Proprioception From a Spinocerebellar Perspective

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I. INTRODUCTION

A. Definition of Proprioception

The term proprioception was coined by Sherrington (299) to describe the sensory information contributing to a sense of self position and movement. The relationship of proprioception to unconscious or more automatic functions has traditionally distinguished it from kinesthesis, or the conscious sense of position and movement. Proprioception has also been associated with a distinct class of sensory receptors, most notably those found in the muscles and related deep tissues, while kinesthesis has been more closely associated with joint and cutaneous receptors (45, 78, 127). The framework we propose here considers how proprioceptive sensory information is organized as it relates to a sense of body position and movement, but without any judgement about which sensory receptors may or may not be involved.

B. Sensory Receptor Basis

Current views of proprioception at the spinal level have, however, been strongly influenced by our understanding about the sensory receptors that contribute to it (for reviews, see Refs. 146, 199, 290). Some of these, the muscle spindles for example, have been studied extensively so the information they transmit to the nervous system is known in great detail (for example, see Refs. 77, 137, 138, 196, 218, 219, 272, 277–280, 296, 325). This knowledge, combined with our knowledge of receptor terminations and functional connectivity, has led to a general understanding of spinal proprioception as a central expression of the sensory receptor input which in turn details local parameters like muscle length and muscle force. The intent of this review is to examine this perspective in an historical context, and through that examination to provide a different framework for understanding spinal proprioception that may be more in tune with current views of sensorimotor processing in other central nervous system (CNS) structures.

II. IMPORTANCE OF PROPRIOCEPTIVE FEEDBACK FOR MOTOR ACTIONS

A. Feed-Forward Control of Directed Movements

Contemporary thinking about motor control has it that many actions belonging to a daily repertoire of motor activity may actually be controlled in a feed-forward manner, i.e., without a direct contribution from sensory feedback (85, 159, 162, 209, 229, 333). Thus a loss of proprioceptive feedback does not prevent movement or the ability to carry out motor tasks. Polit and Bizzi (268, 269) demonstrated this by showing that deafferented monkeys could perform a reach-to-target task successfully without visual aid. However, the behavior was not normal, suggesting further that sensory information may play an important regulatory role even for such over-learned movements as these.

B. Loss of Proprioception Leads to Direction and Amplitude Errors

This issue has now been investigated in a number of different behavioral contexts and with diverse experimental
approaches. Arm movements, particularly reaching movements, have continued to provide a preferred experimental paradigm for investigating the contributions of sensory information in guiding voluntary motor actions (106, 167, 168). For example, studies by the Ghez laboratory on deafferented patients lacking proprioceptive feedback have provided a number of relevant observations. These patients made large directional and amplitude errors when performing a reaching task without visual feedback. The errors were associated with differences in velocity and acceleration for movements in different directions and, according to the authors’ interpretation, might have resulted from a failure to take the inertial properties of the limb into account in programming the initial trajectory (113). Because direction and amplitude errors were partially compensated by allowing patients to view their arm before or during the movement, the authors proposed that visual feedback could assist proprioception or even substitute for it in some way by updating an internal model of the arm. (105).

C. Proprioception May Be Necessary to Develop and Calibrate Internal Models

A variant on the traditional reaching task was used in another study with a similar group of patients to show that a lack of proprioceptive information might also be responsible for deficits in interjoint coordination (107, 287). More recently, Sainburg et al. (286) speculated further that “control of intersegmental dynamics is normally dependent on proprioceptive information to update and maintain neural representations of the musculoskeletal system.” They found that sensory feedback was also required for adaptation to novel intersegmental dynamics. Thus, in agreement with other studies of this genre (64, 110, 183, 297, 317), they concluded “the nervous system uses sensory information to develop and recalibrate internal models of the musculoskeletal system itself.”

These studies, among an increasingly large number on this subject, clearly outline the importance of a proprioception both as a continuous feedback process and also as a component in the central processing of voluntary movements (see Refs. 126, 161, 168, 222, 223, 262, 273 for reviews). Although many of the higher order sensory functions contributing to internal models or intersegmental coordination have been attributed to supraspinal structures like the cerebellum (22, 109, 175, 294, 319, 320), we would like to consider here that an organizational framework for proprioception found at spinal cord levels may also be consistent with such functions.

D. Historical Frameworks for Proprioception Organization

In developing this framework we begin with an overview from a mostly historical perspective that outlines some of the assumptions and observations that drove the research and some of the conclusions that were drawn from them. We show that at least three organizational schemes, considered fundamental to spinal proprioception, were developed over a period of nearly 50 years, beginning with the introduction of the microelectrode. The earliest organizational model regarded primarily the monosynaptic connections between sensory receptors and spinal neurons, leading to a characterization of proprioception based primarily on muscle receptors and localized receptive fields. A later model that developed largely from the use of natural stimulation and a closer attention to polysynaptic pathways still focused on local muscle-based or joint-based representations. A third organizational model, and one we focus on in the latter half of this review, developed from the observation that spinal proprioception may also be organized in terms of global parameters representing the whole limb.

III. SPINAL PROPRIOCEPTION: HISTORICAL OVERVIEW

A. Introduction of Microelectrode Technology

Much of the early work on spinal mechanisms begun by Sherrington and his colleagues and contemporaries (62, 192, 204) was concerned with global aspects of reflex behavior and how sensory and motor mechanisms contributed to them. The emphasis was on behavioral relevance, and it developed from Sherrington’s concept that reflexes formed a basis for a hierarchical organization of the sensorimotor system. This top-down investigative approach was largely surpassed however following the introduction of the microelectrode in the 1950s. The technological breakthrough provided by the microelectrode allowed investigators to examine functional anatomy in great detail at the single-cell level, and it thereby focused research efforts toward the behavior of individual neurons and the specific synaptic interactions between them.

B. Emphasis on Monosynaptic Sensory Connections

Although the microelectrode opened many new avenues of inquiry, it was at the same time an effective technological barrier to a further understanding of neuronal circuitry. The single-cell recording techniques of the time were simply unable to deal effectively with multisynaptic connectivity and large-scale integrative circuits. Therefore, great emphasis was placed on monosynaptic connections, and their functional relevance was elevated to the virtual exclusion of the more complex circuitry. Indeed, it seemed logical that the most direct connections...
were the relevant ones and that less direct or indirect connections were meant only to modify and/or modulate.

C. Topological Projections and Localized Receptive Fields

Two basic concepts from sensory physiology also contributed significantly to the formulation of a general view about the central organization of proprioception. The concepts were the topographical projections of sensory information to and within the CNS, and receptor or modality specificity within the CNS (235, 236, 265, 314). As a consequence of the importance placed on these concepts, much of the effort to understand spinal proprioception was directed at the receptors themselves and at elucidating their specific connections in the spinal cord. The result has been that relatively little attention was paid to understanding whatever composite information might be represented by ensembles of diverse receptors. Moreover, this receptor-specific approach persisted even though most of the synaptic targets of the sensory receptors were found to receive convergent inputs from receptors having different locations and serving different modalities (1, 2, 23, 52, 60, 65, 71, 89, 148, 182, 234, 247, 256, 289). Some better known examples are the convergence of different types of cutaneous receptors onto “wide dynamic range” cells of the spinothalamic system (226) and the convergence of muscle spindle and tendon organ afferents onto common sets of interneurons in specific reflex pathways (224).

Nevertheless, the concept of topological projections has provided a useful framework for understanding function in a number of sensory systems. In cases where the sensory receptors exist in a two-dimensional array, such as the retina or the skin, central organizations can be readily analyzed in terms of a topological mapping that conserves nearest neighbor relationships (e.g., Refs. 43, 44). It has been tempting, therefore, to extend this concept to proprioception, even though its receptors may not be so simply arrayed. Muscle receptors for example are distributed throughout the three-dimensional bulk of individual muscles, and their distribution is not uniform across muscles. Nevertheless, some simple reflex organizations suggested that an appropriate “topology” for proprioception might be defined by the organization of muscles about a single joint, i.e., the agonists and antagonists. For example, it is well established that spinal motoneurons receive direct synaptic input from muscle spindle receptors in the muscle innervated by the motoneuron as well as from synergistic agonists (for reviews, see Refs. 47, 93, 128, 218). Moreover, a consistent reciprocal relationship between receptors and their projections to antagonist muscles is also well established. (141, 193; for reviews, see Refs. 19, 139).

This precise muscle-by-muscle organization may not, however, represent a general organizational pattern. For example, even simple reflex behavior involving more than one joint shows clear interactions across joints (189). Some of these interactions may result from specific reflex pathways such as those linking muscles acting at different joints (49, 239, 242, 244, 295), or the excitation of extensor motoneurons throughout the hindlimb by ankle extensor afferents (125). Heteronymous interactions may also involve presynaptic mechanisms as suggested by studies of afferent-induced modulation of the soleus II reflex during passive cycling movements (230, 231) and stretch of the quadriceps muscle (232).

D. Receptor Specificity and Sensory Integration

The idea that the selective sensitivity or specificity of sensory receptors carries over to the CNS has also influenced how experimental results have been interpreted. This principle is emphasized by the concept of sensory modality, which may be thought of as a class of sensations sharing a common stimulus quality. Although such qualities may not precisely correspond to the specificity of sensory receptors, it is often viewed in those terms. For example, until relatively recently, it was considered well established that position sense and kinesthesia are attributable to joint receptors rather than to muscle receptors (e.g., Ref. 236). Joint-angle sensation was believed to result from the central processing of information from joint receptors that specifically encode joint angle (48, 82, 241, 331). However, it is now clear that muscle spindles, once thought to encode exclusively individual muscle lengths, are also major contributors to the kinesthetic sense of position and movement (46, 51, 219–221, 326, 327). This example illustrates how an ensemble of information from diverse sensory receptors may contribute to a given “modality.”

IV. A MODEL TO STUDY SPINAL PROPRIOCEPTION: THE DORSAL SPINOCEREBELLAR TRACT

A. Dorsal Spinocerebellar Tract Projects Proprioceptive Information Centrally

One of the major central projections of the muscle receptors is over spinocerebellar systems. Thus the spinocerebellar neurons may be considered as a kind of end point for the processing of proprioceptive sensory information at the lowest levels in the nervous system where the synaptic connectivity between sensory receptors and central neurons can be studied. Consequently, with the advent of the microelectrode, spinocerebellar neurons
became a particularly attractive target for study along with the spinal motoneurons, since both were large cells and accessible to intracellular recording, and they were both direct targets for sensory input from muscle receptors.

Two major groups of spinocerebellar neurons contribute to dorsal and ventral spinocerebellar tracts (DSCT and VSCT, respectively), and together they provide the major direct sensory projection from the hindlimbs and lower part of the trunk to the cerebellum. Sensory information from the hindlimbs is also relayed by indirect spino-reticulocerebellar pathways and through at least two olivocerebellar pathways, the direct spinoolivocerebellar and the indirect spinoreticulo-olivocerebellar. We consider here only the dorsal spinocerebellar neurons, since they are most likely to represent the purely sensory aspects of the proprioceptive information directed centrally. The ventral spinocerebellar neurons have been shown to encode some form of motor or premotor signal derived from descending pathways in addition to proprioception (13–15, 198, 202). A parallel system serving the forelimbs includes the direct cuneocerebellar and rostral spinocerebellar tracts (118, 258) and other indirect pathways via the lateral reticular nucleus and the inferior olive.

B. Location and Morphology of DSCT Neurons

The cells of origin of the DSCT are classically described as residing in Clarke’s column in Rexed’s lamina VII of the lumbar and thoracic spinal cord segments (Fig. 1A; Refs. 30, 195, 255, 314, see also Ref. 257 for a review). However, the development of anatomical tracers like wheat germ agglutinin (WGA)-horseradish peroxidase (HRP) led to the identification of several other groups of neurons that also belong to the DSCT. These cells are located throughout the intermediate and dorsal laminae of the thoracic and lumbosacral segments of the spinal cord (72, 210, 214, 217). DSCT axons terminate as mossy

![Fig. 1](http://physrev.physiology.org/)

**FIG. 1.** Neurons of the dorsal spinocerebellar tract (DSCT). A: camera lucida reconstruction of a Clarke’s column DSCT neuron filled intracellularly with horseradish peroxidase (HRP). These are large multipolar neurons with a dendritic arborization that extends beyond the boundaries of Clarke’s column (dashed line). [From Walmsley and Nicol (324).] B: muscle receptor axons form giant synaptic terminals on Clarke’s column neurons. The morphology of a giant synapse is illustrated by this reconstruction. [Modified from Szentagothai and Albert (315).] C: the giant synapses give rise to large amplitude unitary excitatory postsynaptic potentials (EPSPs). An example is illustrated in this intracellular recording from a DSCT neuron, showing a train of 2- to 4-mV unitary EPSPs evoked by a 50-g load placed on the soleus tendon. [From Eide et al. (74).] D: maximal stimulation of the low-threshold afferents in a muscle nerve may activate from 10 to 20 giant synapses synchronously. The record illustrated here shows a 20-mV maximal EPSP evoked in the same neuron as C by stimulation of the gastrocnemius-soleus nerve. [From Eide et al. (76).]
fibers in the cerebellar cortex of lobules I–V in the anterior lobe and in the posterior lobe vermis and paramedian lobe (117, 213, 215, 216). In addition to the cortical projection, there is recent evidence that DSCT fibers also terminate in the medial and interpositus cerebellar nuclei (211, 212).

V. EARLY STUDIES OF DORSAL SPINOCEREBELLAR TRACT

A. Electrical Stimulation Reveals Direct Sensory Connections

DSCT studies that began in the 1950s gave rise to a model for central proprioception that consisted of spinal projection neurons relaying receptor-specific and highly localized sensory information to higher centers that integrate the information (in this case, to the cerebellum).

The earliest results showed that the synapses between muscle receptors and DSCT neurons, unlike those with motoneurons, were “giant synapses” (see Fig. 1B, Ref. 315) that could faithfully follow high-frequency repetitive stimulation of low-threshold muscle sensory fibers (Ia afferents; Refs. 132, 225). It was therefore reasonable to presume that transmission at this muscle receptor-DSCT cell synapse comprised a high-fidelity relay. This interpretation was further supported by later intracellular recordings showing that stimulation of these same afferents evoked larger amplitude and longer duration excitatory postsynaptic potentials (EPSPs) in DSCT neurons than in motoneurons (see Fig. 1, C and D; Refs. 59, 70, 74–76, 225). Thus most of the earlier research on the DSCT was based on the assumption that the direct, monosynaptic input from sensory receptors was the only functionally relevant input.

B. Functional Framework Based on Receptor Type and Localization

For over a decade, electrical activation of afferent input was the primary “functional” means used to examine the connectivity patterns between peripheral nerves and DSCT neurons. Despite the anatomical complexity of Clarke’s column shown to contain both large multipolar projection neurons (Fig. 1A) and interneurons (194, 282), most of the electrophysiological research focused on the shortest latency responses to nerve stimulation. These studies led to an elaborate set of divisions and subclasses based on both modality and receptor specificity (201). According to this classification, the DSCT consisted of proprioceptive and exteroceptive subdivisions, each being further parceled into subclasses depending on the main type of afferent input. Thus neurons in the proprioceptive subdivision were shown to receive monosynaptic excitation either from muscle spindles (primary or group Ia afferents, with minor convergence from secondary or group II afferents) or Golgi tendon organ (group Ib) afferents with a high degree of spatial discrimination (70, 200, 203). Another three groups of DSCT neurons were distinguished within the exteroceptive subdivision. One group was activated from touch and pressure receptors in the skin, another from slowly adapting pressure receptors in the footpads, and the third by receptors that elicited flexion reflexes (133, 178, 201, 334).

Although little attention was paid to polysynaptic pathways, it was nevertheless evident from even the earliest studies (191) that single shock electrical stimulation evoked substantial long-latency responses. Because many of these responses were inhibitory, they were viewed as another example of the well-known surround inhibition that was shown to provide a sharpening of point-to-point resolution through contrast enhancement in the visual system (132, 190, 191). This interpretation helped to reinforce the notion of a functional organization based on precise topological projections. In fact, reviewing the current status of research on spinocerebellar systems in 1965, Oscarsson concluded: “... DSCT [neurons] carry information about proprioceptive and exteroceptive events with high degree of spatial discrimination ... used in the fine coordination of posture and movement of the individual limb” (257).

Figure 2 summarizes some of the main points of this proposed organization. It shows a number of direct monosynaptic connections from specific receptor types (bold arrows) and a few interneurons providing mostly disynaptic inhibition.

VI. NATURAL STIMULATION

A. Responses to Localized Muscle and Cutaneous Stimulation

Later studies departed from the electrical stimulation paradigm by employing more “natural” stimulation such as the stretch of isolated muscles. The aim of these studies was to provide a more functional description of the specific connectivity patterns between sensory afferents and DSCT neurons. However, the focus was still on specific stimuli. For example, work by Jansen and Rudjord and co-workers (153, 156) contributed to a further distinction within the “proprioceptive” division between neurons receiving inputs from only primary or secondary muscle spindle endings. Intracellular responses to muscle activation (Fig. 1C) also allowed an analysis of the functional convergence of afferents from a specific muscle and its effect on DSCT firing (152). The analysis suggested that the convergence increased the fidelity of the information transmission.
Attempts were also made using muscle stretch to characterize the interaction between excitation and inhibition from various muscles onto individual DSCT neurons (151, 154, 155). These studies concentrated on the cellular mechanisms of inhibition and concluded that both presynaptic and postsynaptic mechanisms were involved.

A more in-depth analysis of the cutaneous input to the DSCT was also attempted by Mann (205), who extended the earlier observations by Lundberg and Oscarsson through the use of natural cutaneous stimulation to characterize receptive fields and receptor specificity. He found that only about one-fifth of the recorded neurons were strictly cutaneous, and their receptive fields were not discretely organized, being larger proximally and occasionally being “broken receptive fields.” A small fraction of cells received a combination of cutaneous and deep (interpreted as muscle) inputs, and interestingly, the cutaneous and deep receptive fields were often not congruent. Although he did not study the inhibitory effects on DSCT discharges systematically, he did note that cutaneous inhibitory fields had irregular shapes that were usually eccentric to and not surrounding the excitatory fields. He also found that 20% of the DSCT neurons recorded in this study could not be activated by any localized peripheral stimulus (mute cells).

B. Recognition of Potential Complexity of DSCT Circuitry

Mann (206) pointed out the potential complexity of DSCT organization emerging from this study again in a later review. Although he did not dispute the classification originally proposed by Lundberg and Oscarsson (see Fig. 2), he did raise concerns about oversimplifications that were made about the functional organization of the DSCT. Mann concluded the review by remarking: “The DSCT has received a good deal of attention, perhaps because of its accessibility and presumed simplicity. The accessibility is real, but its simplicity may be brought into question . . . A clear separation of cutaneous and muscle DSCT is no [longer] possible . . . Thus it seems useful to think of the DSCT as a mixed tract rather than to invent new terminology for the cutaneous subdivision, confusing an already somewhat muddy taxonomic picture”. Mann also questioned the specificity of DSCT neurons originally classified as group Ia and group II: “Coded in the discharge of group Ia and group II DSCT cells is the length of a muscle under stretch, and the coded information has been altered little by the imposition of the synapse . . . It is well documented however, that receptors of more than one muscle group can cause a given cell to discharge leading one to question how well the length information
for one muscle can be isolated from the DSCT discharge when another muscle is stretched simultaneously."

C. Functional Framework Remains Focused on Receptor Type and Localization

Although Mann’s review had the merit of pointing out limitations in the classical approach and the resulting view of the DSCT, it ultimately failed to provide a clear alternative functional framework. In fact, the traditional thinking about sensory projections was also evident in the interpretations given to results from a pioneering behavioral study by Arshavsky et al. (12) in which they recorded DSCT activity during treadmill locomotion in decerebrate cats. For example, they observed that at least 50% of the DSCT neurons were active in more than one phase of the step cycle, but they attributed this behavior to receptor input from biartic- ular muscles and did not consider the possibility of convergence mechanisms from multiple hindlimb muscles. Consequently, they concluded that “our findings confirm the view, based on the study of the afferent connexions of DSCT neurones, that the DSCT transmits information about the activity (i.e., the phase and the strength of the contraction) of separate muscles or of a few synergists.”

Thus the use of natural stimulation did not lead to a fundamentally different model of spinocerebellar organization because it was still subject to the same methodological limitations and to the same basic assumptions. The focus on isolated stimuli failed to acknowledge an integrative role for the spinal circuitry, so the implied function of the DSCT was to relay a high-fidelity copy of highly localized sensory information to the cerebellum. Any integrative function required for appropriate sensorimotor integration was the exclusive purview of the cerebellum and other central structures.

VII. POLYSYNAPTIC PATHWAYS

A. Widespread Sensory Convergence Onto DSCT

This relay model was challenged when it could be shown that converging polysynaptic pathways play an extensive role in the activity of the DSCT neurons. The issue was revisited through a series of studies that introduced more quantitative analytical techniques employing a sensitive cross-correlation analysis (180, 249) to characterize DSCT responses to electrical stimulation of hindlimb peripheral nerves (179). The results of this analysis showed that most DSCT neurons respond to stimulation of flexor and extensor nerves in the proximal and distal hindlimb. This implied a much larger pattern of convergence than was previously assumed from intracellular recordings, and it contributed to the finding that the most common DSCT responses, accounting for ~80% of the total responses, were polysynaptically mediated. Figure 3 shows examples from a single cell reported in that study illustrating long-duration inhibitory (type 2) and long-latency excitatory (type 3) responses.

FIG. 3. Cross-correlation analysis revealed a variety of responses to peripheral nerve stimulation and a greater degree of convergence than had been seen with intracellular recording. Extracellular action potential recordings from a single DSCT neuron in response to electrical stimulation of muscle nerves were used to generate cross-correlograms to quantify the poststimulus time probability density of spike occurrence. These records show the time course of excitability changes from the mean firing level (dashed lines) following single shocks to the sensory axons in four different muscle nerves. They illustrate a convergence of sensory input from receptors in the hamstring and quadriceps muscles proximally and the gastrocnemius-soleus and anterior tibial muscles distally. A: type 1 (monosynaptic) response to hamstring nerve stimulation. B: type 2 (inhibitory) response with long duration evoked by quadriceps nerve stimulation. C: type 3 response (oligosynaptic excitatory) response to anterior tibial nerve stimulation that differs from the type 1 monosynaptic response by its longer latency and often longer duration. D: a very weak type 2 (inhibitory) response with a short duration evoked by stimulation of the gastrocnemius-soleus muscle nerve. [Redrawn from Knox et al. (179).]
B. Further Evidence for Polysynaptic Pathways

By the early 1980s, the role of interneuronal networks in the function of DSCT neurons had become more apparent. The available evidence for some of the circuitry underlying the polysynaptic organization of spinocerebellar systems was summarized in a review by Bloedel and Courville (28). Their concept of the spinocerebellar circuitry now included both excitatory and inhibitory interneurons interposed between the sensory receptors and the DSCT projection cells as summarized in Figure 4.

The issue of polysynaptic convergence also became the “leit motif” of a long series of experiments by Osborn and Poppele (248–254) that spanned almost a decade. In these studies, DSCT responses to several types of sensory stimulation, from electrical nerve stimulation to passive ankle joint movements, were analyzed with a variety of quantitative techniques to gain insight about the functional significance of the pattern of sensory convergence in the DSCT.

The results of these studies led to several new observations about the organization of the DSCT circuitry. First, they found that muscle contraction is the most potent single stimulus and inhibition the most common response to that stimulus (248). Then, by extrapolating from large population samples, they showed that >60% of the DSCT population representing sensory input from the entire hindlimb responds to stimulation of primary afferents from a single muscle group (the gastrocnemius-soleus), and mostly via polysynaptic pathways. Thus not only did the DSCT neurons appear to be strongly modulated by muscle force, but also “the information carried by the DSCT is not discretely organized muscle by muscle.” They went on to observe that “the role of integrating afferent information from the various muscles and joints of the limb no longer seems to be the exclusive province of the cerebellum, but also appears to be shared by spinal centers such as the DSCT” (250).

C. Localized Stimuli Affect Most of the DSCT Population

Although each separate stimulus seems to affect a substantial fraction of the DSCT population, more complex stimuli like joint rotations can affect nearly the entire population (88%, Ref. 46). Thus it became evident that even relatively localized stimuli such as single joint movements have a widespread effect when they activate a variety of receptor types simultaneously (e.g., cutaneous, muscular, and joint receptors). Furthermore, the response patterns evoked by these more comprehensive stimuli were distributed differently across the population than were those evoked by more discrete stimuli. This was evident in the comparison of responses to stretch of
the gastrocnemius-soleus with those evoked by passive ankle flexion (254). The two stimuli were designed so they stretched the muscles identically, but they elicited different response components in the population. This result implied that converging input from nonmuscle receptors or from other muscles acting at the ankle joint can modify the activity of DSCT cells so that the same local stimulus, in this case stretch of gastrocnemius-soleus, can evoke a different behavior in another context. It was a clear demonstration that DSCT responses do not merely reflect the activity in specific classes of sensory receptors.

Although the polysynaptic model of spinal proprioception that emerged from these studies seemed more difficult to place in a functional framework than the simpler direct-relay models, it did seem to be more consistent with the anatomy of the system. For example, Walmsley and Nicol (324) argued against a topographical arrangement of muscle input within the DSCT based on a study of muscle projections using intracellular recording and WGA-HRP filling. They found that neurons activated monosynaptically from ankle extensors were scattered throughout Clarke’s column, and they generally received converging input from more than one muscle. Along this same line, Zytnicki et al. (339) found a large heterogeneity in the responses evoked in DSCT neurons by contraction of the anterior tibialis muscle. A convergence of cutaneous sensory inputs was also implied by the results of Kim et al. (177), who examined responses to stimuli applied to the skin of the cat footpad.

D. Connectivity of DSCT Neurons Outside Clarke’s Column

The increasing evidence that various neuronal subgroups residing outside Clarke’s column also contribute axons to the DSCT (119, 210, 211) suggests further that these subpopulations might also have distributed connectivity patterns. Two studies in the late 1980s provided careful examinations of the inputs to these non-Clarke’s column neurons. One study characterized the sensory input to DSCT neurons located caudal to Clarke’s column in laminae V and VI of the lumbar spinal cord (11). These authors found an extensive mono- and disynaptic pattern of convergence from electrically stimulated muscle as well as cutaneous and joint nerves compatible with a major integrative role for these neurons. A similar experimental approach was used by Edgley and Jankowska (73) to investigate the connectivity of more rostral dorsal horn spinocerebellar neurons. These neurons were found to receive extensive monosynaptic convergence from group II muscle afferents, as well as from joint and cutaneous afferents. Unlike the neurons studied by Aoyama et al. (11), however, they did not seem to receive input from group I muscle afferents.

VIII. PARALLEL DISTRIBUTED NETWORK

A. DSCT Circuitry Resembles a Parallel Distributed Network

Rather than suggesting a specific functional organization, the large-scale sensory convergence onto DSCT neurons and associated polysynaptic circuitry resembled instead a parallel distributed neural network having a widespread interconnectivity. The analogy to a neural network was reinforced by the results from a set of experiments using a variety of stimuli including muscle stretch or contraction and joint ankle flexion/extension (253). Cells that responded similarly to one of these stimuli generally showed different response profiles for other stimuli. In fact, it was not possible to predict a cell’s response to one type of stimulus from its response to another. This argued strongly against any clear-cut functional distinctions among DSCT neurons and led to a proposed scheme in which divergent projections from sensory receptors (input layer) project onto various interneuronal pathways comprising a “hidden layer” in a neuronal network. The weighted pattern of convergence of sensory information from the hidden layer to the individual units of the output layer (the DSCT neurons) determined their firing properties (253; Fig. 5).

B. Similarity With Other Spinal Sensory Networks

More generally, the parallel distributed organization proposed for the DSCT circuitry resembles analogous distributed networks that have been proposed for the control of various types of spinal reflexes. The scratch reflex in the turtle is one example in which distributed activity of broadly tuned propriospinal interneurons coordinate two forms of scratch reflex behavior (rostral or pocket scratch) (25, 26). The network controlling this reflex behavior contains shared components with the circuitry devoted to the control of swimming behavior, and it might also be distributed bilaterally (83, 84, 307, 308). Another example is the wiping reflex in the frog (108) in which an irritating stimulus on the frog skin can evoke a precise foot wipe directed at the stimulus using different limb configurations that depend on stimulus location. Stimulating boundary areas between two adjacent wiping zones can elicit the limb configuration of either zone with similar probability, suggesting that a distributed organization might also govern this behavior (171, 172).
dependent reflex reversals (7, 67, 68, 90, 118, 258, 263, 309; see also Refs. 63, 261, 285, 336 for reviews) and positive force feedback (10, 111, 115, 129, 263, 275, 276) motivated a proposal for a much less specific organization. This organizational scheme developed from the notion of a parliamentary principle originally introduced by Bässler (20, 21), which was an alternative to the idea that distinct interneuronal groups might control distinct phases of the locomotion cycle. It was based on experimental evidence from the stick insect showing that interneurons are all active throughout the phases of locomotion. From this observation, Bässler conceptualized a population-coding scheme for the control of locomotion whereby each interneuron contributed with its level of activity to all the locomotion phases in a manner analogous to the way a member of parliament contributes to a decision with a vote.

The control scheme for mammalian locomotion proposed by Prochaska (274) is similar to this in principle, since it postulates that weighted contributions from various spinal interneuronal network modules might govern locomotion and reflex behavior in general (see Fig. 6). Prochaska (274) attempts to account for reflex variability using the formalism of fuzzy logic, wherein behaviors are selected according to a set of imprecisely defined or “fuzzy” rules relating specific sensory variables to specific motor actions. One basis for such circuit interactions might be the interneurons that are shared among different spinal circuits. In fact, it is likely that a number of interneurons contribute to the control of more than one motor behavior, for example, posture and locomotion (41, 42, 121, 140, 142, 312, 313, or for a detailed review, see Ref. 147). Interneurons may also be shared between reflex and ascending systems. At least one class of inhibitory interneurons that makes synaptic contact with both DSCT neurons and motoneurons (134) may provide for a coupling of afferent information processing between the two pathways. On the other hand, collaterals of primary sensory afferents directed to either DSCT or spinal motoneu-

![Diagram of the DSCT circuitry proposed by Osborn and Poppele (253)](Modified from Osborn and Poppele (253).)
rons may also be under differential supraspinal (cortical) control via presynaptic inhibition (135, 136, 149, 150, 197). Differential presynaptic control of different sensory afferent branches might, therefore, represent a mechanism by which the activity of the two networks could also be uncoupled. Thus even these relatively simple mechanisms can lead to a number of possible outcomes.

IX. INFORMATION ENCODED BY DORSAL SPINOCEREBELLAR TRACT ACTIVITY

A. Nonlinear Interactions Require a Normal Behavioral Repertoire for Study

Even though the parallel distributed network organization of the DSCT bears an obvious resemblance to spinal organization schemes that have been recently proposed to account for reflex behavior, this analogy did not help to provide any clear functional insights. Neither did the experimental paradigms used to study the DSCT, since they addressed primarily questions of connectivity. Nevertheless, it was generally supposed that a functional model would eventually result from these studies. In particular, it was assumed that if a sufficient number of selective (i.e., well controlled) and discrete stimuli were tested, then a synthesis of resulting observations would ultimately define the total functional organization. However, the experimental results proved this assumption to be invalid because it failed to account for the nonlinear interactions among stimuli. It is unlikely therefore that the functional significance of the circuitry can be fully appreciated unless the stimuli engage a sufficiently complete set of peripheral mechanisms in the same spatial and temporal order as occurs in normal behavior.

B. New Functional Framework Based on Whole Limb Rather Than on Localized Parameters

The need to adequately engage sensory input was particularly well illustrated for the DSCT circuitry by an experiment in which DSCT responses to bidirectional, single-joint rotations were compared with those for bidirectional perturbations of the whole limb (33). The result was that neurons responding to ankle-only flexion with the same time course of activity showed a variety of response waveforms to ankle-only extension, whereas bidirectional limb movements consistently produced opposite response waveforms for oppositely directed limb movements (see Fig. 7). Thus only when the sensory input from the whole limb was activated in a normal behavioral pattern did the responses of this system show a clear and consistent relationship to the stimulation. Even though the single joint stimuli produced robust and often large-amplitude responses (177, 253, 254),
there was no consistent pattern across neurons that related them to the stimulus parameters.

This experiment provided the first clear, direct evidence that the output of the spinal sensory circuitry might be related to whole limb parameters rather than to local parameters like muscle lengths or individual joint movements. Moreover, the same study showed that the activity of DSCT neurons is broadly tuned for limb movement direction and for the position of the hindfoot. These observations set the stage for a completely different functional concept for spinal proprioception by raising the question of the extent to which global versus local limb parameters are represented in the activity of DSCT neurons.

C. DSCT Neurons Encode a Linear Representation of Foot Position and Movement

This question was examined systematically by recording DSCT unit activity during passive placement of the cat hindfoot over most of its parasagittal workspace. The response data were related to limb kinematics to determine whether they best represented individual joint angles or more global limb parameters (see Figs. 8A and 9A for definitions). Kinematic parameters that included multiple joint angles always explained a greater fraction of the variance in unit activity than did any single joint representation (38). In fact, linear relationships between unit activity level and the polar coordinates of limb axis length and orientation consistently explained the greatest percentage of variance in unit activity. Examples of this relationship are illustrated in Figure 8, C–F. These three-dimensional plots show a planar relationship between unit firing activity and the limb end-point position given by the coordinates of the limb axis.

Another feature of the DSCT responses to passive limb placement is that the activity of many neurons may also relate to the direction of limb movement as it goes from one position to another. In other words, movement and positional parameters can be represented simultaneously by the activity of individual DSCT neurons, but they are not represented independently. The amplitude of the movement response was found to be linearly dependent on the level of position-related activity (34). This relationship between inputs is reminiscent of the interaction between retinal and eye (or head) position signals first described by Andersen et al. (5) for neurons of the parietal cortex. The amplitude of the retinal receptive field response of those neurons was found to be modulated by the eye or head position. This type of modulation, resulting from a multiplicative type of interaction between the two signals, is commonly referred to as “gain field” modulation. Gain fields have now been demon-
strated for several CNS structures involved in oculomotor control (39, 323) and spatial orientation (207, 237, 238, 316). Although the functional interpretation of gain fields is still debated, they appear to represent a neural mechanism by which information about multiple parameters may be compressed and combined in a single unit’s activity, and they have also been interpreted as evidence for coordinate transformations (4, 6, 288, 302, 310, 338, for reviews; see Ref. 40).

X. REFERENCE FRAMES TO FORMALIZE RELATIONSHIPS

A. Muscle- and Joint-Based Reference Frames

One way to formalize the relationship between unit activity and limb kinematics is through the definition of a reference frame, which is a spatial domain in which parameters of interest can vary (305). For example, a pri-
mary reference frame for muscle receptors is the spatial
domain of the muscle, and the coordinates for effective
stimuli in that frame of reference might be the one-dimen-
sional coordinate of muscle length. From the relationship
between muscles and joints, we may also define another
reference frame for muscle receptors that is joint based.
The coordinates in this reference frame would be the
relevant joint angles.

B. Limb- Versus Joint-Based Reference Frames
and Biomechanical Factors

The reference frame for a DSCT neuron, which com-
bines signals from receptors in different muscles and
joints, each having a separate reference frame, depends
entirely on exactly how the signals are combined. For
example, a combination of joint angles might be weighted
such that the resultant is equivalent to the length or
orientation of the limb axis, thereby transforming the
joint-based reference frame to a limb-based reference
frame. Or the combination might simply represent a sum
or difference of joint angles, in which case the reference
frame would still be joint based. Thus the fact that DSCT
neurons might receive convergent inputs from more than
one joint does not in itself imply anything about a refer-
ence frame for the resulting information.

The question then is whether DSCT activity is based
on the reference frames of the sensory receptors or on
some derived reference frame that results from central
processing. The difficulty in distinguishing between these
possibilities is that mechanical constraints in the limb
result in a correlation between joint angles and more
global limb parameters. Therefore, even a clear relation-
ship between unit activity and limb axis parameters is not
necessarily indicative of a centrally organized coordinate
transformation.

XI. INTERACTION BETWEEN BIOMECHANICAL
AND NEURAL FACTORS

A. Joint-Angle Covariance Reduces Limb
Degrees of Freedom

To explore this issue further, it is important then to
examine how the limb segments and joints interact. The
cat hindlimb may be considered as a 3-degree-of-freedom
linkage of segments allowing for two-dimensional move-
ment of the end point in a parasagittal plane. This rela-
tionship illustrates an important point about limb motor
control, namely, the need to deal with extra degrees of
freedom. In the cat hindlimbs for example, movements
about three joints must be controlled to achieve limb
end-point movements that are confined to a two-dimen-

FIG. 9. Covariation of cat hindlimb joint angles for
passive and active postures. For a given hindlimb post-
ture, the angles at the hip (h), knee (k), and ankle (a)
illustrated in A are plotted versus one another in a
three-dimensional joint-angle space. Joint-angle mea-
surements made while the hind foot of an anesthetized
cat was placed in the 20 positions indicated in Figure
8B all fall within a single plane indicated by the joint-
angle covariance plane drawn in B for data pooled
from six animals (38). When alert cats were required to
maintain stance on a tilted platform, the joint angles
also showed a planar covariance as illustrated in C.
[Replotted from Lacquaniti and Maioli (187).] Although
the joint angles were confined to a linear covariance
plane both during active stance and passive limb place-
ment, the planes had different orientations. The covari-
ance plane determined from joint angles measured
during active stance was rotated $-90^\circ$ in the ankle-hip
plane with respect to the covariance plane determined
for the anesthetized cat. This observation is consistent
with a control strategy that may take advantage of
biomechanical joint-angle constraints by modulating
joint-angle relationships, in this case by reversing the
relationship between hip and ankle joints.
sional workspace. However, there is a tight coupling among the three joint angles in the cat hindlimbs during both passive and active limb movements that effectively reduces the limb degrees of freedom from three to two (38, 188), implying in this case there may be no extra degrees of freedom to control. This reduction is illustrated by the finding that the relationship among the three joint angles of the hindlimb shows a planar or two-dimensional covariance over a large range of limb positions. Thus the data representing limb positions in a three-dimensional joint-angle space fall on a plane rather than being scattered throughout the space as expected if joint angles varied independently (see Fig. 9).

The basis for the joint-angle coupling that leads to this behavior in the passive limb is presumably biomechanical, as indicated by post mortem assessment (38). For example, the biomechanical properties of biarticular muscles that span two joints from origin to insertion as well as more passive structures such as ligaments undoubtedly have a role in coupling forces across joints. During movement there may also be inertial coupling between limb segments as well.

Behavioral studies of posture in cats have suggested that neural control of the limb may actually take advantage of these biomechanical constraints (186–188). Cats trained to maintain stance on a tilting support platform also showed a linear covariation of joint angles during this task (187; Fig. 9C). However, the joint-angle covariance pattern in this case is somewhat different from that described in the passive limb (Fig. 9B). First, the coupling among joint angles is tighter, suggesting that neural control may actually reduce further any independent motion in the individual limb segments. Second, the orientation of the covariance plane is different due mostly to a sign inversion of the relationship between the hip and the ankle angles (compare Fig. 9, B and C). These observations suggest that the limb biomechanics may provide a basis for the planar joint-angle covariance that effectively reduces the limb’s degrees of freedom. A reduction in degrees of freedom may then simplify control strategies for maintaining stance, since the problem of mapping sets of joint angles into foot positions (188) can be solved by appropriately adjusting the relationships among limb segments. In this case, it would involve somehow reversing the passive relationship between hip and ankle angles. Sensory input that is also constrained by the biomechanical coupling is more likely to support this type of control strategy based on global limb parameters rather than one that controls joints independently.

B. Implications of Joint-Angle Covariance for Motor Behavior

Recently intersegmental covariations have also been observed and studied during locomotion (27, 120, 298; see also Ref. 184 for a review). These studies extended the observations made during standing behavior to the kinematics of locomotion and also pointed out that limb axis length and orientation represent kinematic invariance across various types of gait. Lacquaniti et al. (184) proposed from these observations that “the CPG [central pattern generator] may control limb segment motion by encoding the waveform of the elevation angles. In response to these kinematic reference signals, the appropriate muscle synergies would be determined in a subordinate and flexible manner to adapt to the current mechanical constraints.”

The biomechanical properties of the limb may also provide a substrate for interjoint coordination at the reflex level (114, 181, 335; see also Ref. 243 for a review). Muscle length-dependent excitatory connections exist between muscles with synergistic biomechanical actions across joints (242, 245), whereas force-dependent, inhibitory pathways link muscles that exert torque in different directions (31, 32, 145, 300). Therefore, the action of these connections could result in a stronger across-joint coordination that complements the biomechanical coupling.

These results suggest that biomechanical interjoint coupling may be utilized and perhaps fine-tuned by the CNS in controlling the limb. Such interplay between controller and the controlled plant could play an important role in the process by which the nervous system copes with the potentially complex multi degree-of-freedom control problem. In essence, purely biomechanical factors establish a reduction in the limb degrees of freedom that is reinforced and modified by spinal reflex pathways that interconnect muscles acting at different joints. Consequently, the role and the computational load of the higher level control may be effectively simplified.

C. Implications of Joint-Angle Covariance for Sensory Representations

The relevant functional implication for sensory information processing is that receptor activity throughout the limb is also likely to be correlated because of the strong biomechanical coupling among segments. For example, the activity of receptors located in muscles acting at the hip and the ankle might reflect the covariation of the angular motion of the two joint angles by showing a high level of temporal correlation; that is, the activity of a hip extensor muscle receptor can also transmit information about ankle joint motion. Patterns of correlated activity across receptors along with a large degree of sensory convergence could potentially bias the activity within the spinal circuitry. The result would be that the activity of spinal neurons would appear to relate to global hindlimb parameters even though it might simply reflect the joint-angle covariation without additional sensory transformations by the spinal circuitry.
XII. REFERENCE FRAMES FOR DORSAL SPINOCEREBELLAR TRACT ACTIVITY

A. Can We Distinguish Between End Point- and Joint-Based Reference Frames?

The question for the DSCT then is the extent to which the activity of these neurons is referenced to the joint-angle covariance or to more abstract limb parameters such as the limb end-point position. In the passive limb there is a single relationship between limb end point and a linear combination of joint angles and thus a unique limb geometry for each end-point position (38). Therefore, the finding under passive conditions that DSCT cells encode limb length and orientation, or effectively limb end-point position is not surprising. In fact, because of the biomechanical coupling, we could expect this result even if the cells received only a minimal sensory convergence across joints.

However, a number of observations suggested that DSCT activity does reflect a contribution from the spinal circuitry in elaborating a representation of limb axis length and orientation. One is that among the cells that responded independently to all three hindlimb joint angles, those that related similarly to one joint angle could show different relationships with the other two (38). In other words, the pattern of joint-angle convergence expressed by these cells was not fixed to the biomechanical joint covariance. The relationship between DSCT activity and joint angles could be weighted differently across cells as in a network or fuzzy logic type of organization. The other observation was that the cells are broadly tuned with respect to limb axis parameters (33), and the preferred tuning directions are clustered along and perpendicular to an axis roughly coincident with the limb axis (34; see Fig. 8E). This observation provided an indirect indication that the weightings of inputs from various limb segments might be biased toward an explicit representation of the whole limb.

The crucial test of this issue was to alter the joint angles and end-point position separately (35, 37). By constraining the movement at specific joints, sets of limb end-point positions could be imposed that were each associated with a different joint-angle covariance pattern. The responses of DSCT neurons for each position in which the limb was free to move was compared with those obtained with joint constraints. The result was that about one-half the sample cell population studied exhibited the same response to the two different joint-angle covariance patterns across limb end-point positions. These cells were clearly able to signal the position of the limb end point for at least two different sets of limb geometry, that is, they somehow derived the end-point position independently from the biomechanical constraints. The other cells continued to signal a linear representation of the limb length and orientation, or limb end-point position, but it was a different representation in the two cases. The activity of these cells was clearly influenced by the joint-angle covariance.

B. Evidence for a Kinematic-Based Reference Frame

These studies in the anesthetized cat ignored, however, an obvious source of sensory input to the DSCT, namely, the inputs activated by muscle forces and joint torques. Thus the finding that DSCT activity encodes end-point position cannot be taken to rule out more elaborate representations based on joint torques or limb compliance. The reason is that all these variables are highly correlated in the passive limb. Moreover, DSCT cells in particular have been found to be very sensitive to sensory inputs activated by muscle contraction (200, 248, 252, 339), so it seems reasonable that muscle force or joint torque could as well be represented explicitly by DSCT activity. If so, it brings into question any conclusion about DSCT encoding of hindlimb parameters in an end point-based reference frame, since the position of the limb end point is potentially independent from joint torques.

This issue was investigated by comparing responses to passive limb positions with and without muscle stimulation (36). In this experiment, various muscle groups were activated by electrical stimulation of dissected ventral root filaments. For a given foot position, this generally resulted in a stiffening of the limb with only modest changes in joint-angle kinematics. The underlying assumption of the experiment was that if the reference frame for DSCT responses were based to any extent on kinematics or muscle forces, then the muscle tension perturbations produced by this stimulus would be expected to alter the presumed kinematic representation. In fact, we might expect a substantial disruption of the DSCT representation since the stimulus was somewhat artificial and unrelated to the structured pattern of muscle activation occurring during normal behavior. Instead, the general finding was that the cells’ preferred tuning directions based on limb position were mostly unchanged by the muscle activation.

The result was complicated though by the fact that most of the cells did respond to the muscle stimulation, and while most of them (59%) nevertheless showed no significant change in their position-related activity, many cells (41%) did show changes. Closer examination of these changes showed that they resulted from uniform increases or decreases in response levels across positions. The effect of the muscle stimulation therefore was to alter the cells’ sensitivity to limb position, but this sensitivity or gain change was uniform over the entire
workspace. Thus it did not significantly alter the cells’ preferred tuning directions, or region in the limb workspace where a cell was most active (also referred to as the preferred maximal activity gradient direction in Ref. 36). Preferred tuning directions determined from responses recorded for passive limb positions were found to differ from those determined for responses recorded during muscle stimulation by less than \( \pm 15^\circ \) for about three-quarters of the cells studied. In fact, as illustrated by the difference angles in Figure 10, many cells that exhibited large differences in tuning direction when the knee joint was constrained showed essentially no difference during muscle stimulation.

Therefore, when limb forces were altered while maintaining limb geometry and joint-angle covariance nearly constant, the spatial tuning behavior of the DSCT cells was largely invariant. This result was interpreted as consistent with a kinematic reference frame for DSCT representations. Thus, in noting that the spatial variables appear to define reference frames for DSCT activity, Bosco and Poppele (36) concluded that “... whatever force information is encoded by the DSCT is encoded in a kinematic reference frame.”

XIII. HOW DOES DISTAL SPINOCEREBELLAR TRACT RELATE TO HIGHER ORDER SENSORY STRUCTURES: EVIDENCE FROM SENSORY CORTEX AND CEREBELLUM

What seems to emerge from this analysis is a framework for proprioception that involves a highly flexible network organization based in some way on whole limb kinematics. The functional organization underlying this framework originates with the biomechanical linkages in the limb. Afferent information from limb receptors is then processed further through a distributed neural network in the spinal cord (see Fig. 11). Although we examined only the evidence from the dorsal spino-cerebellar system to support this view, we also implied that spinal circuitry in general may be organized in a similar manner, at least with respect to the distributed nature of sensory processing. Here we will examine the extent to which other CNS structures may exhibit an organization similar to that described for the DSCT. An important consideration implied by such comparisons is the extent to which a common type of organization might be necessary for communication between spinal cord and central structures.

A. Broad Directional Tuning

One prominent feature of the proposed spinal organization is broad directional tuning. Although studies of central sensory processing have mostly focused on receptive field organization and mapping the body surface (50, 80, 88, 94, 160, 164, 235, 240, 270), there is evidence that a distributed processing of sensory information by broadly tuned cortical neurons may serve as a potential neural mechanism for tactile stimulus localization (246, 271, 337). This issue remains controversial though because the relevance of topographical maps for sensory processing of both kinesthetic sense and tactile discrimination in the somatosensory cortex is far from settled (for different perspectives on this issue, see Refs. 143, 163, 283, 328).

Broad directional tuning with respect to limb kinematic parameters was first characterized in the primate motor cortex (16, 95, 97, 103, 233, 292), and the same type of unit behavior has now been observed in many CNS structures involved in sensorimotor control. In particular, neurons in the sensory (53, 167, 281) and parietal cortex (16, 56, 81, 167, 169, 170), the cerebellum (69, 91, 96), and basal ganglia (3, 57, 58, 61, 102, 144, 322) have all been observed to be broadly tuned to the direction of arm movements. Although there is not yet a general agreement about the functional implications of the broad tuning, it is generally accepted it can provide for a parallel processing of global limb variables (101, 104, 293).

B. Representation of Global Limb Parameters

A relationship to global limb parameters is another feature of the spino-cerebellar organization of propriocep-
tion. This topic has received considerable attention in studies of motor areas, but it is less often the focus of sensory area studies. Although Gardner and Costanzo (55, 98, 99) pointed out nearly two decades ago that the activity of sensory cortical neurons might also relate to the global kinematic parameters of limb movement and posture, the issue was not revisited until relatively recently. Two studies employing the center-out reaching task incorporated by Georgopoulos et al. (100, 103) showed that most of the neurons in the primary sensory cortex (SI) receiving tactile or deep (mainly muscle) receptor information were broadly tuned for movement direction and arm position (53, 281). For reasons we discussed above, the latter investigators also pointed out that the directional tuning could be explained to a certain extent by peripheral receptor properties. Nevertheless, some of their findings were strongly suggestive of a more distributed processing of sensory information based on more global limb parameters.

A subsequent SI study extended the two-dimensional reaching paradigm to three dimensions by training monkeys to grasp a manipulandum within a large workspace (318). This study showed specifically that the activity of SI neurons related best to linear combinations of joint or segment angles rather than to single joint angles. About half of the neurons were modulated by end-point displacements along a single axis in space, and many other neurons were modulated for hand displacements in a plane, that is, along two perpendicular axes. Only a few cells were found to be modulated along all three axes.

C. A Common Coordinate System for Encoding Spatial Information

The majority of the neurons in these cortical studies were modulated for hand displacements in the anteropos-
terior direction, i.e., for arm flexion and extension, and this bias did not appear to depend on the locations of the neurons’ receptive fields or their modalities (tactile or deep) (281). This type of anisotropy in the distribution of preferred directions that is strongly biased along the axis of flexion-extension of the arm is quite different from that seen in motor cortex, where preferred directions have been found to be uniformly distributed (103). However, the same bias has also been observed in the cerebellum (96), and it bears a strong resemblance to the distributional bias observed for DSCT neurons that tended to align with the limb axis (34). This type of preferred-direction clustering along coordinate axes might be expected if information were encoded in a coordinate reference frame (17, 18, 116, 173, 174, 208, 267, 301, 332; see Ref. 305 for a review), implying then that spinal, cerebellar, and cortical sensory neurons may share a similar limb-based coordinate system for encoding spatial information (see Fig. 12).

This idea was extended by an analysis of the behavior of neurons in area 5 of the parietal cortex. Lacquaniti et al. (185) fitted regression models to recordings made while monkeys performed three-dimensional reaching movements in three separate workspaces (81) to test different assumptions about possible coordinate systems. Their analysis showed that the most parsimonious description of area 5 neuronal activity was a coordinate system for the representation of hand position based on distance and direction from the shoulder. In support of this idea, there was a strong tendency for parietal neurons to be tuned along one of the three coordinate axes (elevation, azimuth, and distance or the equivalent elbow angle). This is also consistent with the psychophysical observation that these same spatial parameters may be processed by the nervous system independently (24, 29, 79, 86, 87, 112, 228, 284, 303, 304).

D. Kinematic and Kinetic Representations

It seems therefore that there is increasing experimental support for a global representation of limb parameters by central neurons in various sensorimotor structures. In addition, however, the activity of these neurons can and often does relate to both limb kinematic (position, movement) and kinetic (force, joint torque) parameters (e.g., Ref. 281). However, a feature of the proposed spinocerebellar organization of proprioception is its emphasis on limb kinematics. The extent to which other sensory structures may share this emphasis has not yet been directly investigated.

One recent study of SI neurons addressed the issue indirectly by examining neuronal activity with external loads applied to the manipulandum. The loads modified the pattern of muscle activation required for the execution of the reaching movements and led to changes in the activity of a large fraction of SI neurons. However, the loading effect was examined only in relation to activity levels during the center holding time (that is, when the monkey’s hand is grasping the manipulandum at the center of the workspace). Furthermore, only two examples were given (see Fig. 9 in Ref. 281) to show the effect of the load on the directional activity, and they suggest that the activity was mainly associated with the gain of the response rather than the cells’ preferred directions. Although it is difficult to generalize from this, the result appears to be similar to the DSCT result. In parietal area
5 however, neuronal activity was found to be invariant with respect to limb kinematics under the same experimental conditions (170), implying a kinematic-based reference frame in that structure.

XIV. SIGNIFICANCE OF KINEMATIC-BASED REFERENCE FRAMES FOR DORSAL SPINOCEREBELLAR TRACT ACTIVITY

A. A Basic Kinematic Reference Frame for Proprioception

The evidence in support of a kinematic-based reference frame at various levels of sensorimotor processing is still sketchy and somewhat indirect. Nevertheless, we believe from the results of the DSCT studies that this basic idea can provide a plausible framework for evaluating the functional significance of at least the early stages of proprioceptive information processing.

The evidence for a gain field-like interaction between limb position responses and the responses to both movement direction (34) and muscle force (36) suggests one way in which various proprioceptive parameters might interact within a basic kinematic reference frame; that is, they may modulate the sensitivity of a kinematic response. Furthermore, the finding that about half of the cells in the DSCT appear to represent limb parameters in terms of the limb end point while a similar fraction are instead influenced by specific limb geometries is an intriguing one that may suggest different functional interpretations. For example, these behaviors could represent the outputs from two stages in a transformation from a joint-based to end point-based reference frame (e.g., Refs. 165, 166). Another possibility comes from a consideration of the possible role of DSCT in cerebellar function.

B. Alternative Proposal for Proprioceptive Feedback in Cerebellar Regulation of Posture

The existence of two roughly equal neuronal subpopulations projecting to the cerebellar cortex suggested to us that they might underlie some kind of comparison between end point-related and joint angle-related signals. For example, one way the cerebellum might influence reflex behavior during posture and locomotion could be to ensure that muscle activation patterns and, therefore, joint torques, would be such that the desired limb end-point positions are mapped onto a set of joint angles within a given covariance plane; that is, it might play a role, through its modulation of reflexes, in modifying the passive biomechanical coupling across joints to produce the active patterns observed in stance and locomotion. The sensory feedback via dorsal spinocerebellar pathways could provide a measure of how well the reflex-induced coupling achieves the desired covariance pattern.

One way this might occur is by sensing a mismatch between end point-related and joint angle-related signals carried independently by two neuronal subpopulations. Because each DSCT cell’s activity encodes an end-point position, a comparison between cells that encode end point invariantly and those that encode end point differently for different joint configurations could provide an error signal for deviations from a desired joint covariance. Figure 12 illustrates a hypothetical example of two such cells based on the joint constraint model (35, 36). When the limb is free to move according to its passive compliance, both cells respond in a similar way to different limb postures. Thus the difference between their firing rates for any posture is some constant value. However, when the relative joint compliance is changed, in this case by constraining the knee joint, the cells no longer respond similarly. Thus a comparison of the behavior of two such cells during limb movement could reveal changes in the joint-angle covariance (Fig. 13).

To implement this comparison in the cerebellum would require an appropriate DSCT projection pattern. The projection could also provide for a summation of oppositely phased responses to achieve the desired difference. [DSCT neurons are typically divided into 2 groups of similar size with opposite response phase (33, 34, 251–254; see also Figs. 8 and 12).] Thus if the DSCT projection to the cerebellum were to bring together matching end point-related signals of opposite phase from the two DSCT subpopulations within a given joint-angle covariance pattern, then a linear summation of their activity by cerebellar cortical neurons could provide the desired comparison. The resulting cerebellar output activity could conceivably direct a modulation of reflex activity to reestablish a desired joint-angle covariance.

This example is not intended as an explanation of cerebellar function, since the DSCT is only one of many inputs to the cerebellum. It is presented here to illustrate how the framework proposed for the organization of proprioception with the DSCT might contribute to a possible regulation of joint-angle covariance. Nevertheless, it is not unreasonable to consider a mechanism of this kind. In fact, the type of DSCT convergence envisioned to take place in the spinocerebellar cortex is analogous to the linear summation of mossy fiber directional signals representing head and eye velocity that occurs in the cerebellar flocculus of the goldfish (259, 260).
XV. SUMMARY

A. Role of Limb Biomechanics in Global Limb Representations

We have presented here a possible framework for interpreting proprioceptive signals at the spinal level. It is based on the premise that global limb information rather than localized receptor-like proprioceptive information is encoded by the nervous system. Within a basic global framework, information is encoded by a distributed system in which each neural element may still bias the global information according to some local detail. For example, the DSCT data suggest that details about stiffness at a single joint might be contained in a population signal that encodes a representation of the limb end point that may then depend on the joint covariance resulting from specific levels of joint stiffness.

This global sensory representation is not organized entirely by the neural circuitry however. It begins in the periphery with the biomechanical structure of the limb. Biomechanical constraints ensure that the activity from individual sensory receptors will be correlated in certain ways that depend on whole limb parameters. Therefore, even a minimum of central sensory convergence could lead to global representations with this peripheral apparatus (37, 38, 281).

B. Significance of Kinematic-Based Representations

We also suggest that this framework could be based on limb kinematics. If so, it is noteworthy that while many participating sensory receptors are associated with muscles and some even specifically tuned to muscle force, nevertheless their ensemble is capable of encoding limb kinematics. In other words, inputs from receptors located...
in individual muscles or associated deep structures as well as in the skin are assembled at very early stages of central processing to provide a representation of limb kinematics. Because this occurs at these earliest stages, it suggests that the peripheral apparatus may also in some way play a role in its determination. The result, however, is that centrally directed sensory information may be encoded in a framework common to that of central motor activity that relates to limb kinematics. It may therefore be analogous to the situation in the superior colliculus where sensory information from various modalities is mapped congruently within a retinotopic map (227, 306) that may be modified or transformed by gaze (123, 124, 157, 158); that is, the sensory information is combined and integrated through a common coding framework. Although the retinal projection may provide the basis for a common framework for eye, head, and body movement control, limb biomechanics and associated proprioceptors appear to provide the basis for a common framework for limb movement control.

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REFERENCES


34. BOSCO G AND POPPELE RE. Representation of multiple kinematic
83. Feld EC and Stein PS. Spinal cord coordination of hindlimb move-


A. LUNDBERG A AND WEIGHT F. Functional organization of connexions  
197. LOMELI J, QUEVEDO J, LINARES P, AND RUDOMIN P. Local control of  
183. ACKNER JR AND DIZIO P. Rapid adaptation to Coriolis force pertur-  
184. LAQUANITI F AND MAIOLI C. Independent control of limb position  
190. LAPORTE Y AND LUNDBERG A. Functional organization of the dorsal  
April 2001  
182. LABELLA LA AND MCCREA DA. Evidence for restricted central con-  
187. LAQUANITI F AND MAIOLI C. Motor patterns in walking.  
185. MAGNUS R. Studies in physiology of posture.  
200. LUNDBERG A AND OSCARSSON O. Functional organization of the dorsal  
195. LOYD DPC AND MCINTYRE AK. Dorsal column conduction of group  
192. LIU CN. Afferent nerves to Clarke's and the lateral cuneate nuclei in  
196. LACQUANITI F AND MAIORI C. Control of limb geometry in cat posture.  
198. LUNDBERG A. Function of the ventral spinocerebellar tract. A new  
203. LUNDBERG A AND WINSBURY G. Functional organization of the dorsal  
181. KUO AD AND ZAJAC FE. Human standing posture: multi-joint move-  
191. LAPORTE Y, LE TAILLANTER M, LOPIANO L, AND MAIORI C. The control of  
188. LACQUANITI F AND MAIORI C. Coordinate transformations in the con-  
197. LACQUANITI F, GUGION E, BIANCHI L, FERRAINA S, AND CAMINTI R.  
189. LAPORTE Y AND LUNDBERG A. Functional organization of the dorsal  
193. LACQUANITI F, GUIDO M, AND ZAGO M. Motor patterns in motor tasks  
194. LIU CN. Afferent nerves to Clarke's and the lateral cuneate nuclei in  
205. MANN MD. Axons of dorsal spinocerebellar tract which respond to  
222. MESSIER J AND KALASKA JF. Differential effect of task conditions on


330. Whelan PJ and Pearson KG. Comparison of the effects of stimulating extensor group I afferents on cycle period during walk-


