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SIGNALING OF KINESTHETIC INFORMATION BY PERIPHERAL SENSORY RECEPTORS

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KINESTHESIA[1]: SENSATIONS ASSOCIATED WITH JOINT POSITION AND MOVEMENT

The relative position of our skeletal body parts is determined by the angles of our joints. In the absence of visual cues, joint angle information becomes conscious through a mental image of our body (body image). Introspective attention to the body image indicates that we have the following sensory information concerning a particular joint: knowledge of 1. the angle both when the joint is moving and stationary, and an awareness of 2. the direction and 3. the speed of angular changes. These three types of information can vary independently (e.g. a given position can be reached by movements

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[1] In the strict sense, "kinesthesia" refers only to sensations associated with joint movement. There seems to be no general term for sensations experienced both during joint movement and when the joint is stationary. Therefore, in this review we use the term kinesthesia to include sensations that occur under both static and dynamic conditions.

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in two or more directions that can occur at different speeds) and so each is considered a different attribute of kinesthetic sensibility. We propose to refer to each of these different types of conscious information by a separate term: we will call type 1 *joint position information;* type 2, *joint direction information;* and type 3, *joint speed information.*

There is also an intensive aspect to kinesthetic experience. We consider the sensory intensity of a stimulus to be proportional to its ability to attract a person's attention and, in the context of kinesthesia, the term refers to stimuli that affect the body image. Kinesthetic intensity is less when a joint is stationary than during joint movement and the intensity increases as the rate of movement increases. If the rate of movement is kept constant there is little change in perceived intensity as the joint is moved passively over most of its range. Kinesthetic intensity differs from conscious information about joint position, speed, and direction since it is present in the absence of joint movement and is enhanced in proportion to the speed of rotation without being much influenced by its direction.

The body image, as we perceive it, is invested with skin and flesh, and when stimuli unrelated to joint angle are applied to the skin and deeper tissues, the body image is enhanced. For example, if the tips of two fingers touch a surface, there is an immediate increase in the clarity with which the relative position of the two fingers is perceived. Since the cutaneous input from the fingertips contains no information about finger position, this input must facilitate a signal from other receptor populations capable of measuring joint angle. Such a facilitatory interaction is reasonable; part of the information available about a cutaneous or subcutaneous stimulus is its location, and this is assessed in terms of the body image.

Non-angle-related inputs that refresh the body image but do not shift it may be said to have a "secondary" or "facilitatory" role in kinesthesia. Receptors whose discharge changes as a function of joint angle have a potential "primary" or "specific" role since they might produce an appropriate shift in body image during a change in joint angle. If these receptors are tonic, they might also provide ongoing signals that specify the position of the joint in the absence of movement.

Before considering how the different types of conscious information are elaborated by the central nervous system, we review the role of various peripheral receptors in the measurement of joint angle.

SENSORY RECEPTORS THAT MEASURE JOINT ANGLE

Articular Receptors

Articular mechanoreceptors have been considered important for many years in supplying joint position information (see Matthews 1982, this volume), but recent evidence suggests that they are less well designed for this function than was originally believed. The knee joint of the cat has been studied most extensively; and it has been found that articular receptors signal mainly whether the knee is at or near the end of its range (Skoglund 1956, Burgess & Clark 1969, McCall et al 1974, Clark & Burgess 1975, Grigg 1975, McIntyre et al 1978, Carli et al 1979, Ferrell 1980). Monkey knee joint articular receptors behave similarly (Grigg & Greenspan 1977). This suggests that articular receptor activity might produce the deep pressure sensations that are felt in the vicinity of the joint as the end of the range is approached. One way to assess the sensory function of these receptors is to inject local anesthetic into the knee joint cavity. This silences almost all articular receptors in the cat (Clark et al 1979, Ferrell 1980) and monkey (Clark et al 1979) knee joint except some of those that respond only to external pressure on the articular tissues (Clark 1975). When human subjects are similarly injected, simple motor tasks such as walking are unimpaired and the most obvious sensory defect that can be identified by introspection is a reduction in the deep pressure sensations at the end of the range. Careful tests have shown no deterioration in subjects' ability to detect a slow passive change in knee joint angle of 5 deg (Clark et al 1979), which ordinarily is a difficult task. Therefore, the evidence is good that knee articular receptors do not have an important primary or facilitatory role in signaling joint position but do contribute to deep pressure sensations.

The next question is whether the knee joint is typical. Elbow (Millar 1975) and wrist (Tracey 1979) articular receptors resemble those of the knee in signaling primarily near the end of the range. However, those in the hip (Carli et al 1979) respond over a large fraction of this joint's working range. Nevertheless, removal of almost all hip articular receptors during joint replacement surgery produces little kinesthetic impairment (Grigg et al 1973). No electrophysiological recordings have been published of activity from articular receptors in the finger joints, but eliminating the metacarpal-phalangeal articular receptors by joint replacement surgery (Cross & McCloskey 1973) or injecting the cavity with local anesthetic (F. J. Clark, K. W. Horch, and P. R. Burgess, unpublished observations) does not impair kinesthetic position sensations. However, joint pressure and pain sensations are noticeably dulled by intracapsular anesthetic injections.

In summary, there is no evidence at present that articular receptors in any joint are important for the conscious awareness of joint position. Other kinesthetic attributes have yet to be studied quantitatively but casual observations suggest that information about the speed and direction of joint movement is little impaired by the loss of articular receptor activity. Instead, articular mechanoreceptors appear to contribute to the deep pressure sensations that occur toward the end of a joint's range. Although some articular receptors respond at both ends of a joint's range and so do not provide an obvious angle-related signal, others respond only at one end. To further test whether the latter can shift the body image, it would be desirable to investigate their action in the absence of muscle and cutaneous receptor activity. So far, an experiment of this type has not been successfully carried out.

Cutaneous Receptors

Cutaneous receptors provide angle-related signals when the skin covering one side of a joint is stretched (Hulliger et al 1979) or when the position of a joint brings skin surfaces into contact. Anesthetizing the skin around the knee joint, either alone or in combination with an injection into the joint cavity, produces no alteration in appreciation of joint position or change in body image that can be detected introspectively. Performance in a difficult task involving discrimination of slowly produced 5 deg angular changes was not diminished under these conditions (Clark et al 1979). However, when a finger was anesthetized, which eliminated both cutaneous and deep sensibility, there was a profound sense of loss and the finger largely disappeared from the body image. It is not surprising that kinesthetic sensibility was impaired under these conditions (Browne et al 1954, Provins 1958, Goodwin et al 1972), but it is difficult to know how much of this was due to the loss of non-angle-related inputs necessary for the elaboration of the body image and how much was due to the loss of specific kinesthetic signals. It is clear that signals from skin and/or deeper connective tissue receptors around the interphalangeal joints can shift the body image, although comparatively rapid movements of the joint are required (Gandevia & McCloskey 1976) and the actual position of the joint is largely unknown.

In summary, there is no evidence at present that cutaneous receptors around the knee make an important contribution to conscious information about the position of this joint. This presumably applies also to other joints proximal to the hand and foot. However, it would be desirable to test further whether angle-related signals from these cutaneous receptors can shift the perceived angle of a proximal joint by investigating their action in the absence of input from joint and muscle receptors. After a digit is anesthetized, its body image representation is less clear and what is left of the digital image fails to shift appropriately with changes in joint angle. This indicates that receptors in the finger supply important primary or facilitatory kinesthetic inputs. Neither input appears to arise from articular receptors since selective anesthesia or removal of these receptors produces little impairment.

Muscle Receptors

If neither joint receptors nor cutaneous receptors (except perhaps for the digits) provide an important primary input for our awareness of joint position, muscle receptors become the most likely candidates. Moreover, there is direct evidence that muscle receptors are involved in kinesthesia. Vibrating the tendon of a muscle produces an illusion, after a delay of a second or so, that the joint is being displaced in a direction so as to stretch the vibrating muscle (Eklund 1972, Goodwin et al 1972, Matthews 1982). The illusion incorporates both a sense of joint movement and a sense of altered joint position. The effective vibrations are at amplitudes that would excite mainly the primary spindle endings, and perhaps some secondaries, but not the tendon organs to any extent. This does not rule out a role for tendon organs in kinesthesia (Rymer & D'Almeida 1980), but in the discussion below the emphasis is on the receptors in muscle spindles.

Table 1 lists the muscles that cross the cat ankle joint. A number of these also cross either the knee or the toe joints, and plantaris and extensor digitorum longus cross all three. Of the five muscles that cross only the ankle joint, there are two—soleus and tibialis anterior—that signal primarily on the flexion-extension axis (Table 2, Figure 1). Figures 2 and 3 show average input-output functions for the primary (Figures 2A and B) and the secondary (Figure 3A) muscle spindle endings in these two muscles. The input-output functions were constructed from measurements made during a staircase stimulus sequence that started at that end of the range where the muscle was unstretched and proceeded to the opposite end of the range and back again in steps of 6–8 deg. Each position was held for 16–18 sec and the rate of movement from one position to the next was 40 deg/sec. The upper and lower curves in Figures 2A and 3A show the discharge during movement (dynamic input-output functions). In constructing the dynamic input-output function for an individual receptor, each value was plotted at the position where the movement terminated. A number of these individual dynamic functions have been averaged to generate the average dynamic functions in Figures 2A and 3A. Enclosed within these dynamic curves are static input-output functions constructed from measurements made at each position 2 sec and 15 sec after the movements were over. The 15 sec curves lie within the 2 sec functions. These data were collected from cats sufficiently deeply anesthetized that they had little motor tone. Present evidence suggests that relaxed human subjects also have little alpha or gamma tone (Vallbo 1974a, Burke et al 1976, 1978) and the input-output functions in Figures 2 and 3 would presumably resemble those of primate spindles in relaxed muscles when the ankle joint is moved passively (Hagbarth et al 1973, Cheney & Preston 1976). We assume that this is the case in the discussion below.

HOW MUCH OF A JOINT'S RANGE IS SIGNALED BY MUSCLE RECEPTORS UNDER PASSIVE AND ACTIVE CONDITIONS? Under passive conditions, muscle receptors signal over the joint's entire range, with ago-

Table 1 Muscles influencing ankle joint[a]

Muscle	Joints crossed between origin and insertion		
	Knee	Ankle	Toe
Medial gastrocnemius	+	+	0
Lateral gastrocnemius	+	+	0
Plantaris	+	+	+
Soleus	0	+	0
Flexor digitorum longus	0	+	+
Flexor hallucis longus	0	+	+
Tibialis posterior	0	+	0
Peroneus longus	0	+	0
Peroneus brevis	0	+	0
Peroneus tertius	0	+	+
Tibialis anterior	0	+	0
Extensor digitorum longus	+	+	+

[a] The muscles influencing the ankle are listed together with any other joints crossed. Plantaris does not cross the toe joints directly but inserts into the flexor digitorum brevis.

nist and antagonist muscles dividing the range about equally between them (Figures 2 and 3). When the joint is moved into the noncoded region for a particular muscle, the muscle's tendon goes slack, as can easily be verified with one's own Achilles tendon. This means that in order to read spindle discharge in terms of joint angle, it must be known whether the extrafusal muscle fibers are contracted since extrafusal contraction, by taking up the slack in the tendon, makes it possible for the spindles in a muscle to signal over the entire range. However, extrafusal contraction alone tends to unload the spindles and it is not surprising, therefore, that the gamma motor system is recruited together with the alpha motor system during most motor acts (Vallbo 1974b, Hagbarth et al 1975). The level of gamma activity must also be known to interpret spindle discharge in terms of joint angle since increased fusimotor drive can alter spindle discharge in the absence of a change in joint angle. The afferent response to a given level of fusimotor drive changes with the length of the muscle, due to the length-tension relationship of the intrafusal fibers (Lewis & Proske 1972), and this also has to be adjusted for. A further complication would arise if the intrafusal fibers fatigued, since the relationship between the gamma output and the afferent signal would then be altered at all muscle lengths. Fortunately, the fusimotor system appears to be relatively fatigue resistant (Emonet-Dénand & Laporte 1978).

Table 2 Responses of primary spindle receptors in certain muscles to different positions of the ankle joint[a]

	Soleus	Tibialis anterior	Peroneus longus	Peroneus brevis	Tibialis posterior
Flexion	++	0	0	+	0
Flexion + add & cw twist[b]	+++	0	++	+++	0
Flexion + abd & ccw twist	+++	0	0	0	+++
Extension	0	++	+	0	0
Extension + add & cw twist	0	++	+++	++	0
Extension + abd & ccw twist	0	+++	0	0	++

[a] The number of plus signs indicates the relative strength of the response, +++ designating the maximal response to the most effective stimulus. In each case, the stimulus was strong, i.e. near the end of the range. All values are based on measurements from at least three animals.

[b] add = adduction; abd = abduction; cw = clockwise; ccw = counterclockwise.

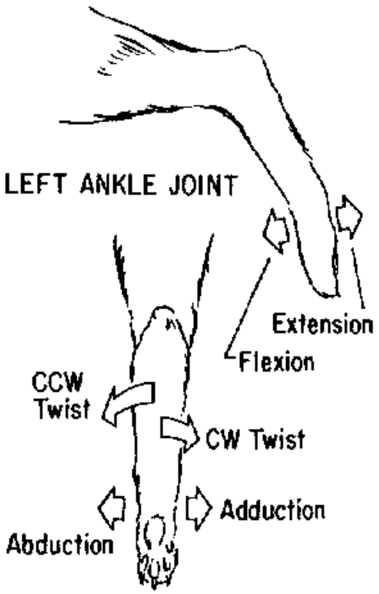

Figure 1 A drawing of the left ankle joint of a cat illustrates the axes of joint rotation tested. Adduction was often combined with clockwise twist and abduction with counterclockwise twist.

"PLACE" AND "FREQUENCY" CODES FOR SIGNALING JOINT ANGLE

A fundamental question in kinesthesia is the nature of the code used by the peripheral receptors to signal joint position. A *place code* is one in which individual receptors are spatially tuned so that each signals over only a limited portion of the range. The joint angle is then specified by just which receptors are active. Figures 2 and 3 indicate that although some place

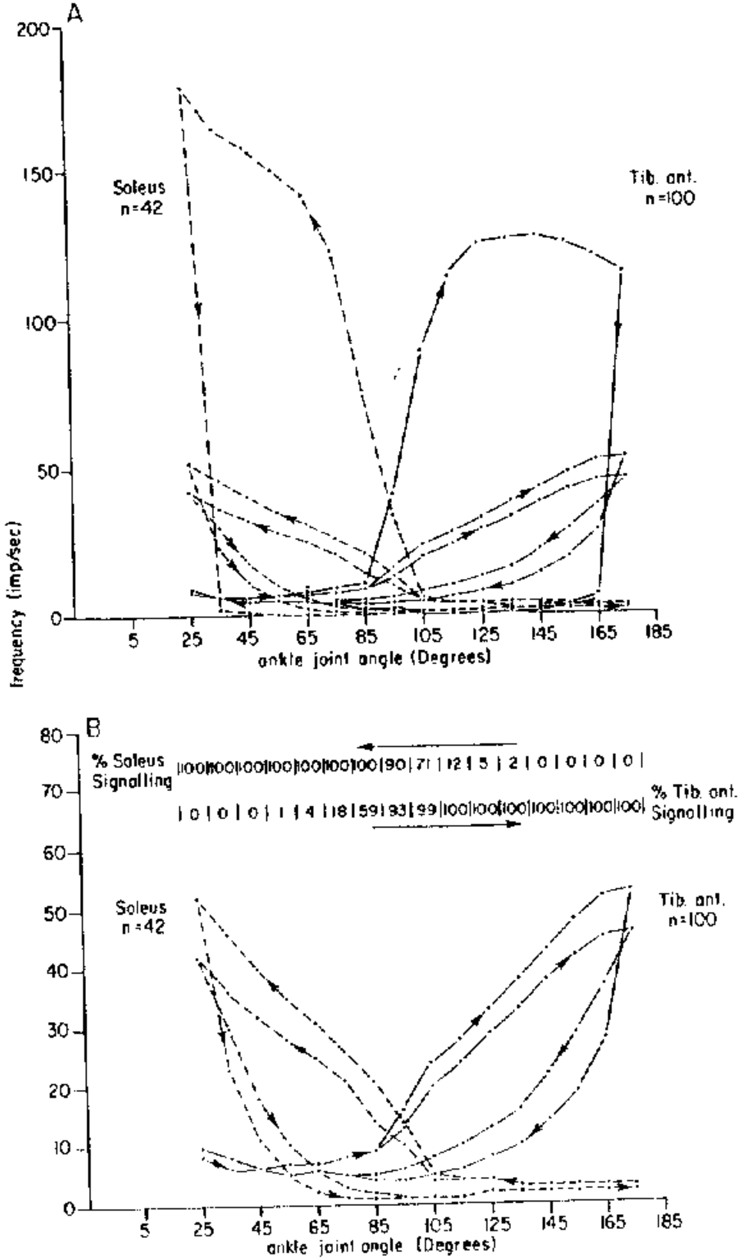

Figure 2 The responses of 100 primary (phasic) muscle spindle receptors from tibialis anterior and 42 primary endings from soleus have been averaged and are graphed as a function of ankle joint angle. Dynamic input-output (I-O) functions are shown in *A* as well as 2 sec and 15 sec static functions (see text). The I-O functions of individual receptors were averaged

coding is possible as a muscle comes under tension, over much of a muscle's signaling range the position of the joint during muscle lengthening is coded by an increase in the discharge of fibers that are already active. During a strong isometric contraction, the possibility of recruiting spindle receptors at different positions during muscle lengthening would be even more limited because most of the spindles would have been set into activity by fusimotor activity (Vallbo 1974b, Burke et al 1978). Thus, joint position appears to be signaled to an important degree by the level of activity in two populations of afferent fibers, each from an antagonistic muscle or muscle group. This might be called an *opponent frequency code.*

EVIDENCE FOR CENTRAL PROCESSING OF THE PERIPHERAL FREQUENCY CODE: RATE SENSITIVITY, ADAPTATION, AND LINEAR DIRECTIONALITY Proceeding on the evidence that the level of spindle discharge is involved in specifying joint angle, Figures 2 and 3 indicate that if the frequency of discharge is read directly, the angle cannot be known with any precision. During movement, spindle discharge exhibits rate sensitivity. This property is well developed among primary endings (Figure 2A) and their activity is determined much more by the speed of joint movement than by joint angle (Cooper 1961, Harvey & Matthews 1961). The secondary endings are also rate-sensitive; the difference in discharge between the dynamic input-output functions and the 2 sec static input-output functions during muscle lengthening in Figure 3A would result in an angular error of about 21 deg for tibialis anterior secondary receptors and 20 deg for soleus secondaries. (How this calculation was made is shown in Figure 3B.)

Adaptation of the discharge after the limb becomes stationary ("static adaptation") also changes the relationship between spindle discharge frequency and joint angle. In the case of the secondary endings, this would cause a position error of 4 deg for tibialis anterior and 5 deg for soleus

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by dividing the flexion-extension axis into 10 deg bins and summing the discharge frequencies of all the measurements that fell within a particular bin and dividing by the number of receptors contributing. If an individual receptor contributed more than one measurement to a bin, these were averaged before being added to the other measurements. In *B*, the 2 sec and 15 sec curves in *A* have been expanded and the percentage of primary endings signaling at each angle is indicted for both tibialis anterior and soleus. An ending was considered to be signaling if its discharge had increased by an amount equal to 5% of its total change in frequency over the range coded. The percentages given apply to the 2 sec static responses during muscle lengthening. The 5% level was exceeded a little sooner during movement and a little later for the 15 sec static case. Thirty-eight percent of the soleus primary endings and 54% of the tibialis anterior endings had resting activity at angles where their discharge was not influenced by changes in joint position.

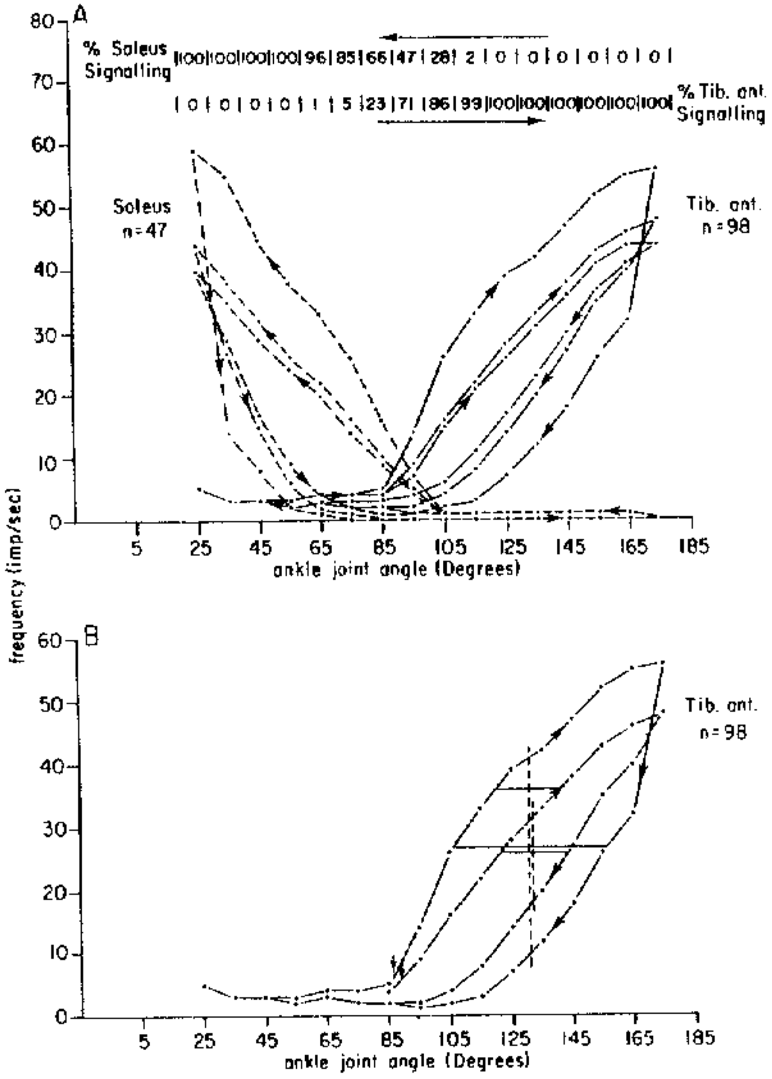

Figure 3 *A* shows the responses of 98 secondary (tonic) muscle spindle receptors in tibialis anterior and 47 secondary endings in soleus, averaged and graphed as in Figure 2, and under the same stimulus conditions. The percentage of secondary endings signaling at each angle is indicated for both muscles. Eight percent of the soleus secondary endings and 20% of the tibialis anterior secondaries had resting activity at angles where changes in joint position were not coded. *B* illustrates how rate and linear directionality errors were calculated. The responses during movement and 2 sec after movement was over are shown for secondary endings in tibialis anterior. The threshold, defined as an increase equal to 5% of the frequency change over the coded region, occurred at 87 deg for the average movement response and at 89 deg for the 2 sec static curve during muscle lengthening (vertical arrows). Linear directionality errors were estimated by measuring the angular (horizontal) distance between the lengthening and shortening I-O functions where they were equidistant from a vertical line placed half way through the coded region. The dotted vertical line at 131 deg is at the half-way point for the dynamic response and the dotted line at 132 deg is half way for the 2 sec static function. Accordingly, the length of the middle horizontal line (50 deg) is the linear directionality error of the dynamic functions and the length of the lowest horizontal line (22 deg) gives this error for the 2 sec static functions. Rate errors during muscle stretch were calculated in a similar fashion as the angular (horizontal) distance between the dynamic I-O function and the 2 sec static I-O function where these functions were equidistant from the vertical line half way through the dynamic response (uppermost horizontal line, 21 deg). Adaptation errors were considered to be equal to the angular distance between the 2 sec and 15 sec static I-O functions where they were equidistant from the vertical line half way through the 2 sec static response. The 15 sec static functions have been omitted from *B* for simplicity but are shown in *A*. Rate, adaptation, and linear directionality errors calculated in this fashion may have no particular biological relevance and are meant simply to express the frequency differences produced by rate sensitivity, adaptation, and linear directionality in such a way that they can be related to joint angle.

receptors during the 13 sec that elapsed between the 2 sec and 15 sec readings (Figure 3A). The error would be greater in the case of the primary endings, amounting to 10 deg for tibialis anterior and 16 deg for soleus receptors during this same 13 sec period (Figure 2B). These error calculations were made as described in Figure 3B and refer to muscle lengthening.

Still another disparity between frequency of discharge and joint position results from the "linear directionality" of the endings. Linear directionality refers to a difference in neural discharge at a given joint position when that position is reached by moving in different directions along the same path. Linear directionality is evident both during movement and after the joint becomes stationary. Figure 3B shows how we estimated the angular error introduced by linear directionality.

Linear directionality is exaggerated during movement because of the rate sensitivity of the endings. The primary endings (Figure 2A) were actually silenced during muscle shortening and for this reason primary endings are unable to signal joint position or joint speed during shortening at rates higher than about 10 deg/sec. Linear directionality is greater 2 sec after movement ceases than after 15 sec because of the static adaptation of the receptors. The primary endings in soleus had 50 deg of linear directionality error at 2 sec and 34 deg at 15 sec. The corresponding values for tibialis anterior primaries were 56 deg and 34 deg.

Secondary endings have less linear directionality than primary endings but the errors are nevertheless appreciable. During movements at 40 deg/sec, the errors were 52 deg for secondaries in soleus and 50 deg for those in tibialis anterior. Under static conditions, the secondary endings in soleus had an error of 33 deg at 2 sec and 26 deg at 15 sec. The corresponding values for tibialis anterior secondaries were 22 deg and 14 deg.

If left uncorrected, errors of this magnitude would seriously degrade an animal's information about limb position. Human subjects experience little rate or adaptation error: if a relaxed limb is moved briskly to a particular angle and then stopped and held stationary, the perceived position of the joint remains fixed in spite of the decline in receptor discharge. During a step-wise stimulus sequence like that used in the animal studies, relaxed human subjects experience linear directionality errors of less than 5 deg. Present evidence suggests that primates and cats have spindles with similar properties, and that relaxed muscles receive little fusimotor support. Therefore, it is likely that the frequency of discharge of the receptors is not used directly to specify joint angle but that the central nervous system "processes" this input in some way.

COULD SOLEUS AND TIBIALIS ANTERIOR SPINDLES SPECIFY ANKLE POSITION ON THE FLEXION-EXTENSION AXIS WITHOUT THE PARTICIPATION OF RECEPTORS IN OTHER MUSCLES? Soleus and tibialis anterior are the two muscles of those specific to the ankle joint that would appear to be best situated to signal flexion and extension. However, tibialis anterior spindles are excited by ankle abduction and by counterclockwise twist of the foot and soleus receptors are excited by abduction, adduction, clockwise, and counterclockwise twist (Table 2, Figure 1). If tibialis anterior spindle activity were to be inhibited within the central nervous system by activity arising from spindles in tibialis posterior (Table 2), and if soleus spindle activity were to be inhibited by tibialis posterior and peroneal spindle discharge, the tibialis anterior and soleus signals would become more specific for ankle extension and flexion.

ROLE OF MULTIJOINT MUSCLES IN SIGNALING JOINT ANGLE Of the 12 muscles that cross the ankle joint, only 5 are confined to the ankle joint alone (Table 1). It is not yet obvious how the spindles in multijoint muscles can signal joint angle since their discharge at a given ankle joint position can be greatly altered by changes in the position of the knee or toe joints. For example, the spindles in extensor digitorum longus are well excited by ankle extension but their discharge at any position over the extension half of the range can be greatly enhanced by toe flexion. One way in which multijoint muscle receptors might contribute to joint position signaling is for their discharge to be channeled into different central circuits depending on changes in activity from joint specific muscles. Thus, spindles in extensor digitorum longus would contribute to the signaling of ankle extension if tibialis anterior were being stretched but the short toe extensors were not, and would contribute to the signaling of toe flexion if the short toe extensors were being lengthened but tibialis anterior was not. Some support for this idea comes from tendon vibration studies. Vibrating the tendon of tibialis anterior causes an illusion of ankle extension when the joint is stationary. Vibrating the tendon of extensor digitorum longus does not produce any very clear illusions unless the ankle is passively extended, in which case the ankle extension is felt to be greater than it actually is, or unless the toes are passively flexed, which produces an illusory exaggeration of toe flexion. It would appear that the illusions from a multijoint muscle are referred primarily to the joint being moved. However, these results must be interpreted with caution because tendon vibration produces patterns of input that are unlikely to occur in nature and the nervous system may respond in ways that are not indicative of its normal behavior.

SOME POSSIBLE CENTRAL NEURAL CIRCUITS FOR KINESTHETIC SENSIBILITY

In this section we speculate on how the various kinds of conscious kinesthetic information described at the beginning of this review are elaborated by the central nervous system. Only the passive case is considered; i.e. the joint is rotated by an external force with the subject relaxed. Present evidence suggests a good correspondence between the behavior of anesthetized cat and relaxed human ankle joint muscle spindles under these conditions (Hagbarth et al 1973) and therefore the detailed information available for the cat (Figures 2 and 3) is used to discuss how the central circuits might function.

Joint Position Information

CORRECTING FOR RECEPTOR RATE SENSITIVITY, ADAPTATION, AND LINEAR DIRECTIONALITY During muscle stretch, the problem faced by the kinesthetic system is similar to that confronted by the tactile system during skin indentation. The rate sensitivity of cutaneous mechanoreceptors causes a largely rate dependent discharge to occur while the skin is being indented, and this discharge then declines after the movement stops because of receptor adaptation. There is evidence for an integrator in the circuit signaling skin indentation depth which helps convert the rate sensitive receptor signal into a largely rate independent awareness of altered skin position (D. A. Poulos, K. W. Horch, R. P. Tuckett, J. Mei, and P. R. Burgess, unpublished observations). A similar mechanism could serve for joint position information. What is required is that the excitation set up by a nerve impulse persist in the integrator so that it can add to the excitation produced by the next impulse. This persistent excitation would be independent of any nerve impulses produced by the integrator itself. The rate at which the integrator charges and discharges would have to be matched to the dynamic properties of the receptors, if the system were to function properly. However, this model, which works well for the skin, encounters a serious problem when applied to spindle receptor behavior during muscle shortening. The receptor discharge after a shortening movement gradually builds up rather than declining and an integrator would exaggerate this build up, thereby enhancing the error.

The situation in the light of present understanding can be summarized as follows. The central nervous system must be equipped to extract a reliable position signal from spindle discharge that is both rate and directionally sensitive. Integration of the input (in the mathematical sense) can help compensate for rate sensitivity during muscle stretch but there are problems in producing a properly controlled reduction in the level of the integrator during muscle shortening. However, since humans, and presumably other animals, have relatively small rate and linear directionality errors under passive conditions, the sensory input must have been "corrected" in some way.

IS THE FREQUENCY CODE IN THE PERIPHERY CONVERTED INTO A PLACE CODE WITHIN THE CENTRAL NERVOUS SYSTEM? Another basic question about conscious joint position information is whether the frequency code in the periphery is converted into a place code within the central nervous system. It is generally thought that "spatial" sensations use place codes centrally; i.e. when the perceived location of something that is being sensed changes, this occurs because there is a change in the locus of neural activity in the brain. If we apply this idea to kinesthesia, a perceived change in the location of a body part due to an alteration in joint angle should be associated with a wave or front of activity that moves through the brain. Moreover, the subjective experience is one of the whole anatomical entity, skin and flesh alike, being relocated. The most literal interpretation of this is that muscle spindle receptors propel the central somatotopic representations of the skin and deeper tissues through brain space.

Joint Direction Information

Perhaps the easiest way to detect the fact that joint movement is occurring as well as the direction of that movement is to compare the discharge of the primary and secondary endings. When the muscle is lengthening, the discharge of the primary endings is enhanced much more than that of the secondaries. During muscle shortening, the discharge of the primary endings is greatly suppressed, that of the secondaries less so. Measuring the discharge of the primary endings alone would not, for receptors lacking resting activity, distinguish muscle shortening from the absence of movement in a noncoded portion of the range. An alternative method for determining the direction of movement—by assessing whether the discharge of the secondary endings is increasing or decreasing—would not be so prompt as the comparison of primary and secondary discharge because of the great sensitivity of the primary endings to changes in the direction of movement.

Joint Speed Information

Although primary muscle spindle receptors provide a signal largely proportional to the speed of joint movement during muscle lengthening, they are silent during passive muscle shortening at velocities above about 10 deg/sec, in the absence of fusimotor support. If the same method is to be used by the central nervous system for measuring speed of joint rotation during both passive lengthening and shortening, the secondary endings will have to provide the signal (Figures 2A and 3A). One possibility is to measure the rate of change of the secondary discharge.

Kinesthetic Intensity Sensations

Kinesthesia is like most other spatial sensory experiences in that moving from one location to another is not associated with any obvious change in perceived intensity; however, the discharge of the muscle spindle receptors increases progressively as the joint is moved from an intermediate position to the end of the range (Figures 2 and 3). This is the only instance known to us where progressively increasing afferent input is not reflected in an increasingly intense sensation. The kinesthetic intensity circuit may monitor the size of the wave of activity that we have postulated results from conversion of the peripheral frequency code into a central place code. A mechanism of this sort would also account for the fact that intensity sensations are about the same whether a muscle is lengthening or shortening, even though the overall level of spindle discharge is much higher during lengthening. The fact that the intensity is felt to increase with the rapidity of joint rotation would be explained if the intensity circuit receives additional inputs from nonspindle muscle and connective tissue receptors that are rapidly adapting.

The speculative character of this discussion on the properties of central neural circuits for kinesthetic sensibility indicates how little is actually known about information-processing in this sensory modality. How the circuits might have to change to accommodate the effects of efferent activity is equally unknown and adds additional complexity to the problem. More research will be required to determine whether the circuitry we have postulated is actually present.

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