Does the nervous system depend on kinesthetic information to control natural limb movements?

S. C. Gandevia and David Burke
Department of Clinical Neurophysiology, The Prince Henry and Prince of Wales Hospitals, Sydney, N.S.W., and the Prince of Wales Medical Research Institute, University of New South Wales, Sydney, Australia

Abstract: This target article draws together two groups of experimental studies on the control of human movement through peripheral feedback and centrally generated signals of motor commands. First, during natural movement, feedback from muscle, psychophysical and microelectrode evidence suggests that joint and cutaneous afferents change in human subjects these changes have reflex and kinesthetic consequences. Recent second, the role of centrally generated motor commands in the control of normal movements and movements following acute and conditions, but that this is inadequate for normal movement; deficits in motor performance arise when the reliance on proprioceptive functionally useful input from a range of peripheral receptors as well as from internally generated command signals. The unanswered questions that remain suggest a number of avenues for further research.

Keywords: deafferentation, kinesthesia, motor commands; motor control, muscle, joint, and cutaneous afferents

Movements are produced under a wide range of circumstances: They may be performed rapidly, with minimal time for feedback compensation (i.e., "ballistic movements"), or they may be performed slowly; they may be guided in part by visual or auditory cues, or even driven by metabolic demand (e.g., respiration). Furthermore, the exact trajectories of repeated movements vary so that the neural drive that generates them and the resultant feedback differ (e.g., Abend et al. 1982; Bernstein 1967). Throughout the literature on movement control, there has been studies of feedback mechanisms (including their spinal circuits) and central output mechanisms (ranging from the motor cortex to motoneurons), with less investigation of the dependence of the motor output on available feedback. Thus, there is a lack of studies considered natural movements are not clear. Perhaps there has been so much to establish about the properties of the motor organization of motor output and motor feedback that their task-dependent interaction during movement has received less attention. Furthermore, kinaesthetic control can operate at an apparently unconscious but not necessarily unimportant level.

This target article was formulated as part of a public debate about whether or not afferent feedback is necessary for movement control. Our objective is to show that human cutaneous, joint, and muscle afferents respond to movements, influence perception, and evoke reflex changes during movement. Because some motor tasks have proceeded well with limited feedback, we have reviewed the role of perceived motor commands in movement control and described some of the deficits ascribed to proprioceptive loss. A less restricted review has recently been published by Prochazka (1989).

1. Sensory feedback and its effects during movement

1.1. Discharge of skin, joint, and muscle receptors during movement

Specialized receptors in the skin, joints, and muscles of a limb respond to appropriate movement whether it is active or passive. The technique of microneurography introduced by Valbo and Hagbarth (1980) has allowed documentation of the properties of afferent fibers in cooperative human subjects. Not only can an afferent's peripheral properties then be determined, but also the central responses to microiontophoresis of substances applied to the palm may discharge in the palm (see sect. 1.2). The development of these techniques in human subjects has proceeded contemporaneously with methods to record from single peripheral nerves to freely moving animals (e.g., Loeb et al. 1977; Prochazka et al. 1976). Although microneurography does not yet allow the freedom to record in walking human movements. With the hand in a rest position, however, there is little background discharge in any of the cutaneous receptors except the SA II mechanoreceptors, of which approximately one third have a background discharge. Discharges during movement are much more common than static responses to different maintained positions. Responses to voluntary movement are similar in intensity to those associated with cutaneous stimuli applied to their receptive fields. Cutaneous afferents sometimes discharge only toward one end of a movement range (i.e., unidirectional response; Fig. 1A), but usually discharge in both flexion and extension. Marked changes in discharge rate occur toward extreme angular positions for both active (Hulliger et al. 1979) and passive (Burke et al. 1986) movements. Static responsiveness to changes in joint angle have been documented for SA II receptors (Fig. 1A), with the discharge rate usually increasing as the end of an angular range is approached (see also Kainbo 1975). Receptors responding to movement are usually located in the digit moved, whereas responses in the palm may discharge with movement of one or two nearby digits.

Discharges in the form of "kneejerk" like responses in movement control. The proprioceptive function of cutaneous afferents in human movement control is such that the hand may show considerable "regional" specialization. Thus the input from cutaneous afferents should provide information on the occurrence of movement, the region of the hand involved in the movement, and the rate of oscillatory movements (particularly from PC [FA II] and RA [HI] afferents), but less information on static joint angles (see Table 1 for definitions of abbreviations). Receptors in the denser innervated finger pulp maintain minimal background discharge rates the response to new contact with grasp objects. Provided that their receptive fields contact the surface of an object, RA, PC, and SA I afferents may generate near-sinusoidal bursts at up to 300 Hz in response to imperceptible slippage between surface and skin (Johansson & Westling 1987; 1989; Kunesch et al. 1988; see also Westling & Johansson 1987). The reflex responses evoked by such tactile stimuli have a greater relative importance than in non-grasp tasks (see sect. 1.1.3).

Dispute has long surrounded the properties of cutaneous joint afferents in the cat (e.g., Boyd & Roberts 1985; Burgess & Clarke 1966; Clark 1977; Forster 1980; Skoglund 1956; Tracey 1979; for review see Proko et al. 1988). If data are pooled from two large micro- neurographic surveys in human subjects, they suggest that digit joint afferents probably subserve less than 10%
Figure 1A. Data from four SA II units with receptive fields in the hand. The static discharge rate during voluntary "staircase" movements is plotted against the angle of the joint. Units with decreasing relationships are on the left and those with increasing relationships are on the right. Many other slowly adapting cutaneous afferents discharge toward both movement extremes (e.g., Burke et al. 1988). Data redrawn from Hulliger et al. (1979).

1B. Left: Responses of a single joint afferent associated with the interphalangeal joint of the thumb to sustained pressure and passive joint movement in three axes of rotation: abduction (lateral stress to the distal phalanx), full flexion, and extension (external rotation of the distal phalanx). Right: Perceptual matching during microstimulation of the same joint afferent. The subject recorded the perceived movements by flexing the interphalangeal joint of the contralateral thumb. Changes in joint angle were recorded by a potentiometer (upper trace in both panels). Stimulus pulses delivered to the intralaminar recording site are represented in the lower traces (0.35 V, 0.1 msec, 20 Hz train). In both examples, the latency from the onset of stimulation to the onset of perceived joint rotation was 350 msec. Reproduced from McCloskey et al. (1980).

of the large-diameter afferent fibers in the digital nerves. Nearly all joint afferents innervating the metacarpophalangeal or interphalangeal joints of the hand were recruited or accelerated their discharge during passive movements (Burke et al. 1988). The discharges were sustained, with minimal adaptation, at the extremes of the physiological range (Fig. 1). The overall capacity of the 19 joint receptors to signal static angular position was limited. Of the 68 afferents that discharged across the angular range, the responses of two were unidirectional (i.e., monotonically increasing with joint angle). The majority discharged in more than one axis of joint rotation (e.g., flexion-extension, abduction-adduction), some discharging to nonphysiological bending and torsional stresses on the joint. Thus, only a minority of the slowly adapting joint afferents provide detailed information about joint angle, whereas nearly all can signal that movement is near or has exceeded, usual physiological limits. Overall, broad agreement exists between the types of movement responses displayed by joint receptors in humans and those in experimental animals, but no comparable data for single units are yet available for the digital joints in other primates. Each slowly adapting joint receptor can also be activated by strong focal pressure to a region of the joint, but the level of pressure required suggests that such a response occurs rarely during common manipulative tasks. Comparable data have been noted for the majority of articular afferents in the cat (Aloisi et al. 1988). The responses of joint receptors innervating the metacarpophalangeal and the interphalangeal joints were not qualitatively different. This observation is relevant because some midrange "units" in the cat hindlimb are actually muscle spindle afferents projecting in a joint nerve (Clark & Burgess 1975; McCloskey et al. 1978; Rossi & Grigg 1982). The focal receptive fields for the human digital joint afferents are not consistent with a muscle afferent origin. Joint receptors in experimental animals may respond to muscle contraction (McIntyre et al. 1979, Millar 1973), although the forces required are relatively large and must be exerted near the movement extreme which excites the receptor (Grigg & Greenspan 1977). Representation of human joint afferents to graded voluntary contractions have not yet been measured, but those in our sample did not respond to switch contractions of intrinsic muscles of the hand (Burke et al. 1988). Paciniform corpuscles outnumber Ruffini endings by 2-3 to 1 in primate digital joints (Satihan & Devanandan 1983) but the behavior of the former is difficult to study because they have wide receptive fields involving much of the hand.

Muscle spindle endings are abundant in intrinsic muscles of the primate hand compared with other limb muscles (Devanandan et al. 1983). Whereas it is easy to equate the high number of specialized cutaneous receptors in the finger pulp with the high tactile acuity of this region, the high density of muscle spindle endings in distal muscles (expressed in terms of muscle weight) should not be equated automatically with high proprioceptive acuity. So far, several studies have failed to document increasing acuity for position and movement detection of joints in a proximo-distal direction (e.g., Clark et al. 1985; 1986; Guelich-Schiebler 1989; Hall & McCloskey 1983; Taylor & McCloskey 1990a). The sensitivity of muscle spindle endings depends on their location within the muscle, their indirect coupling to the tendon (e.g., Griffiths 1987, Hoffer et al. 1989, Meyer & Lohmann et al. 1974) and their in-series coupling to adjacent muscle fibers (Burke et al. 1987). The data in Fig. 2A are redrawn from Meyer & Lohmann et al. (1974). Variability in the responsiveness of muscle spindle endings may be accounted for by differential lengthening of spindles located in different parts of the muscle. This problem may be greater in humans, given the larger size of their muscles, although it has not yet been formally studied. Certainly, there is a wide range of sensitivity to ramp stretch in human spindle endings under passive conditions.

The functionally important calculation of muscle spindle "numbers" remains a puzzle. It may not be their density or absolute number in a muscle that is critical but the number of muscle spindles per motor unit. When calculated in this way values for the intrinsic muscles of the hand are high but closer to values for other muscles. This calculation is relevant as individual spindles can monitor precisely the discharge of nearby motor units and reflexly affect the discharge of these motor units as suggested by Binder and Stuart (1980); see also Camerone et al. (1990), McKeon & Burke (1983); for review see Windhorst et al. (1989). However, if spindle numbers are expressed relative to the number of muscle fibers (arguably a more relevant transformation given the distributed territory of a motor unit), then the intrinsic hand muscles with motor units containing few muscles fibers are richly endowed with proprioceptors.

The discharge rate of muscle spindle endings increases monotonically with increasing passive stretch (Edin & Vallbo 1980a, Vallbo 1974a). During a voluntary contraction at different muscle lengths against a standard load, however, the spindle discharge rates commonly remain constant (Hulliger et al. 1985) and do not provide a simple index of static muscle length. Directional information is available from the spindle discharge during slow isometric movements of the metacarpophalangeal joints (2-5/sec) generated by relatively low forces (<30% maximum; Hulliger et al. 1985; see also Burke et al. 1978a), but again position "sensitivity" is reduced compared with that during passive stretch. Most muscle spindle endings innervating finger extensor muscles (17/25) discharged with a pure stretch response (no response with shortening) during voluntary and passive movements about the metacarpophalangeal joint of fingers.

Figure 2A. Data from the extensor digitorum longus of the cat show the relationship between muscle extension and the static discharge of typical muscle spindle endings (open circles) in a peripheral section of the muscle (lower part of graph) and a central section of the muscle (upper part). The actual lengthening in different sections of the muscle was measured (filled circles) and the data have been superimposed. Thus the intramuscular location of a muscle spindle ending is an important determinant of its proprioceptive function. Data redrawn from Fluhr et al. (1978).

2B. Relationship between the density of muscle spindles (expressed as number per g) and Golgi tendon organs for a range of muscles in the cat. FCR: flexor carpi radialis; EDB: extensor digitorum brevis; FDL: flexor digitorum longus; MG: medial gastrocnemius. Data from Betterman et al. (1978) and Richmond & Stuart (1985).
The behavior of tendon organs is broadly consistent with the view developed above for muscle spindle endings, namely, that movement-stimulation suggests they preserve information about the dynamics of a portion of a whole muscle. The discharge of Golgi tendon organs in the resting state during walking is strongly coupled with the EMG to abolish the spindle activity presumably due to the recruitment of additional motor units, occurring only during slow changes in muscle force (Appelhans & Prochazka 1984). We conclude that specialized joint, cutaneous, and intramuscular receptors discharge during normal movements although motor units will not discharge unless the joint is under moderate tension. Coding by cutaneous receptors remote and adjacent to joint requires further study, as does the mechanism underling the variability in coding by individual muscle spindle afferents. Another way to determine the role of spindle and tendon organ feedback would be to compare the population inputs from muscle afferents in a variety of muscles including intrinsic and extrinsic hand muscles during normal movements.

1.2. Sensations of limb "movement" originating in peripheral receptors

Hughlings Jackson (1931) introduced the concept that movements could be graded on a scale from the "most automatic" to the "least automatic," with the implication that the latter movements are those requiring a proproceptive strategy (Peck et al. 1984). Because the limb musculature is organized into three joint units, the reference to the discharge of other than the primary receptor would need to descript the signal from the spindle endings relative to the relative movement of each joint. Further specialization of the sensory input from the lumbaris is indicated by its lack of Golgi tendon organ afferent medial longitudinal bundle fibers (Cordo 1990). In the lumbaris, the sensory input to the lumbaris has been described as being more complex than in other muscles, involving both muscle and joint receptors (Kendall et al. 1968; Merton 1953). However, while not theoreatically necessary for control of movement, perceptual access for proproceptive information to the brain, joint, and muscle receptors should provide the CNS with greater flexibility of control, particularly for small slow movements and isolated movements that are part of the end of rapid movements, and also in the transition from one movement sequence to another (Cordo 1990). Such access to perception is presumably also critical when learning a new skill.

As shown above, movement of the joint and muscle, and recurrent feedback to the CNS is critical for the development of voluntary movement. This is particularly true for the developing CNS, where the sensory input to the CNS is critical for the development of voluntary movement. This is particularly true for the developing CNS, where the sensory input to the CNS is critical for the development of voluntary movement. This is particularly true for the developing CNS, where the sensory input to the CNS is critical for the development of voluntary movement. This is particularly true for the developing CNS, where the sensory input to the CNS is critical for the development of voluntary movement.
evolve illusory movements and may even detect a single stimulus (Gandevia 1985). The CNS appears able to interpret closely whether a change in spindle discharge is due to an external perturbation or to voluntarily generated activity presumably by reference to signals of motor command or corollary discharge (McCloskey 1975: 1981; see also sect. 2.1), so that the same proprioceptive input may evoke different sensations dependent upon the initial "set" of the subject. All proprioceptive signals must be interpreted by the CNS against a background input from other sources such as the visual, auditory, axial muscle, and vestibular systems (e.g., Biguer et al. 1988; Curtin et al. 1988). Thus, for example, vision of the limb can attenuate or even abolish the illusory phenomena attributed to muscle spindle endings (e.g., Gandevia 1985; Goodwin et al. 1972), but when vision is prevented, proprioceptive cues can affect apparent visual localization (e.g., Levine & Lackner 1970). The degree of perceptual "trade-off" between competing signals may be complete (as in the case of visual inputs reducing the stimulation of muscle spindle movements or more subtle but known before stimulation of single joint afferents). Furthermore, perception of limb position may be more accurate than that of a constituent joint within (Vorfeld 1982).

1.2.2. Muscle spindle afferents and nonlinearities.

Muscle spindle output is position specific (extent of the spindle action) by movement- and contraction-history of the parent muscle. Specific "afferents" in muscle spindle responsiveness after contraction "shortening" of the muscle, possibly due to postcontractory depression of muscle spindle receptors or their central projections (Macefield & Burke 1990). Joint and cutaneous inputs could help "realize" any perceptual maps derived from muscle spindle endings.

1.2.3. How many muscles are required? Most joints are crossed by more than one muscle so that signals from muscle spindle endings will be available from more than one source. The relationship between spindle discharge and joint angle differs for different muscles crossing a joint (Burgess et al. 1982). For joints with movements in more than one axis, unique determination of joint "position" will require analysis of the inputs from more than one agonist-antagonist pair or from extramuscular receptors. For example, differences in the signals from muscle spindle endings in the interossei and lumbricals acting on one finger would provide information about the position of the metacarpophalangeal joint in the plane of abduction/adduction. Observations have confirmed that both the antagonist and agonist can contribute to movement detection for proximal (e.g., Gilhodes et al. 1986; Roll & Vedel 1982) and for the distal phalanx (Gandevia et al. 1983). Short muscles crossing few joints would aid resolution of absolute angular positions.

For movements involving joints and muscle groups proximal to the hand the ability to detect passive movements is similar if the parameters of movement are expressed as relative changes in muscle length (Hall & McCloskey 1983). It is uncertain whether this finding can be extended to all muscle groups, particularly the intrinsic muscles of the hand. However, observations based on pulling the surgically severed tendon of extensor hallucis longus suggest that it behaves with lower "sensitivity" to changes in muscle length (McCloskey et al. 1985a); other proprioceptive inputs are required to explain full acuity at the metacarpophalangeal joint. Simultaneous measurement of human spindle responsiveness and thresholds for movement detection would allow the neural mechanisms involved in the psychophysical experiments to be examined more precisely. The potential "counterparts" in the receptors to the intrinsic and extrinsic muscles of the hand is exemplified by a study entitled "Tactile discrimination of thickness," in which the authors were forced to conclude that discrimination of the thickness of objects placed between the thumb and index finger is largely derived from muscle spindle endings rather than cutaneous tactile receptors (John et al. 1989, see also Edin & Abb 1991). The distance from the tip of the index finger was only 75 mm, corresponding to angular deviations of 0.1°.

1.2.4. Signals underlying static position sense. To study the ability to perceive small changes in static position of joints, Clark and colleagues moved joints at extremely low angular velocities (<2°/min), below those at which subjects report any sensation of movement (Clark et al. 1985, 1986). An approximate threshold for detection of changes in position is now available for a number of mechanisms using these extremely slow displacements. Although there is disagreement about the extent to which this capacity is available for the proximal interphalangeal joint (Clark et al. 1985), the statement of "false" proprioception for the hand is only for proximal joints if the movement parameters are expressed in terms of absolute angular motion (Hall & McCloskey 1983). This observation alone suggests that different neural mechanisms subserve detection of "position." Given results with anesthesia of the skin and joint, and of mixed nerves, the ability to detect position changes is likely to be dependent in part upon input from muscle spindle endings, at least for the knee and ankle joints. As for sensation of more rapid movements, the responsible mechanisms for static position sense may differ for various joints, particularly since muscle "disengagement" at the distal interphalangeal joint produces little impairment of the thresholds for detection of joint angle. Muscle contraction at the final position fails to enhance the position signals for finger joints (Table 2: Taylor & McCloskey 1990a). This suggests that theafferent activity evoked by a weak muscle contraction does not convey unique information about position and that any corollary motor signals do not make a precise map of joint position.

1.2.5. Interaction between muscle and nonmuscle kinesiologic signals. Proprioceptive afferent activity for applied movements in some joint muscles (hand, knee and ankle) is not impaired by local cutaneous (and joint) anesthesia (Clark et al. 1979, 1985; see also Barrack et al. 1983a), but it is abolished by anesthesia of the forearm (e.g., Brown et al. 1954; Ferrar & Smith 1959; Gandevia & McCloskey 1970). This impairment occurs even if the anesthesia is remote from the joint moved; anesthesia of the finger pulp affects activity for more proximal joints of the finger (Clark et al. 1986) and anesthesia of fingers adjacent to the one being moved impairs its performance (Gandevia & McCloskey 1976). Proprioceptive afferent for joint movements is facilitated tonically by a digital nerve input, probably derived from SA II and joint receptors with a background discharge (Table 1).

Some specific pro pr oceptive input can be extracted from the discharge of cutaneous afferents. This was facilitated for the distal interphalangeal joint of the finger when the muscle and joint afferents contributions to movement sensation had been removed (Ferrill et al. 1987). Cutaneous afferents within the radial nerve respond to finger movements and can presumably contribute to detection of applied movements (Edin & Abb 1991). Microstimulation of occasional cutaneous afferents is reassuring receptors in the distal phalanx can evoke sensations of movement consistent with the natural behavior of the afferent (Macefield et al. 1990). In the hand, the additional fact that direct input to skin and joint receptors in movement detection is likely to be especially important, at least across the usual angular range. The
role of cutaneous afferents may vary according to tactile stimuli present around the joint. This is exemplified by the finding that the variance of estimates of knee position may be reduced by cutaneous anesthesia, as if this removed "noise" from detection (Clark et al. 1985). One implication of this work is the need for more research within the CNS of the different sources of proprioceptive input.

During the reinstatement of muscle spindle afferents as key contributors to kinesthesia, the potential role of joint receptors was often ignored. Evidence set out below, however, acts as a prudent reminder not to expect intramuscular receptors to provide all the relevant proprioceptive cues under every natural condition. Furthermore, the functionally important contribution to proprioceptive performance from intramuscular, joint, and cutaneous signals (specific and nonspecific) may differ for distal, proximal, and truncal joints.

1.2.6. Contributions of joint afferents to movement sensation at the human distal interphalangeal joint. If the hand is postured appropriately, the long finger extensors and flexors and the intrinsic extensor mechanism can be disengaged so that proprioceptive sensation at the distal interphalangeal joint is due only to cutaneous and joint afferents (Gandevia & McCloskey 1976). With this muscle disengagement, the ability to detect the direction of applied flexion and extension movements within the midrange of joint positions deteriorates markedly, but the residual acuity is in part dependent upon joint afferents. A dependence on joint receptors was suggested by the improvement in performance in flexion expansion, and the further improvement (but not abolition) with intracutaneous anesthesia (Clark et al. 1985; Ferrell et al. 1987). The magnitude of the estimated contribution of joint receptors differed slightly in the studies of Ferrell et al. (1985) and Clark et al. (1989), but the data have been pooled in Figure 5A. When muscles were disengaged so that only joint and cutaneous afferents could contribute, performance was unaffected by cutaneous anesthesia over the dorsum of the joint. That the sensitivity and number of cutaneous and joint afferent fibers responding to the imposed movements is small (sect. 1.1) used not be important if the discharge of individual afferents can be perceived. The results of Taylor and McCloskey (1990a) using imperceptibly slow movements to assess "position" sense at the distal interphalangeal joint confirm that performance need not depend upon intramuscular receptors.

Joint removal offers a seemingly direct way to assess whether proprioceptive acuity requires an input from joint receptors. In human subjects, replacement of diseased joints is associated with minimal impairment of position sense and functional performance (e.g., Cross & McCloskey 1973; Grigg et al. 1973; cf. Karanjia & Ferguson 1983). However, it is likely that the impairments underestimate the potential joint afferent contribution, because tests have usually assessed performance in the midrange of movement, not toward the angular extremes. Barrack et al. (1983b) documented an impairment of movement sensation with aging and this was more marked in patients with degenerative arthritis at the knee (irrespective of joint replacement). These findings suggest a proprioceptive role for joint receptors, but such patients commonly have wasted muscles, presumably due to "disuse," and the possibility remains that intramuscular receptors were also involved. A deterioration in walking was reported for the cat after acute anesthesia of the knee joint (Ferrell et al. 1985).

1.2.7. Signaling the extremes of angular range. The label "map" set up by muscle spindle endings is unsuited to signal the physiological limits of joint rotation. Artificial activation of muscle receptors is sufficient for subjects to report that joints have moved into anatomically impossibly positions (e.g., Crandall 1977; Gandevia 1985), although a signal closer to the true position can be extracted if required (Sittig et al. 1985). Against this, the discharge of digital joint receptors is well suited to signal the movement extreme, although a single afferent may not specify uniquely which extreme. One study that examined position sense across a broad angular range for the proximal interphalangeal joint of the index finger documented misalignment between the affected and control sides when the contributions from joint and cutaneous afferents were abolished (Ferrell & Smith 1989). When the joint of the target finger was positioned near the extreme of flexion (or extension), the joint of the anesthesized finger had to be hyperflexed (or hyperextended) to align the perceived locations of the two fingers (Fig. 5B). This distortion of the extremes of the flexion-extension range remained after anesthesia of the joint alone.

Some unmeasured and small changes in uninnervated joint afferents from the cat knee respond to joint movement in the midrange, but particularly to twisting movements (Grigg et al. 1986; Schubale & Schmidt 1983). With experimentally induced joint inflammation or effusion, the population of joint afferents is sensitized and the proportion of the complete complement of joint receptors responding across the full angular range and at the extremes increases (e.g., Ferrell 1987; Grigg et al. 1986). Thus, under these conditions, kinesthetic awareness of the joint would be heightened and protective reflexes dependent on joint afferents would occur for smaller mechanical disturbances.

1.2.8. Microstimulation of joint and muscle afferents. Stimulation of individual large-diameter cutaneous afferents evokes sensations localized to their receptive fields with particular tactile qualities depending on the afferent class (Table 3; Macfeld et al. 1990; Oeho & Toerekbjörk 1983; Schady & Toerekbjörk 1983; Valbo et al. 1984). The probability of obtaining these sensations is virtually 100% for afferents innervating the distal part of the digits, but the probability diminishes for more proximal sites in the hand. An exception is that stimulation of single SA II afferents rarely evokes sensations with a tactile quality. Early indirect arguments that the methodology was faulty (Wall & McMahon 1985) have been refuted (Toerekbjörk et al. 1987; see also Calame & Stein 1988).

Microstimulation of joint afferents innervating the in

---

Table 3. Perceptual responses attributed to selective microstimulation of large-diameter cutaneous, joint, or muscle afferents innervating the hand

<table>
<thead>
<tr>
<th>Receptor class</th>
<th>Sample size</th>
<th>Occurrence of sensation (%)</th>
<th>Single stimulus perception</th>
<th>Character of sensation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cutaneous RA (FA I)</td>
<td>(60)</td>
<td>~90</td>
<td>+</td>
<td>tap, flutter, or vibration depending on stimulus frequency</td>
</tr>
<tr>
<td>Cutaneous PC (FA II)</td>
<td>(14)</td>
<td>~85</td>
<td>?+</td>
<td>vibration (dull)</td>
</tr>
<tr>
<td>Cutaneous SA</td>
<td>(50)</td>
<td>~80</td>
<td>+</td>
<td>low pressure or indentation</td>
</tr>
<tr>
<td>Cutaneous SA II</td>
<td>18</td>
<td>~10*</td>
<td>-</td>
<td>joint movement when receptive field over distal interphalangeal joint</td>
</tr>
<tr>
<td>Joint</td>
<td>11</td>
<td>~70</td>
<td>-</td>
<td>local deep pressure, joint movement or stress</td>
</tr>
<tr>
<td>Muscle spindle ending</td>
<td>13</td>
<td>&lt;10**</td>
<td>-</td>
<td>?</td>
</tr>
<tr>
<td>Tendon organ afferent</td>
<td>5</td>
<td>?</td>
<td>?</td>
<td>low motor threshold</td>
</tr>
</tbody>
</table>

*The usual lack of perceptual responses to stimulation of SA II afferents is confirmed by Schady & Toerekbjörk (1983). **A single stimulus to a group of presumed primary spindle endings evokes a sensation consistent with muscle lengthening (Gandevia 1985).

---

The table above provides information on the perceptual responses attributed to selective microstimulation of large-diameter cutaneous, joint, or muscle afferents innervating the hand. The table includes information on the occurrence of sensation, single stimulus perception, and the character of sensation for different receptor classes, such as cutaneous RA (FA I), cutaneous PC (FA II), cutaneous SA, and cutaneous SA II. The table also highlights that the usual lack of perceptual responses to stimulation of SA II afferents is confirmed by Schady & Toerekbjörk (1983).
1.3. Evidence that afferents from skin, joint, and muscle exert reflex effects during natural movements through spinal pathways

That proprioceptive afferents have a critical role in motor control can be supported by demonstration of their reflex effects during voluntary movement. This section reviews this evidence and seeks to emphasize the variety of reflex effects that can be documented in studies on human subjects.

The relative importance of spinal and long-loop (supraspinal) reflex circuits in compensating for phasic disturbances of voluntary movement has been hotly debated (for reviews of human and animal data, see Katayama et al. 1983; MacKay & Murphy 1979; Marsden et al. 1983; Matthews 1991; Froggatt 1997). At the spinal level, complex intersegmental machinery governs transmission of sensory feedback and descending commands to the motor pool (Janssens & Lundberg 1981). In addition, feedback from muscle spindles in soleus to homonymous motorneurons, the soleus IA projections to antagonists (see below), between segmental efferent and afferent nerves, and across joints (such as the ankle) have also been studied extensively (e.g., Bayoumi & Ashley 1988; Mao et al. 1984; Pierrot-Deseilligny et al. 1981b). The pattern of group II input to motor units from different sets of receptors indicates that when a limb is in the concentric phase of a movement, even when subjects respond in a reactive-time task (e.g., Burke et al. 1980; Valko 1971). Clearly, the sensitivity of muscle spindle afferents to a movement will change as a result of fusimotor drive during the contraction, but there are little data on whether the spindle response to a perturbation would be increased or decreased (Morgan et al. 1994). Furthermore, the fusimotor system does not appear to operate as an effective gain-control for the stretch reflex, regardless of whether the disturbance is phasic or tonic (Burke 1991).

The existence of a y-motor system implies that it ought to be possible to alter the spindle pathway without changing the input to the motor neuron pool. Voluntary muscle contraction is accompanied by activation of fusimotor neurons sufficient to increase the discharge of spindle afferents (e.g., Valko 1971; Burke 1988, 1994), for example, after review see Burke 1981; Valko et al. 1979). The data in Figure 6 illustrate the effects of stimulating the fusimotor drive via microstimulation of the spinal motoneuron pool. The fusimotor drive interacts with other muscle-contracting mechanisms, such as the contractile apparatus of the muscle (e.g., Gadeviana 1985).

When a muscle is activated, the afferent discharge is increased, and in some subjects, even a single stimulus evokes a peristaltic reflex that widens the muscle (Figure 3). Using microstimulation with trains of stimuli we confirmed that most S1 SII Afferents innervate the vasa vasorum and that these efferents could induce contraction of the muscle (Figure 4). However, stimulation of two S1 SII afferents with repetitive fields over the dorsum of the fingers during flexion of the interphalangeal joint of the finger evoked a comparable sensation on microstimulation. Such afferents could contribute to proprioceptive sensation when stimulated in isolation, and presumably they could also have subverted the proprioceptive afferent volley and joint and muscle mechanoreceptors (e.g., Clarke et al. 1989; Ferrell et al. 1987). Clearly, joint, muscle, and even cutaneous afferents can provide sensory input to afferent projections connected to the natural movement. The studies described above highlight the greater spatial summation required for perceptions evoked by afferent inputs compared with other afferents from the hand. The difference probably disappears for more proximal sites in the limb where cutaneous sensitivity is less acute. Heat, muscle tension, and movement control

The strength of spinal reflex pathways can be altered by mechanical stimulation of the afferent volley. In general, the strength of spinal reflex pathways enhances the excitability of the active motoneuron pool and suppresses that of the antagonistic muscle, particularly at the onset of the contraction. Examples are given below.

11.3.1. Presynaptic inhibition of IA afferent terminals on motoneurons. The contracting muscle at the onset of a voluntary contraction is decreased, but presynaptic inhibition of IA afferent projections to the motoneurone pool of soleus muscles is increased (Figure 6). Stronger contractions of soleus produce greater suppression of presynaptic inhibition of IA afferent fibers exciting soleus (Iles et al. 1987). With voluntary contraction of the soleus, the H-reflex is potentiated, presumably by suppression of background presynaptic inhibition (e.g., Schiappett et al. 1988). Rapid relaxation of a contraction is associated with temporary enhanced presynaptic inhibition, which subsequently subsides to the resting level (Schiappett & Crema 1984, Schiappett et al. 1986). When subjects stand upright, presynaptic inhibition of the fibers to soleus motoneurons increases, while there is a rapid relaxation to quadriceps motoneurons decreases, with little change in presynaptic inhibition of Ia fibers to tibialis anterior motoneurons (Schiappett et al. 1984, 1986). When subjects stand upright, presynaptic inhibition of Ia fibers to soleus motoneurons increases, while there is a rapid relaxation to quadriceps motoneurons decreases, with little change in presynaptic inhibition of Ia fibers to tibialis anterior motoneurons (Schiappett et al. 1984, 1986).

When subjects stand upright, presynaptic inhibition of Ia fibers to soleus motoneurons increases, while there is a rapid relaxation to quadriceps motoneurons decreases, with little change in presynaptic inhibition of Ia fibers to tibialis anterior motoneurons (Schiappett et al. 1984, 1986).

When subjects stand upright, presynaptic inhibition of Ia fibers to soleus motoneurons increases, while there is a rapid relaxation to quadriceps motoneurons decreases, with little change in presynaptic inhibition of Ia fibers to tibialis anterior motoneurons (Schiappett et al. 1984, 1986).
Changes in the IA inhibitory interneuron (Delwaide & others, 1988).

### 1.3.2. An oligosynaptic propriospinal-like pathway has been demonstrated in the human upper and lower limbs, analogous to the C3-C4 propriospinal system which transmits descending commands to motoneurons for forelimb target reaching movements in the cat (Atsermerk & others, 1981). At the onset of and during a weak contraction, transmission in this pathway is more effective (Baldissara & Perreot-Desailly, 1989; Burke & others, 1992; Hulthvorn & others, 1986). Using spatial facilitation, Malgras and Perreot-Desailly (1988) and Burke and others (1992) have demonstrated poststimulus time histograms and reflex studies, respectively, a wide divergence between cutaneous and muscle afferents onto the interneuronal component in the spared segment of the spinal cord necessary for integrative descending commands with the target reaching movements in the spinal cord (Niesen & Perreot-Desailly, 1991).

### 1.3.3. Transmission in excitatory and inhibitory IB reflex pathways can be modulated by voluntary contraction, with facilitation of heteronymous excitatory pathways to a contracting muscle and with suppression of the autogenous disynaptic inhibitory pathway (Fourner & others, 1983).

Suppression via the disynaptic inhibitory pathway increases with contraction strength. Cutaneous influences on the transmission in IB reflex pathways have been demonstrated in the cat (Lundberg & others, 1977) and in the human lower and upper limbs (Cavallari & others, 1986). Perreot-Desailly & others, 1981a; see also Perreot-Desailly & others, 1982). Cutaneous facilitation of transmission in IB reflex pathways might be of functional significance in curtailting a movement. For example, in the upper limb, input from skin on the dorsum of the hand facilitates transmission in IB inhibitory pathways to efferent motoneurons and in IB excitatory pathways to hand flexors, so that hand contact could help to terminate an extension movement of the hand. Evidence for convergence between human knee joint afferents and IB afferents projecting to thigh muscles has been difficult to obtain during a voluntary contraction of the target muscles (Brooke & McIlroy, 1989), possibly because the knee positions studied did not include full flexion or full extension (positions in which joint afferent discharge is likely to be maximal; see sect 1.1: also Bassendine & Ferrell, 1981). However, joint afferents excited by joint effusion inhibit quadriceps motoneurons (e.g., Ili & others, 1984; Wood & others, 1988).

### 1.3.5. The projection of group II muscle spindles afferents

A. Angular displacement

B. Spindle discharge

Figure 8A. Compensation following randomized disturbances to thumb tracking movements. The subject flexed the distal joint of the thumb against a constant torque of 0.1 Nm, and in some trials, this torque was maintained at 2% 30 ms after the start of the recording sweep. This torque change was too small to be detected by the subject (lower record). In the upper records, when larger disturbances were included unpredictably within the sequence, complete recovery was evident following the 2% 1% torque changes by the end of the sweep (left traces). There were corresponding changes in the integrated EMG records (right) from surface electrodes over flexor pollicis longus. When small disturbances were given alone (bottom traces), there was no positional correction and no change in EMG. Effective recovery was also dependent upon the context of the disturbance and the subject's response to the represented. Reproduced from Marden & others (1983).

8B. Unloading responses resulting from natural irregularities in a slow voluntary shortening movement. Response of a dynamic muscle spindle receptor in a human subject. Five traces superimposed. Traces are, from above, standardized spindle potentials; ankle joint angle; ankle anterior EMG. The initial event initiating the irregularity appears to be a grouping of EMG potentials. This burst is accompanied by a burst of spindle activity (i.e., afferent co-activation). The vertical line indicates the onset of the small irregularities in movement accompanying the EMG and spindle afferent burst. Following the shortening there is a reflex reduction in EMG. Reproduced from Burke & others (1976a).

---

**References**


---

**Figure 7A.** Peristimulus time histogram (PSTH) of the discharge of a muscle spindle ending in tibialis anterior recorded while the subject was standing. The arrow, a brief train of stimuli (5 pulses at 300 Hz) was delivered to the subject at 5400 ms. This median was initially silent and was given a background discharge (9-10 Hz) by direct stimulation of the tendon. Upper trace is the cumulative sum (CUSUM), middle trace is the PSTH, and lower trace is the rectified averaged EMG from tibialis anterior. The reference value of a change in EMG. Vertical calibration is 10 nV. Reproduced from Asanis & others (1996a).

---

**Figure 8A.** Compensation following randomized disturbances to thumb tracking movements. The subject flexed the distal joint of the thumb against a constant torque of 0.1 Nm, and in some trials, this torque was changed by 2% 30 ms after the start of the recording sweep. This torque change was too small to be detected by the subject (lower record). In the upper records, when larger disturbances were included unpredictably within the sequence, complete recovery was evident following the 2% 1% torque changes by the end of the sweep (left traces). There were corresponding changes in the integrated EMG records (right) from surface electrodes over flexor pollicis longus. When small disturbances were given alone (bottom traces), there was no positional correction and no change in EMG. Effective recovery was also dependent upon the context of the disturbance and the subject’s response to the represented. Reproduced from Marden & others (1983).

---

**Figure 8B.** Unloading responses resulting from natural irregularities in a slow voluntary shortening movement. Response of a dynamic muscle spindle receptor in a human subject. Five traces superimposed. Traces are, from above, standardized spindle potentials; ankle joint angle; ankle anterior EMG. The initial event initiating the irregularity appears to be a grouping of EMG potentials. This burst is accompanied by a burst of spindle activity (i.e., afferent co-activation). The vertical line indicates the onset of the small irregularities in movement accompanying the EMG and spindle afferent burst. Following the shortening there is a reflex reduction in EMG. Reproduced from Burke & others (1976a).
the hand by the most trenchant of critics (Matthews 1980). As shown in Figure 8A, the inhibitory reflex response is, in general, only adequate to compensate fully for small disturbances (Fig. 8A; Marsden et al. 1983). In situations where a sudden perturbation causes a reflex movement to return the limb toward its unperturbed trajectory and, in a second experiment, found that the return to the control trajectory was essentially identical to the responses to those effectively in those trials in which the perturbation evoked a reflex response. So-called long-latency "reflex" effects operate only on the stretched muscle but also on functionally-related muscles (Cole & Abbas 1987) as well as on remote muscles to ensure a more appropriate trajectory. Indeed, in their "Gieren et al. 1988; Soechting & Lacquaniti 1988). Reflex feedback also plays a major role in unperturbed movements, to help smooth unintended irregularities that might occur in the course of the movement (Burke et al. 1978; Vallois 1973). These can be sensed by spindles in the contracting muscle (Vallois 1973) and lead to a rapid alteration in EMG activity (Burke et al. 1978; Jakubowicz & Fadala 1980). An example is shown in Figure 3B. In accurate position- or force-matching tasks, the gain of the reflex opposition to a very slow disturbance varies appropriately for the task given to the subject (Cobefeda & McCloskey 1987). The reason for this variability is not known. The behaviourally significant feature of the reflex effect is probably an important change in the CNS that is due to a change in the importance of the reflex in the CNS. This plasticity would be meaningful if the nervous system required feedback control of performance.

2. Motor commands and movement without peripheral feedback

2.1. Sensations of force, timing, and centrally generated motor commands

If we state that centrally generated commands for movement are important in controlling it, we may admit no more than that the CNS is not necessary for movement and can therefore be dismissed as a possible cause of movement changes (e.g. Alexander et al.'s view of the CNS and can produce movement (cf. Alexander et al.'s, this paper). However, because such signals must be relaid upon when the CNS is not functioning, this brief discussion is warranted of several of their properties and how they might influence perception. There seems to be a relationship between the sensations related to limb movement to endogenous signals that are mediated by internal signals whereas in other areas of neural control (notably for eye movements), the central action of command signals is well established at the perceptual level (e.g., Guthrie et al. 1983). In a recent review Matthews et al. (1983) pointed to the likely conservation in evolution of such commands to control movements based on feedback from such that "it is naive to suppose that they are not involved and to treat a search for them with the microscope as being rather like trying to find the soul" (see also Robinson's and Pons's articles, this issue). Their various roles in both motor control and movement (e.g., see Gaudet 1987; McCloskey 1981). Although there are difficulties in capturing these reflexes during active movement of the upper limb (Burke 1987), subjects do report that they are probably pivotal for understanding motor control. This is consistent with experiments that approach described below go some way toward opening the door for studies of what Stellington (1900) referred to as the "inward balance of the" nervous system".

Centrally generated commands must exist prior to voluntary movement, but it is difficult to define the point at which they give rise to perceptual effects. Based on the relatively timing of the "will to move" and an apparent absence of discrimination, motor output, and other considerations, it appears that the motor commands are likely to be present from the time of the motor cortex event. However, this is not consistent with the beginning of the LBM event (see below). It may be that the motor commands are present from the time of the motor cortex event, but could not be detected with current techniques. In many cases, the ability to perceive the CNS from making rapid voluntary movements in response to limb, even unperceived stimuli (Taylor & McCloskey 1990b). A similar conclusion on the timing of motor action was reached by McCloskey et al. (1983), who showed that subjects could time when a muscle contracts using either of two signals: one central, generated prior to neural activity in motoneurons, and the other peripheral, a signal which is detectable by an observer in some cases. The perception of these signals, however, does not provide evidence for the existence of the CNS acting on. An indication of the resolution afforded by centrally generated signals was provided by Gandevia and Roth well (1982). Subjects have, or can rapidly acquire, the ability to discriminate between movement and without reference to peripheral inputs (e.g. sensory) as 'the will to move' and the perceived timing of voluntary movements. There have been a number of attempts to demonstrate that movement is centrally driven, but require a peripheral signal for selection (sensation of effort instead). First, the subject may be instructed to generate a force to match an external reference force (Thompson et al. 1990). This was consistent with this view that control of movements is achieved by a combination of voluntary commands. An alternative explanation that needs to be excluded for this and related studies (Hutton et al. 1987) is that subjects are able to attend to a signal of the CNS as a cue to the commands, which can then affect the CNS. A combination of voluntary commands. The first two mechanisms would be available following deafferentation, while the second mechanism is predicted to fail together. The ability to attend to an absolute peripheral force signal does not apply to all experimental situations: Muscles that are used all the time do not prefer to indicate that perceived force or heaviness is increasing even when instructed to concentrate on the absolute force or tension (e.g., Jones & Hunter 1985). Second, there is electrophysiological evidence for a cortico- projection of group Ib afferents (McIntyre et al. 1984) with segregation of the input from tendon organ and Golgi tendon organs (Ferrell & Smith 1989; Smith & Ferrell 1989; 1989). Third, position sense is distorted by progressively loading the contracting muscles (Ferrell & Smith 1989). Roland
Performance after deafferentation has been recently reassessed in patients with large-fiber sensory neuropathies and central deafferentation syndromes, and in patients with surgical deafferentation. In the description below, emphasis is given to the consistent deficits observed in a group of six patients with large-fiber sensory neuropathy by Sanes et al. (1985). Similar findings are evident in reports of smaller numbers of patients with this syndrome (e.g., Cole 1986; Cole et al. 1986; Forget & Lamarre 1987; Ghez et al. 1990; Rothwell et al. 1982b). These patients display "premotor deafferentation" (e.g., Jeannerod et al. 1984; Nakazato & Takeya 1981; Volpe et al. 1979).

After deafferentation, patients have a wide-based gait, difficulty in making repeated finger movements without vision, and difficulty in maintaining a posture, especially when vision is excluded. Thus, when attempting to maintain angular position against one of a series of flexor or extensor torques with muscles across the wrist, the meaning of error during 29 sec of "postural maintenance" was about 6° for a group of six patients whereas it was usually less than 1° in control subjects (Sanes et al. 1985). Errors did not grow with the size of the load (Fig. 9A). Comparable errors developed on removal of visual feedback when movements of specified amplitudes were required against a spring. The initial movement was similar to that of normal subjects when visual feedback of position was permitted but the position accuracy attained under visual control could not be maintained (Fig. 9B). Introduction of an unexpected viscous load at the onset of movement resulted in a slower movement of reduced extent in the patient group, a finding which corroborates data from normal subjects (Day & Marsden 1969). This data suggests that the hypothesis that movement endpoints can be determined solely by the properties of a simple mass-spring system (see Bizi et al., this issue), is invalid. In some patients, particularly of small amplitude (3° at wrist in the study of Sanes et al., 1985), were associated with large errors in both the dynamic and static phases, and occasional small movements led to the wrong direction. These and other data (e.g., Brink & Mackel 1987, Sanes et al. 1983a; 1983b) highlight the need for specific feedback for precise "verifying" contractions. A loss of joint position control and symptoms relating to data well suited for such tasks (Fromm & Evarts 1981).

In deafferented patients, abnormally large degrees of contraction of the agonist muscle produced movements the classical bi- or triphasic EMG pattern occurred in an agonist-antagonist pair. However, although this centrally generated pattern remained after deafferentation (Forget & Lamarre 1987; see also Bizi et al. 1984), the antagonistic burst (leading to limb deceleration) no longer changed in proportion of the initial agonist burst. Furthermore, the timing of the antagonist burst was more variable. In deafferented patients, the ability to match torque (or weight) was extant, but it was not as good as in normal subjects. The deficit appeared especially for low forces, and it showed hysteresis. Forces presented in ascending order were better matched than those in descending order (Sanes et al. 1980). In normal subjects, there is poor accuracy for judgment of relatively low forces (Gandevia & Kibbeath 1990; Newell et al. 1984). This impaired sense of motor command or effect may reflect a defective capacity to calibrate this signal in accordance with a pro-ceptual signal (see Gandevia & McCloskey 1978). Deafferented patients also exhibit a poorer ability to make accurate jointpoint matching movements with the upper limb (Ghez et al. 1989).

Other aspects of motor performance should be measured in patients with deafferentation, including improvement in performance over time (Cole 1986) and the ability to perform sequences of movements in which afferent signals are required to trigger the next component of the sequence (Cordo 1980; see also Benevento et al. 1988, Johansson & Westling 1986a, 1986b). The latter studies highlight the ability of central motor control to be rapidly recalibrated even within a single movement block based on afferent inputs from the limb when the relationship between force required and movement produced is altered unexpectedly. Thus, an unexpected change in the case will be liftable, but replaced accurately on the ground. Formal measurements of muscle strength have not been reported yet in these patients although weaknesses defined by the testing factors for their performance. These measurements, if also obtained prior to deafferentation, could indicate the degree of facilitation mediated through the motor-sensory loop. Unfortunately, the number of individuals in both groups is too small for this to be done. This delay may also be difficult to interpret because of the wide range of normal strength. Finally, deficits in timing of muscle movements in highly stereotyped tasks such as respiration and locomotion will probably also be revealed; these have been documented for the paw-shake response after hindlimbs deafferentation in cats (e.g., Koshland & Smith 1969). An alternative way to do the capacity of centrally generated commands and of peripheral inputs to drive motorneurons involves recording the discharge of single motor axons destined for particular intrinsic muscles of the hand. Recording the discharge of single motor axons from the median nerve led to the development of a complete anesthetic block of the ulnar nerve so that the capacity of subjects to discharge motorneurons supplying intrinsic muscles of the hand could be assessed when there was no tonic or phasic feedback from homonymous and heteronymous muscles in the hand (due to the ulnar block) and no phasic feedback from cutaneous and joint afferents innervating the hand (Gandevia et al. 1990). The skin and joints of most of the hand remained silent, because skin and joint afferents transmitted the unanesthetized median nerve. Although this acute muscle paralysis and deafferentation is artificial, any ability to drive intrinsic hand motorneurons repre-
Behavioral and Brain Sciences (1992) 15:4

Can sense be made of spinal interneuron circuits?

D. A. McCrea
Department of Physiology, Faculty of Medicine, University of Manitoba.
Winnipeg, Manitoba, Canada, R3E 0N9
Electronic mail: dmc@um.umanitoba.ca

Abstract: It is increasingly clear that spinal reflex systems cannot be described in terms of simple and constant reflex actions. The extensive convergence of segmental and descending systems onto spinal interneurons suggests that spinal interneurons are not reflex systems but rather form a crucial component in reflex systems which mediate the activation of voluntary and reflex movements. The notion that descending systems simply modulate the gain of spinal interneurons has been tempered by the observation that spinal interneurons can differentiate and mediate control of specific motoneurons. Spinal reflex systems are complex and current approaches will continue to provide insight into motor systems. During movement, several neural mechanisms act to reduce the functional complexity of motor systems by inhibiting some of the parallel reflex pathways available to segmental afferents and descending systems. For example, the flexion reflex system is discussed as an example of the flexibility of spinal interneuron systems as a useful conceptual construct. Examples are provided of the kinds of experiments that can be developed using current approaches to spinal interneuron systems.

Keywords: flexion reflex, interneuron, motor control, motor activity, pain-sensing inhibition, reflexes, spinal cord

1. Introduction

This target article addresses some current issues concerning interneurons involved in spinal motor pathways. Despite the wealth of detailed information about the anatomy, behavior, and synaptic action of spinal interneurons, some feel that a clearer understanding of the function of spinal pathways is necessary. Moreover, in the past the focus has been on corticomotor and reticulomotor pathways in turn leading to theades of spinal reflexes. In this discussion, I suggest that a massive convergence and divergence of functional systems has been revealed in recent studies of spinal interneurons. In this discussion, I propose that the theme will be developed that behavior involves not only neural mechanisms that influence the operational complexity of these systems but also that we must consider the relationship of interneurons to each other. This interaction between interneurons will be dominant and others will be less important. This dominance may change as the movement progresses. It has become increasingly apparent that individual interneurons often receive a small portion of the input that influences the entire population of interneurons involved in a specific motor pathway. The input to interneurons is often made possible by the divergence of afferent systems to generate fine movements as well as the grosser movements that are often thought to be characteristic of reflexes. Sense is being made of spinal interneurons in spinal reflexes. In addition, techniques used in the past will continue to provide insight into the organization of motor systems seen in the interneurons. Renshaw cells, interneurons mediating reflexes from Ib tendon organ afferents (Harries & Jankowska 1985a; 1985b), lamina VIII crossed interneurons (Harries & Jankowska 1985b), group II interneurons located in caudal lumbar segments (Lundberg et al. 1977a), group II interneurons in mid-lumbar segments (Edgley & Jankowska 1977b) and their activity during fictive locomotion (Shephard et al. 1980), interneurons active in the DOPA preparation (e.g., Jankowska et al. 1987a), interneurons involved in pyramidal inhibition (Budimowicz et al. 1987), interneurons in lumbar propriospinal pathways (Vasquez et al. 1989), efferent co-phonics (reviewed in Edgley & Jankowska 1987), interneurons involved in fictive scratching (e.g., Dijkstra et al. 1981), and cervical propriospinal cells (Lundberg 1978b). Recent demonstrations of divergent pathways in cat (Fleischman et al. 1985) and cat (Edgley & Wallace 1987) may not hold true for spinal reflex systems. (For more details about the interneurons mentioned, see reviews by Baldissera et al. 1981; Jankowska 1982; Lundberg 1978b; McCrea 1986.)

The view of spinal reflex function suggests that particular spinal afferents have specific reflex actions mediated by discrete populations of interneurons and that the activation of these pathways results in reflex movements. Included is the idea that reflex movements are a class of...