developed from observations in animals ranging from insects to humans, at all levels of their respective nervous systems. With this broad applicability in mind, let us now examine some of the terminology in the field and attempt to tighten up on the underlying definitions.

9.2. SET

At the beginning of this review it was suggested that Evarts' version of Woodworth's definition ("a state of readiness to receive a stimulus that has not yet arrived or a state of readiness to make a movement") though simple, lacks in specificity. For example it would be consistent with the definition as it stands to posit that the state of the readiness is restricted to cognitive areas of the brain. There is nothing specifically to indicate that preparatory changes in transmission occur within the motor control loops themselves. Indeed the very term 'readiness' lacks precision. It could be interpreted purely in terms of preparatory neural firing, or in terms of performance (the subject's response was faster and more accurate, therefore there must have been increased readiness).

One option is to reject the term set altogether on the grounds that it has become too hazy and ill-defined. The problem with this is that one does need a term to describe the state of a complex control system whose internal elements have been adjusted to respond appropriately to incoming stimuli. *Set* and *tuning* have fairly specific meanings in technology and are in widespread use: engines, engine components, radios and many other electronic devices are set or tuned; industrial robots and computer programs are set or 'set up' with parameter lists or sub-programs to perform particular tasks. Perhaps the closest analogy of all is to be found in recent software models of neural networks, in which learning takes place by the reward-based setting of connections between large arrays of elements transforming sensory information into motor output (e.g. Edelman and Finkel, 1983).

If we are to retain the term set in neurophysiology, then we should at least try to sharpen up its definition. The first thing to decide is what should be included and what should not. Certain mechanisms discussed above seem to fall safely within the generally accepted meaning of set, and can be included without too much difficulty in a definition: (1) task-dependence of reflex gain (Nashner, 1976; DiCaprio and Clarac, 1981; Bässler, 1983; Akazawa *et al.*, 1983; Capaday and Stein, 1987); (2) task- and context-dependence of fusimotor action (Prochazka *et al.*, 1985); (3) increased transmission to sensory cortex related to (a) exploration (Vierck, 1978; Chapin and Woodward, 1982a; Palmer *et al.*, 1985) and (b) motivation (Poranen and Hyvärinen, 1982; Nelson, 1987); (4) increased transmission to motor cortex during precision movements (Fromm and Evarts, 1977); (5) increased discharge of neurons in a variety of CNS areas prior to movement (reviewed by Evarts *et al.*, 1984); (6) changes in sensorimotor transforma-

tions brought about by conditioning (e.g. Kandel, 1984).

It is much harder to decide whether to include whole sequences of activation or gain control (motor programs). For instance, the predictable time course of reflex responses to skin stimuli in gait was described by Grillner (1975) as being a "set central program": spinal pattern generators were set to run stereotyped programs, of which phasic control of reflex transmission was one. The danger of including sub-programs such as this in the ambit of set is that the term can quickly become all-encompassing: the locomotor sub-program does not differ in principle from the motor program to play a violin sonata. Every long sequence of pre-planned action can then be viewed as a set program and the term set becomes virtually useless. On the other hand, it is difficult to jettison motor programs outright as they do represent a recognised element of the accepted meaning of set. Is there some formula by which simple sub-programs can be retained, while complex programs are excluded? One possibility is to define set solely in terms of programs underlying simple, cyclical or short-duration tasks. This turns out to be too restrictive: suppose that proprioceptive sensitivity is high and steady throughout a complex motor task performed under stressful conditions; because the task is complex, set may not be used, even though in this case context rather than task evoked the simple change in transmission, and set would otherwise seem the ideal descriptor. To cover this, let us couch the definition in terms of sensorimotor parameter control with the limited inclusion of certain sub-programs: "A sensorimotor set is a state in which transmission parameters in various sensorimotor pathways have been adjusted to suit a particular task or context. This includes parameter adjustments evoked by conditioning, and parameter schedules in stereotyped tasks such as gait." The tenuous element in this definition is the final phrase regarding parameter schedules and only further usage will reveal whether it belongs or not.

9.3. EXECUTIVE, PERMISSIVE AND COMMAND FUNCTIONS

In the synthesis so far we have concentrated largely on the moment-to-moment transformation of sensory input into motor output. The implication has been that there is a higher level of CNS organisation at which detailed sequences of motor commands are generated. In essence this is just an extension of the command neuron concept (Kupfermann and Weiss, 1978), which has run into difficulties because candidate neurons in invertebrates have nearly always been found to receive movement-related feedback (Davies, 1985). The issue is not new. Bernstein (1940) argued strongly against a centralised command structure remote from the periphery: "the decisive role in the achievement of motor control must be played by *afferentation* . . . The central effectors achieve coordination of movements only by plastically reacting to the totality of the signals from the afferent field, adapting the impulses transmitted to the situation that actually obtains at the periphery. Co-ordination lies basically not in the character and accuracy of a tetanic effector impulse but in the accuracy of some sort of preparatory effector impulses *which organise and prepare the periphery* for the reception of the right impulse at the right moment."

Apart from the question of whether the 'higher' command centres do or do not receive feedback, there is the more fundamental issue of whether the whole notion of 'higher' and 'lower' centres should in fact be scrapped. The hierarchical schemes of CNS motor organisation, dating back to the late eighteenth century have been attacked as being "old-fashioned" (Davies, 1985; but cf. Pearson *et al.*, 1985). To take their place, models have been proposed which tend to feature current electronic and computer technology, e.g. tape recorders, parallel processing and distributed function (Hoyle, 1975; Davis, 1985). To some extent the whole debate on hierarchy can be side-stepped: whether or not there are specialised centres from which commands flow 'downstream', one may posit that pre-set motor programs are formulated and held *somewhere* in the CNS. The most compelling evidence for this arrangement is found in situations in which a whole sequence of purposive movements is unleashed by a trigger stimulus, and once under way, is virtually impossible to abort. Examples have been reported in species ranging from invertebrates (e.g. Hoyle, 1975; Brodfuehrer and Friesen, 1986) to humans: subjects attempting to 'abort' a motor response failed 20% of the time at 150 msec prior to the response and 90% of the time at 100 msec (Slater-Hammel, 1960).

Requin (1985), in a thoughtful review of attention and preparation, stressed the difference between *processing* stages in preparation (e.g. the selection of appropriate responses) and *selective perceptual and motor set* influencing the implementation of these responses. To illustrate the distinction, Requin identified three types of units he and his colleagues have observed in motor cortex of monkeys performing a choice reaction time task (Fig. 8): (1) true motor units: purely movement-related cells unaffected by set; (2) true pre-setting units: cells whose firing was unrelated to movement and was changed only by a cue providing the animal with information about the intended movement; (3) transitional cells with both pre-setting and motor unit behaviour. The true motor units were labelled as executive, because they received program instructions and conveyed orders to the spinal cord; the true pre-setting neurons were labelled as permissive, because they were targets for pre-setting processes related to instruction. The role of the transitional cells was seen as instruction-related setting of spinal centres just in advance of the commands from the 'true motor units'. This conception is similar to that of Evarts *et al.* (1984) who categorised motor cortex cells into two main types, 'transient' (equivalent to Requin's true motor units) and 'tonic set cells' (equivalent to pre-setting units). However Evarts speculated that the role of the tonic set cells, which respond primarily to the instruction stimulus, was to influence the routing of motor commands to the transient cells, rather than to influence the spinal cord directly.

Broadly speaking one could equate the functions of Requin's 'permissive' cells and Evarts' 'set' cells with parameter control. The ambivalence of the 'executive'

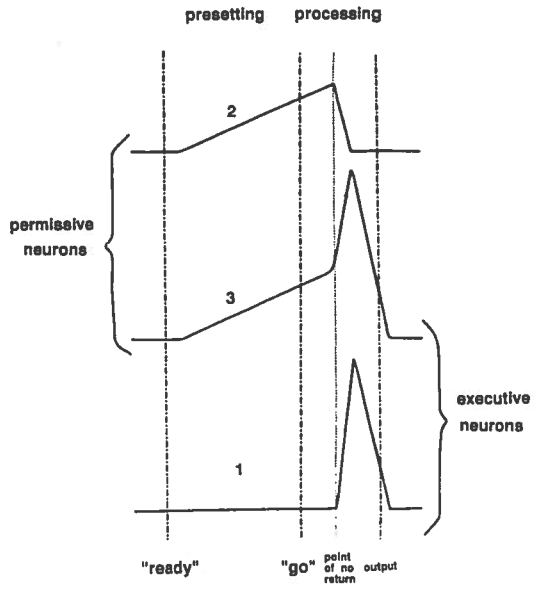

FIG. 8. Schematic of main kinds of units recorded in monkey motor cortex whose activity is related to movement in reaction-time tasks. The activity of units labelled permissive is preparation related; the activity of units labelled executive is movement related. Type 3 units show both behaviours. Reproduced from Requin (1985) with permission of the author and the Intl. Assoc. for Study of Attention and Performance.

cells, namely that they supposedly issue commands but can only do so on receipt of 'instructions', echoes the confusion surrounding the command neuron concept, and supports the notion of command by network consensus (Davis, 1985). For our purposes, it is sufficient to note that there is a conceptual separation of command and pre-setting functions, and that the evidence for a role in parameter control is just as strong for the cerebral cortex as it is for the cerebellum.

9.4. MODALITY AND PATHWAY SWITCHING: HYBRID CONTROL

In the discussion on parameters and variables, multivariate control in so-called hybrid systems was briefly alluded to. The operation of such systems can be quite simple: for example, an unloaded robot arm must move rapidly and accurately to a new position. The relevant output variables are displacement and velocity, and because the load is small and invariant, feedback gains can be set to relatively high levels without causing instability. The arm is then required to manipulate a fragile load of unknown mass: this calls for control of grasp force, greater stability margins, and a compliant response to sudden loading. For these new requirements, the appropriate parametric adjustments would be to reduce length and velocity feedback and to increase feedback from sensors monitoring actuator force and grasp force. In industrial hybrid robots, the task generally proceeds in pre-ordained stages, and feedback parameters are reset from a schedule or look-up chart whenever a new stage is reached. In advanced systems, the parameters could be continuously varied between stages; furthermore in unpredictable situations where rapid triggering of responses might be necessary, some of the monitored variables might be more useful than others, so transmission parameters could be weighted to reflect this.

Are we overdoing the cybernetic analogy here? What if a significant proportion of movements is carried out 'open-loop', for example by central command networks generating programs honed by re-entrant information on previously successful or unsuccessful performance (Hoyle, 1975; Edelman and Finkel, 1983)? In fact there is no conflict, because parametric control or modality switching in sensory pathways does not pre-suppose an automaton-like arrangement of elemental feedback loops. For instance the fact that proprioceptive sensitivity increases by almost an order of magnitude when movements are imposed says nothing about how this augmented input is used. To maintain stability, transmission in simple reflex loops might well be suppressed under these circumstances (e.g. human H-reflexes seem to be reduced in difficult beam-walking compared to normal walking) (Llewellyn *et al.*, 1989). On the other hand, we have seen that the elevated proprioceptive input does seem to get through to the cerebral cortex (see Section 7.5), there to be subjected to further parametric controls (Evarts *et al.*, 1984; MacKay and Murphy, 1979b). Thus a given modality may be weighted differently in different pathways. Admittedly the only clear-cut example of modality-specific gain control related to task is the phase-dependence of different reflexes in gait: those elicited by skin stimulation can be modulated quite differently than those elicited by muscle stretch (Forssberg *et al.*, 1975; Akazawa *et al.*, 1982). Task-related switching from cutaneous to proprioceptive input to cerebral cortex has been suspected in the past (Dyhre-Poulsen, 1978) but has not been rigorously proven. This is clearly an important issue, on which further progress could be made with current techniques.

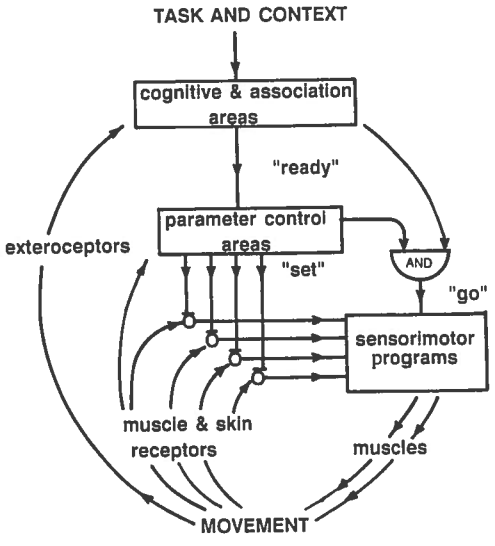

FIG. 9. Schematic illustrating task-related parametric control of multi-variate feedback in mammalian motor systems.

9.5. CONCLUDING REMARKS

A recurring concept in motor control physiology is that the goal of a motor act crucially determines its planning and performance (James, 1890; Bernstein, 1967; Granit, 1977; Evarts *et al.*, 1984). A related notion developed in this review is that in a control system the nature of the controlled variable is determined by the nature of the feedback signal (Taylor and Gottlieb, 1985): with multi-variate feedback the relative importance of each controlled (state) variable is determined by the relative magnitude of its respective feedback parameter. If one agrees with Bernstein that "the decisive role in the achievement of motor control must be played by *afferentation*", then it follows that the goal of a motor act (and the context in which it is to be performed) determines the magnitude of the sensory transmission parameters likely to produce the most appropriate response (Fig. 9). In this review we have seen many examples of task and context-dependent sensory transmission in widely ranging species and widely ranging motor behaviours. From all this it seems safe to conclude that anticipatory gain control of sensory transmission is indeed a fundamental strategy of motor systems.

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Appendix: Terms related to "set"

alertness
anticipation (receptor and effector)
anxiety
arousal
attention
attitude (Einstellung)
contingent variations
determination, determinierende Tendenz
directing tendency
dichotic listening (cocktail party effect)
disposition
expectation, expectancy
filtering
foresight
goal-set
habit
hypothesis
intention
mental set
mind set
motor set
neural set
orienting
parametric gain control
permanent set
postural set
prediction
preparation, preparatory set
pre-programming
pre-setting
priming
processing
readiness (Bereitschaft)
set (Einstellung)
set to react, set to perceive
situation-set
startle
task-set (Aufgabe)
temporary set
tuning, pre-tuning
unconscious set
voluntary set