

3. Proprioceptive feedback and movement regulation

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“YOU CAN ONLY CONTROL WHAT YOU SENSE.” This statement summarizes the current view of sensorimotor control (243) and underlies most of the material in this chapter. As we will see, the removal of sensory feedback to the central nervous system (CNS) has long been known to impair, though not abolish, motor function, particularly in tasks requiring dexterity and context-dependent control. However, it is only in the last decade or two that the flexibility in the use of sensory feedback by the CNS has become fully apparent. In this period, the field of sensorimotor control has truly flourished. Guesswork regarding the nature of the feedback signals to the CNS in voluntary movement has been replaced

by hard data on the activity of single afferents and ensembles of afferents of different sensory modalities. In many species the responses of CNS neurons to incoming information depend heavily on behavioral context and attentional mechanisms. Perhaps of most importance, there has been a major conceptual shift in formulating hypotheses of sensorimotor control. Models based on reflex arcs and servo loops controlling single muscles are now being augmented by multivariate models that incorporate state- and context-dependent rules. Technology, which 40 years ago provided the framework of servo-control theory for analyzing limb stretch reflexes and oculomotor control, now offers a rich diversity of additional op-

tions, including control structures ostensibly modeled on the CNS itself (e.g., expert systems, neural networks, “fuzzy” logic control systems). With fewer conceptual constraints in the way, the hunt is now on to identify the sensorimotor rules and neuronal circuitry that govern the control of movements in various animal species. It is understood that few of these rules are likely to be rigidly fixed. The CNS can clearly modify, modulate, or override any of its control subsystems to cope with changes in task and context. Furthermore, it is apparent that vertebrates and invertebrates share some basic mechanisms of sensorimotor control. Thus, although the focus of this chapter is on mammalian systems, invertebrate systems are discussed where appropriate.

SENSORY FEEDBACK: HISTORICAL BACKGROUND

Reflected Action: The “Sentient Principle”

Ideas regarding the sensory control of movement date back to Descartes in the mid seventeenth century. Interesting accounts of the historical development of the subject may be found in Brazier (45, 46). Briefly, Descartes posited that there was a flow of sensory “spirits” along the “marrow” of nerves leading to the CNS. Motor spirits were directed back toward the muscles along hollow canals in the same nerves. The sensory input supposedly opened valves or pores in the pineal gland, thus controlling motor output. Over the next 200 years, the idea of a “sentient principle” underlying motor actions was further developed and studied empirically. The existence of separate sensory and motor nerve fibers was suggested by Jiří Procházka in 1780 and then verified experimentally in the famous studies of Bell and Magendie. By the end of the nineteenth century, Hall and others had shown that the spinal cord had a considerable autonomy in its reflex responses.

Perhaps the most influential theory of all regarding reflexes was that of Sechenov (1863), who proposed that all animal and human behavior could essentially be reduced to reflex action (307). Sechenov asserted that higher brain function comprised three elements: sensory inflow, a central reflexive process governed by physical laws, and motor output. “Willed” movements were held to arise as a consequence of residual or remembered sensory inputs, triggered internally. Sechenov suggested that reflexive motor output could be evoked by small fractions of past sensory input. This led him to formulate the idea of conditioned reflexes, which his student Pavlov developed into a major field of inquiry. Complex, goal-directed actions were seen as chains of simple

reflexes, each of which elicited the next reflex in sequence. Interestingly, Sechenov’s views brought him into conflict with the government and judiciary of the time, because it was felt that criminal acts could potentially be defended on the grounds that they were reflex chains over which the accused had no control.

The study of reflexes entered the modern era of scientific measurement with the work of Horsley, Sherrington, Hughlings Jackson, Adrian, Magnus, Graham Brown, and others. This period has been extensively reviewed elsewhere (46, 84, 148, 238). By 1930 the following concepts and mechanisms had been identified and studied: action potential frequency code, proprioception, exteroception, neuronal excitation and inhibition, reflex integration and plasticity, decerebrate rigidity, righting reflexes, positive supporting reaction, reflex stepping, and motor functions of cerebellum and motor cortex. The midbrain reticular formation had been linked to attention and arousal (229). In the 1950s and 1960s, the advent of intracellular recording enabled Eccles, Lloyd, Lundberg, and Laporte to analyze reflex connections at the cellular level (reviewed in 19, 187). By the mid 1960s the signaling properties of muscle spindles and tendon organs, and the modulating action of fusimotor efferent fibers on muscle spindles, had been elucidated in great detail by B.H.C. Matthews, P.B.C. Matthews, Hunt, Kuffler, Boyd, Houk, and others (178). The wealth of new knowledge about the individual components of the motor system set the stage for the development of comprehensive hypotheses of sensorimotor control, an enterprise that continues to this day.

Motor Effects of Sensory Loss

One way to determine the role of sensory input is selectively to abolish it, for example, by transecting the sensory nerves entering the CNS, and then to look for deficits in motor performance. This was first done by Magendie (46), and has since been carried out in numerous different ways in animals ranging from insects, lobsters, and crabs (23, 71, 167, 350) to amphibia, reptiles, birds, fish, and mammals, including humans (157, 256, 257, 297, 298). In nearly all cases, purposeful or rhythmic motor action persisted after deafferentation, but accuracy and adaptability were diminished (see Chapter 4).

Although deafferentation experiments seem simple enough in principle, the results have been varied and confusing, engendering much controversy and debate. For example, Mott and Sherrington maintained that deafferentated monkeys had profound

and enduring deficits in limb movements (250), but Munk strongly disagreed, claiming that after recovery the animals' motor performance was remarkably good (251). With hindsight, most of the inconsistencies in the published accounts can be attributed to the following factors. First, the full capability of a deafferented limb is only expressed if the contralateral limb is also deafferented or bound (251, 321). Second, tiny remnants of sensory input may suffice for reasonable control, especially of simple movements (140, 298). Third, nervous systems are good at developing new motor strategies to circumvent deficits, making these less obvious (75). Fourth, ischemic deafferentation generally produces pain and unusual sensations, which themselves can alter motor output (183, 205). Finally, deficits are prominent when tasks are complex (133). They may be missed if testing is too simple.

With these complications in mind, the following conclusions regarding deafferentation are now fairly secure:

1. the basic ability to produce voluntary force and move limbs is preserved after deafferentation. However, movements are generally uncoordinated and inaccurate, especially when visual guidance is absent (133, 257, 294, 297).

2. coordination of the different segments of the primate hand in precision tasks is particularly im-

paired (Fig. 3.1). The accuracy of spatial orientation, fractionated movements and anticipatory preshaping of the hand is reduced, and writing may be severely affected (79, 138, 205, 328).

3. Gait is possible after deafferentation, but again it tends to be irregular and uncoordinated. This holds true in vertebrates and invertebrates alike (23, 24, 25, 72, 137, 140). In humans who have lost limb proprioception, gait is severely impaired and requires conscious attention (75). If neck proprioception is also lost, gait becomes virtually impossible (328).

4. Control of tasks involving simultaneous changes in several variables, coordination of several limb segments, or adaptation to changes in the external environment is impaired. Thus, fastening buttons or holding a cup are difficult and sometimes impossible without visual guidance (133, 294, 298).

Central Pattern Generators and Sensory Feedback

A very important concept that emerged from deafferentation studies was the idea that there are neuronal assemblies in the CNS that can generate basic patterns of motor output for rhythmic activities such as walking, breathing, chewing, swimming, and flying, without sensory input (50, 157, 263, 350). In 1911, Graham Brown posited an "intrinsic factor"

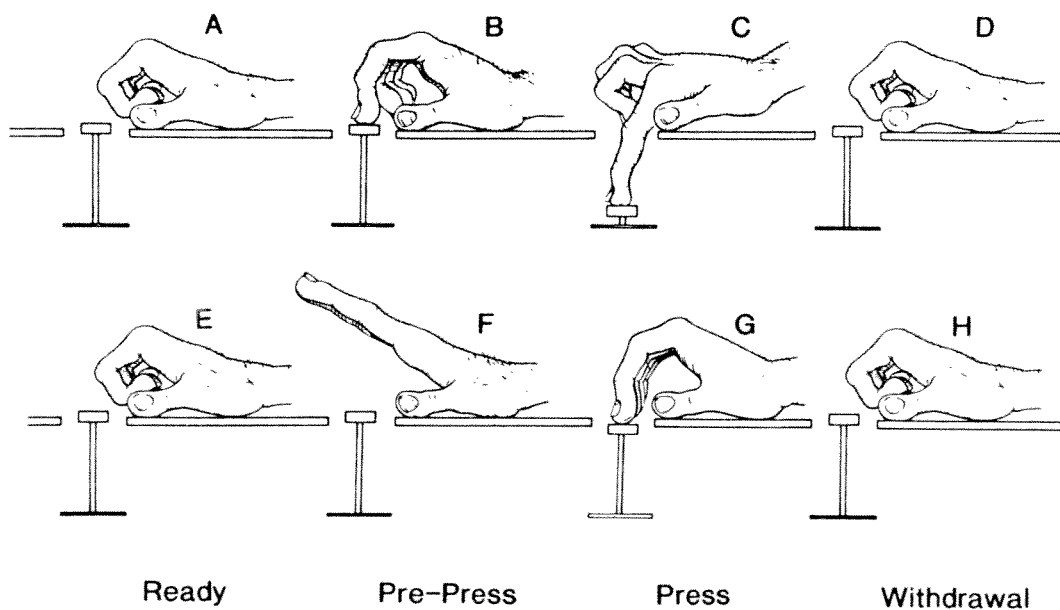


FIG. 3.1. Effect of selective deafferentation on hand control in a macaque monkey. Finger movements in a key-pressing task, before (*top*) and after (*bottom*) a cuneate fasciculus lesion. The pre-movement start position was similar in normal and lesioned animals (A and E), as was the final position (D and H). However, the individual control of fingers was dramatically lost after the

lesion (compare F to B). The fingers extended, bore down on the key in unison (G) and finished in a tightly flexed power grip (H). From here a return to position F, with the fingers fully extended, was not uncommon, with multiple cycles of F-G-H in rapid succession. [Reproduced from Cooper et al. (79).]

for locomotion in the spinal cord, on the grounds that coordinated activation of flexors and extensors could be seen after the cord had been isolated from descending supraspinal input and from all afferent input (50). Grillner coined the term “central pattern generator” to describe the hypothetical intrinsic circuitry (157). Just how well the spinal central pattern generator functioned in isolation from sensory input became a matter of some debate. Most groups acknowledged that after deafferentation the locomotor rhythm was more labile [cats (160); crabs (167); stick insects (24)]. Yet many intricate details of normal muscle coordination could be found in selected recordings from muscle nerves in deafferentated walking cats (Fig. 3.2). Other authors stressed the variability of the data, particularly in relation to bifunctional muscles (23, 224, 263). It has even been

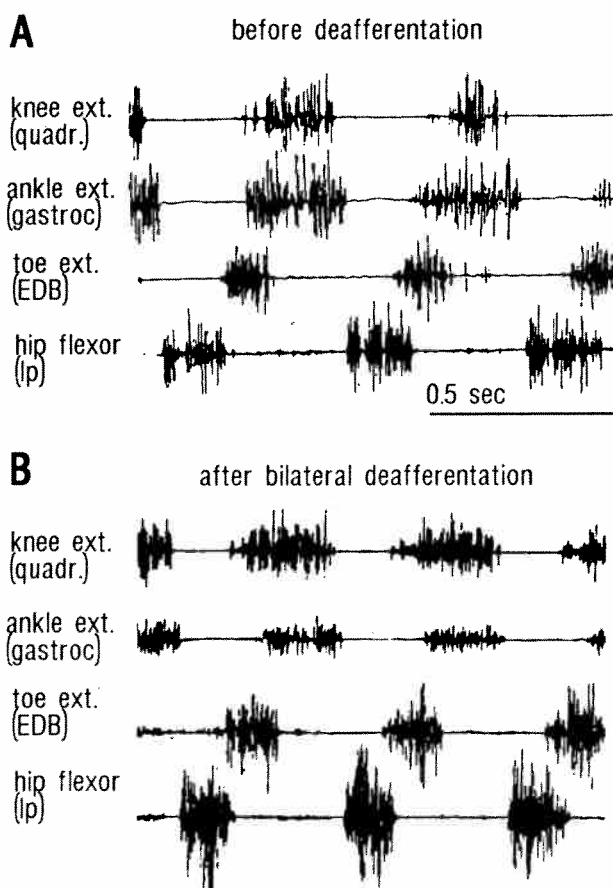


FIG. 3.2. Electromyogram recordings from four hindlimb muscles in a decerebrate cat induced to walk on a treadmill by electrical stimulation of the midbrain locomotor area. The relative timing of the bursts of activity is remarkably similar before (A) and after (B) bilateral hindlimb deafferentation. ext., extensor; quadr., quadriceps; gastroc, gastrocnemius; EDB, extensor digitorum brevis; Ip, iliopsoas. [Adapted from Grillner and Zangger (160).]

suggested that the activation patterns of the bifunctional muscles in 3:4-dihydroxyphenylalanine (DOPA)-induced fictive locomotion are those of backward rather than forward locomotion (51).

In certain specific cases, movements in a normal animal can be attributed fairly clearly to central programming. For example, in cockroaches, afferent feedback in fast walking is too delayed to have a reflex effect within a given cycle, the duration of which is 40 ms or less (88, 355). At most, the sensory input might affect the motor program in ensuing steps [one-step-ahead control; (195)]. In locusts, sensory input influences the wing-beat cycle *following* the one in which it was elicited (266). In rapid ballistic movements in humans, sensory feedback is also too slow to modify the motor output (90). Human subjects and monkeys must plan in advance the force of certain movements, based on visual judgment and prior memory (133). The neural activity involved in this planning has been recorded in several different ways. Indeed, even the simple co-contraction strategy that humans use to stiffen limbs when learning novel tasks may be viewed as a centrally generated motor program (32, 247).

Grillner (1975) suggested that in locomotion, reflexes are “prepared to operate but (are) without any effect so long as the movement proceeds according to the set central program” (157). This notion has its origins in the “Reafferenzprinzip” of von Holst (339) and remains influential to this day (6, 18, 22). Somewhat at odds with this view is the evidence that sensory input during gait can have a very strong effect indeed. For example, when a rhythmically air-stepping animal is lowered to the ground, the instant a limb gains firm ground support, the rhythm slows or ceases (23, 24, 102, 136). The hindlimbs of spinal cats walking on a split-belt treadmill adapt their cadence to each belt separately (125). Obstruction of hip movement (9, 159) or loading of extensor muscles (78, 102) can completely suppress rhythmicity in a leg, while the other legs continue to cycle. In the absence of sensory feedback, obstacles or inclines are not compensated for, and if the animal is not supported it falls (137, 140). Rossignol (see Chapter 5) deals in more detail with the relationship of sensory input to the locomotor pattern generator. For our present purposes, we may conclude that:

1. The CNS can autonomously generate detailed patterns of muscle activity that can form the substrate of complex movements.
2. To be useful, these motor patterns must be under direct feedback control. They are modulated and at times overruled by sensory-evoked control mechanisms in the CNS.

3. In some animals, generation of the locomotor rhythm depends entirely on sensorimotor interaction (i.e., sensory input is an integral and necessary part of the locomotor pattern generator) (23, 24).

STRUCTURE AND RESPONSE PROPERTIES OF PROPRIOCEPTORS

Many types of sensory receptor contribute to motor control in different animals, and several reviews detail the morphology and functional properties of these receptors in vertebrates (148, 178, 185, 189, 238, 280, 285) and invertebrates (22, 24, 56, 57, 71, 127). In the following summary, the emphasis will be on mammalian proprioceptors, although corresponding invertebrate analogs will be mentioned.

The word “proprioception” refers to the sensing of the body’s own movements (see also Chapter 4). In 1821 Charles Bell assumed that muscles contained sensory elements that contributed both to conscious “muscle sense” and to the subconscious reflex control of movement (46). This view prevailed through the 1940s. However, by the 1950s, neurophysiologists had for various reasons rejected a conscious sensorial role for muscle proprioception. It was not until 1972, when it was shown that the selective activation of muscle receptors with vibration-evoked illusions of movement, that this role was reinstated (143). In the meantime, clinicians had continued to think of proprioception in kinesthetic terms, evaluating it according to their patients’ perception of imposed movements of the extremities. In this chapter, we will take the broad view. Any receptor that can signal position or movement about joints qualifies as a proprioceptor, regardless of whether the information reaches consciousness, or for that matter whether it demonstrably contributes to movement control.

By and large, limb proprioceptors sense one of two variables: displacement and force. The transduction process generally introduces dynamic components of response and various nonlinearities. In mammals, limb displacement is sensed by muscle spindle, joint, ligamentous, and skin receptors (178, 189, 238, 349). The invertebrate displacement sensors are chordotonal organs, thoracicocoxal muscle receptor organs, and various hair sensilla (127). In receptors with efferent innervation (muscle spindles and thoracicocoxal muscle receptor organs), the CNS modulates the gain of the afferent response to muscle stretch and adds a tonic component of firing or a “bias” (57). Mammalian tendon organs signal the force produced by a few motor units (175). Small ensembles of tendon organs can provide information

about whole-muscle force (283), but there is disagreement about the fidelity of this information (174, 185). The invertebrate analogs of tendon organs, campaniform sensilla, act like strain gauges, detecting strain in the external cuticle that gives indirect and nonlinear information about limb loading (127). Mammalian joint and ligamentous receptors respond best to extremes of joint angle, though some midrange signaling occurs (52, 118). It is debatable whether joint and ligamentous receptors make a significant contribution to the sensory input required for controlling normal movements (189).

Muscle Spindles

In the last 40 years, more effort has gone into understanding the structure, functioning, and reflex action of muscle spindles than of all the other mammalian mechanoreceptors combined. This is because it was long assumed that spindles were the most important proprioceptors for movement control. It is now apparent that the spindles’ “poor relations,” the tendon organs, may be just as important for controlling cyclical movements such as locomotion (78, 102). Spindle afferents make monosynaptic connections with α -motoneurons, so they offered an accessible portal for studying central synaptic action. Finally, the nature and function of the γ -fusimotor supply to spindles intrigued many researchers and continues to do so. Boyd, Gladden, and Hulliger have written excellent reviews on muscle spindles and fusimotor action (41, 42, 178). What follows is a brief and necessarily incomplete summary and update of certain aspects of this work, selected to facilitate the functional emphasis of this chapter.

Spindle Structure. Depending on its size, a mammalian muscle may contain up to 500 spindles (20, 42, 340). These are located amongst the extrafusal muscle fibers, sometimes in association with one or more tendon organs (1, 230, 290). Spindles range in length from 0.5–10 mm, corresponding to 10%–20% of extrafusal fiber length (287, 343). They consist of six to ten intrafusal muscle fibers attached at each end (pole) to the surrounding extrafusal fibers (Fig. 3.3). A central capsular enlargement that gives the spindle its fusiform shape and hence its name contains one or two primary and one to five secondary sensory endings spiralled around noncontractile portions of the intrafusal fibers (20, 41). The endings project into the muscle nerve via group Ia (primary) and group II (secondary) afferent axons (21, 42). The capsule protects the endings from the large swings in electrolyte concentrations that accompany extrafusal contractions. Each spindle is innervated

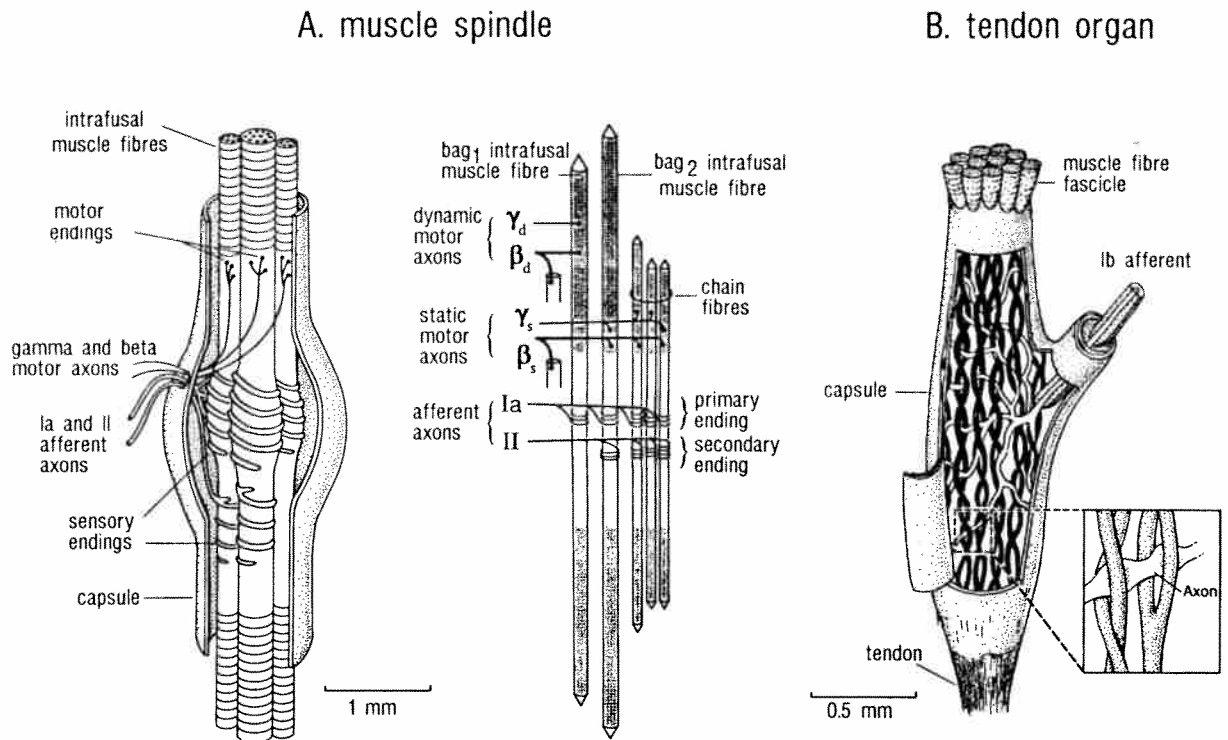


FIG. 3.3. Schematic of a mammalian muscle spindle (A) and Golgi tendon organ (B). The γ - and β -fusimotor axons innervate six to ten intrafusal muscle fibers (not all shown). The β -motoneurons also innervate extrafusal muscle fibers as indicated. The central regions of the intrafusal fibers, around which the group Ia and II sensory afferents spiral, are noncontractile. When the polar ends of the intrafusal fibers contract in response to γ and/or β activity, the sensory regions are stretched, causing increased

Ia and II firing. Dynamic fusimotor action stiffens the bag₁ intrafusal muscle fiber, so that when the ends of the spindle are stretched, more of the stretch is imparted to the sensory region, thus sensitizing the Ia ending. The terminal branches of the tendon organ are entwined amongst the musculotendinous strands of 10–20 motor units, and “sample” the active force produced by them. [Adapted from Kandel et al. (193) and Zelena and Soukup (354).]

by 10–12 γ -fusimotor axons and often by a β -skel-etofusimotor axon, which also innervates surrounding extrafusal muscle (114).

The morphological details of the sensory and motor innervation of muscle spindles were debated for many years, principally by Ian Boyd and David Barker (reviewed in 178). The consensus now is that the typical limb spindle in cats, monkeys, and humans contains three types of intrafusal muscle fiber: a dynamic bag₁ (DB1 or b₁), a static bag₂ (SB2 or b₂), and 2–11 chain (c) fibers. A functional separation of chain fibers into long and short has been suggested (201). Activation of each intrafusal fiber has specific effects on afferent responses to length changes. The b₁ fiber is selectively activated by dynamic fusimotor (γ_d) or skeletofusimotor (β_d) axons, although nonselective activation along with b₂ and chain fibers may sometimes occur (113). The b₂ and chain fibers are activated selectively or concomitantly by static fusimotor or skeletofusimotor (γ_s or β_s) axons. Some spindles, notably the minor members of tandem or compound spindles in neck mus-

cles, lack b₁ fibers (1, 20, 201). Their primary afferents are consequently called b_{2c} afferents. Neck b_{2c} afferents have stretch-response properties and conduction velocities intermediate between those of limb primary and secondary spindle afferents (101, 290). In hindlimb muscles, up to 30% of primary endings may be of the b_{2c} type (326).

Spindle Response Properties. The length-response characteristics of spindle primary and secondary endings with and without fusimotor action have been characterized in great detail over the last 50 years (reviewed in 41, 113, 178, 238). Though there are some minor variations between species, basic spindle characteristics, elucidated in acute experiments and summarized in Figure 3.4, are remarkably similar in cats, monkeys, and humans (70, 256, 273). Both primary and secondary endings transduce length changes dynamically, the primary endings having somewhat larger velocity- and acceleration-sensitive components of response (i.e., slightly more phase advance for sinusoidal inputs and larger step-

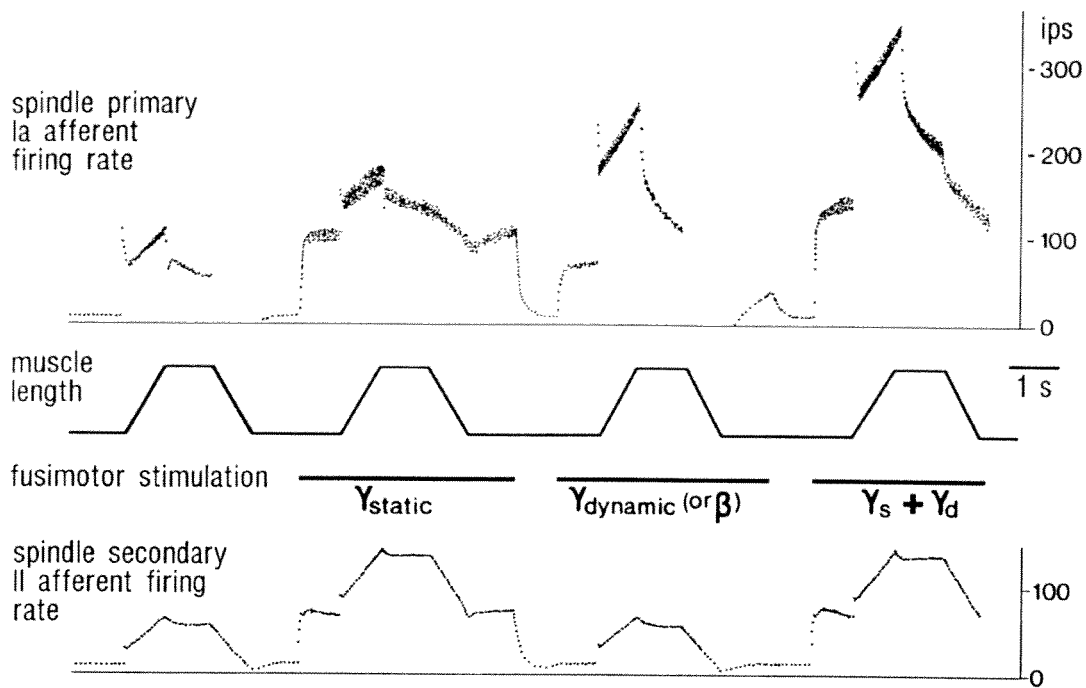


FIG. 3.4. Schematic summary of the firing rate responses of group Ia and II spindle afferents to trapezoidal length changes with and without concomitant fusimotor stimulation. The firing rates shown are typical of displacements of about 10% of rest-length and velocities of 0.05 rest-length/s. The horizontal bars

indicate periods of fusimotor stimulation at 100/s. Note the big increase in Ia stretch sensitivity with γ_d stimulation and the strong biasing effect of γ_s stimulation. Combined γ_d and γ_s stimulation gives occlusion effects. ips, imp/s. [Adapted from Prochazka (278).]

changes in firing at the onset of ramp stretches). The responses of both types of ending show many nonlinearities, notably length-, velocity-, and amplitude-dependent sensitivity (27, 68, 180, 240); aftereffects of muscle contraction; history of length changes and fusimotor modulation (49, 249, 286, 346); nonlinear velocity scaling (176, 271, 299); irregularity of discharge intervals (154, 241); and local unloading effects of extrafusal muscle contraction (36, 170). There is a large range of stretch-sensitivities between individual group Ia and II afferents, notably in relation to the velocity-sensitive components of response. Effectively, there is a continuum of behavior from group II afferents with low displacement- and velocity-sensitivity, to group Ia afferents, which can be highly velocity-sensitive (17, 304, 347).

From a functional point of view, the most important aspects of fusimotor action can be summarized as follows. When muscle displacements are small (<0.5% of muscle rest length), pure γ_d action, mediated by b_1 fibers, slightly *decreases* the stretch-sensitivity or gain of Ia afferents and adds some bias (141). Phase advance, which in the absence of fusimotor action ranges from 45–90 degrees for sinusoidal length changes in the range 1–4 Hz, is slightly *reduced* by γ_d action. For larger amplitude length

changes, γ_d action increases Ia stretch-sensitivity up to fivefold (43). Phase advance may increase slightly (180) or decrease slightly (68). Strong γ_s action adds a relatively large bias to both Ia and II firing and generally attenuates Ia stretch-sensitivity by 50% or more for all amplitudes of length change (68, 87, 180). Paradoxically, *weak* γ_s action can *increase* Ia sensitivity (179). In either case, phase appears to be little affected.

Although γ_d fibers occasionally have an intermediate (b_1b_2) action on primary endings, they rarely if ever activate secondary endings. Of the six to nine γ_s axons acting on a secondary ending, each adds some bias, most attenuate its sensitivity to very small dynamic stretches (<1% rest length), and two or three attenuate its response to large-amplitude stretches too (48, 68, 87). However, one or two of the γ_s axons may substantially *increase* the secondary ending's sensitivity to stretches greater than 4% rest length, presumably via b_2 intrafusal fibers (186). In some ways, the action of these γ_s fibers on secondary endings is quite similar to the action of γ_d fibers on primary endings. Indeed, one could even argue that the overall repertoire of fusimotor control of spindle primary and secondary endings differs in detail rather than in any fundamental way.

The internal disposition, strength, and sensory innervation of the three types of intrafusal muscle fiber presumably determine the particular type of fusimotor action on a given primary or secondary ending. This can range from “pure” chain-type action (biasing, driving of Ia’s, reduced stretch-sensitivity) to b_2 action (strong biasing, stretch-sensitivity decreased in Ia afferents, increased in II afferents), to “pure” b_1 action (minimal effects on II’s, moderate biasing, and large increases in stretch-sensitivity in Ia’s) (41, 113, 326).

The terms *dynamic* and *static* fusimotor action are misleading, in that both types of action alter mainly the *gain* and *offset* rather than the *dynamics* of Ia and II responses to stretch. Matthews originally coined the terms to distinguish the strong γ_s biasing action on Ia afferents at constant (static) muscle length from the large increases in Ia response to (dynamic) length changes evoked by γ_d fibers (236). Subsequently, it was claimed that γ_d action selectively increases velocity-sensitivity of Ia afferents (208), but this was based on an association of velocity response with the *slopes* of firing rate in ramp stretches (a nonlinear property discussed below). In fact, if the *initial steps* in rate are taken as the velocity components, and the slopes are taken as the length responses, γ_d action does not significantly change the ratio, nor does it change the frequency of singularities in sinusoidal frequency–response plots (68).

Spindle Models. Various mathematical models of these properties have been developed. Though it has always been recognized that nonlinearities are a major problem, several very useful linear frequency–response analyses have been published (68, 87, 141, 166, 177, 241, 272). Representative transfer functions relating firing rate to input are as follows:

spindle Ia afferents, displacement inputs less than 0.5% rest-length (68):

$$\frac{K_1 s(s + 0.4)(s + 11)(s + 44)}{(s + 0.04)(s + 0.8)} \quad (1)$$

spindle Ia afferents, displacement inputs greater than 0.5% rest-length (68):

$$\frac{K_2 s(s + 0.4)(s + 4)(s + 44)}{(s + 0.04)(s + 0.8)} \quad (2)$$

spindle II afferents, all displacement inputs (68, 272):

$$\frac{K_3(s + 0.4)(s + 11)}{(s + 0.8)} \quad (3)$$

where K_1 , K_2 , and K_3 are gain constants and s is the Laplace frequency-domain operator.

As we saw above, γ action, either static or dynamic, changes the gain of spindle afferent responses but has little effect on the dynamics. γ action can therefore be characterized by changes in the gain constants alone (γ_d : increased K_1 or K_2 ; γ_s : decreased K_1 or K_2 , increased K_3). Ia afferents are more velocity-sensitive as temperature drops, and this may be represented by reducing the “44” parameter in the $(s + 44)$ terms (272). However, a limitation of the linear models is that velocity-sensitive components of Ia responses to ramps do not scale *linearly* with increasing velocity (237). Schäfer et al. (172, 299) and Houk et al. (176) proposed a power-law relationship between Ia responses and velocity of stretch:

$$\text{Ia firing rate} = \text{constant} \times \text{velocity}^n \quad (4)$$

The mean value of the exponent n was 0.56 in Schäfer’s hands or 0.3 according to Houk. Schäfer’s analysis was restricted to the dynamic index (the decrement in firing at the end of a ramp stretch). Houk et al. (176) found that the addition of a length-dependent term:

$$\text{Ia firing rate} = \text{constant} \times \text{length} \times \text{velocity}^{0.3} \quad (5)$$

characterized the response of Ia afferents during ramp stretches of different velocities. The initial step in Ia firing at the onset of a ramp stretch was represented by two more terms added to equation 5, specifying firing rate and muscle length offsets r_0 and l_0 :

$$(\text{Ia firing rate} - r_0) = \text{constant} \times (\text{length} - l_0) \times \text{velocity}^{0.3} \quad (6)$$

An interesting nonlinearity predicted by equation 6 is that the size of the initial step in firing rate depends on the muscle length at which the ramp stretch starts. This produces an increase in the ratio of the velocity response (step in firing rate at stretch onset) to the displacement response (slope of firing rate profile). Poppele (271) also reported changes in this ratio, but in relation to stretch velocity rather than initial length, a result that is *not* predicted by equation 6.

Details aside, the important point is that the Ia response is clearly a nonlinear function of length and velocity. Other nonlinear models have been published by Hasan (165) and Schaafsma et al. (300), the latter including muscle length-tension properties and spike-encoding mechanisms. So far, it is the linear transfer functions (68, 272) that have proved most accessible and practical to modelers, although

the problem of nonlinearity, particularly in relation to velocity scaling, always lurks in the background. For all their lack of precision and generality, linear models are useful in revealing fusimotor modulation of muscle spindle firing in awake animals (see Fig. 3.9) and gain and stability in the stretch-reflex arc (28, 184, 291). Admittedly, the conclusions would be strengthened if they were validated with the more accurate but computationally demanding nonlinear models.

Tendon Organs

Structure and Response Properties. Tendon organs are encapsulated corpuscles 0.2–1 mm long. Over 90% are located at musculotendinous junctions or tendinous inscriptions (21). Their sensory endings, which project into the muscle nerve as group Ib axons, are entwined amongst the tendinous strands of 10–20 motor units, a given motor unit engaging one to six tendon organs (185, 285, 288). In the absence of muscle contraction, most tendon organs have a high threshold to imposed muscle stretch (235). Thus, tendon organs were initially considered to be “overload protectors,” firing only when muscle force approached injurious levels. This idea was dispelled when it was shown that the adequate stimulus for tendon organs was active contraction of the motor units with which they were associated (175, 188). Even in the absence of active contraction, when the rates of applied muscle stretch were matched to those in the step cycle, 46 of 53 tendon organs were activated (319). Indeed, it is now quite clear that tendon organs as an ensemble respond over the full physiological range of muscle force (5, 83, 174).

Tendon Organ Models. Because it is impossible to monitor force from the small group of motor units that innervate a tendon organ, it is difficult to determine precise input–output characteristics for the receptor. Nonetheless, some frequency analyses have been performed by applying feedback-controlled force signals to whole muscle (8, 177). This indicated that tendon organs had a high-pass filtering property, or dynamic component of response, similar to that of spindle II endings (5). Tendon organ Ib afferents, all force inputs (177):

$$\frac{K(s + 0.15)(s + 1.5)(s + 16)}{(s + 0.20)(s + 2.0)(s + 37)} \quad (5)$$

where K is a gain constant. Another similarity with spindle II afferents is that Ib afferents tend to fire fairly regularly, except at low levels of active force, when unfused twitch contractions of newly recruited motor units summate and “beat,” causing charac-

teristic bursts of Ib firing (155, 174). The Anderson transfer function, used in conjunction with monitored force, gave a good fit to the firing profile of a Ib afferent recorded in a conscious cat (8, 15). There are various sources of nonlinearity in Ib transduction. First, a given ending may be unloaded by contractions of muscle fibers not inserting into the receptor capsule (175, 320, 354). Second, the relationship between whole-muscle force and the force produced by the tendon organ’s cohort of motor units is unlikely to be perfectly linear. Third, at low active forces, the beating effects alluded to above are seen and, as each new motor unit is recruited, a characteristic step in firing rate occurs (15, 83, 334). Thus the attractive simplification that tendon organs provide a more-or-less linear representation of whole-muscle force is problematic and has been debated for some time (35, 83, 155, 174, 185).

Spindle and Tendon Organ Densities: A Clue as to Function?

There are 25,000–30,000 muscle spindles in the human body: 4,000 in each arm and 7,000 in each leg (42, 340). Muscles vary tremendously in the number of spindles and tendon organs they contain. This has often been seen as a clue to unraveling their function (1, 21, 59, 185, 238, 340). Some intrinsic hand muscles that contain large numbers of spindles have no tendon organs at all (185). Other muscles, notably the diaphragm, the digastric muscle, intrinsic muscles of the larynx, and extraocular muscles in some species, have no spindles (238).

One interpretation of these differences is that muscles engaged in fine control have the most proprioceptors. For example, in the cat forepaw, which can perform delicate manipulative tasks, the fifth interosseus has 119 spindles/g; whereas lateral gastrocnemius, a hindlimb extensor, has only five spindles/g (69). Some deep neck muscles have up to 500 spindles/g (1). Granit suggested that these muscles control precise movements and so they require elaborate spindle control (148). However, this was challenged by Banks and Stacey (20), who reviewed data on 75 muscles in different species and found that spindle density depended not so much on muscle function as on size. The average number of spindles n in a muscle of weight w grams was:

$$n = 38 w^{0.42} \quad (8)$$

derived from:

$$\log_{10} n = 1.58 + 0.32 \log_{10} w \quad (9)$$

Roughly speaking, equation 8 says that the number of spindles = $38 \times$ cube root of muscle weight in

grams. Thus, a 64 g muscle should have about 152 spindles. On this basis, the cat fifth interosseus has only 5% more spindles than expected from its size, about the same as the hindlimb extensor soleus (20). Buxton and Peck (59) put an interesting slant on the issue. They claimed that the number of spindles acting about a joint correlated better with the summed range-of-motion or motor complexity of the joint than the net weight of the muscles. Contrary to previous ideas, it was argued that proximal muscles had more range-of-motion and were richer in spindles than distal ones (305). However, the numbers of spindles were calculated from summed muscle weights. This is probably invalid, as equation 9 applies only to individual muscles. Regardless of how the numbers are computed, however, it is true that the intervertebral neck muscles have a "bewildering number of spindles" (80). The spindles and tendon organs are arranged in complexes that in some cases stretch continuously from one end of a muscle to the other (1). Furthermore, the control of movements of the head is undoubtedly complex. Precise muscle contractions are required to hold the head upright and oriented; the head must provide a stable platform for the visual system, even during large movements of the trunk. In quadrupeds, the mouth is used for feeding, for grooming, and for manipulating objects, all of which require accurate head movement. The high spindle densities in neck muscles are therefore consistent with the idea that the greater the motor demands, the more spindles are required; however, in human psychophysical experiments, the resolution of head movements was found to be somewhat *lower* than that in the limbs, hands, and digits (327). In short, the hypothesis that spindle numbers are related to motor skill is simple and didactically appealing, but unfortunately it is not supported by all of the available evidence.

Proprioceptors in Joints, Ligaments, and Skin

Mechanoreceptors in joint capsules, joint ligaments, and skin are anatomically well placed to provide proprioceptive feedback, but it has been surprisingly difficult to establish their role precisely. Until the late 1960s, joint receptors were assumed to mediate position sense and to signal joint position over the full range of motion (44). However, in an important series of experiments, Burgess and Clark found that most joint receptors in the cat knee were actually quite unresponsive in the midrange (52, 73). This finding has been debated ever since. Ferrell (118), for example, disputed the emphasis of Burgess and Clark's results, claiming that a substantial propor-

tion of units in the cat knee posterior articular nerve responded in the midrange. Tracey (332) recorded from 110 cat wrist joint receptors and obtained results in broad agreement with Burgess and Clark, in that the receptors started firing only when the wrist was pushed into a fairly flexed position, but Zalkind (353) found slowly adapting afferents in cat wrist joint that fired over the whole range of motion. Intercostal joint receptors (139), hip joint afferents (66), and temporomandibular joint receptors (219) were reported to signal across all joint angles. Some of the full-range afferents in the cat posterior knee joint nerve apparently originate in either muscle spindles or tendon organs in nearby muscles (73, 153, 245). Loading of the joint capsule by muscle contraction sensitizes joint receptors, in some cases enough to confer midrange responsiveness on them (156).

On balance, studies in reduced preparations indicated that joint capsular and ligamentous afferents are capable of signaling limb position and movement at the extremes of motion and in some joints over the full range of motion. Given that single-unit discharges are discernable in recordings from whole joint nerves (118), the total number of receptors signaling midrange movement is probably quite low compared to the number of surrounding muscle and skin receptors responding to the same movement. Joint afferents have conduction velocities mainly in the group II range (52), and their segmental reflex connections with α -motoneurons are less direct than those of muscle spindles (187, 189). Their contribution to kinesthesia and sensorimotor control probably complements that of the other proprioceptors (242, see Chapter 4) and they may have a special role in inhibiting muscles when joints are damaged (183).

Receptors in the glabrous or hairy skin overlying joints and muscle respond both phasically and tonically to movement (349) and so are good candidates for a role in proprioception. Furthermore, there is a huge number of skin receptors in the extremities. The human hand has an estimated 17,000 skin mechanoreceptors with myelinated afferent fibers (190), compared to a population in the whole arm of about 4,000 muscle spindles, 2,500 tendon organs, and perhaps a few hundred midrange joint receptors. The skin receptors best suited to signal position are slowly adapting type II receptors, which respond to stretching of the skin, in some cases several centimeters from the point of maximal strain (173). Slowly adapting type I skin receptors respond more locally, fire less regularly, and adapt more rapidly. Additionally, there are at least four kinds of hair follicle and rapidly adapting glabrous skin receptors

that respond to the dynamic components of hair deflection or skin stretch (349).

Invertebrate Proprioceptors

The response properties of the invertebrate displacement sensors of the chordotonal organs and thoracicocoxal muscle receptor organs have been studied in several species. In general these receptors have high-pass characteristics comparable to those of mammalian muscle spindles. For example, in recordings from various single afferents innervating femoral chordotonal organs in stick insects, units were encountered that were predominantly length-sensitive, velocity-sensitive, acceleration-sensitive, or admixtures of the three (23, 24). Crustacean thoracicocoxal muscle receptor organs have two types of sensory afferents, T and S, which are analogous to mammalian spindle Ia and II afferents (57). They are nonspiking, transmitting signals to the CNS electronically, but in all other respects their responses to length changes and their efferent control by Rm1 and Rm2 motoneurons (equivalent to γ - and β -motoneurons) are astonishingly similar to those of muscle spindle endings. Campaniform sensilla, located in the external cuticle of many invertebrates, show high-pass characteristics comparable to those of their mammalian analogs, the tendon organs. High-pass frequency response characteristics have also been reported for other classes of invertebrate proprioceptors including locust forewing stretch receptors (266) and cockroach femoral tactile spines (274).

RESPONSE PROPERTIES OF PROPRIOCEPTORS DURING ACTIVE MOVEMENT

Methodology

Until the 1960s, no recordings had been obtained from sensory afferents during unrestrained voluntary movement in any species. Yet there was already a wealth of data on their passive properties in anesthetized animals and on their activity during reflexive hindlimb movements and respiration in lightly anesthetized, spinalized or decerebrate animals. In the 1960s, various theories were proposed on how the sensory endings might fire during normal movements and how the afferent input might be used by the CNS in controlling these movements. With hindsight, some of the assumptions were more or less right and some were more or less wrong. In the following, most of the emphasis will be on the data

obtained since 1967 on the firing of proprioceptive afferents in normal voluntary movements.

Hagbarth and Vallbo (1967) pioneered the neurography technique of recording from single sensory nerve fibers using semimicroelectrodes inserted into peripheral nerves of awake human subjects (Fig. 3.5A). The importance of this work in elucidating natural sensory activity during movement cannot be overstated. It coincided with the studies of muscle receptors in decerebrate locomotor cats (309). Other methods have since been developed to record from first-order afferents in normal cats and monkeys [Fig. 3.5; (74, 124, 142, 216, 276, 301)]. A large body of information on sensory input during voluntary movement now exists. While much has been clarified, particularly with regard to tendon organ and skin receptor activity, the firing patterns of muscle spindles and the fusimotor activity that shapes them remain somewhat controversial. Nonetheless, for certain classes of movement such as slow, rhythmical muscle contractions in humans and locomotion in the cat, the firing profiles of spindles and tendon organs are now well characterized, allowing a fairly detailed analysis of sensorimotor interactions.

Although recordings from spindle afferents have been obtained during voluntary movement in humans, cats, and monkeys, it has been virtually impossible to obtain equivalent data on γ -motoneurons (but see 221, 289). In fact it is rather fortunate that spindle-afferents rather than γ -efferents are accessible, because spindles are innervated by up to a dozen γ -motoneurons and it would be difficult indeed to infer spindle afferent behavior from kinematics and the firing of single γ -motoneurons alone. This is not to say that γ recordings should not be pursued in the conscious animal; information about type-specific γ activity is of great interest in relation to arousal, sensory set, and central rhythm generation. But the resultant *sensory* signals are in fact more crucial for understanding the basics of the sensory control of movement.

Muscle Spindles

Involuntary Movements in Animals. The earliest clues regarding fusimotor control of muscle spindle sensitivity in active movements came from recordings in decerebrate cats (111). Spindles in reflexly activated muscles often increased their firing, even when the muscles shortened. This led to the notion of α - γ linkage (148), whereby γ action was posited to keep spindles taut and responsive in the face of extrafusal shortening (209, 238, 268). The early data also showed that γ -fusimotor neurons could fire spontaneously in the absence of detectable muscle activity

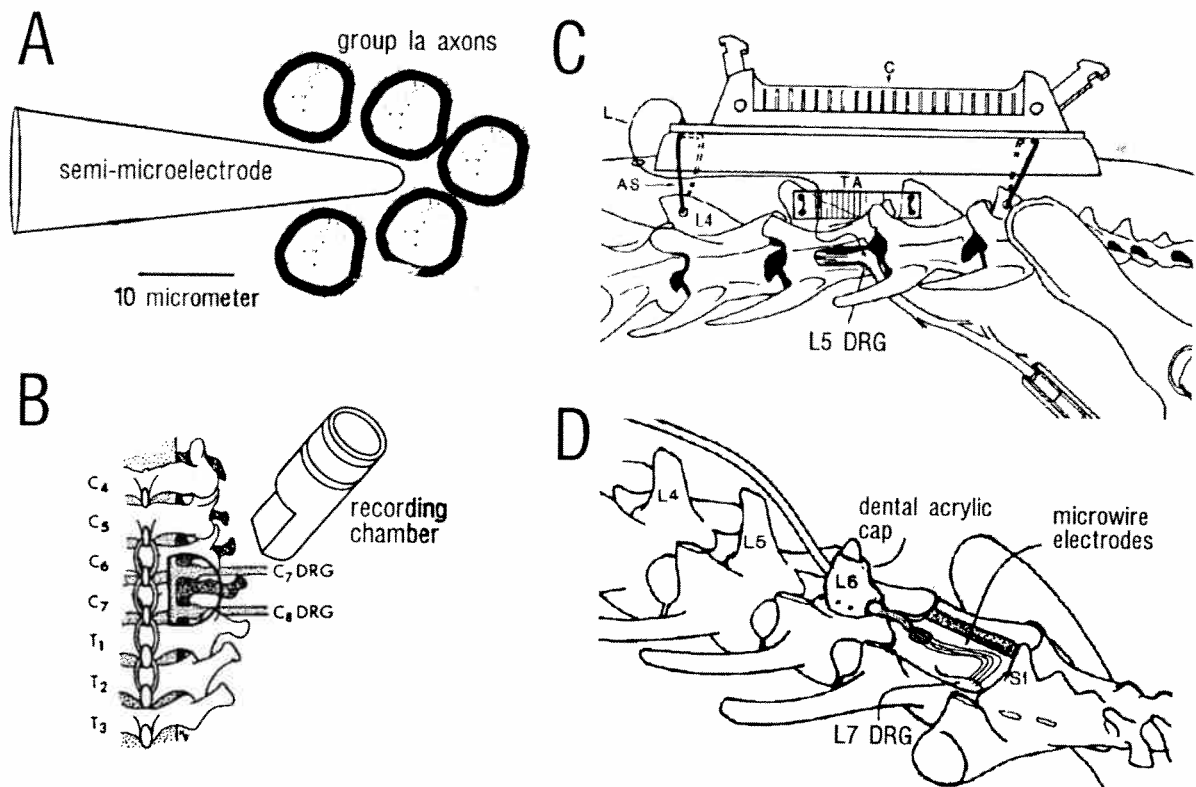


FIG. 3.5. Techniques to record from single nerve fibers in conscious humans (A), monkeys (B), and cats (C and D). A, Schematic profile of a neurography electrode pushed amongst Ia axons in a peripheral nerve (shown in cross section). The uninsulated portion of tip is about $30\ \mu\text{m}$ long. Single-unit selectivity probably relies on proximity of tip to a node of Ranvier of an axon. [Adapted from Wall and McMahon (341).] B, Exploded view of recording chamber over monkey cervical (C7, C8) dorsal root ganglia (DRG). Holes drilled through the lateral ver-

tebral processes allow access to DRG by microelectrodes lowered in chamber. [Adapted from Schieber et al. (302).] C, Loeb's "hat-pin" microwire implants in cat lumbar (L5) dorsal root ganglion (DRG). Microwire lead from DRG is stabilized on a Silastic sheet sutured between L5 and L6 vertebral spinous processes, then tunneled up to connector back-pack. D, Floating microwire variant of C, showing stabilization of cable shield in dental acrylic cap on L7 spinous process. Microwires are also stuck and/or sutured to dura mater. [C and D adapted from Prochazka (276).]

and that they generally had lower thresholds than α -motoneurons to electrical stimulation within the CNS, particularly within the reticular formation (151), to mechanical stimuli such as twisting the ear (150), and to noxious stimulation (182, 189, 191).

Spindle afferent and γ -efferent firing was also recorded during involuntary *rhythmical* motor activity in many different reduced preparations. This material has been reviewed several times (148, 178, 222, 238, 275) and so only the salient points are summarized here. Recordings during *respiration* in anesthetized cats generally supported the idea of phasic, α -linked γ activity, but tonic γ firing was also observed (152). The first recordings from spindle afferents during *locomotor* movements were obtained in high decerebrate cats (309). Firing was closely linked to phasic bursts of muscle activity rather than stretch, again suggesting a dominance of α -linked γ action. But in subsequent recordings (308), length changes were the more powerful modulatory influ-

ence, so it was hard to draw firm conclusions from these studies. Several other research groups have recorded from spindles in decerebrate or decorticate cats generating locomotor rhythms. The experimental techniques, conditions, and constraints varied between laboratories (33, 60, 252, 267, 312). The picture that has emerged from the reduced locomotor preparations is that γ activity is partly linked to α activity and partly independent of it. This is neatly illustrated in Figure 3.6, which shows the neural traffic in a muscle nerve during locomotion in a thalamic cat. The afferent and efferent components of activity were separated analytically on the basis of delays between two recording sites (33). The spindle Ia and II firing profiles in this figure are somewhat distorted versions of the muscle length profile. γ Firing is modulated roughly in phase with α activity, about a "carrier" frequency (i.e., bias or offset). The phasic component of γ action presumably maintained the spindle afferent discharge dur-

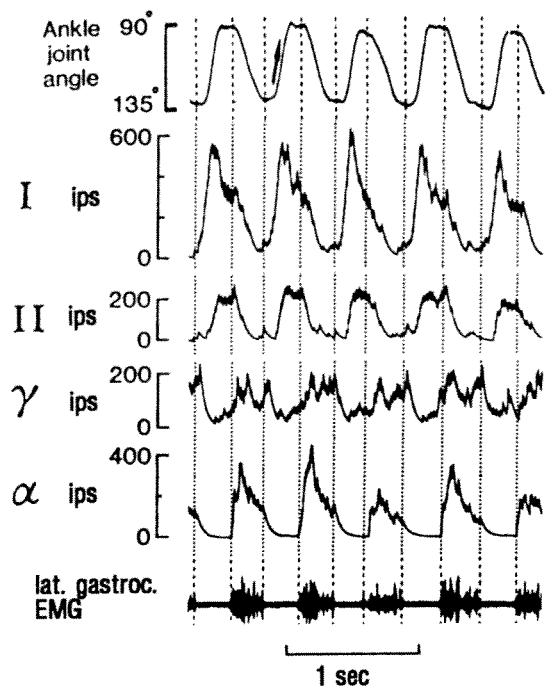


FIG. 3.6. Activity of group I and II afferent fibers and α and γ motor fibers during spontaneous air-stepping movements in high decerebrate cats. The mean firing rate profiles were estimated by electronically sorting afferent and efferent signals in a branch of the nerve to lateral gastrocnemius muscle. The technique does not differentiate between spindle Ia and tendon organ Ib afferent activity, but in this experiment Ia activity probably dominated the group I record, because there was no ground contact or weight bearing. Muscle lengthening is shown by the arrow. Both Ia and II afferents fired mainly during muscle stretch. The γ activity was modulated in time with the α bursts and whole-muscle electromyogram and there was an additional tonic offset or bias (i.e., there were both phasic and tonic components of γ discharge). [Adapted from Bessou et al. (33).]

ing extrafusal shortening and the tonic component set the underlying spindle afferent bias and sensitivity, depending on the admixture of γ_d and γ_s activity involved.

There has been much speculation on whether γ_d and γ_s fibers have distinct firing patterns during rhythmical movement. Some data indicate phasic α - γ_d linkage with tonic γ_s activity, some indicate α - γ_s linkage with γ_d tonic, and some indicate muscle-specific combinations (see Table 3.1, later). A case has also been made for coactivation of γ_d , β_d and fatigue-resistant type S motor units in "tonic" muscles and γ_s , β_s and fast-twitch type F motor units in "phasic" muscles (34). β -Motoneurons are α -motoneurons that innervate spindles, so they presumably fire at rates typical of motor units: 5–20 imp/s. Spindles are rarely innervated by more than one β -motoneuron, so β -fusimotor action, although guaranteed to be α -linked, is probably relatively weak

compared to the action of a cohort of 10–12 γ -motoneurons firing at much higher rates. This weak β action may, however, be amplified or potentiated by concomitant γ action (112).

Voluntary Movements in Animals. The firing of spindle afferents recorded during chewing and other jaw movements in awake cats (74, 322) and monkeys (142, 204, 234) was generally related to muscle length, albeit with additional electromyogram (EMG)-linked components resulting from presumed α -linked γ and β action. Single-unit activity has also been recorded with microelectrodes from the cervical dorsal roots of awake cats and monkeys [Fig. 3.5B,C,D; (77, 124, 301, 302)]. Because the stability of the recording situation was precarious, the monkeys were not anesthetized during afferent identification. Several units with convincing spindle Ia-like responses to muscle twitches and vibration were characterized in slow tracking movements and self-paced rapid movements (330). In the rapid movements the afferents responded mainly to displacement, with phase advances consistent with the dynamic transfer characteristics of Ia afferents. However, during slow tracking (Fig. 3.7), some units fired as much during muscle shortening as lengthening. Although some of this could be ascribed to α - γ linkage, there were various features that indicated significant independence of α and γ activity (301, 302, 330). In contrast, the units recorded by Flament et al. (124) all increased their firing during isometric contractions, indicating α - γ linkage.

The firing of muscle afferents recorded in awake, walking cats (see Fig. 3.5C and D) has been combined in small ensembles according to muscle group and receptor type (Fig. 3.8). Some interesting facts and figures emerge from these data. First, the data showed that ensembles of as few as four or five afferents can provide the CNS with high-resolution information on muscle length and force. After the data of four or five afferents are averaged, the addition of more afferents does not substantially change the ensemble profile. Second, when the linear model of equation 2 is applied to the averaged length signals, the resulting profiles match the corresponding ensemble firing rates well (Fig. 3.9). This means that to a first approximation spindle afferents signal muscle length and velocity in the step cycle. Third, deviations from the modeled profiles suggest some α -linked γ action and mechanical transients related to tendon stretch, muscle "bounce," or muscle slackening (170, 287). Finally, if the firing of all the spindles in a typical cat hindlimb muscle is summed, the peak Ia input to the CNS in the step cycle is 20–40 kimp/s (283). The net monosynaptic reflex action of

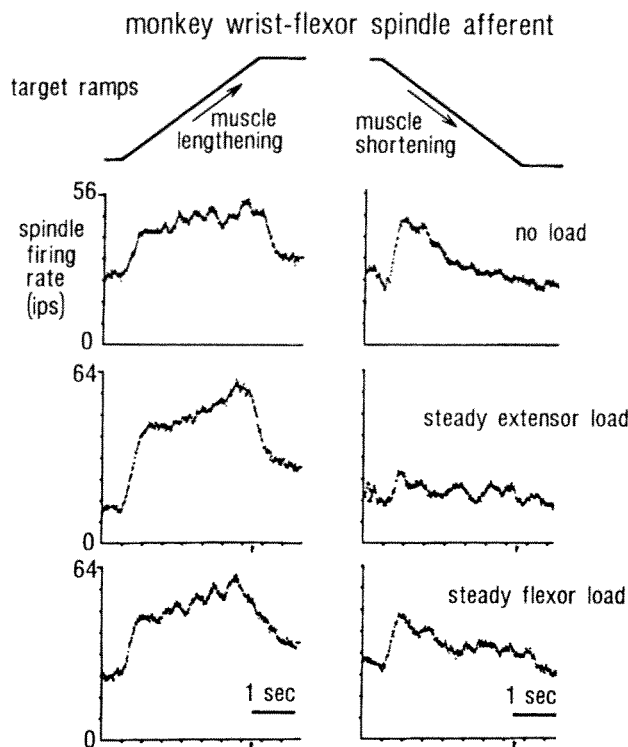


FIG. 3.7. Firing rate profiles of a monkey wrist-flexor spindle afferent recorded during voluntary wrist movements tracking a displayed ramp-and-hold target. Each profile is an average of several trials. Actual wrist movement was not shown, but it is assumed that tracking was good. Six combinations of movement and loading condition are shown. Left column, wrist extension trials (muscle lengthens); right column, wrist flexion (muscle shortens). Top row, no load; middle row, steady extensor load; bottom, flexor load. During muscle lengthening, afferent increases its firing rate. At onset of shortening, smaller increases in rate are seen, indicating some γ action. Relationship to loading conditions was interpreted as evidence for independence of γ and α activity. [Adapted from Schieber and Thach (302).]

this is nearly enough to depolarize low-threshold α -motoneurons from rest to firing threshold [(278); see also Chapter 1]. Note that if a 20 kimp/s signal were played through a loudspeaker, it would be so high pitched as to be inaudible.

Voluntary Movements in Humans. In the 1970s, Hagbarth and Vallbo did many neurography trials and trained students and visiting scientists in the technique. Neurography was independently developed in Munich (318) and Paris (292). As a result, hundreds of recordings from single muscle and skin afferents have now been documented by different groups around the world (131, 161, 178, 190, 349). Spindle afferents of various muscles of the hand, arm, and leg have been studied in different sensorimotor tasks and contexts. Certain basic firing properties have

been observed repeatedly and are now established beyond reasonable doubt:

1. In relaxed muscles, spindle afferents behave like passive stretch receptors, increasing their firing in response to muscle stretch and decreasing it during shortening (Fig. 3.10A). The stretch-sensitivities of the afferents, expressed in terms of proportional changes in muscle length, are similar to those of deafferented spindles in cats (107, 238, 334), baboons (70), and isolated human muscle (257, 273).

2. α - γ Coactivation: when muscles are voluntarily activated there are clear signs of accompanying fusimotor activation: increased spindle afferent firing in isometric contractions (Fig. 3.10B) or maintained firing if the muscle shortens (Fig. 3.11). This implies a “hard-wired” α - γ linkage, as posited by Granit (148) and reaffirmed by Hagbarth (161) and Rothwell et al. (293). In the early neurography work the EMG-linked component of γ action seemed to dominate spindle afferent responses, particularly in isometric data of the type in Fig. 3.10B. In the late 1970s, spindle afferent recordings in cats and monkeys performing normal movements indicated that changes in muscle length generally overrode the effect of α -linked γ action. Correspondingly, in the more recent human neurography experiments, when muscles contracting against loads were allowed to lengthen and shorten, the spindle firing also usually reflected the muscle length changes rather than the EMG (Fig. 3.11).

3. Firing rates of human spindles during active movements are quite low: usually in the range of 0–30 imp/s. Maximal rates of up to 85 imp/s have been seen in faster movements and tremor (336). By comparison, in cat gait, Ia firing rates of 50–200 imp/s were typical and rates greater than 600 imp/s occurred in imposed movements or unusual tasks (145, 217, 218, 283). Monkey jaw Ia afferents fired at 0–250 imp/s during eating and up to 360 imp/s in rapid movements (142, 204).

4. Human spindles fire in segmented bursts during rapid muscle stretch (162). It was posited (109) that these bursts could cause the M1, M2, and M3 segments of EMG response to rapid stretch (207, 232). Data in awake cats lent support to this idea, showing Ia bursts during rapid stretch and corresponding EMG bursts at monosynaptic latencies (15, 284). However, this hypothesis has been overshadowed to some extent by new evidence that EMG responses at M2/M3 latency are mediated by long-loop transcortical pathways (62, 239).

Task-Related Fusimotor Set. Motor tasks with elements of novelty, difficulty, or arousal are often as-

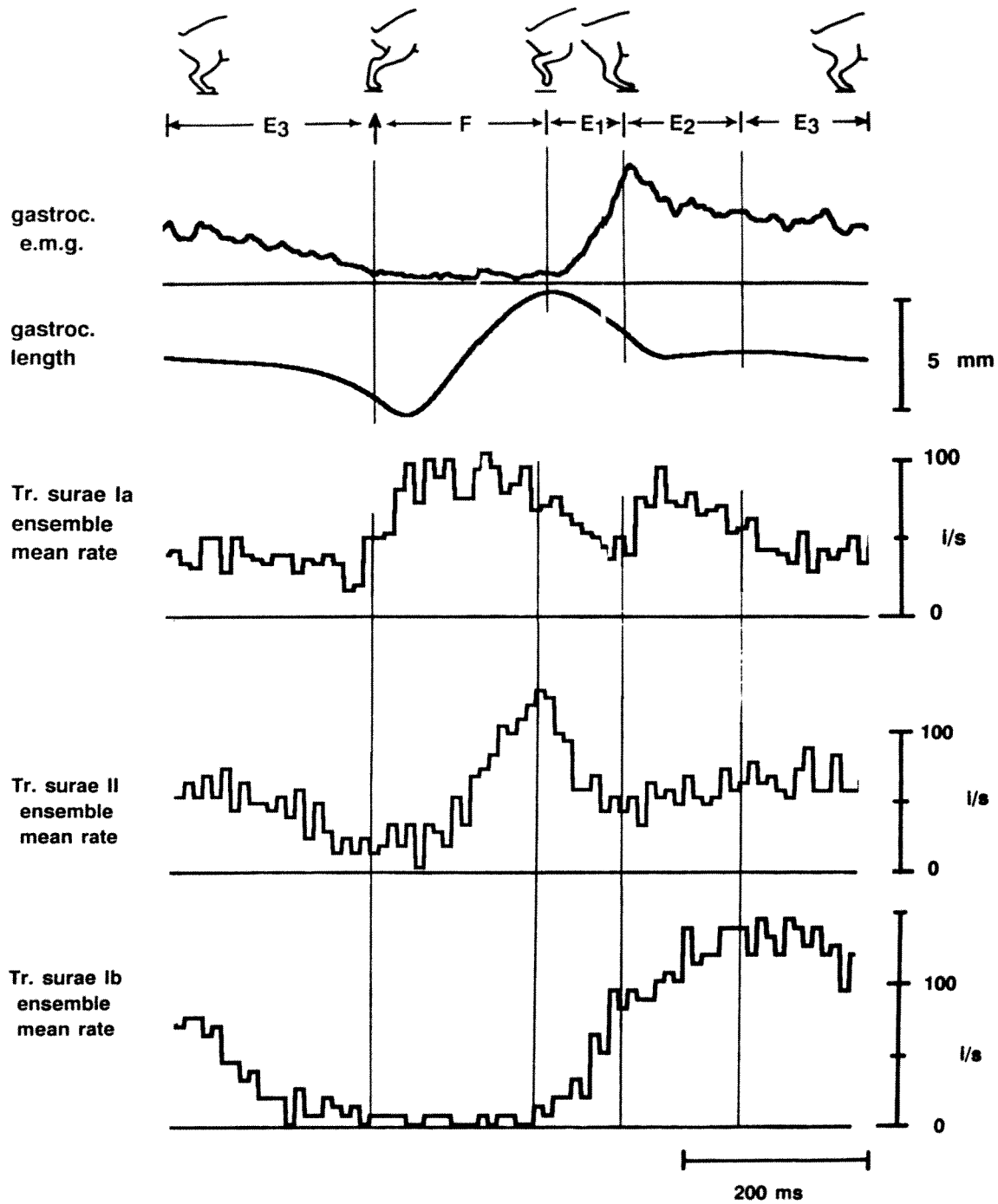


FIG. 3.8. Mean firing rate profiles of the three types of large-diameter afferents in cat triceps surae muscles in the step cycle. The ensemble data were averaged from chronic recordings of nine Ia afferents, two II afferents, and four Ib afferents. Each afferent contributed four step cycles. The firing rate profiles are event histograms of 10 ms bin width calibrated in terms of mean

firing rate. The electromyogram and length averages were obtained from the Ia data only, but were similar for the II and Ib recordings. Note the high peak firing rate of tendon organ Ib afferents during the stance phase. [Adapted from Prochazka et al. (283).]

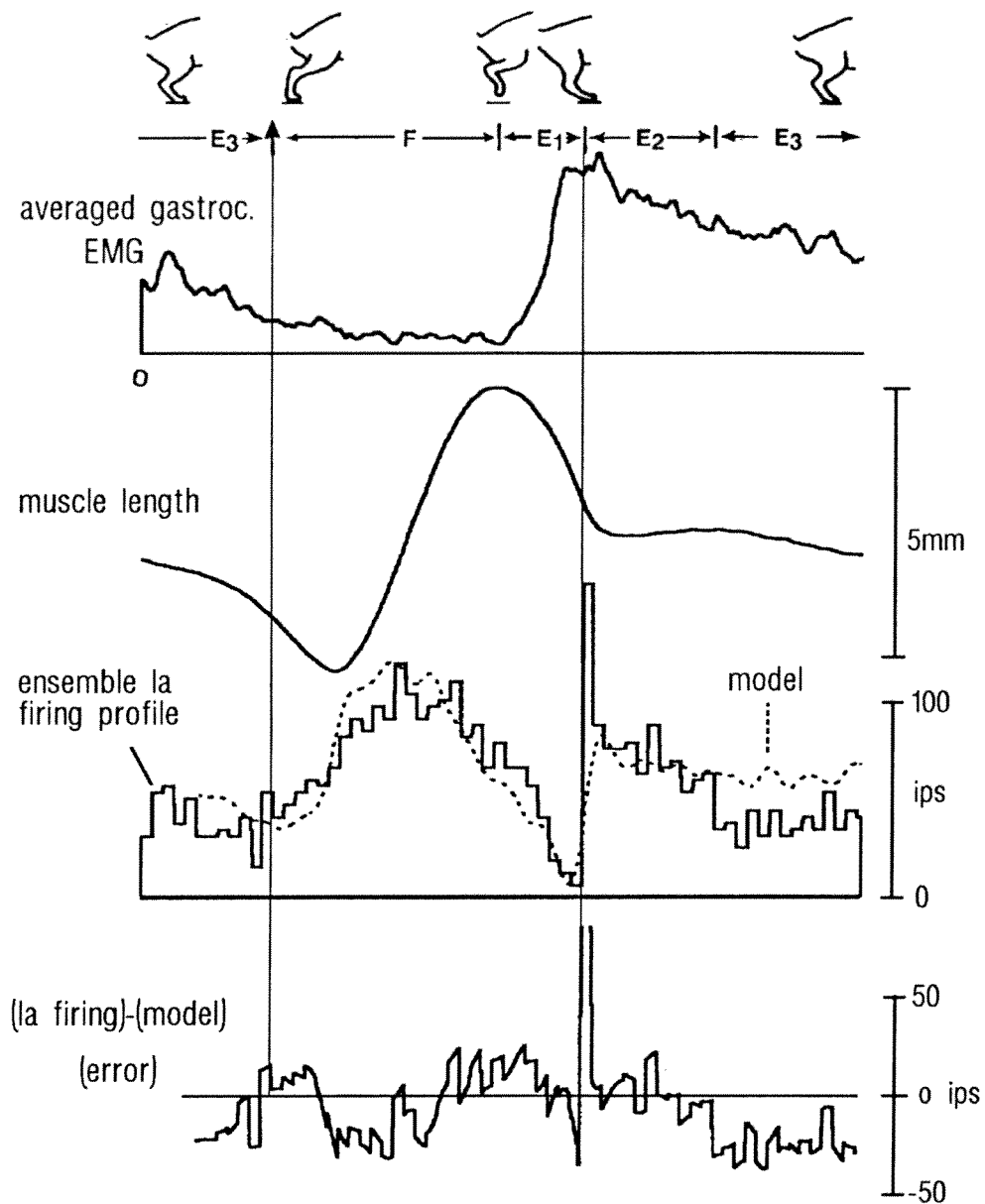


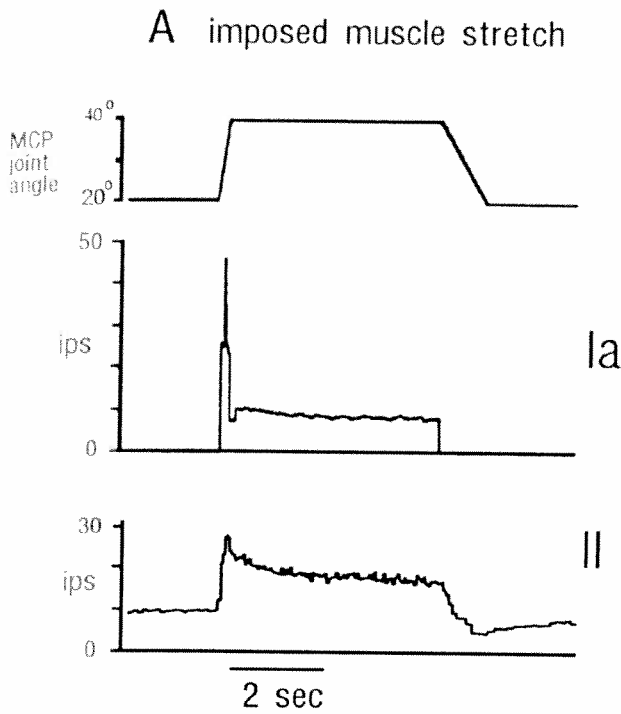
FIG. 3.9. Same Ia data as in Figure 3.8, but this time aligned to the moment of foot contact, thus exaggerating the contact-related Ia firing transient. *Dashed curve* was obtained by digitally filtering the length profile using equation 2. *Bottom trace* shows difference between ensemble profile and model (i.e., the firing rate not accounted for). The modulation depth of the ensemble

profile is 108 imp/s; that of the error signal is 67 imp/s. The error reflects factors such as fusimotor modulation, tendon compliance effects, and muscle unloading. There is no clear relationship between the error and the electromyogram, indicating that α -linked components of γ action were not dominant.

sociated with high spindle Ia stretch-sensitivity and firing rates in cats [(282); Fig. 3.12]. The task- and context-dependence of γ_d activation that this implies has been associated with the general phenomenon of preparatory set (117). Elevated fusimotor set has been inferred in several tasks and contexts, but the most reliable way to evoke it in conscious cats is to impose movements on a limb. This presumably evokes a state of increased alertness or wariness in

the animals. The Ia firing rates during imposed movements can be quite astonishing (>600 imp/s). With firing rates such as these, the net Ia input to the CNS from all of the spindles in the cat hindlimb may transiently exceed 0.2 Mimp/s (277).

The notion of fusimotor set presupposes α - γ independence, particularly in relation to γ_d -motoneurons. Consequently, in human neurography experiments, evidence for convincing and significant γ



B isometric contractions

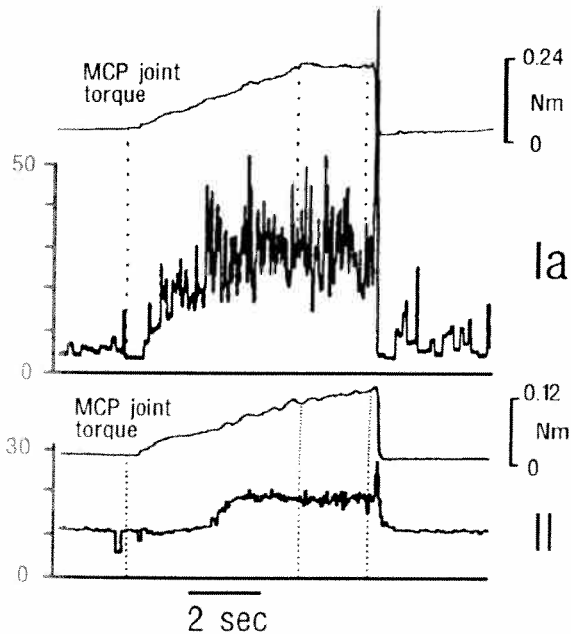


FIG. 3.10. Activity of a human spindle primary (group Ia) and secondary (group II) afferent of a finger extensor in imposed movements and voluntary isometric contractions. A, Both afferents responded to muscle stretch. As the muscle shortened, the group Ia afferent fell silent and the group II afferent reduced its firing rate. B, Both endings showed increased firing during isometric contractions of the receptor-bearing muscle, monitored as torque about the metacarpophalangeal (MCP) joint. [Adapted from Edin and Vallbo (108).]

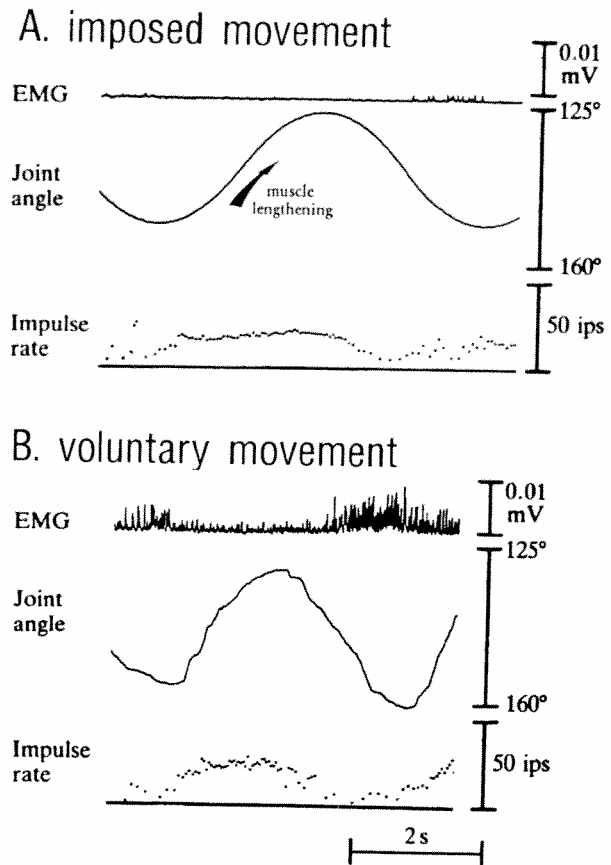


FIG. 3.11. Response of a human muscle spindle afferent of a finger extensor to imposed movements and voluntary movements against a small external load opposing finger extension. A, The afferent responded to the imposed sinusoidal displacement and maintained its firing during muscle shortening, indicating some fusimotor action. There was minimal electromyographic activity during the imposed movements. B, The spindle responded to the active movements in much the same way. There was no evidence in this case of additional firing linked to the voluntary electromyogram, as would be expected from α - γ co-activation. [Adapted from Al-Falahe et al. (4).]

action independent of α activity has been sought. So far little independence has been found (3, 10, 54, 55, 130, 289, 336). Table 3.1 summarizes the various hypotheses regarding the central control of γ_s - and γ_d -motoneurons. Clearly, both α -linked and tonic components of γ activity are implicated throughout. The tonic components of γ drive are task- or set-related in most cases.

As already mentioned, spindle firing rates are low in human neurography compared to those in the cat and monkey recordings. It is unclear at this stage whether this represents a genuine species difference, or whether it is merely a consequence of experimental design. In neurography, the risk of dislodging electrodes from their location in peripheral nerves places constraints on the speed and freedom of

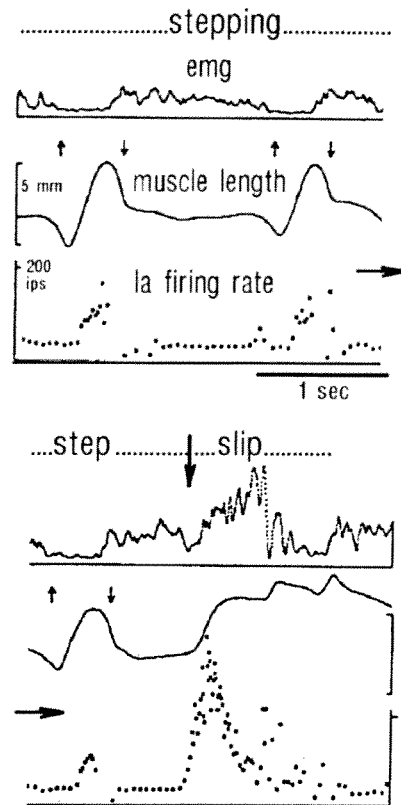


FIG. 3.12. Ankle extensor Ia firing illustrating a sudden change in stretch-sensitivity when the hindlimb of a cat walking along a table surface slipped on the edge of the table. The record is continuous from upper to lower panel. At the moment marked with the arrow, the cat slipped and crouched, the receptor-bearing muscle actively lengthened, and the spindle afferent responded with firing rates of nearly 400 imp/s. This was interpreted as a sudden task- or context-related increase in γ_d action, exemplifying "fusimotor set." [Adapted from Prochazka et al. (281).]

movement. When movement velocities are matched, the species differences are not so marked. Thus in slow hand movements, monkey spindles fired at 0–80 imp/s (124, 302). In alert cats performing slow hindlimb limb movements, firing rates were also often in the 0–80 imp/s range (personal observations). It should be remembered that animals brought into an unfamiliar laboratory for recording sessions are likely to be aroused, alert, and suspicious, whereas human subjects can rationalize the situation, and although discomfort is involved, they are unlikely to maintain a heightened state of motor readiness. The somewhat higher firing rates in animals performing comparable slow movements and the much higher rates associated with novel tasks and imposed forces may therefore be due to increased arousal and attention in the animal subjects. Equivalent states of arousal, alertness, and anxiety occur in normal daily

life in humans, but it is difficult to reproduce them in the neurography setting. The question of whether humans exhibit fusimotor set is therefore still open.

Central Control of the Fusimotor System. Fusimotor set also presupposes that there are areas in the CNS that selectively activate γ -motoneurons. Granit and Kaada (1952) found that stimulation of the brain-stem reticular formation produced fusimotor excitation along with generalized motor arousal (151). This association of γ activity with diffuse arousal was soon overshadowed by the theory of phasic, α -linked activation. However, Appelberg (11, 12) later found that stimulation of a region dorsal and caudal to the red nucleus selectively activated γ_d -motoneurons. Appelberg called this region the mesencephalic area for dynamic control (MesADC). Although the location of the MesADC and its specificity in controlling only *dynamic* fusimotor activity has been questioned, recent results have confirmed that γ_d action is readily elicited from regions both caudal and rostral to the red nucleus (324). This effect was seen in jaw muscle spindles as well as in hindlimb spindles (323), indicating that brainstem control of γ_d action is diffuse and widespread. In fact, the MesADC may be part of a larger subcortical system involved in attentional and orienting mechanisms (229), of which fusimotor set is but one example. Other areas implicated in γ_d control are the motor cortex (338) and habenular nucleus (95). γ_s Activity has been evoked from regions caudal and dorsal to the red nucleus (158, 324), the vestibular nuclei (65), and substantia nigra pars reticulata (345). Note that some of these putative fusimotor control centers may have neuromodulatory rather than direct motor functions.

Several lines of evidence have also implicated the cerebellum in fusimotor control (100, 110, 135, 149, 151, 302, 329, 330). Indeed, cerebellar hypotonia and ataxia are sometimes explained in terms of fusimotor dysfunction. However, these ideas have been undermined by a recent study in conscious cats, in which spindle afferents were monitored before and during ataxia resulting from lidocaine inactivation of the cerebellar nuclei (145). Task-dependent fusimotor modulation of spindle responses was not detectably changed during the ataxia. It was concluded that the cerebellum was not a major controller of the fusimotor system, and that the ataxia observed did not result from disordered fusimotion.

Spontaneous and reflex-evoked γ activity has been recorded in acute spinal cats (30). There was indirect evidence that γ_s and γ_d fibers were affected reciprocally by intravenous DOPA in this preparation. In acute DOPA-treated spinal locomotor cats, phasic γ

TABLE 3.1. Summary of Hypotheses Regarding CNS Control of γ Activity

Preparation	Muscles and Movement	γ -Fusimotor Profile		References
		γ	γ_i	
Decerebrate or anesthetized cat	Hindlimb, reflexive	α -Linked (γ_i ?) + some tonic or reflex-evoked firing		149–151, 158
Decerebrate or anesthetized cat	Intercostal: respiration, coughing	α -Linked + tonic or reflex-evoked firing		81, 85, 115, 306
Decerebrate or spinal locomotor cat	Hindlimb extensors: locomotion	α -Linked		308, 309, 312
Anesthetized cat	Intercostal: respiration	Tonic	α -Linked	152
Anesthetized cat	Jaw closers: reflex chewing	α -Linked	Tonic	14, 95, 147
Decerebrate locomotor cat	Hindlimb <i>flexors</i> : locomotion	α -Linked	Tonic	33, 60, 252, 253, 267
Decerebrate locomotor cat	Hindlimb <i>extensors</i> : locomotion	Tonic	α -Linked	33, 60, 252, 253, 267
Normal monkey + cat	Jaw closers: chewing, lapping	Tonic & some α -linked		74, 142, 204, 234, 322
Normal cat	Hindlimb: locomotion	Tonic + some α -linked	Task-/set-related + some α -linked	145, 218, 277, 281, 282
Human	Hand, arm and leg: isometric and tracking	Mainly α -linked, some set-/task-related		3, 54, 108, 130, 161, 163, 289, 293
Normal monkey	Forearm: isometric and tracking	Task-related + some α -linked		110, 124, 301, 302

activity has been reported (312) and in chronic spinal locomotor cats, spindle firing patterns suggested intense, tonic γ activity (Pearson, personal communication). The fact that the spinal preparation shows generalized fusimotor activation that is in part independent of phasic α activity indicates that at least some of the interneuronal circuitry of fusimotor control resides in the spinal cord.

Tendon Organs

Animal Data. Hindlimb Ib afferents in the awake cat typically fire in the range 0–150 imp/s during active muscle contractions in stepping and greater than 400 imp/s in rapid imposed stretch (15, 215, 283). Extensor forces in slow cat gait usually reach about 15% of maximal isometric force (342). This is somewhat higher than the forces attained in the human Ib recordings mentioned above, where firing rates were in the range of 0–50 imp/s. Staircase firing increments (Fig. 3.13) and other nonlinearities are smoothed away in ensemble firing profiles of as few as four Ib endings (Fig. 3.8) but it has been argued that these discontinuities might actually convey useful information to the CNS about motor unit recruitment and local mechanical events in the muscle (1, 35).

Surprisingly, the ensemble data indicated that the net firing rates of all the tendon organ Ib afferents of ankle extensor muscles rivaled that of the corresponding spindle Ia and II populations during the stance phase of the step cycle (Fig. 3.8). There has recently been a complete reappraisal of the role of extensor Ib input in relation to reflexes and locomotor pattern generation and accordingly the details of Ib firing during the step cycle have assumed a greater importance (see below).

Human Neurography Data. Recordings from Ib afferents are scarce in the neurographic literature, as they are in the chronic animal data. Most human Ib afferents were silent in relaxed muscle and fired during active muscle contraction at rates in the range of 0–50 imp/s (4, 10, 107). Again, for stability reasons peak forces were low (~0.08 Newton meter at metacarpophalangeal joint: i.e., probably <15% maximal voluntary torque). Unlike spindle afferents, human Ib endings never showed signs of unloading in isometric contractions (108). An interesting property of Ib firing is the staircase nature of increases and decreases in firing rate during smooth increases and decreases in muscle force [Fig. 3.13; (108)]. This was first described by Vallbo (334) and was later corroborated in decerebrate cats (183) and then in awake cats (15). It presumably reflects progressive recruit-

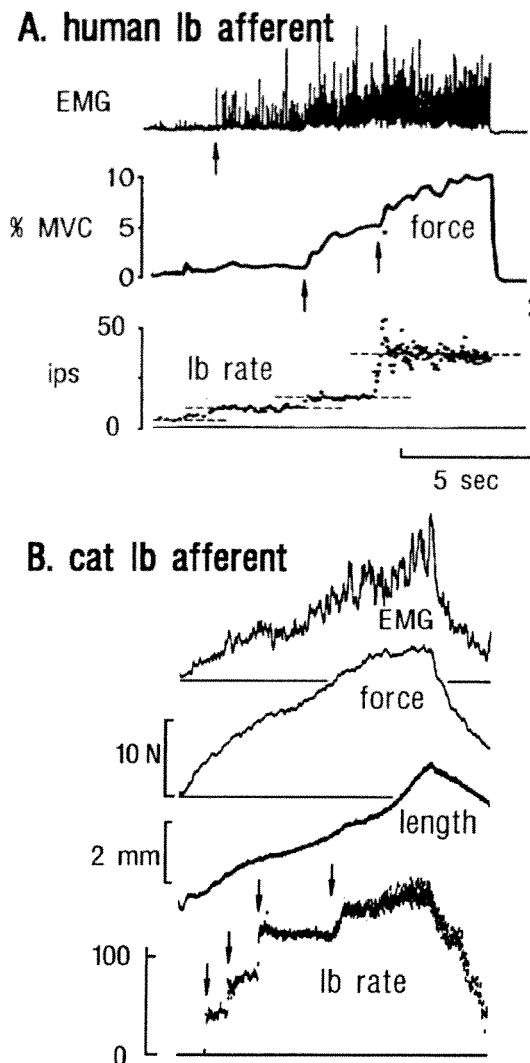


FIG. 3.13. Firing of single Golgi tendon organ afferents during slowly increasing muscle force in (A) a human finger extensor muscle and (B) an ankle extensor muscle in the awake cat. The arrows indicate increments in firing rate attributed to progressive recruitment of motor units. The rate increments and overall range of firing rate of the human tendon organ were smaller than in the cat: finger extensor force was expressed as a percentage of maximal voluntary contraction (% MVC). For comparison, in the cat 10 N measured at the footpads is roughly equivalent to 15% maximal force (343). [A Adapted from Edin and Vallbo (108), B from Appenteng and Prochazka (15).]

ment and derecruitment of motor units. As previously mentioned, this and other nonlinearities have raised the question of whether tendon organs can possibly signal whole-muscle force (185).

Skin and Joint Afferents

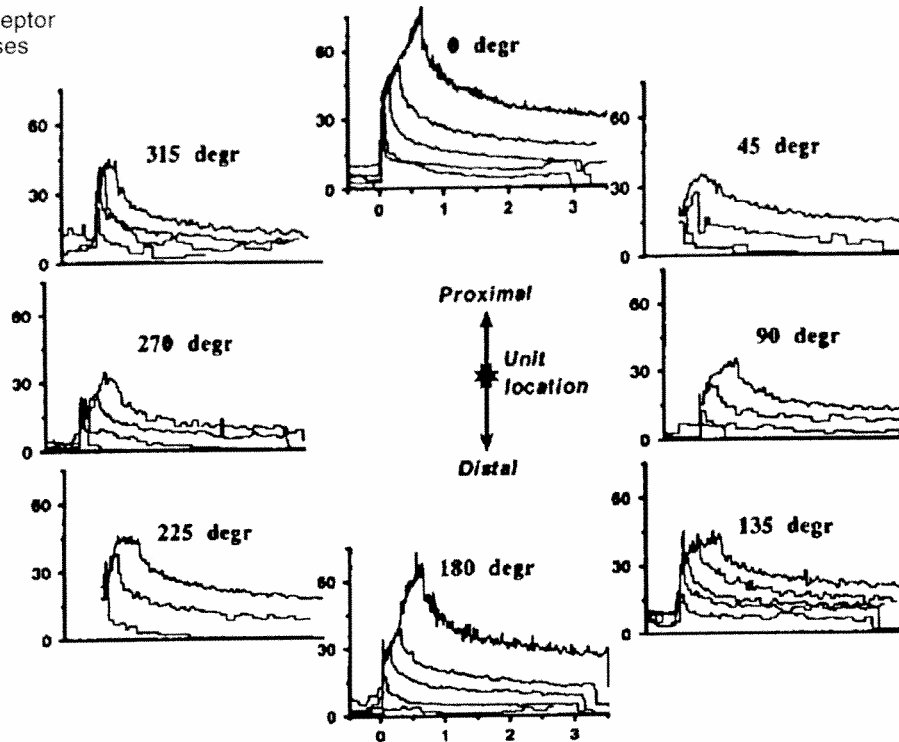
Animal Data. Although skin afferents have been encountered more often than muscle afferents in chronic animal studies, very few recordings have

been documented in the literature. This may be because skin afferent firing during movement was perceived as being fairly predictable, though actually this is not always the case. Receptors in the skin in the vicinity of the jaw can signal jaw movement in a reproducible manner and could therefore provide proprioceptive information to the CNS (13). Not surprisingly, skin and hair follicle receptors in and around the footpad in the cat's paw signal foot touch-down and some fire throughout stance (171, 215, 216, 333).

Chronic data on the firing of joint receptors in animals is even more scanty (215, 216). This is not too surprising, as joint receptors are far outnumbered by skin and muscle receptors so the likelihood of encountering them in random samples of dorsal root fibers is low. Their afferents are smaller than many muscle and skin afferents, so they are less likely to produce discriminable action potentials. Finally, differentiating them from spindle afferents is problematic, especially if suxamethonium is not used. The few data that exist indicate that some joint afferents fire throughout the step cycle, while others scarcely fire at all in the midrange (216).

Human Data. Neurographic studies have shown that slowly adapting type II skin receptors signal the stretching of skin over nearby joints, which could provide proprioceptive signals to the CNS [(53, 105, 106, 181, 196, 248); see also Chapter 4]. However, two objections must be dealt with before this can be accepted. First, slowly adapting type II afferents are rather nonspecific in their response to the direction of skin stretching. Edin (105) characterized this in vectorial terms, showing that although a given receptor has a preferred strain axis, it also responds, albeit at lower firing rates, to strain in all other directions (Fig. 3.14). Nonspecific directional sensitivity raises the problem of ambiguity in the information signaled, in that a given receptor, say over the metacarpals, may respond just as vigorously to being stretched by movement of one finger as it does to movement of another. Edin has an interesting answer to this objection. If convergence is allowed, the information from an ensemble of slowly adapting type II skin receptors on the back of the hand would in theory provide a sensory population vector that would reliably differentiate individual finger movements. Edin has shown this both by neurography and by measuring skin strain at a matrix of points on the back of the hand during finger movements (Edin, personal communication). In fact, by observing one's own hand during finger movements, and by focusing on the tactile sensation in the finger

A. skin receptor responses



B. strain sensitivity vectors

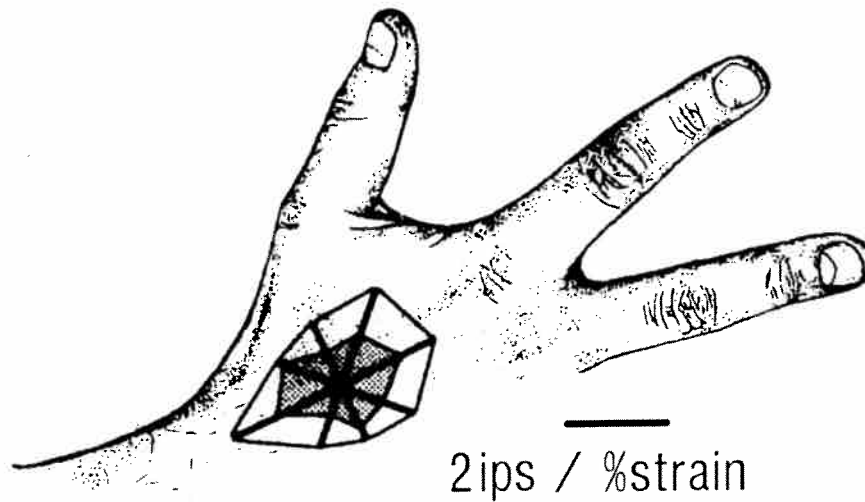


FIG. 3.14. SAI skin receptor responses to stretching the skin in the receptive field at the angles shown (0 degrees is along forearm axis). Each plot shows the firing rate responses to five skin stretches applied along the angular axis indicated and causing strains of 1.25%, 2.5%, 5%, 10%, and 20%, respectively. The sensitivity along a given axis was expressed as the adapted

response per % strain (i.e., $\text{imp} \cdot \text{s}^{-1} \cdot \% \text{strain}^{-1}$), and superimposed on the diagram of the hand as a vector with appropriate length and orientation. This receptor would presumably respond best to flexion of the forefinger, but it might also respond to flexion of the other fingers and the thumb. [Adapted from Edin (105).]

webs, it is easy to convince oneself of Edin's argument.

The second objection is that some skin areas contain afferents that signal over the whole range of joint movement while others do not. For example, palmar glabrous skin afferents responded only at the extremes of finger joint displacement (53, 225), whereas nonglabrous receptors on the back of the hand responded over the full range of motion (10). Given that different joints are associated with different proportions of glabrous and hairy skin, skin-mediated proprioceptive acuity would be rather uneven.

If skin receptors contribute to *conscious* proprioception (248), one might expect that electrical stimulation of them would give rise to kinesthetic illusions. In human neurography it is claimed possible to stimulate through the recording needle and excite only the axon being recorded from (225, 335, but cf. 341). When this was done in 18 slowly adapting type II skin afferents, movement sensations resulted in two cases (225). In the same experiment stimulation of single spindle afferents did *not* give rise to kinesthetic sensations even though ensemble spindle input evoked by muscle vibration and whole-nerve electrical stimulation clearly does [(129); see also Chapter 4]. The positive result in single slowly adapting type II skin receptors is thus powerful evidence that skin afferents play an important role in proprioception. Recently, Edin's sensory vector matrix has been tested in reverse in the author's laboratory by D.F. Collins. Skin afferents at a set of points on the back of the hand and over the finger joints were stimulated electrically and mechanically. This produced weak illusions of finger movement, which were greatly augmented by tendon vibration.

Joint receptors have occasionally been recorded neurographically (53, 104, 181, 225), though it is worth noting that differentiating joint afferents from group II spindle afferents is problematic (280). The firing profiles indicated that the afferents signaled over a fair range of joint angle. Human psychophysical experiments designed to evaluate the contributions of muscle, skin, and joint receptors to kinesthesia have been somewhat inconsistent. Several groups found that local anesthesia of joint afferents did not interfere significantly with position sense, whereas inactivation of muscle afferents did (73, 296). Position sense was fairly normal in patients who had undergone total replacement of knee joints (86), hip joints (194), finger joints, and toe joints (86). On the other hand, Ferrell and Smith (120) anesthetized the proximal interphalangeal joint in a human subject and found inaccuracies in position matching, particularly at the extremes of joint angle.

Anesthetizing the knee joint capsule in cats led to marked motor and kinesthetic deficits (119). At this point the relative contributions of joint and skin receptors to kinesthesia and motor control are still unresolved.

Invertebrate Proprioceptors

There is very little information on the firing of proprioceptive afferents during free movement in invertebrates. Wilson and Gettrup (351) first recorded from wing stretch receptors during tethered flight in grasshoppers. Zill and his colleagues (211, 212, 355) found that tibial campaniform sensilla fired rhythmically in relation to force and cuticular strain in certain parts of the cockroach step cycle. As the cadence increased to 24 steps/s there was a progressive phase shift between bursts of afferent and efferent activity. This and other evidence suggested that proprioceptive feedback in rapid stepping was too delayed to contribute reflexly within the same step cycle. A switch to open-loop control in rapid gait was posited. Under these circumstances proprioceptive signals may be used to provide overall postural information and one-step-ahead control.

FEEDBACK CONTROL

Basic Concepts, Definitions, and Types of Control System

In the last few years there has been a move to integrate the mass of information on simple reflexes into an overall view of how multisegmented limbs are controlled. To gain some perspective, let us first summarize some basic concepts and design features of engineering control systems. In robotics, the essence of control is to guide actuators to move loads in a desired manner. The desired movement is termed the *input* and the actual movement is the *output*. In a closed-loop control system, the output produced by the actuator is monitored by a sensor, fed back and compared to the input, producing an *error* signal. The error signal is passed on through one or more elements back to the actuator, thus closing the loop. The signal transmitted around the loop is generally altered ("conditioned") by each element (e.g., dynamic filtering). This may be an unavoidable property of the element or it may be added to compensate for unwanted filtering elsewhere in the loop (269). In the simplest case, if the load-moving properties of the actuator are understood and there are no obstacles, it is enough to supply a predesigned input signal to the actuator, to move the load as required. Al-

though there is no feedback as such and the system therefore operates “open-loop,” the nature of the input signal derives from prior feedback comparisons of outputs and inputs. Most factory robots operate open-loop, their tasks being divided into stages, the sequential completion of which is sensed by switches or position sensors. In sophisticated robots, several variables may be sensed and used in complex ways to control actuators. As Levine and Loeb (210) entertainingly remarked, you need only look in a mirror “to see an example of a very satisfactory nonlinear MIMO control system.” The similarity to neural sensorimotor control is compelling, so let us identify some basic control systems.

Proportional Control. Actuators are driven in proportion to the error between command signals and sensory signals. The error signal is usually filtered dynamically to improve performance [differentiation to speed up response, integration to attain zero final error, the combination being termed proportional-integral-differential (PID) control].

Finite State (Conditional) Control. Finite state systems were first formulated in relation to production-line processes. In these systems, actuators are driven according to rules such as: *IF* this sensory condition is satisfied *AND* that sensory condition is satisfied *THEN* do such-and-such (331). If one thinks of all the available sensory inputs as comprising a multidimensional vector, a rule or state is satisfied when the vector falls within a region of vector space “belonging” to that rule. In some systems, rules are derived using automatic induction algorithms in which the relative importance of different sensors emerges quantitatively [i.e., some sensors are more equal than others (195)].

Adaptive (Self-Organizing) Control. Internal transmission properties of the controller (e.g., compensation parameters) are modified or tuned on the basis of performance assessments or parameter identification in preceding time segments. In essence, a supervisory controller assesses performance and adjusts parameters in the basic controller (e.g., when the load changes). Because there are many ways to assess performance and to change parameters, adaptive controller design is virtually an art form (98, 269).

Predictive (Feedforward) Control. Parametric changes are generated in advance of expected loading conditions. For example, transmission delays (e.g., to and from extraterrestrial robots such as moon buggies) may be overcome by using an internal model of the actuator/load, which provides an immediate

simulated output suitable for local closed-loop operation. A copy of the simulated output is passed through an analog delay line and compared with the “real” delayed output, allowing follow-up error correction (315, cf. 339).

Neural Networks: Sensorimotor Maps. An orderly array of artificial “neurons” with large numbers of “synaptic” interconnections is set up within a digital processor to transform sensory inputs into motor outputs. Appropriate transformations are “learnt” by strengthening or weakening the interconnections according to the success or failure of repeated trials of a sensorimotor task (“knowledge of results”). This process may be viewed as a form of feedback control. There are various types of network structure and numerous “teaching” algorithms (192). The map or engram thus learnt can subsequently be used open-loop (no feedback) to transform multivariate commands or sensory inputs into desired responses.

Fuzzy Logic. Inputs from sensors are assigned “membership” functions. A membership function translates a particular value from a sensor into a measure of the “truth” of a linguistic description of state such as “the leg is in early swing.” For example, suppose leg extensor force is high. The likely truth of the statement “the leg is in early swing” is very low, whereas the likely truth of “the leg is in late stance” is quite high. Because the description of state is imprecise, it is termed “fuzzy.” Each fuzzy sensory state is coupled with a corresponding fuzzy motor state such as “activate flexors strongly and extensors weakly.” The corresponding *motor* membership function is scaled according to the “truth” accorded its related sensory state. Several motor membership functions are then condensed into a discrete value using a “defuzzification” algorithm. This discrete value drives the actuator(s) (98, 199). In “neuro-fuzzy” controllers, the membership functions themselves are adjusted to optimize performance criteria. In essence, fuzzy systems allow multiple sensory modalities to be weighted and combined according to linguistically recognizable rules. This feature makes them interesting in relation to neural control (see below).

From the 1950s to the mid-1980s, neurophysiologists were somewhat mesmerized by the first of the above schemes, proportional feedback control. This was partly due to successful modeling of the oculomotor system and partly to some basic structural similarities between the stretch reflex arc and servo loops (238). Proportional feedback models are useful in describing the control of one or two variables such as muscle length and force. But when multi-

variate, complex movements such as those in posture and locomotion are considered, they quickly become unmanageable (210). Some of the other systems may then be more applicable. It is interesting that all six control schemes listed above are now being applied to the practical problem of controlling human movements artificially (168, 270, 279).

Proprioceptive Control

This section deals with current and emerging views on proprioceptive control strategies and the way reflexes and higher level control are combined to produce normal movement. Several excellent and exhaustive reviews have appeared recently on reflex integration in the spinal cord [(19, 187, 244); see also Chapter 1]. The emphasis in what follows will therefore not be on spinal reflex mechanisms, but rather on current attempts to understand proprioceptive feedback in a general sense and in relation to the control schemes just summarized.

Proportional Control (Stretch Reflexes). It was recognized many years ago that the stretch reflex arc is analogous to a proportional feedback control loop. The length sensors, muscle spindles, feed back a signal related to muscle stretch. Motoneurons (the comparators) subtract this from the descending command for muscle shortening (the "input" signal). The difference (error) drives the muscle to shorten. Note that the descending command to *shorten* is opposite in sign to the *lengthening* signal from spindles; summing the two is equivalent to subtraction, which is consistent with negative feedback.

Given this compelling analogy and the many studies of the spindle-mediated stretch reflex over nearly a century, the role of the stretch reflex in controlling movement is still remarkably elusive. On the one hand, it is clear that a volley of action potentials evoked in the Ia afferents of a muscle by a tendon tap or nerve stimulus can produce a reflex twitch of homonymous and synergistic muscles that can move a limb. On the other hand, when displacements are applied to a limb, the components of EMG response attributable to spinal reflexes are relatively small (164, 207, 232). Perturbing forces are transmitted through skin and underlying tissue, simultaneously stretching, jarring, and unloading many receptors in skin, ligament, muscle, and tendon. Yet the afferents of the stretched muscles seem to dominate the responses, because inactivating or bypassing the other sensory modalities has little effect (28, 91, 231). The long-latency reflexes are larger and more forceful than the monosynaptic or short-latency oligosynaptic components. They are mediated partly via trans-

cortical pathways (62, 238) and partly via segmental reflex action evoked by Ia activity that continues as the displacement unfolds (134, 162). They are also under volitional control, so their designation as reflexes is a loose one. The functional role of Ib input in load compensation in the human arm is unclear. In theory, concomitant force and length feedback of varying relative weight should result in spring-like behavior of varying compliance, but attempts to verify this in human subjects have been inconclusive (82). Ib feedback plays an important role in modulating postural and locomotor reflexes (93).

It is often said that reflex gains are low. What does this mean? In theory, gain around a feedback loop may be measured by detaching the sensor, applying a displacement to it, and measuring the actuator's response. The response-to-stimulus ratio is, by definition, the open-loop gain (i.e., the overall product of the gain of each element all the way around the loop). This experiment is possible in invertebrates whose proprioceptors are anatomically separate from muscles: thus stretch-reflex gain has been measured as a function of frequency in different behavioral states in stick insects (24). During load compensation the gains ranged from 1–11. Comparable indirect estimates have been derived in humans, gains being in the range of 0–2 (28). The gains in these very different species were similar in the sense that they were much lower than gains in electronic circuits or robotic devices. This is presumably because load-moving muscles develop phase lags greater than 180 degrees in a frequency range of 0–10 Hz, which restricts the gains attainable without reflexes becoming unstable.

Reflex gain should be seen in context. The function of the stretch reflex is to resist load perturbations and maintain stability. In general, the closed-loop operation of a feedback loop with an open loop gain x reduces the deflection otherwise caused by a force perturbation by $1/(1 + x)$. Thus an open loop gain of just 1 would reduce the deflection of a tonically activated muscle by 50% (i.e., muscle stiffness is effectively doubled). If the inherent muscle stiffness itself is high—for example, because of agonist-antagonist co-contraction (32)—the force resulting from the stretch reflex is also high because the reflex multiplies the effect of the inherent stiffness (28, 311). Thus although stretch reflex gains in animals are numerically low by technological standards, they are functionally significant in the biological context (61). In some cases they may be increased to cause a "useful" instability (26, 303). Animal movements are smooth rather than robotic (i.e., load compensation is compliant rather than stiff). It is therefore appropriate that stretch reflexes are not very strong.

Many experiments have shown that stretch reflex gain varies with intention, task, and sensory context (47, 117, 123, 164). The longer latency electromyographic responses in humans are under strong volitional control and in certain cases are inhibited or even reversed (63, 99, 202, 247, 254). Mono- or oligosynaptic H-reflexes during stepping are lower than in quiet stance, and in running they are lower still (63, 64). H-reflexes are also attenuated in difficult tasks (214) and when muscles are co-activated (258). Although it is generally assumed that gain is modulated by presynaptic inhibition as part of the central motor program, this may also be due to movement-evoked reafference (76).

Positive Force Feedback? In cats it has recently been shown that extensor Ib-mediated reflexes, which are inhibitory during quiet stance, completely reverse and become excitatory during the stance phase of gait (78, 264). In invertebrates reflexes also reverse when going from rest to active movement (25). In principle, positive force feedback should be destabilizing. However, provided that the open-loop gain of positive force feedback remains less than 1, the operation of a positive Ib reflex arc is stable and in fact mimics rather well the behavior of the cat limb during gait. This has been modeled in the author's laboratory with the help of Dr. David Bennett, using both physical actuators operating under positive force feedback and mathematical control-systems models (manuscript in preparation). As positive force feedback gain approaches 1, a force applied to the actuator is resisted, much as in a length servo. However, unlike a length servo, this occurs at whatever length the output happens to be when the system is turned on (cf. lead-pipe rigidity). In combination with weak negative length feedback (loop gain ~ 1), the system reproduces command displacements and responds to external perturbations like a spring whose stiffness rapidly increases as force feedback open-loop gain approaches 1.

At this stage it is unclear whether this excitatory Ib action during cat gait really does constitute positive force feedback or whether the Ib input acts at the level of the locomotor pattern generator, triggering the stance/swing transition in a finite-state manner (see below). The issue is currently being tackled in two or three laboratories: essentially, if *proportional* excitatory responses to Ib input can be demonstrated during gait, this would support the idea of proportional positive feedback. This is not to say that the two mechanisms are mutually exclusive; Ib input could still also "trigger" the pattern generator within a finite-state structure.

Inherent Feedback Due to Muscle Properties. In early feedback models of the stretch reflex, the actuator, muscle, was treated as a pure force generator. But it has long been known that in the absence of reflexes, contracting muscles respond to imposed stretch like stiff springs. Partridge (260) equated this to a sort of "intrinsic" length feedback. The great innovation of the equilibrium-point hypotheses of Feldman (31) and Bizzi (37) was to include this nonneural component of feedback explicitly. Feldman's concept is illustrated in simple form in Fig. 3.15. The load-bearing hand is at an equilibrium position, which results from a spring-like deflection from an internally set "virtual" position. The deflection depends on the load and the inherent muscle stiffness *augmented* by the stretch reflex. In theory, the "virtual" or unloaded position is revealed by removing the load (while distracting the subject and so avoiding adaptive responses). If the weight of the forearm is neglected, a notional position is reached which Feldman termed λ . Assuming that the nonreflexive com-

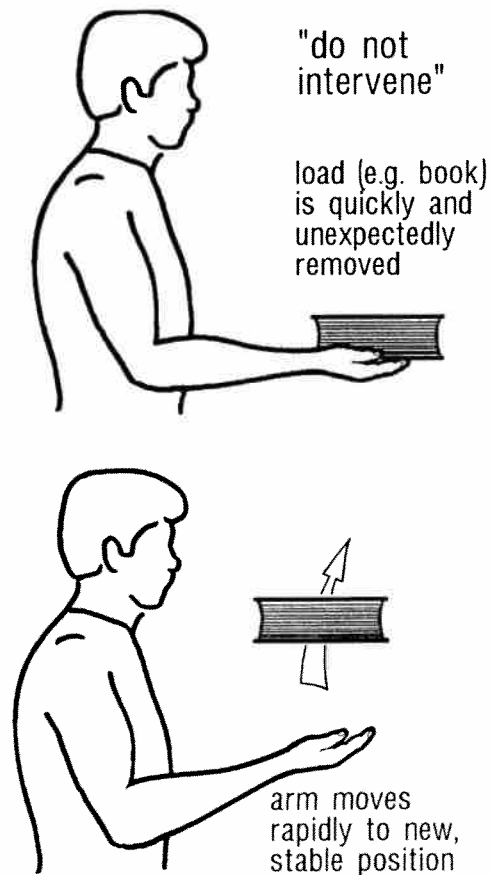


FIG. 3.15. Schematic illustrating the equilibrium point hypothesis. When the book is removed, the arm flexes to a new stable position, close to the threshold of the stretch reflex (the virtual position λ). [Adapted from McCloskey and Prochazka (243).]

mand is set constant throughout, λ corresponds to the muscle length at which the stretch reflex neither adds to nor subtracts from the set level of activation of motoneurons innervating the muscle. Feldman referred to this as the displacement threshold of the stretch reflex. Muscle length can clearly be changed either by changing the centrally generated set level, or by changing the reflex threshold. In fact it has been argued that these amount to the same thing (243).

There is no denying the basic appeal of the equilibrium-point concept: a notational command point moves along a centrally generated trajectory, dragging a load around via a spring (206, 316). In a sense, this is a general way of looking at any load-moving control system. However, some of the details are problematic and have caused a great deal of controversy. For example, in the λ theory, there has been an insistence on the invariance of reflex gain (31) in the face of overwhelming evidence that in fact reflex gain is modulated in relation to task and context, through the mechanisms of presynaptic inhibition, fusimotor activation, and muscle nonlinearities. Strongly activated muscles can only shorten so far, so when large loads are involved, one must assume that virtual trajectories are compressed into small regions close to the anatomical boundaries of the work space. Resolution then becomes a problem. Nonetheless, by placing intrinsic muscle properties in the center of the control scheme, equilibrium-point theories have had a major impact on the field.

Finite State Control: The Logic of Postural Constraints. In 1975, Forssberg and colleagues made the important discovery that during locomotion in the chronic spinal cat, responses elicited by mechanical stimuli impeding the forward swing of the leg actually reversed when the stimuli were applied during the stance phase (126). This was later confirmed in normal cats (97, 344) and humans (29). The topic is reviewed by Rossignol (Chapter 5) so we need only consider the broader ramifications here.

The phase-dependent reversal of reflexes may be viewed as a special case of finite-state control, the rules being of the type:

- Rule 1. *IF* swing phase
 AND skin stimulus
 THEN lift and place leg;
 IF stance phase
 AND skin stimulus
 THEN extend leg and prolong stance.

The rules developed in active prosthetic and orthotic devices show interesting parallels with those

identified in animal species (270, 279). For example, the rule for switching from stance to swing in several designs of above-knee prostheses has the following form:

- Rule 2. *IF* extensor force low
 AND hip extended
 THEN initiate swing.

The same rule was identified quite independently in cat, cockroach, lobster, and stick insect [(9, 24, 25, 71, 159, 265); Fig. 3.16]. The rule-base for flexion onset does not stop with the ipsilateral leg. If the contralateral leg has not ended *its* swing phase, ipsilateral flexion does not occur; *IF* stance *AND* contralateral swing *THEN* delay flexion and prolong stance. This is best illustrated in "foot-in-hole" experiments, where an unexpected absence of contralateral ground support causes a delay in swing-onset in the load-bearing leg (144.) Yet in a gallop, both legs can be in the air at the same time, indicating that the contralateral ground-support condition only applies in slow walking. A more complete version of rule 2 is therefore:

- Rule 3: *IF* gait slow
 AND contralateral limb loaded
 AND extensor force low
 AND hip extended
 THEN initiate swing,
 ELSE prolong stance.

Certain sensory combinations or motor tasks may trigger "override" rules. An obstacle impeding forward swing evokes skin input from the dorsum of the foot that causes the normal swing phase to be aborted and replaced with a stereotyped lifting and placing of the foot: rule 1, the stumble reaction. In above-knee prostheses this is specifically designated a "hazard" state (270). Nociceptive input and input from high-threshold joint afferents may terminate stance and so they may also be viewed as triggering override rules (183). Another type of override is presumably required in *backward* walking (see Chapter 8). Here, swing is initiated when the hip is maximally *flexed* and the gastrocnemii (but not soleus) are still loaded. It remains to be seen whether an entirely new rule is required or whether it is possible to modify rule 3 to fit this situation. Furthermore, the relative difficulty cats and dogs seem to have in walking backwards may indicate that the required variant of rule 3 is not "hard-wired."

The rules discussed so far relate largely to sensory input. Centrally generated programs must also be taken into account. As mentioned earlier, animals

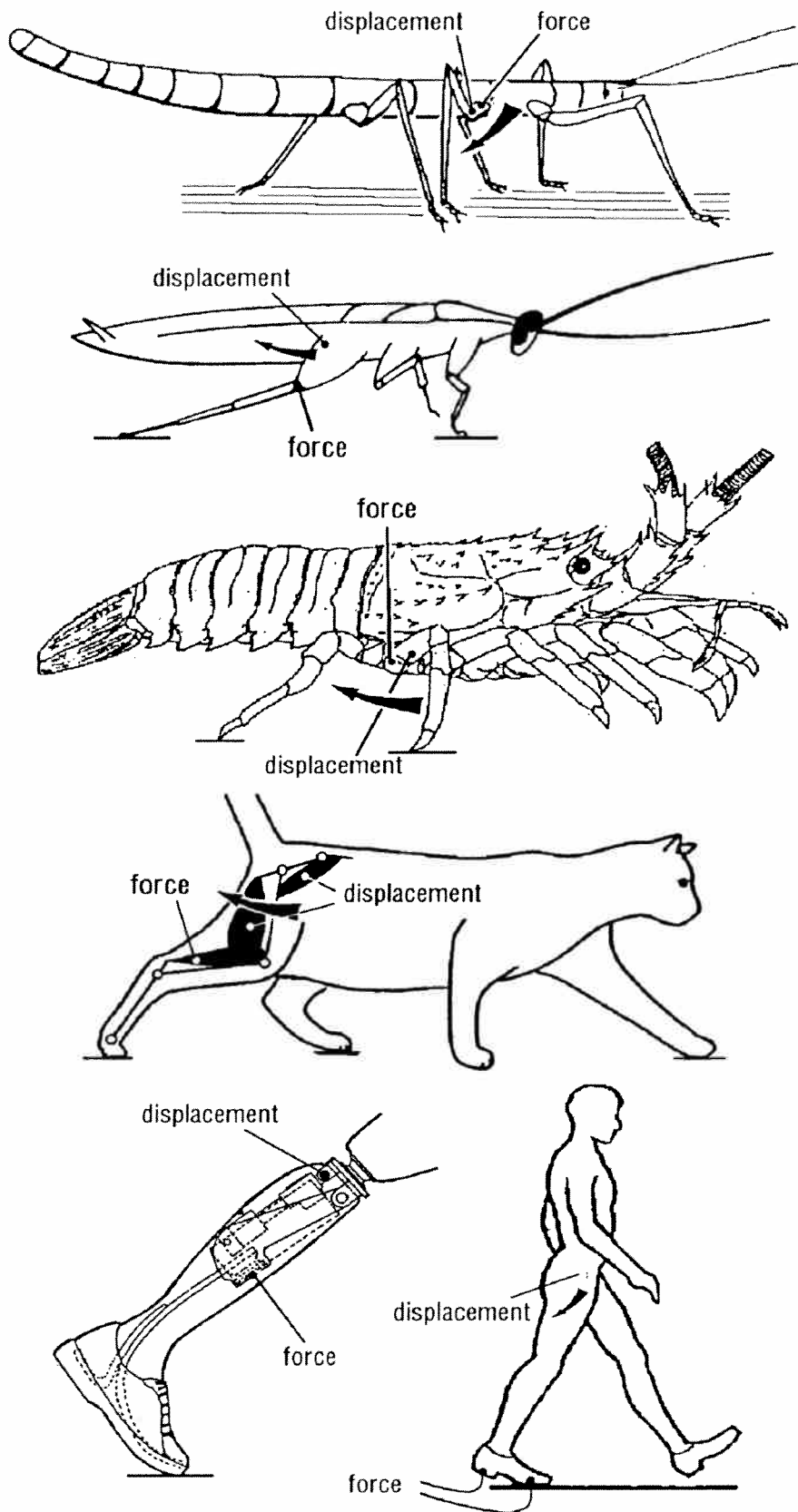


FIG. 3.16. Schematics of stick insect, locust, lobster, cat, active leg prosthesis, and man using functional electrical stimulation. In each case, pairs of sensory variables are indicated that have been shown to be used in a conditional way to initiate the swing

phase of gait (i.e., *IF* displacement exceeds threshold *AND* force has declined below threshold, *THEN* initiate flexion). Approximate positions of identified sensors (natural and artificial) are shown. [Adapted from Prochazka (279).]

held above the ground may "air-step" (136). Swing phases are rhythmically and consistently triggered even though rule 3 is not satisfied. This may be explained in terms of the default operation of a central oscillator that cycles autonomously in the absence of sensory input. When the foot contacts the ground, sensory input is restored and the oscillator is dominated by it according to rule 3. A very similar relationship is seen in scratch responses in cats: if the hindlimb is held in an extended position, the scratching rhythm is suppressed (89). If the paw misses its target or only makes light contact, the extensor phase is relatively short. When firm contact is made, the extensor phase lengthens. In this case not only are limb sensors implicated, but so too are mechanoreceptors of the paw, head, and neck (67). Postural responses to translation of ground support may in fact also be viewed as default programs upon which sensory input is overlaid [(227, 228); Chapter 7]. Other pattern generators under sensory control include those for respiration, mastication (220), and paw-shaking (198). In all of these situations it is possible to identify proportional, finite state, adaptive, and/or predictive mechanisms interacting with basic pattern generators.

"IF-THEN" rules simply provide a description of the association of inputs and outputs in movements that have multiple phases and are subject to postural constraints. They are compatible with proportional control and the central generation of temporal patterns and synergies. Indeed, it is hard to see how "real" motor sequences such as those in gait could be described *without* combining some form of conditional logic with intrinsic central pattern generator and proportional control mechanisms. One can now also begin to speculate on how the logic might be implemented in the spinal cord. For example, rule 2 might be achieved by facilitation of the "swing generator" by hip flexor Ia feedback (200) and disinhibition of it by extensor Ib feedback (265). Alternatively, the extensor half-center might be held in the ON state by extensor Ib facilitation (in addition to direct positive Ib feedback to motoneurons). With the decline of Ib activity at the end of stance, the central oscillator is released, and swing is initiated with support from hip flexor Ia feedback (169). Hazard states such as the stumble corrective reaction and nociceptive gating would require powerful and direct reflex pathways that could override and reset the central pattern generator.

This approach is new in spinal cord research, which has hitherto focused largely on cellular mechanisms and isolated reflexes. Motor strategies and rules are inferred from studies of normal movement (e.g., 24, 144, 261). The neuronal circuitry that ex-

ecutes these rules is then sought in a goal-directed manner so that the functionally important circuits are targeted (6, 146, 244, 264, 325).

Proprioception and the Higher Centers: Adaptive or Predictive Control. A sign of *adaptive* control is that parameters are adjusted as movements proceed. A sign of *prediction* is that parameters are adjusted in advance of expected motor tasks or sensory input. It goes virtually without saying that nervous systems are adaptive/predictive controllers par excellence. Responses to external stimuli can change from one trial to the next according to performance. For example, Nashner (1976) showed that reflex responses to stance perturbations in humans were suppressed over three or four trials if they were arranged to destabilize posture (254). With simpler perturbations, responses actually reversed from one trial to the next, according to stimulus direction (255). These changes were too rapid to be explained in terms of preparatory set; instead, a fast selection of the appropriate synergy based on the evolving sensory input was posited. Selection may rely on feedback from particular groups of receptors, as suggested by a remarkable series of experiments by Dietz and colleagues in which underwater stance platforms and elastic straps were used to modify weight-bearing conditions (93, 94). Brooke and McIlroy (1995) found that when postural stimuli were unpredictable, whole portions of response could be deleted from one trial to the next (47). It was as though the responses of a given muscle were pieced together from prestored patterns, according to intent, uncertainty, and sensory information about the task and the postural conditions preceding it. Indeed, a common theme of much recent work is that the CNS has a repertoire of responses, synergies, and cyclical patterns, which it can modulate, select, and combine according to context and sensory state (161, 311). Some of this is done in a predictive manner, suggestive of preparatory set (117), and some is done as the movements evolve (76, 92, 314).

Where in the mammalian CNS does the prediction and selection occur? First, it should be understood that sensory input is generally gated or filtered before it reaches the higher centers. For example, routine or irrelevant *tactile* input to cortex is attenuated while "relevant" signals are enhanced (2, 310). This modulation occurs at brainstem, thalamic, and cortical levels. Other than fusimotor effects, little is known about gating of *proprioceptive* input to higher centers (6, 122). Enhanced proprioceptive transmission has been posited, but not proved, for tasks that require attention and are associated with increased γ_d action (103, 277). The inferior ol-

may control proprioceptive transmission to the cerebellum: olivary neurons in conscious monkeys are most responsive to novel stimuli (132) and reafferent signals are attenuated in the spinoolivocerebellar pathway during locomotion, whereas novel stimuli are not (213). Cerebellar cortical neurons show activity in anticipation of skin and proprioceptive stimuli (313). Interestingly, the mesencephalic system implicated in γ_a control sends collaterals to parts of the olive (12). This is consistent with the idea that the rubrobulbospinal system is a general area for preparatory set, adaptation, and proprioceptive gain control.

Spinocerebellar tract neurons encode *combinations* of sensory input from a whole limb, global variables such as displacement of the foot with respect to the body (39, 337), or information on interneuronal state (223). After processing through the cortex, sensory responses in cerebellar nuclear cells are even more complex (38, 40, 226, 317, 337). At this stage, just how the cerebellum uses proprioceptive information is a matter of speculation, but much evidence points to predictive and adaptive functions (38, 246, 313).

Proprioceptive input reaches the motor cortex via the dorsal column nuclei, nucleus Z, the thalamus, area 3a, and somatosensory cortex (16, 203, 259, 262, 348). Stimulation of motor cortex produces illusions of movement (7). In monkeys, limb perturbations evoke responses in motor cortical cells (58, 116, 122, 128) and, in some cases, stimulation of the same cells excites motor units of the perturbed muscles, demonstrating a transcortical feedback loop (121). Like the cerebellum, the motor cortex has long been implicated in sensorimotor prediction and adaptation (96, 117, 197, 233). Mechanisms may include presynaptic inhibition (295), selection of motor programs, and fusimotor control (338).

Multivariate "Fuzzy" Logic. We have discussed proprioceptive control in terms of servo loops, conditional logic, and predictive mechanisms. In conclusion, we should consider analogies with connectionist systems, which perform adaptive feedback control and which have structures at least superficially analogous to neuronal circuitry. In neural nets, information is processed by virtue of learnt "synaptic" weights or connections of different strengths between large numbers of simple summing elements. In fuzzy logic the weighting takes the form of "membership functions." The way the weighting is determined varies from one system to another and need not concern us here. The important thing is to recognize some basic analogies with neural control:

1. Weighting functions are used to process and combine input from many sensors and to control many outputs simultaneously: "parliamentary principle" (24).

2. Performance is matched to task and context by altering the weighting of signals: "response selection" (47).

3. The relative importance of different types of sensor may vary: "task-dependent reflex reversal" (264, 325).

4. The activity of internal, "hidden layer" elements is poorly related either to sensory inputs or motor outputs: "unrelated" cortical neurons (121).

5. Executive circuits evaluate or predict performance on the basis of multimodal sensory input and make appropriate parametric modifications: cerebellum (329).

6. These circuits might be separate and discrete from the main control loops, but must have two-way links with them: "accessory gain control" (226, 255).

The neural net concept of "hidden layer" cells is useful because it offers an explanation for the fact that some cortical neurons fire in relation to motor tasks but neighboring neurons do not (121). However, a disadvantage of neural net models is that the way they function is hard to analyze and categorize in terms of a rule base. Fuzzy controllers are interesting because their sensorimotor mapping is more explicit. Furthermore, they are more "biological" than finite state systems in that they work with graded rather than all-or-nothing sensory states. Whereas the finite-state rule for switching from stance to swing might require extensor force to be less than 5 N *and* hip angle to exceed 120 degrees, a fuzzy system would assign weights to muscle force, joint angle, and other inputs, and would trigger swing if the mean of the corresponding output functions was close enough to the "swing" end of the scale. A strikingly similar mechanism was suggested by Bässler (24) for the control of locomotion in stick insects: "As in a parliament, the stimulus not only activates the coalition government responsible for the performance of the response but also activates the opposition." In other words, as extensor force declines and the hip extends, the votes for initiating swing increase while those for maintaining stance decline. Votes are weighted according to the population represented by each "seat." The switch occurs when the total number of votes and their relative weight crosses a threshold. Groups of interneurons could be viewed as belonging to a party with a particular policy: "If the leg is quite extended, we will turn the flexors on strongly and the extensors

weakly." Votes for a party (membership in it) are maximal under certain political (sensory) circumstances.

Artificial systems in which available sensors are "awarded" weightings according to their importance in predicting or controlling motor tasks (168, 195) may be of great value in understanding proprioception. Among the interesting research topics in the future will be to establish the control logic and relative weighting accorded sensory input from skin, joint, ligament, muscle spindle, and tendon organ afferents in different sensorimotor contexts.

CONCLUSION

The last decade has seen a proliferation of new ideas on the nature and use of proprioceptive feedback in natural behavior. The notion of stereotyped, immutable reflexes somehow coordinated by a complex motor program has been overshadowed by the various control schemes described above, in which proprioception plays a variable but often crucial role. The empirical and theoretical possibilities have opened up tremendously. Because sensorimotor interactions provide one of the few accessible windows into the internal workings of nervous systems, progress in this area will continue to have an important impact on neuroscience as a whole.

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