# Sensory feedback to the cerebral cortex during voluntary movement in man

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**Abstract:** This article describes a series of experiments directed toward the following questions: (1) Do signals from musculotendinous receptors reach consciousness? (2) Does feed-forward information of muscular force and expected extent of voluntary movement exist? To answer these questions data from voluntary compression of springs and strain-gauge have been analysed in healthy young subjects and in patients with unilateral focal lesions of the cerebral hemispheres.

By successive elimination of information from other sources it was possible to verify that receptors in muscles and tendons do signal movement magnitude and muscular tension to the cerebral cortex, and that this information does indeed reach consciousness. There also exists a feed-forward mechanism signalling parameters of voluntary contraction. However, it is unclear whether peripheral, subcortical, or intracortical loops are directly involved. Perception of signals of muscular tension is abolished by lesions of the contralateral cortex near the central sulcus. It is possible that there exist separate cortical projection areas for kinaesthetic signals from muscles and from joints.

**Keywords:** consciousness, discrimination, kinaesthesia, motor feedback, muscle receptors, perception, voluntary movement

Are our muscles "insentient"? Do signals from musculotendinous receptors remain unconscious? Or do signals from receptors in muscles and tendons provide man with conscious information about the force exerted and the extent of movement during voluntary contraction? This article is an attempt to give a consistent answer to these questions.

The motor system is the part of the nervous system that controls contraction of striate muscles. The nervous impulses that initiate voluntary muscular contractions are presumed to originate in the cerebral cortex and thence to spread to subcortical parts of the motor system. By way of the large ($\alpha$) motoneurones and smaller ($\gamma$) motoneurones in the anterior horn of the spinal cord, these impulses are transmitted through the peripheral nerves to the respective motor endplates. At the motor endplates the nervous impulses release a chemical transmitter (acetylcholine), which in turn excites the two types of muscular fibers and induces contraction.

Voluntary contraction need not be accompanied by movement. Under some circumstances, when the muscles are used to oppose external forces, there is no movement of the joints and the length of the muscles remains constant (isometric contraction).

Voluntary movements, like all other movements of solid objects, consist of operations in time and space specified by physical parameters. When, for example, a person lifts a cup of tea to his lips, this voluntary movement is specified by the trajectory of the teacup, the force vectors, the acceleration and velocity at every point, the total length of the path, the locus of origin, and the time of onset. Voluntary movements of this kind are normally carried out quickly and precisely (by adults) and without information concerning the total mass of the cup or its contents.

There are two types of explanations of the often surprising precision with which we move our limbs. One is that the motor system calculates in advance the values of movement parameters sufficiently accurately to assure successful performance. The other type of explanation is based on the fact that every muscular contraction inevitably changes the state of receptors in muscles

and tendons and normally also of those in joints and skin (Figure 1). These receptors are able to measure the parameters of voluntary contraction and transmit this information to the motor system. The motor system is then thought to control voluntary contraction under the guidance of sensory feedback from these receptors. Although there is no contradiction between these two explanations, physiologists disagree as to the relative importance of specific motor commands versus sensory feedback.

Another and equally important dimension in the understanding of the physiological organization of voluntary motor control is the question of the *levels* in the central nervous system at which the desired values of voluntary contraction parameters are calculated; or, in other words, the extent to which voluntary contractions are automatisms. Because man is able, consciously, to vary the parameters of voluntary contraction in an infinite number of ways, one might be tempted to believe that, at the moment they are triggered, descending signals from the cerebral cortex provide the desired values of the contraction parameters in coded form. The task left for the subcortical part of the motor system would then consist solely of compensating for unexpected events during the movement or contraction (for instance, should the aforementioned teacup prove unexpectedly heavy). In this model, sensory feedback has a dual role: partly to provide concurrent sensory feedback to the subcortical parts of the motor system about the parameters of contraction, and partly to update cerebral cortical information concerning the consequences of voluntary contraction in the peripheral field of action; the latter would be for later use in the programming of further voluntary contractions. The contrasting view is that coded motor output from the cerebral cortex does not specify trajectories, force vectors, velocity, acceleration, and so forth, but merely constitutes a message for the subcortical motor systems concerning the ultimate goal of the voluntary contraction. The rest of the motor organization of voluntary contraction would then be carried out automatically, with calculation and control of contraction parameters left to the subcortical motor system; sensory feed-
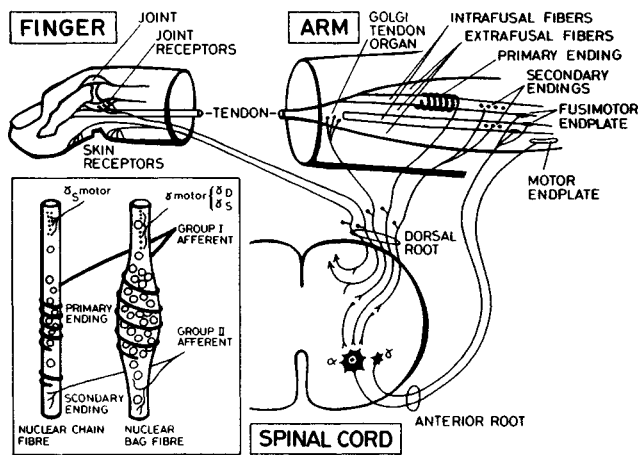
Figure 1. Simplified diagram of the sources of afferent information during voluntary contraction. The muscles that move the finger are located in the forearm. Muscles consist of two types of muscular fibers. *Extrafusal* fibers do the muscular work and are innervated by α-motoneurones in the anterior horn of the spinal cord. Each α-motoneurone innervates some 20–200 extrafusal fibers. The α-motoneurone and the extrafusal muscle fibers it innervates are called a *motor unit*. The *intrafusal fibres*, components of the muscle spindles are specially developed contractile sense organs arranged in parallel with the extrafusal fibers. Muscle spindles may be further divided into two classes on a morphological basis: nuclear bag fibers and nuclear chain fibers. Both have two kinds of receptors: the *primary endings*, which mainly record muscular length and velocity; and the *secondary endings*, whose function is still obscure. The functional pattern of these two receptors is complicated because they are contractile and can be activated by four different routes: (1) by a change in muscle length; (2) as the result of impulses from the α-motoneurones (in other words, during muscle contraction and relaxation); (3) directly from the α-motoneurones (so-called β-innervation); (4) by the γ-motoneurones that innervate the muscular part of the receptors. The matter is further complicated because there exist two types of γ-*motoneurones*: γ-*static* and γ-*dynamic* fusimotor neurones. Each type has small separate contacts with the intrafusal fibers, where a neurotransmitter substance is released, which in turn excites the muscular part of the muscle spindle Electrical stimulation of the γ-dynamic neurones increases the sensitivity of the primary endings to the velocity of a linear stretch of the muscle; stimulation of the γ-static neurones increases the number of impulses from the secondary endings. Nuclear bag fibers are thought to receive innervation from the γ-dynamic fusimotor neurones while nuclear chain fibers are thought to be innervated by γ-static fibers (P. B. C. Matthews, 1972). In this way, the muscle spindles can be "tuned" to give a very differentiated response during voluntary contractions

The extrafusal fibers are likewise subdivided into two types: *slow-twitch fibers* (or "red" fibers) and *fast-twitch fibers* (or "white" fibers). These names refer to the color and the velocity of contraction upon brisk electrical stimulation

In series with the extrafusal fibers are the *Golgi tendon organs*, which measure muscular tension and changes in tension. If a muscular contraction leads to a movement of the joints, then joint receptors signal the change in position. In addition, mechanoreceptors in the skin and subjacent tissue can signal changes at the skin surface as well as pressure if the movement is opposed by some external object. To this afferent information must be added signals from tendon organs and primary and secondary endings The sensory part of the peripheral nerve carries afferent fibers from skin receptors, joint receptors, Golgi tendon organs (*groups Ib*–afferents), primary endings (*group Ia*–afferents) and secondary endings (*group II*–afferents) to the spinal cord Here the afferents from the spindles activate α-motoneurones such that these neurones fire a short burst of impulses that can once again reactivate the whole system.

back from receptors in muscles and tendons would be transmitted exclusively to this part of the motor system. There would be no need for sensory feedback from these receptors to the cerebral cortex, because the latter could make no use of such afferent information, any more than a driver can use the magnitude of propulsive and restrictive force vectors from road and air friction in order to change speed. Although this highly developed servo

system is supposed to compensate for all unexpected events during contraction, the cerebral cortex needs some additional information as to whether the ultimate goal has indeed been attained. Ordinary visual and auditory feedback, eventually in combination with some information from the skin and the joints, is usually sufficient.

These four explanations are neither topical physiological models nor theories, therefore no references have been given. Rather, they are four extreme viewpoints that provide cornerstones for various existing theories concerning the role of sensory feedback in voluntary motor control.

The vast majority of investigations of the afferent signals from muscle spindles and tendon organs have been carried out on anaesthetized animals whose muscles have been subjected to various forms of stretch; hence little is known about the sensory function of musculotendinous receptors during voluntary contraction in man. The results from animal experiments of this kind have gradually led to the view that one of the main functions of the muscle spindle is in the servo control of muscular contraction (Merton, 1951, 1953). A simplified diagram of the elements in the muscle servo is shown in Figure 2. The most important detector element in the loops is the muscle spindle. As muscle spindles not only react to muscular contractions, but do so in a way that is controlled by efferent impulses from γ-motoneurones, it is quite difficult to ascertain whether or not these sense organs can really measure some of the parameters previously mentioned (extent of movement, velocity, acceleration). This was exactly the type of argument raised by Rose and Mountcastle (1960) when they stated that muscular receptors could not measure joint angles or extent of movement. This more theoretical rejection of man's faculty to perceive signals from muscle spindles was supported by experiments of Chambers and Gilliat (1954), Provins (1958), and Merton (1964). These authors anaesthetized the skin and joints of the fingers in human beings and found that this abolished sensation of passive finger movement, while active movements of the joints continued to be made with approximately the same positional accuracy as in the unanaesthetized state (Merton, 1964). Apparently this was not due to impulses from muscle spindles, because when anaesthetized subjects were instructed to oppose passive movement by muscular contraction, they showed no improvement in perception of stationary joint angles (Provins, 1958).

Further experiments were set up to prove that it was impossible for man and animals to perceive signals from either muscle spindles or from tendon organs. For example, Gelfan and Carter (1967) conclude:

"The problem of 'conscious proprioception,' whether there is awareness of muscle length and tension changes, was investigated in volunteer patients whose muscle tendons available at the wrist and ankle were exposed under local anesthesia restricted to the skin. All subjects tested uniformly failed to detect length and tension changes when only the muscles were stretched. The signals from the tension and stretch receptors did not contribute to the kinesthetic sense when the joints of the fingers, hand or foot were also moved. None of the sensations experienced, including awareness of position and movement of joints, were referable to signals from muscle spindles or Golgi tendon organs. It was concluded that there is no muscle sense in man."

In addition, Swett, Bourassa, and Inoue (1964) and Swett and Bourassa (1967) showed that it is impossible to condition a cat to respond (by pressing a bar) to electrical stimulation of afferents from primary endings and Golgi tendon organs. On the basis of these and other experiments (e.g., Brindley and Merton, 1960) the conviction soon became widely adopted that it is impossible to perceive signals of muscular tension and change in limb position from musculotendinous receptors (e.g., Rose and Mountcastle, 1960; Matthews, 1964; Gardner, 1967; Merton, 1964a, 1964b, 1970, 1972; Mountcastle and Darian-Smith, 1968; Phillips, 1969).
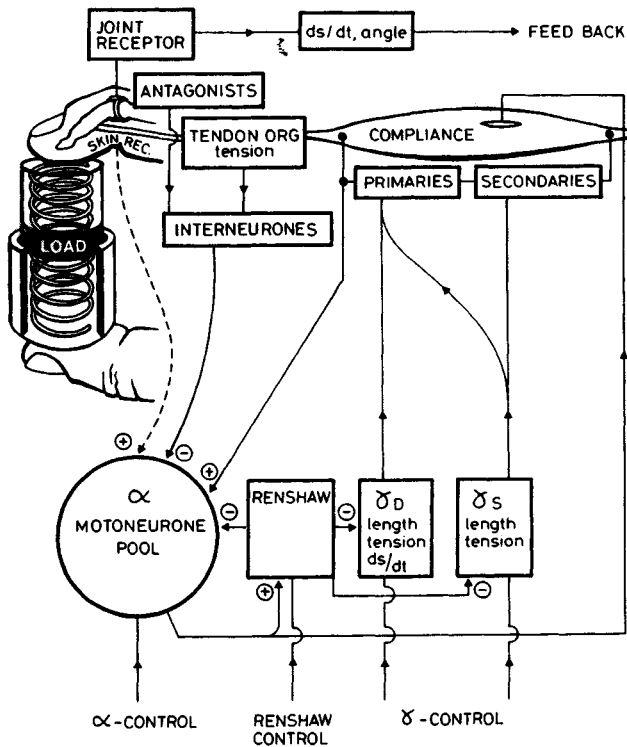
## The feed-forward hypothesis

The physiological models that will be mentioned under this designation all have the common feature that the cerebral cortex is informed a priori about some of the physical parameters of voluntary contractions (Figure 3). Gradually increasing insight into the functions of alpha and gamma motoneurones and muscle spindles has led to the common conviction that voluntary movements are to a large extent automatic in character. It is widely accepted that voluntary contractions are, from the moment they are triggered in the cerebral cortex, under the control of subcortical and hence automatic mechanisms, and that disturbances are partially or entirely compensated by the muscle servo mechanism. In the 1960s, afferent signals from muscular receptors and Golgi-tendon organs were considered to be subjectively inaccessible features of the internal working of the servo mechanism. It was thought that if sensory feedback from Golgi organs and muscle spindles reached consciousness this would only serve to disturb the action of the muscle servo, because any



Figure 2. Schematic survey of interrelations of some components of the "muscle servo." The main principle is this: If α-innervation is initially too weak and extrafusal fiber tension too small to overcome the external load (symbolized by the coil spring), the muscle is stretched over and above the preprogrammed length during contraction and along with it are stretched the parallel coupled muscle spindles. This releases increased impulses in the spindle afferents (group Ia and II), which polysynaptically increases the impulses from the already active α-motoneurones to the extrafusal fibers and causes a recruitment of previously inactive α-motoneurones; the muscle is thereby supplied by new active motor units. The net effect depends, of course, on how the γ-dynamic and γ-static neurones are biased from their control centers, and also on the time lag between intra- and extrafusal activation during voluntary contraction. These two questions and that of whether the α-motoneurones are preset to a desired length or to a desired tension have generated some of the main physiological controversies in the last twenty-five years. In addition, at the spinal level the system is modulated by negative feedback from Renshaw cells and, at very high tensions, by negative feedback from Golgi tendon organs. The broken line symbolizes facilitating effects on the α-motoneurones to the flexor muscles in the limbs. This facilitation is probably mediated at supraspinal levels. (A pair of muscles with opposing effects on a joint are called agonists and antagonists. If the movement is a flexion of a joint, all flexor muscles are agonists, and all extensors are antagonists.)

Even when muscle and tendon receptors are excluded, there are other sources that may supply the cerebral cortex with information about the parameters of voluntary contraction (Figure 1). It is well known that phasic and tonic receptors in the joint capsules measure joint position (Goldscheider, 1898; Boyd and Roberts, 1953; Skoglund, 1956) as well as length, velocity, and direction of movement (Skoglund, 1956, 1973). In primates, afferents from these receptors are known to project to the cerebral cortex (Mountcastle and Powell, 1959; Werner and Mountcastle, 1963). In addition, it is possible that receptors in the connective tissue around joints measure tension (Skoglund, 1956; Millar, 1972). However, sensory feedback from these receptors and from others around joints cannot be the cause of the continued accuracy of voluntary movements in Merton's subjects since the signals from these receptors were all blocked by anaesthesia. As the muscles were held to be insentient, it was necessary to formulate a new hypothesis in terms of which the necessary information for a sense of position during anaesthesia was ascribed to a central origin.
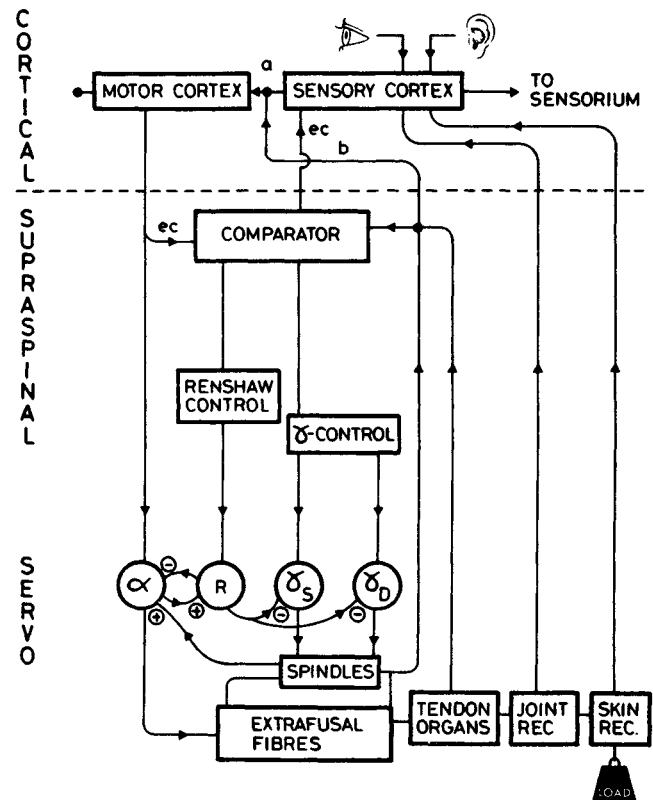


Figure 3. Block diagram of some of the main elements in the feed-forward hypothesis. The blocks do not refer to anatomical entities. Before it was known that group I and group II afferents from muscle spindles projected to the cerebral cortex, it was supposed that every self-induced muscular contraction was accompanied by corollary discharges from motor areas into sensory systems serving to prepare the latter for the expected changes that would ordinarily result from the movement (the path ec in the figure). After it became known that both group I and group II afferents project to the cerebral cortex, this path (b) was mainly thought of as the afferent link in a transcortical load compensation reflex. In addition, it is possible that afferents from skin and joints can participate in the transcortical load-compensation reflex. The comparator receives information about descending motor impulses and this information is compared with afferent feedback from the spindles and tendon organs. If any disturbance occurs during contraction, it will be compensated by impulses from the comparator to the Renshaw and γ-control, which in turn set the new bias of the muscle servo. The afferent information signalling to the cortex that contraction has been appropriately carried out comes from skin and joint receptors and sometimes, in addition, from the eye and ear. Information from these sources reaches the sensorium, that from other peripheral sources information does not.

misalignment between desired and actual muscular length and tension was already taken care of automatically by the muscle servo (Merton, 1964a). The discovery that spindle afferents did indeed project to the cerebral cortex (see below) only led to the interpretation that these projections were the afferent path of a transcortical servo loop (Phillips, 1969, Merton, 1970, 1972). The muscles were still held to be insentient.

On the basis of man's evident capacity to adjust his commands to the motoneurones in proportion to the requirements of expected performance, Merton (1964a, 1964b) reintroduced the concept "sense of effort." The sense of effort was a kind of conscious "feeling of innervation" that accompanied the departure of voluntary impulses from the cortex (1964a, 1964b, 1970). In the version of von Holst (1954), an "efference copy" of the motor command is stored, that is, the coded output from the cerebral cortex "leaves a copy of itself somewhere in the central nervous system to which the reafference (sensory feedback) of this movement compares as the negative of a photograph compares to its print." If there is no mismatch between the efference copy and the sensory feedback, nothing further happens; if there is, the difference will have certain effects according to the particular organization of the motor system for the species studied, which for primates and man should mean that the muscle servo compensates for the difference. Yet, it is not clear where this efference copy is stored and where the comparison takes place in the central nervous system. In Sperry's (1950) version of the same principle, "corollary discharges" issue from the motor cortex to the sensory cortex to be compared with the sensory feedback from the periphery.

The vagueness with which the feed-forward hypothesis is expressed makes empirical testing difficult. The problem is that the nature of the motor command from the cerebral cortex is not specified. There is no evidence for the claim that replicas of outgoing motor commands are stored somewhere in the central nervous system or reach the sensory cortex. It is especially unclear whether feed-forward impulses contain any information about the parameters of voluntary contraction. Yet Merton (1964a) mentions "that we know through our sense of effort which way our eyes are pointing in the dark, and in the thumb experiment the subject knows through his sense of effort how far he had moved the pointer." Gandevia and McCloskey (1977a) use "sense of effort" in another way, to refer to centrally generated sensations concerned with the estimation of weights and tensions. Finally, Kennedy (1973) has stated that the relation between the requisite contraction and control parameters is genetically determined.

Thus, according to the feed-forward hypothesis, it is postulated that the cerebral cortex or other parts of the central nervous system receive information about the nature of outgoing motor commands via intercortical connections or subcortical loops and that this information reaches consciousness. Although the nature of the descending motor commands from the cerebral cortex is usually not specified, some authors have provided various hints as to how such voluntary contraction parameters might be available to the subject a priori. These parameters are position, magnitude of movement, force, and estimated load. In the pages that follow, the validity of the feed-forward hypothesis with respect to the first three of these parameters will be examined.

### Specification of the hypothesis to be investigated

The hypothesis that I shall attempt to support with some recent experimental results is the opposite of the one just presented. I propose to show that information about tension and change in limb position is supplied to the human cerebral cortex by receptors in muscles and tendons during voluntary muscular contraction, and, further, that this information does indeed reach consciousness.

Although consciousness is a diffuse and ill-defined concept, I feel obliged to use it because this was the way the present problem was introduced by previous authors (e.g., Merton, 1964a, 1964b, 1970, 1972; Gelfan and Carter, 1967). To make my hypothesis amenable to empirical testing, I shall use operational criteria for consciousness. If the concept is to have any empirical content, it must have something to do with the capacity to perform *discrimination*. To discriminate is to be able, upon verbal instruction, to distinguish between two physical inputs and make a decision about the respective magnitudes of one or more parameters. Similarly, matching of two physical inputs along one or more parameters should be one of the distinctive marks of consciousness.

To find out whether information about tension and movement path length reaches consciousness, it is not sufficient to show that potentials from group Ib and Ia afferents (see legend to Figure I) can be recorded from the human cortex or scalp: such projections may merely be the afferent link in a cortical automatism such as the accommodation reflex in the visual system. But if subjects can discriminate and match degrees of applied tension and movement magnitude, this means that information about tension and extent of movement is indeed conscious. Of course, this need not in itself imply that such information is transmitted from peripheral receptors, for this ability to discriminate could also be based on feed-forward signals.

Consequently, three kinds of experimental evidence are called for: first, a demonstration that information about tension and extent of movement is conscious; second, evidence that movement magnitude and tension signals are transmitted by the receptors in muscles and tendons; third, data showing that afferents from muscle spindles and tendon receptors project to the human cerebral cortex.

As it is far from clear which of the muscular contraction parameters are registered by the various receptors in skin, joints, and muscles, it is necessary to introduce some sensory functions that define the relation between contraction parameters and sensation. *Kinaesthesia* means feeling of movement, but is often used synonymously with "position sense." This has caused a confusion among the static and dynamic proprioceptive functions. *Kinaesthesia* is used in this article to mean *perception of change in the position of a limb due to muscular contraction.* Kinaesthesia would then be sensory feedback occurring only during muscular contraction. The other term, position sense, or, better, *statognosia*, is reserved for *perception of the position of a limb in space.* In clinical neurology, position sense often refers to sensation of passive movement. Sensations of passive movement are, by definition, sensations, induced by external forces, of change in the position of a passive limb in the absence of muscular contraction. The term position sense will not be used here.

The expressions *sense of tension* and *sense of force* are not synonyms, although both tension and force are measured in Newtons. Provided the present hypothesis is correct, man has a sense of tension. Since it is not possible to measure tension directly in man without surgical intervention, the experiments reported below approach the problem through a study of force output during compression with thumb and index finger. The measuring device is interposed between thumb and index finger; dynamics of elastic tissues between measuring device and muscles are ignored.

Kinaesthesia, statognosia, sense of passive movement, and sense of tension are all sensory functions; by definition, this means that the signals upon which these sensations are based reach consciousness. Note that kinaesthesia involves four of the physical parameters of voluntary contraction: direction, extent of movement, velocity, and acceleration. Statognosia involves only spatial position, while sense of tension involves force and its time derivatives. Now the hypothesis can be reformulated to state that kinaesthesia and sense of tension are based, wholly or in part, on signals from receptors in muscles and tendons.

In summary, during voluntary contraction there may exist sensory feedback of tension and kinaesthesia from musculo-

tendinous receptors, joint receptors and cutaneous receptors together with feed-forward information about voluntary force. The relative significance of these sensory mechanisms will be analysed below.

### Experimental evidence for sensory feedback of tension from musculotendinous receptors

The following evidence is based on recent experiments (Roland, 1975; Roland and Ladegaard-Pedersen, 1977) that will be summarized here to an extent sufficient for detailed criticism. First, we attempted to show that tension information was conscious by having subjects (Ss) discriminate the strengths of coil springs. S sat behind a curtain with arms unsupported and right hand extended in front. In order to avoid visual cues, the springs, encapsulated by small cylinders (Figure 2), were never visible to S. Likewise, great care was taken to exclude any unintended tactile or auditory information.

S held the encapsulated spring between thumb and index finger, the three ulnar fingers maximally flexed. Then, on command, the spring was compressed with the index finger. During a two-alternative forced-choice discrimination of spring strength, S's task was to compare two springs of slightly different strength and to choose the stronger one (Figure 4).

When a coil spring is compressed, force at a given moment is related to extent of compression (or movement path length) and acceleration in the following way (Roland and Ladegaard-Pedersen, 1977):

$$P_i = k \cdot s_i + m \frac{d^2s}{dt^2} \tag{1}$$

where $P_i$ is the compressing force at a given moment; k is the spring strength in N/m; $s_i$ is the extent of compression; m is the mass of the upper cylinder plus one third of the spring mass; and $d^2s/dt^2$ is the acceleration. Formally, S's task is to solve two equations, identical with equation (1), in two unknowns ($k_1$ and $k_2$, corresponding to the strength of the first and second spring). This solution is possible only if S "knows" the applied force (P), the path length of the compressing movement (s) and the acceleration $d^2s/dt^2$. In other words, it is not possible to discriminate spring strengths without kinaesthetic as well as force information. However, as is apparent from Figure 1, there are various potential sources that could provide the necessary information: skin receptors, receptors in and around joints, musculotendinous receptors, and feed-forward signals. To clarify the relative significance of these sources, information from skin receptors, joint receptors, and feed-forward signals was suc-

cessively eliminated by anaesthesia and gallamine blockade (see below).

Signals from skin receptors in thumb and index finger were blocked by four dorsal injections of 1.5 ml of 2 percent (w/v) lignocaine (a local anaesthetic) on either side of the proximal phalanx, near the volar surface (see Figure 1). A rubber band was tightened around the proximal phalanx 1.5 cm from the metacarpophalangeal joint to prevent the local anaesthetic from being removed by the circulation of the blood. During the experiments, effectiveness of anaesthesia was checked several times by having S attempt to discriminate a difference of over 20 N/cm² in pressure applied to the fingertips. If S could not distinguish the greater pressure from the lesser, anaesthesia was considered sufficient.

Signals from joint receptors were likewise blocked by lignocaine injections. The joint capsule and adjacent convective tissue were infused with 1.5 – 2.5 ml of 2 percent lignocaine and the same amount was injected into the joint space of the interphalangeal joints, the metacarpophalangeal joints of thumb and index finger and the carpometacarpal joint. If S was unable to detect an approximately 20°/sec passive movement of the joint with muscles relaxed, anaesthesia was sufficient. Thus joint anaesthesia severely impaired the sense of passive movement.

At the start of the discrimination experiment, two springs of different strengths were selected. S was told to compress maximally the first spring, then to release it and compress and release the second, and finally to decide which had been the stronger. The first two springs were always easy to discriminate, but S was told that the rest would be difficult. The rules for two-alternative forced-choice discrimination were then explained (see legend to Figure 4). Apart from this, S received no other training or instructions. Discrimination limits (see legend to Figure 4) for twenty-five different springs were measured under three different conditions: without anaesthesia, with skin anaesthesia, and with combined anaesthesia of skin and joints.

Under the first condition (no anaesthesia), muscular tension and pressure against the fingertips yield the same information. In addition, kinaesthesia might be signalled from three types of receptors: cutaneous, articular, and muscular. With skin anaesthetized, Ss spontaneously stated that, prior to compressing it on command, they were not aware of any spring between their fingers. Discrimination limits were unaffected by the lack of information from skin receptors (Figure 5). When skin and joints were anaesthetized, there were likewise no changes in discrimination limits, despite the lack of information from skin and joints (Figure 5). Under skin and joint anaesthesia, Ss are able to discriminate spring strength only if they have conscious information about the applied force (or tension), the path length of the
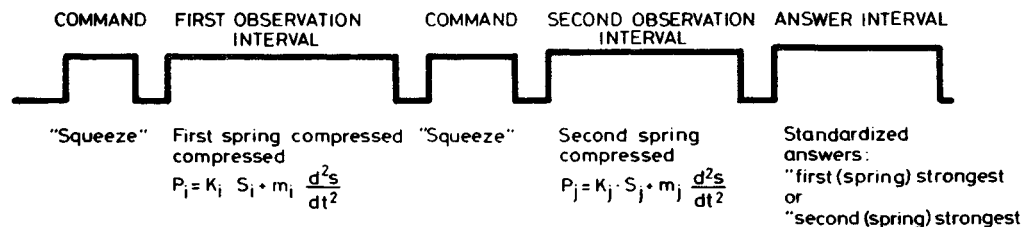


Figure 4. Two-alternative forced-choice discrimination. The figure shows the events in a two-alternative forced-choice discrimination trial. In this modification of the forced-choice procedure, no feedback is given about the correctness of the answers. The order of presentation is always randomized. Here the physical events during spring strength discrimination are used as examples. Ss were instructed to press the springs on the command "Squeeze." They were told to respond either "first stronger" or "last stronger." When trials are repeated with the same two springs (i and j), the probability of a correct answer (pc) can be calculated as:

$$pc = \frac{1}{2}\left(1 + \frac{c_{ji}}{a_{ji}} - \frac{b_{ij}}{a_{ij}}\right)(k_j k_i)$$

in which $a_{ji}$ = number of trials in which spring j is presented as the first spring, $a_{ij}$ = number of trials in which spring i is presented as the first spring, $c_{ji}$ = number of correct answers when spring j is presented in the first observation interval, b = number of incorrect answers when spring i is presented in the first observation interval. Plotting $k_j - k_i$, for any given $k_i$, against the probability of correct answer yields a psychometric curve.

$$pc = [e^{(k_j - k_i)^2/s}]/[1 + e^{(k_j - k_i)^2/s}]$$

The pc values run from 0.5 to 1.00. s is a parameter corresponding to the standard deviation. The *discrimination limit* for $k_i$ is then the differential quotient of the psychometric curve in the interval (0.5–1.0). The discrimination limit corresponds roughly to a probability correct level of 0.75.
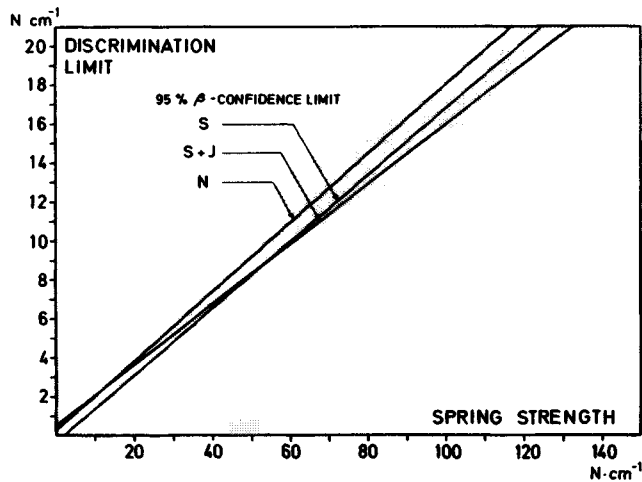
133

Figure 5. Discrimination of spring strength: regression of discrimination limits on spring strength. Each regression line is based on more than 20,000 observations. N: discrimination without anaesthesia; S: discrimination during skin anaesthesia; S + J: discrimination with skin and joints anaesthetized. The hatching shows confidence limits of N. Eleven subjects participated in each experiment. [From Roland & Ladegaard-Pedersen, 1977, reprinted with the permission of the editor of *Brain*.]
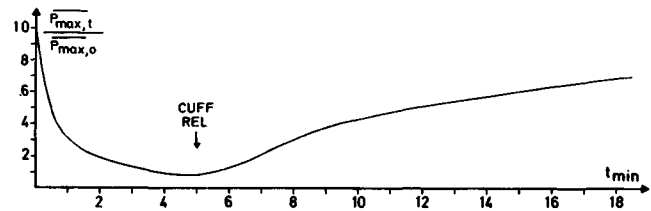


Figure 6. Time course of gallamine induced paresis. At time = 0, gallamine injection is terminated and experiment starts. Ordinate shows average ratio of maximal voluntary force from 11 Ss. $P_{max,o}$ is maximal voluntary force for compression with left thumb and index finger before injection. $P_{max,t}$ is maximum voluntary force at time t. Cuff is released after five minutes. Effects of the ischaemia on the peripheral nerves are thought to subside one minute after cuff release; thus the total ischaemic period is six minutes.

compressing movement, and the acceleration (unless the latter is zero); there being no other cues present it follows that force information is conscious. However, it cannot yet be concluded from this that force information is signalled by musculo-tendinous receptors. If the feed-forward hypothesis is correct, Ss may be managing with only two types of sensory feedback, say, extent of the movement and acceleration, with force signalled via feed-forward loops.

To verify the existence of a sense of tension, the normal relation between motor signals and muscular force must be altered or eliminated, with the magnitude of this change "unknown" to S. The relation between nervous impulses in the motor system and muscular force is most easily changed experimentally at the motor endplate, where neuromuscular transmission can be blocked wholly or in part by curare or curare-like drugs such as gallamine triethiodide. A sphygmomanometer cuff was tightened around the upper arm and inflated to a pressure of 300 mm mercury. Thereafter a retrograde injection of gallamine solution was administered in the forearm veins. After five minutes of ischaemia (occlusion of blood flow), practically all gallamine was attached to the receptor sites (motor endplates) in forearm and hand, and release of the cuff caused only a slight diplopia (double vision). The dose used did not cause total paralysis but allowed S small voluntary contractions amounting to about seven percent of normal maximum isometric force when the effect of gallamine was greatest (Figure 6). The experiments stopped when 75 percent of normal maximum force was restored (Figure 6). The block at the extrafusal motor endplate implies that voluntary contractions are possible only within a narrow range of force in accordance with Figure 6. For example, seven minutes after injection, a maximal voluntary contraction will only result in a muscular force of one-fifth normal maximal voluntary force, but the cortical motor command will still specify maximum force output to the γ-motoneurones and the servo-mechanism. If the feed-forward hypothesis is correct, and there is no sensory feedback of muscular tension, then S would not only fail to recognize such a gallamine-induced paresis, but he would also greatly overestimate the muscular force of the gallamine paretic hand.

The effect of gallamine blockade was therefore investigated in four experiments in which afferent signals from the periphery were restricted to those from receptors in muscles and tendons, with skin and joints anaesthetized as described earlier (Figure 7): (1) compression magnitude matching and spring strength dis-

crimination without gallamine; (2) compression magnitude matching and spring strength discrimination with gallamine induced paresis of one arm; (3) force matching without gallamine; and (4) force matching with gallamine paresis of one arm.

In the gallamine experiments, Ss spontaneously commented upon their weakness within the first two minutes after injection, although they were able to move their fingers. Results of the discrimination and matching experiments were likewise inconsistent with the predictions of the feed-forward hypothesis. Under the feed-forward hypothesis, one would expect that the subjective effort to compress the i-spring with the gallamine paretic hand from 0 to $S_i$ would be much greater than the effort to compress the reference spring (j-spring) from 0 to $S_j$. In the discrimination experiment, therefore, the probability of correct answers should decrease significantly; and in the matching experiment there should be a systematic overestimation of the force of the weakened hand. As is apparent from the results in Figure 7, there was no statistically significant decrease in the probability of correct discrimination of spring strength and there was no systematic error in the force-matching condition with gallamine. However, the accuracy of force-matching decreased after gallamine blockade of the motor endplates, as the measure of uncertainty of matching (the RMS-value) increased.

In the types of voluntary contraction analysed so far, both muscular tension and kinaesthetic parameters change during the contraction. As the decrease in accuracy of force-matching during gallamine blockade might be related to this type of contraction, it was decided to investigate force-matching during conditions in which muscle length was constant (isometric contraction).

The experimental procedure was nearly the same, but instead of compressing springs, S was required to press a strain gauge with his gallamine paretic arm and then match the force of this contraction by pressing the strain gauge with the other arm. Both hands had skin and joints anaesthetized as before. A solution of gallamine in physiological saline was injected into the left arm. First, S pressed the strain gauge with the weakened left thumb and index finger until a specified level of force, as indicated by an audible stop signal, was reached. The actual force of this contraction, called ($P_{set}$), was measured on a peak tension meter. Then S was required to match this force by pressing the strain gauge with the right (nonparetic) thumb and index finger. The force obtained with the right hand is called ($P_{obt}$).

Before the experiment, Ss were told that they would receive an injection of curare and that this would induce paresis. They were informed that although they might notice that great effort was required to obtain any more or less forceful muscular contraction of this limb, it was not in fact their efforts that were of interest but the actual force produced by their left hand. Ss were told to remember the force produced at the moment they heard the stop signal and then to match this force as accurately as possible with their other hand.

MATCH OF LENGTH· CRITERION $S_j = S_i$

A

$$P_j = K_j \cdot S_j + m_j \frac{d^2 s}{dt^2}$$
$$\cong K_j \cdot S_j$$

$$P_j = K_i \cdot S_i + m_i \frac{d^2 s}{dt^2}$$
$$\cong K_j \cdot S_j$$

$S_j \quad S_i$

I

II

MATCH OF FORCE: CRITERION $P_j = P_i$

B

$$error = \log e \frac{P_j}{P_i}$$

$S_j \qquad S_i$

DISCRIMINATION OF SPRING STRENGTH(K)

| | NO OF SUBJECTS | MEAN PROB. CORRECT DISCR. | $\chi^2$ |
|---|---|---|---|
| | 6 | 0.98 | $p > 0.1$ |
| | 15 | 0.89 | |

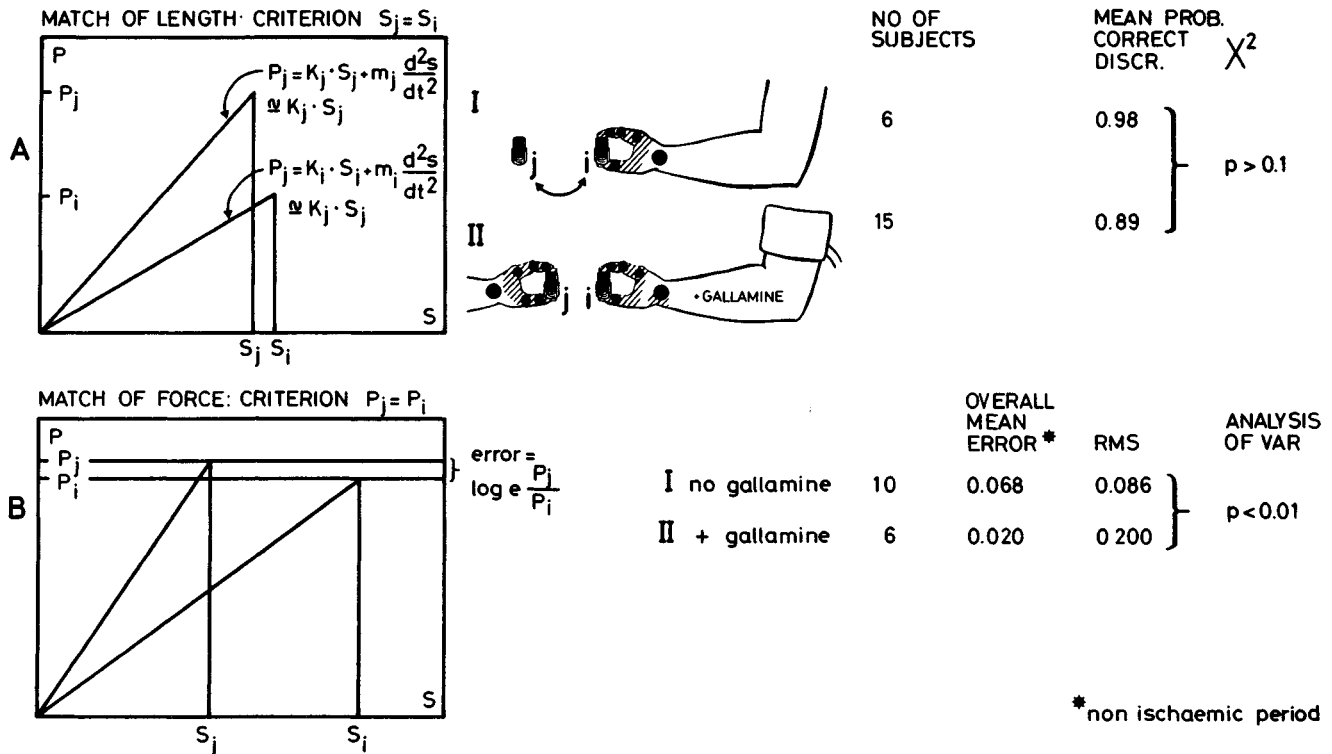| | | OVERALL MEAN ERROR * | RMS | ANALYSIS OF VAR |
|---|---|---|---|---|
| I | no gallamine | 10 | 0.068 | 0.086 | $p < 0.01$ |
| II | + gallamine | 6 | 0.020 | 0 200 | |

*non ischaemic period

Figure 7 Force discrimination and force matching, with and without gallamine blockade. A: In the first experiment (I) S matched compression magnitudes. Indicator spring i (without insertion cylinder) was selected among the twenty-five springs according to a table of random numbers. Skin and joints of the hand were anaesthetized. S pressed the spring down to the prescribed length $S_i$ ($S_i$ likewise determined from a table of random numbers). Compression is slow, with a velocity of approximately 4 mm/sec. A stop signal indicated when $S_i$ was reached. Subsequently Ss matched $S_i$ by compressing a spring of another strength ($k_j$). After this matching, S was asked which of the two springs was the stronger. Because the velocity of compression is approximately constant, the second expression on the right side of the equations vanishes. II: The experiment was repeated, but now the motor endplates in one arm (the "indicator" arm) were blocked by gallamine. Skin and joints of both hands were anaesthetized. As before, S was asked to discriminate spring strengths (the slopes of the curves) under a two-alternative forced-choice paradigm. B: Matching of force. S pressed the first spring (i-spring) slowly down (2 mm/sec) to the prescribed target force ($P_i$). He then received a spring of different strength (j-spring) to be matched with the first. His result ($P_j$) was noted. The error is then $\log_e (P_j/P_i)$. Error was normally distributed. RMS is the root-mean-square or mean value of the standard deviations averaged over all trials. This is a measure of uncertainty of matching. The overall mean error is a measure of systematic deviations from correct matching. I: Matching of force with skin and joints anaesthetized but no gallamine. Here the "reference" arm and the "indicator" arm are the same. II: Matching of force with skin and joints of both hands anaesthetized, but with the "indicator" arm paralyzed by gallamine.

As gallamine does not pass the blood/brain barrier (Cohen, Hood, and Golling, 1968), it has no direct influence on outgoing motor commands from the cerebral cortex; hence, the range within which the sense of effort operates must be assumed to be unchanged, even when the effective force range for voluntary contraction is narrowed by gallamine blockade (Figure 6). Feedforward signals, which require force output, must therefore increase in order to obtain a voluntary contraction of the same strength with a gallamine paretic hand as with a nonparetic hand. The most simple assumption is that these signals increase in proportion to the degree ot paresis. Or that

$$P_{obt}P_{max,o} = P_{set}/P_{max,t} \qquad (2)$$

in which $P_{max,o}$ is the maximum force of the left arm before the gallamine injection and $P_{max,t}$ is the maximum isometric force in the paretic left arm at time t. The expected error in isometric force matching under the feed-forward hypothesis would then be

$$e_e = \log_e (P_{max,o}/P_{max,t}) \qquad (3)$$

The natural logarithm of ($P_{obt}/P_{set}$) is used as the error measure because of its more normal distribution. Equation (2) involves rather strong assumptions, such as the negligibility of the effects of the muscle servo. As it seems reasonable that the effect of the muscle servo should increase with increasing demands of force output, the expected error predicted by equation (3) is too high.

How much too high depends on the gain of the servo and the degree of blockade at the motor endplate, since even the muscle servo has to exert its final effects through the α-motoneurones and the extrafusal motor endplate.

Results are presented in Figure 8, which shows the mean error and standard error of the mean for isometric force matching performance. The mean error reflects systematic deviations from correct matching. As is apparent from Figure 8, no such deviations occurred during the nonischaemic period. The standard error of the mean reflects uncertainty of matching. The standard error was greater in the ischaemic period (first six minutes) than in the nonischaemic period ($p < 0.01$), which stresses the importance of peripheral information in matching. It is further apparent from Figure 8, that Ss indeed perceive the actual force (or tension) of their gallamine paretic arm, and do not rely on any feed-forward signals of force. When anaesthesia is sufficient, Ss have only two main sources of information: receptors in muscles and tendons, and feed-forward signals of central origin. If the muscle servo accounts for the greater part of the final force output from the gallamine paretic hand, then feed-forward signals need increase only slightly, and the assumption about the expected error in equation (3) is no longer valid. But as a consequence, it would not be possible to discriminate spring strength by means of feed-forward information with even approximately the same accuracy as with anaesthesia alone. On the other hand,
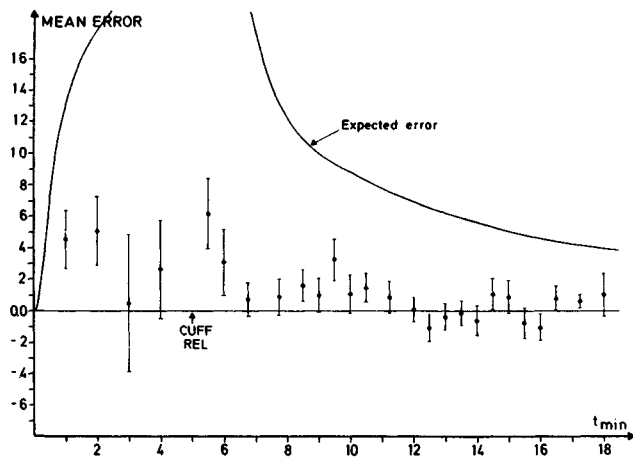
Figure 8. Isometric force matching. The "indicator" arm (Figure 7) is paralyzed with gallamine. The "reference" arm is not. Both hands are skin and joint anaesthetized. Ordinate: mean error = mean of $\log_e (P_{obt}/P_{set})$, in which $P_{set}$ is the prescribed peak force of compression of the strain-gauge with the paralyzed arm ("indicator" arm). Standard error of the mean is indicated. $P_{obt}$ is obtained peak force (or the result of the matching) with the reference arm t: time from start of experiment (see Figure 6). Expected error ($\log_e = P_{max,o}/P_{max,t}$) is the performance expected on the hypothesis that matching was based on corollary discharges or feed-forward signals Note discrepancy between mean and expected error. N = 11. (For further details, see text.) [From Roland & Ladegaard-Pedersen, 1977, reprinted with the permission of the editor of *Brain*.]

if the muscle servo accounts for only a minor part of the final force output from the gallamine-weakened hand, then the prediction about the expected error holds, and its consequence is that the performance depicted in Figure 8 would be impossible unless Ss receive tension information from musculotendinous receptors.

### Some previously overlooked experiments

Some earlier experiments seem to have been overlooked when Rose and Mountcastle (1960) and Gelfan and Carter (1967) concluded that it was impossible for man to perceive signals about tension and extent of movement from musculotendinous receptors. Katz (1925) showed that it is possible to judge the elasticity of an object placed between the teeth, and he believed that receptors in the masticatory muscles were responsible for this faculty (see also Roland, 1973).

Before him, von Frey (1914, 1915) studied the "Kraftsinn," or "sense of force," which in his terminology referred to sensations transmitted by receptor nerves from muscles and tendons. Ss discriminated torque and moment of inertia with the right arm cutaneous sensation reduced by a stiff case tightened around the arm. Von Frey reports the discrimination threshold as being about 5 percent of the stimulating torque, and about one-tenth of this value for the moment of inertia.

Renqvist (1927) used the ergometer of Hill (1922) to investigate flexion-extension movements of the elbow joint. He systematically changed mass, torque, velocity, and acceleration parameters and found that two movements were perceived as equally strong when physical forces were equal.

### Evidence for feed-forward signalling of force during voluntary movement

The experiments on force matching during gallamine block of the motor endplates show that Ss do not rely on feed-forward signals of force. The question of whether or not a feed-forward

mechanism exists, however, is still unanswered. The assumption of equation (2) likewise requires testing.

A small group of new Ss was accordingly instructed to attempt to match with their nonparetic hand their *efforts* in pressing the strain gauge with their gallamine-paretic hand. Skin and joints in both hands were anaesthetized. Instructions and explanations were analogous to those for the isometric force matching experiment described above. Recall that the expected outcome of this experiment would be that $P_{obt} = P_{set} (P_{max,o}/P_{max,t})$; or, as shown in Figure 9, that the logarithmic difference in force level between the nonparetic and gallamine-paretic hand should be equal to the logarithmic difference in maximum force at time t. The results of this experiment are presented in Figure 9. In general, the prediction holds; however, there is a slight but almost constant undershoot that is probably due to the additional force from the muscle servo. So, apparently, man has both a sense of tension and a sense of effort.

### Experimental evidence for feedback of kinaesthesia from muscular receptors

In 1972, Goodwin et al., and Eklund independently and simultaneously published papers on distortion of statognosia in man by vibration of the tendons. Eklund (1972) vibrated the patellar tendon of one of S's legs and then had him track with the other leg the extension induced by the tonic vibration reflex. He found that Ss constantly *under*estimated the extension of the vibrated leg. They apparently did not rely on information from the joints, but followed the information from muscle spindles, which are strongly stimulated by vibration (Brown, Engberg, and Matthews, 1967). The artificially high afferent inflow from the spindles probably caused Ss to judge the quadriceps as stretched more than it actually was.

Goodwin, McCloskey, and Matthews (1972) performed similar experiments on the upper limb, but showed, in addition, that when the biceps tendon was vibrated, the illusion of the arm's being in the direction of stretch persisted during voluntary contractions of low and medium strength. The illusion disappeared during voluntary contractions near maximum force, however. When joints and skin of the hand were anaesthetized by ischaemia from a pressure cuff around the wrist, sensations of passive movement persisted in the fingers, but the prerequisite for this effect was that the forearm muscles be tensed.

In the above experiments, no attempt could be made to quantify the precision of muscular receptors as kinaesthetic recorders because perceptual illusions were involved. Some recent direct approaches to this quantification (Roland, 1975; Roland and Ladegaard-Pedersen, 1977) will now be described.

Kinaesthetic discrimination was investigated with encapsulated springs similar to those used in the experiments described above but with the modification that insertion cylinders of various heights were placed between the bottom of the lower cylinder and the upper cylinder (Figure 10). In this way, the magnitude of movement from top position to bottom could be manipulated. The strengths of the springs were chosen such that a force of 9.80 N gave maximal compression. Thus, the magnitude of the compressing movement from top position to bottom was the quantity to be discriminated during voluntary compression. Under the two-alternative forced-choice paradigm the task was to decide which of the two objects could be compressed more. Discrimination limits were then investigated under the same three conditions as before: no anaesthesia, anaesthesia of the skin, and anaesthesia of skin and joints. Figure 10 shows that discrimination limits were slightly raised during skin anaesthesia. This was partly due to a raised absolute threshold for detection of movement per se, and partly to a raised differential threshold. (The differential threshold or just noticeable difference refers to the discrimination limit when stimulation is well above absolute threshold.) During combined skin and joint anaesthesia, sensation of passive movement disap-
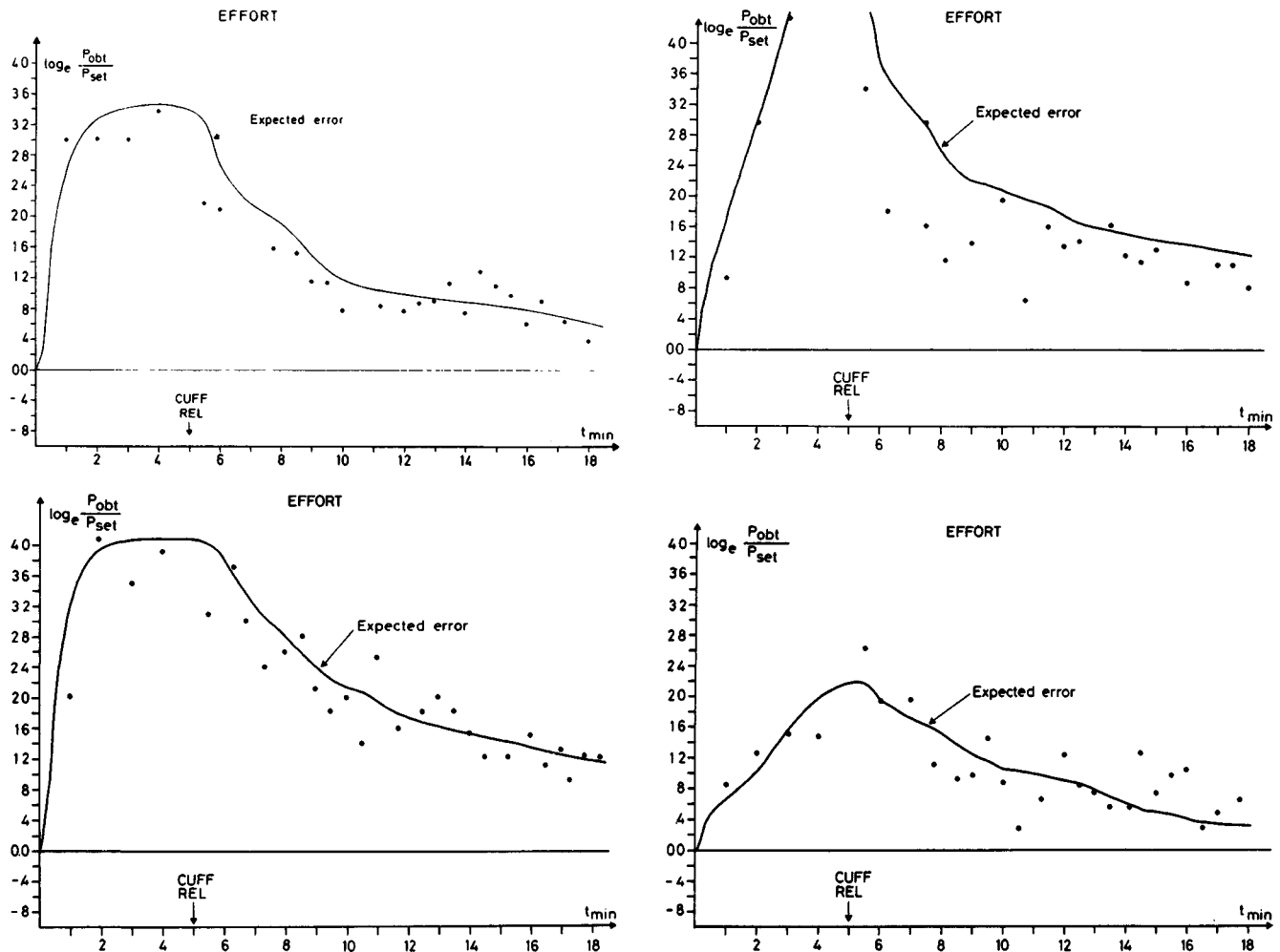
**Figure 9.** Matching of subjective effort. This shows the performance of four Ss in matching the subjective effort of a press on a strain-gauge with a gallamine paretic hand. $P_{set}$ is the force of the gallamine paretic hand; $P_{obt}$ is the force of the non-paretic "reference" hand. Both hands were skin and joint anaesthetized. Data points correspond to the actual matches. The curve is expected error with perfect effort matching through matching of outgoing motor discharges. Note the almost constant undershoot, probably due to the effect of the "muscle servo." (For further details, see text.)

peared, while kinaesthesia was preserved to the same degree as during skin anaesthesia alone (Figure 10).

The effect on kinaesthesia of gallamine block of the motor endplates was also investigated in four experiments in which afferent information from the periphery was restricted to signals from musculotendinous receptors. Skin and joints were anaesthetized as previously. The experiments were: force matching and compression magnitude discrimination and matching, all with and without gallamine block. Figure 11 summarizes the experimental procedures and the results. Ss exhibited a clear impairment in discriminating voluntary movement magnitude during gallamine block. Matching capacity was generally poor in both groups. In both cases, with and without gallamine, the magnitude of error in kinaesthetic matching was correlated with the ratio of the spring strengths (Figure 12). During compression of weak springs, voluntary movement magnitude was generally underestimated, while during compression of strong springs, it was overestimated. Gallamine blockade caused no further decrease in kinaesthetic matching capacity, but ischaemia reduced this capacity considerably (p < 0.01).

In summary, these experiments have shown that muscular receptors do measure extent of voluntary movement, and that this information does reach consciousness, because Ss are still able to perform kinaesthetic discrimination when information from skin and joint receptors has been excluded by anaesthesia. However, while muscular receptors are able to measure movement magnitude, they will not signal equality in the path lengths of two equally long voluntary movements executed with different contraction strengths. On the other hand, skin receptors also seem to play a role in kinaesthesia, probably directly in the initial phase of movement, in which the skin is in contact with the object to be moved.

### Some critical remarks about the experiments

Although these experiments clearly show that signals from musculotendinous receptors do contribute to kinaesthesia and underlie the sense of tension, there are some peculiarities in the action of gallamine that may change the responses of these receptors in a rather unpredictable way. At lower dosages, gallamine seems almost exclusively to block the motor endplates of extrafusal fibers. Under this condition, extrafusal fibers may hence be paralyzed, with intrafusal fibers affected only slightly or not at all (Granit, Homma, and Matthews, 1959; Bessou, Emonet-Dénand, and Laporte, 1965; Emonet-Dénand and Houk, 1968). During a normal voluntary contraction, there is coactivation of $\alpha$- and $\gamma$-motoneurones, such that these cells, and hence the muscle spindles, increase their firing rate in concert at the beginning and during the ascending phase of contraction. (Vallbo, 1971, 1973, 1974). In consequence, afferent input to the $\alpha$-motoneurones increases during the same period, despite the mechanical unloading effect on the spindles. During weak voluntary isometric contractions, the impulse frequencies of
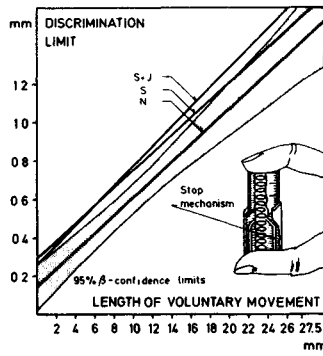
Figure 10. Kinaesthetic discrimination: regression of kinaesthetic discrimination limits on the "free play" (maximal length upper cylinder can be moved). The manipulandum is shown in the figure. The stop mechanism (insertion cylinder) determines the maximal extent of movement, the entity to be discriminated. N: no anaesthesia; S: skin anaesthesia; S + J: skin and joint anaesthesia. Stippled area shows confidence limits of N. Each regression is based on more than 20,000 observations. Average regression for eleven Ss. [From Roland, 1975, reprinted with the permission of *Brain Research*.]

both the primary endings and the secondary endings are linear functions of muscular force. When the extrafusal motor endplate is blocked with gallamine, this relation between muscular force and spindle firing frequency changes, such that the spindles now probably signal only intended rather than actual force. In addition, the mechanical unloading effect on the spindles is reduced

because of muscular weakness. Unfortunately, it is impossible to predict how gallamine changes the position sensitivity of the spindles because discharges from spindle afferents during non-isometric voluntary contractions have not yet been fully investigated. To this it must be added that gallamine has a different effect on the fusimotor endplates. In the cat, Emonet-Dénand and Houk (1968) showed that dosages that barely paralyzed extrafusal fibers also caused a slight block at the γ-dynamic fusimotor endplate. The effect of a rather small further increase in gallamine concentration was a complete block of the γ-dynamic innervation, while the γ-static motor endplate remained resistant. If gallamine acts the same way on human fusimotor endplates, then the dose used in the present study may have caused a partial block of the γ-dynamic innervation. The consequence of this would be changed position and velocity sensitivity of the muscle spindles. This might explain the reduction in discrimination of extent of voluntary movement during gallamine blockade (Figure 11).

However, the actions of gallamine in man are more complex. It is likely that gallamine causes an uneven paresis of the extrafusal motor fibers. Bonde-Petersen et al. (1975) have shown that the nondepolarizing neuromuscular blockers, of which gallamine is one, preferentially paralyze "slow twitch fibers," which are extrafusal muscle fibers displaying a slow increase of tension upon electrical stimulation (see legend to Figure 1). An uneven block of the extrafusal fibers might therefore change the pattern of afferent impulses from the Golgi tendon organs during contraction, since the tendon organs are connected in series with their own "private" group of extrafusal muscle fibers (Houk and
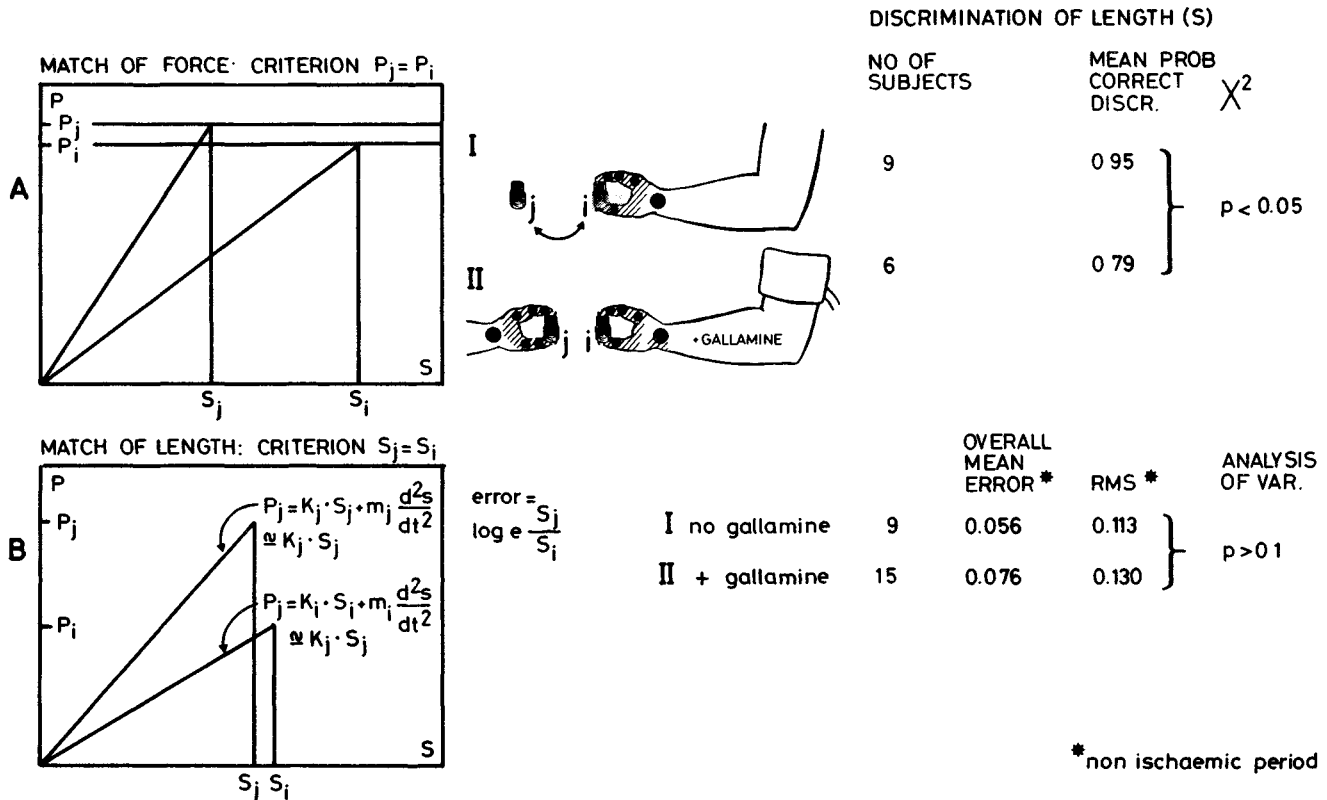


Figure 11. Kinaesthetic discrimination and kinaesthetic matching, with and without gallamine block of the motor endplates. A: In the first experiment (I), S matches force, skin and joint anaesthetized. First, he presses the indicator spring down with a slow velocity of about 4 mm/sec until a prescribed force is obtained ($P_i$). Then the task is to match ($P_i$) with another spring of different strength. When this is accomplished, S is asked which of the two springs was more compressed. Thus the magnitudes of the voluntary movements ($S_i$ and $S_j$) were the entities to be discriminated. The experiment was then repeated (II), but now the arm pressing the i-spring was paralyzed with gallamine. Both the "indicator" hand and nonparetic ("reference") hand were skin and joint anaesthetized as shown in

the Figure. In B, the task is to match extent of voluntary movement first with skin and joint anaesthesia only (I); and then with one arm gallamine paralyzed (II). The first spring (i-spring) is pressed down to a prescribed length ($S_i$). S must then match this length with a spring of different strength ($k_j$). The length obtained this way is called ($S_j$).

Overall mean error is the (time)-average of the mean errors in the nonischaemic period. This is a measure of systematic deviation from a time average error of zero. The RMS-value is a measure of uncertainty in matching. In these experiments force increases linearly with time (and length). Such movements are called "ramp movements." (For further details, see text and legend to Figure 7.)

Henneman, 1967). Thus gallamine probably changes the normal afferent firing pattern from musculotendinous receptors during voluntary contraction in a nonuniform way.

When the skin of thumb and index finger was anaesthetized, the digital nerves were blocked at the base of these fingers. This implies that afferents from the distal and middle joint of the index-finger and the distal joint of the thumb are blocked too. Thus, the skin anaesthesia was actually a combined skin and joint anaesthesia of the distal parts of these fingers. The observed increase in limits for discrimination of voluntary movement magnitude (Figure 10) may therefore be due to concomitant anaesthesia of these joints. This is unlikely, since the movements took place almost entirely in the metacarpophalangeal joint of the index-finger. However, even skin anaesthesia may influence afferent discharges from the muscle spindles. Marsden et al. (1971, 1977) and Dyhre-Poulsen and Djørup (1976) have shown that anaesthesia of the thumb decreases the gain of the muscle servo. Since tendon jerks are not influenced by peripheral anaesthesia and since the effect in the electromyogram appears after 40 – 50 msec, Marsden et al. (1977) have suggested that the facilitating effects of cutaneous afferents are mediated through a transcortical servo loop. More recently, Gandevia and Mc-Closkey (1977b) have shown that flexion movements are facilitated by cutaneous afferent impulses, while extension movements are inhibited. However, this effect of skin anaesthesia should not influence the present results, since the skin was anaesthetized in both standard and comparison trials.

It should be emphasized that the voluntary contraction parameters that have been investigated are not comparable from one experiment to another. Observations from the experiments in which Ss could freely choose their velocity of voluntary contraction (discrimination of spring strength, see Figure 5) showed that they preferred contraction velocities twenty-five times greater than those used in the force matching experiment involving springs and about five times greater than those used in the isometric force matching experiment. These relations are illustrated in Figure 13. If it is reasonable to assume that the tension receptor is more sensitive to changes in force than to force itself, then contraction velocities are of major importance in terms of the number and frequency of the afferent impulses available to the central analyzers. Thus, if the time derivative of force (dP/dt) is a more effective stimulus, then the superiority of



Figure 13. Force time curves for spring strength discrimination, isometric force matching, and spring force matching. The curves reflect stimulus differences for a dynamic tension reporter. The strengths of the two springs 1 and 2 shown in A and C were 4.41 N/cm and 3.92 N/cm, respectively. Ss were skin and joint anaesthetized in all records. In B and C, they were further paralyzed with gallamine during compression of spring 1. B and C are records taken two minutes after cuff release (see Figure 6). The records in A and C were drawn from the time length relations on a film of the discrimination, taken with a high speed camera (film speed 85 pictures per second). In B, S was required to match a force of 12 Newtons with the non-paretic hand by compressing spring 2.

isometric force matching compared to overt force matching with springs stands explained.

In force matching, the entity to be matched is the static force parameter, while in spring strength discrimination, the dynamic parameters (dP/dt and dP/ds) are of principal importance (the strength of a spring being defined as the force relative to the extent of compression). However, Ss still have the possibility of using (dP/dt) as a cue in the isometric force matching experiment, in the case that afferent input from the tension receptor is integrated at the central analyzer. This possibility does not exist in force matching with springs because here the strengths of the chosen springs determine the time derivative of force in the closed loop.

Performance accuracy in the discrimination and matching experiments should not be compared. For several reasons, matching is a rather inaccurate psychophysical procedure. For one, it is not possible to control S's response criterion in the same strict way as under the two-alternative forced choice paradigm.
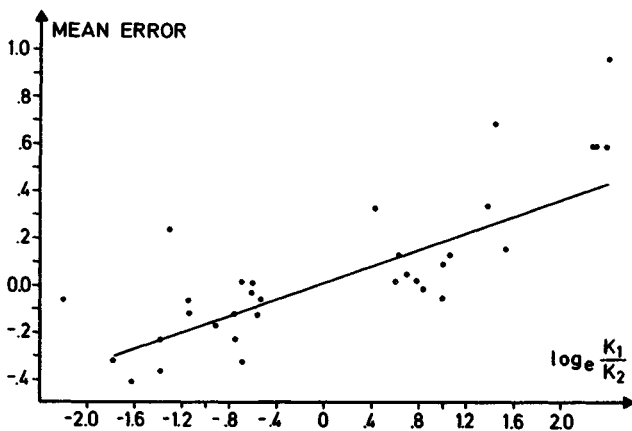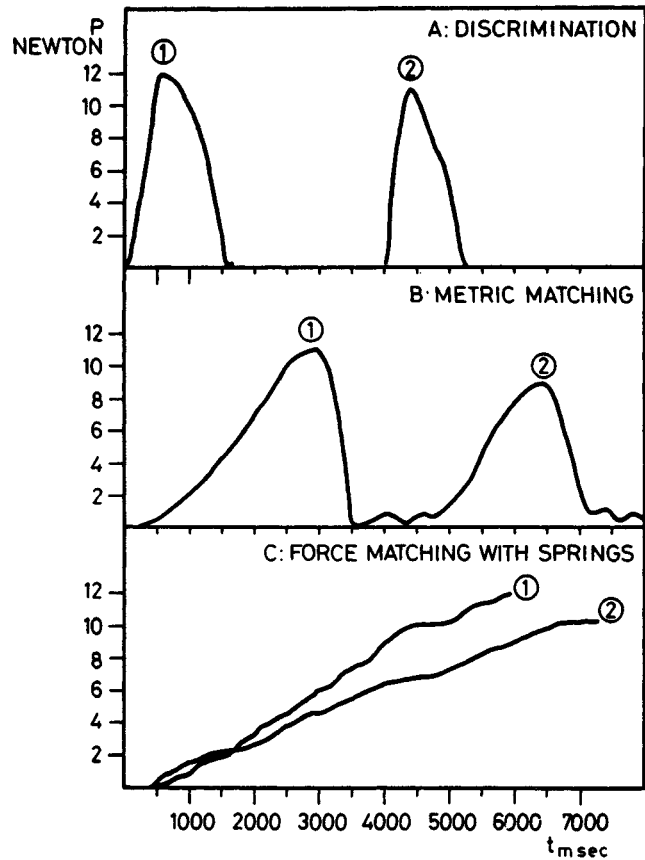


Figure 12. Kinaesthetic error in matching: relation between mean error in matching voluntary movement magnitude and the logarithmic difference in spring strength between first $(k_1 = k_i)$ and second spring $(k_2 = k_j)$ in Figure 11. This figure shows mean errors in kinaesthetic matching without gallamine induced paresis. Each point is mean error of nine Ss. The correlation coefficient $r = 0.63$ ($p < 0.001$). The best fitting straight line for this relation was drawn by graphical methods. Also, the mean error during kinaesthetic matching with gallamine block showed a highly significant correlation with the ratio of spring strengths ($r = 0.73$, $p < 0.001$). [From Roland & Ladegaard-Pedersen, 1977; reprinted with the permission of the editor of *Brain*.]

## Sense of tension as distinct from sense of effort

A recent note by Campbell et al. (1976) reports that "perception of effort with maximum voluntary contractions (during partial curarization) fell in proportion to the reduction in force and

recovered in the same manner subsequently." Campbell and his coworkers conclude that "the sense of effort we have quantified in these experiments is dependent on achievement – i.e., is largely peripheral in origin." What Campbell et al. seem to have measured with their psychological rating scale is probably the sense of tension. The whole matter may be a question of how Ss are instructed. McCloskey, Eberling, and Goodwin (1974) remark that in some of their experiments Ss seem to switch between directing attention to signals of intramuscular tension and a "sense of effort." McCloskey et al. rendered hands insentient by inflating a pressure cuff around the wrist. Ss pulled against a strain-gauge with their anaesthetized hands. When the instruction "keep your effort constant" was given and the triceps tendon was vibrated, in the majority of trials Ss decreased their tension but returned to the previous level when vibration ceased. Sometimes, however, Ss failed, seeming instead to maintain a constant effort.

The well-known experience that objects feel heavier when muscles are fatigued has been analysed by McCloskey et al. (1974). In two experimental series, this common experience was substantiated (although some Ss seem to match weights correctly even with fatigued muscles). These authors put forward the hypothesis that objects feel heavy because an increased command to the muscles is required when the latter are fatigued, with the awareness of this command corresponding to the "sense of effort." Gandevia and McCloskey (1977a, 1977c) have now extended the observations on this sense of effort in some experiments involving the motor endplate blockade by d-tubocurarine (a curare-like agent with approximately the same effects as gallamine). In an experiment on perceived heaviness matching, S was instructed to lift a weight with the thumb of the blocked arm and then, with the other thumb, to match "so that both thumbs feel the same." When maximal voluntary muscular strength was reduced to about 10 percent of normal strength, a 500 g weight was overestimated by 20–40 percent. However, neither the blocked arm nor the reference arm was skin and joint anaesthetized. In another experiment, the thumb of the blocked arm was skin anaesthetized (while the reference arm was not); now the 500 g weight was overestimated by about 400 percent (Gandevia and McCloskey, 1977c, and Figure 5). These results are in harmony with the present ones (see Figures 8 and 9). In the first experiment, Ss presumably used either their sense of tension or the afferent information from skin and joint receptors in their estimation of perceived heaviness. In the second experiment, they almost certainly used their "sense of effort." However, the conclusion that Gandevia and McCloskey (1977c) drew was that Ss relied on their sense of effort in both experiments! Again, instruction may account for the apparent switch between sense of tension and sense of effort: the request to make "both thumbs feel the same" is certainly ambiguous. Likewise, the results of Gandevia and McCloskey (1977c) confirm the hypothesis that when sense of effort is utilized, the observed error in force matching during gallamine blockade is approximately equal to the logarithmic difference in maximum voluntary force at time t (equation 3). We may therefore conclude that man has both a sense of tension and a sense of effort. The main weakness of the feed-forward hypothesis is the vagueness with which the mechanism is formulated. What are the parameters encoded by the postulated signals? Does the anatomical substrate for the feed-forward consist exclusively of intracortical circuits?

It has long been known that, concurrent with voluntary contractions, there are increases in blood pressure and heart rate (Krogh and Lindhard, 1913). These increases are not due to metabolic increases in the muscles, but are a phenomenon concurrent with the transmission of motor signals from the cortex (Freyschuss, 1970; Goodwin et al., 1972). However, since increased heart rate and blood pressure may well be perceived, it cannot be excluded that such sensations provide the basis for the "sense of effort."

As mentioned earlier, when the extrafusal motor endplates have been blocked by gallamine (or d-tubocurarine) the muscle spindles may, because of alpha-gamma coactivation, signal intended instead of actual force during the ascending phase of contraction. It cannot therefore be excluded that afferent signals from muscle spindles are the basis of the sense of effort. Or, to quote Granit et al. (1972), "All these terms (sense of effort, corollary discharges, and so forth) were invented before it was known that the periphery itself is 'corollized' by alpha-gamma linkage to one of our most highly developed sense organs which also projects to the cortex." Until now, none of those who argue for the existence of "corollary discharges," "sense of effort," or feed-forward mechanisms of force registration have been able to exclude these two important potential sources of afferent data for sensations of effort.

However, discrimination of spring strength with anaesthetized hands would be impossible if S did not "know" the force or its time derivative from the first observation interval (Figure 4). S must therefore be able to "remember" the force parameters, at least in the short period between the first and second observation interval. Likewise, matching of "effort" would be impossible during gallamine blockade if S did not "know" the commands to the motoneurones involved in pressing with the gallamine paretic hand. My suggestion, therefore, is that there exists a memory for motor orders. It makes no difference whether this memory is updated by afferent information from muscle spindles, Ruffini-like joint receptors, or subcortical or intercortical loops. The point is that a memory for force parameters exists and that on the basis of this memory Ss apparently have access to information about commands to motoneurones.

### Muscular kinaesthesia as distinct from feed-forward signalling of voluntary movement magnitude and joint kinaesthesia

It is unlikely that feed-forward signals concerning the preprogrammed magnitude of voluntary movement can account for performance when Ss discriminated extent of movement with the skin and joints anaesthetized. The only useful voluntary contraction parameter in this case is the magnitude of the compressing movement with index finger and thumb. However this does not exclude the possible existence of feed-forward signals indicating expected or preprogrammed movement magnitude when voluntary contraction is initiated. The idea of such signals existing is tempting because some mechanism in the cerebral cortex must presumably decide how big a voluntary movement is meant to be. Even if motor commands do contain information about such a preset value of desired movement magnitude, it is unlikely that Ss in the kinaesthetic matching experiment relied upon such signals instead of afferent signals from muscular receptors because they had no a priori information concerning the distance to be moved. The inference that Ss actually relied on peripheral signals is supported by the observation that ischaemia (in combination with gallamine) considerably impaired their performance. The effect of ischaemia on muscle spindles is an increase in firing rate for the first three to five minutes, followed by an abrupt decrease to nearly zero (B.H.C. Matthews, 1933).

Recently there have been a number of studies, particularly from McCloskey's laboratory, providing evidence that muscle afferents should indeed be regarded as contributing to kinaesthesia. Cross and McCloskey (1973) found normal kinaesthesia in patients with joints surgically removed and replaced by prosthesis. Gandevia and McCloskey (1976) showed that muscle receptors increase their reliability in measuring movement path length when the muscles are tensed. McCloskey and Torda (1975) paralysed one arm (with d-tubocurarine) in seven normal Ss and asked them to attempt to move their paralysed but unanaesthetized fingers while blindfolded. All reported inability to move them. If Ss had been relying on feed-

forward signals, the attempt to move should have produced an illusion of movement. However, it is possible that McCloskey and Torda's subjects did receive afferent information from tonic joint receptors and that the steady discharge from these receptors was the afferent information upon which they relied when they stated that they "could not move." Goodwin, McCloskey, and Matthews (1972) made the whole hand anoxic, and at onset of ischaemic paralysis Ss reported no movement illusion when asked to move fingers, even though afferent information from skin and joints was excluded. Thus the feed-forward signals themselves are not sufficient to cause any illusion of movement, even in the absence of information from skin and joint receptors. A muscular kinaesthesia that is distinct from feed-forward signals of expected magnitude of voluntary movement must therefore exist.

The role of joint receptors in kinaesthesia has recently been questioned in some electrophysiological experiments on knee joint receptors in the cat (Burgess and Clark, 1969; Clark and Burgess, 1975; Grigg, 1975). More than half the receptors studied failed to discharge significantly in response to movement in the range intermediate between full flexion and full extension. Other receptors discharged only to bending and twisting procedures, and only a small proportion of phasic receptors (about 15 percent) were capable of producing a response to joint movement in the intermediate range. Likewise, very few fibers in the articular knee nerves yielded slowly adapting responses to joint positions in the intermediate range. However, activation of muscles inserted in the joint capsule could initiate or increase discharge from joint afferents. If these results apply to man, muscular receptors could play a more important role in kinaesthesia, even under normal conditions, than hitherto believed.

In spite of the present results and the cited studies by other authors, it is difficult to explain why Gelfan and Carter (1967) failed to arouse any kinaesthetic sensation in their subjects when they pulled their tendons. Matthews and Simmonds (1974) repeated the experiment with seven Ss operated for a carpal syndrome (compression of a nerve at the wrist). All reported movement of the correct digit when the proper tendon was pulled.

### Which of the musculotendinous receptors are responsible for the sense of tension and kinaesthesia?

The most straightforward answer is: no one knows. As far as the sense of tension is concerned, all three known receptors in muscles and tendons could signal force or tension to the cerebral cortex. Primary endings, secondary endings and Golgi tendon organs all fire linearly to force during voluntary isometric contraction (the primary endings and secondary endings certainly with considerable scatter and irregularity (Vallbo, 1971, 1974) ). One thing that makes the primary endings rather unreliable as tension receptors is that they increase their impulse frequency when the muscle is relaxing (Vallbo, 1970, 1974). But Vallbo studied only very weak voluntary contractions, so it is still uncertain how the spindles behave when the force of the contractions increases.

Certainly, the receptor most suitable for signalling tension is the Golgi tendon organ. In the cat, this receptor has a high dynamic response (to dP/dt) and a slowly adapting static response (to P) upon electrical stimulation of motor nerves (Houk and Henneman, 1967; Alnaes, 1967). The human Golgi tendon organ seems to exhibit the same properties (Vallbo, 1970). The response to increased force and to force during voluntary contraction is more pronounced and more regular in afferents from Golgi tendon organs than in afferents from spindles (Vallbo, 1970, 1974). Owing to these properties, the Golgi tendon organ is implicated as the peripheral receptor for the sense of tension under the most parsimonious explanation of the present findings, for example, that the time derivative of force seems such an im-

portant parameter in force matching and spring strength discrimination.

The question remains open as to which of the two other receptors in the muscle is responsible for muscular kinaesthesia. Inasmuch as no information is available about the behavior of the primary and secondary endings during voluntary non-isometric contractions, it would be premature to infer that one but not the other is the peripheral receptor for muscular kinaesthesia. Until quite recently it was believed that primary endings were highly sensitive to vibration, while secondary endings and tendon organs were not. On this basis it was proposed that the discharges from the primary endings were responsible for the distortion of statognosia and kinaesthesia when the tendons were vibrated. Now Burke et al. (1976a, 1976b) have shown that the primary and secondary endings as well as the Golgi tendon organs in man all respond with discharges phase locked to the vibration cycles. During voluntary isometric contraction the primary and secondary endings increased their discharge.

Stimulation of $\gamma$-static neurones in primates increases the sensitivity of the primary and secondary endings to movement magnitude (muscle stretch). Stimulation of $\gamma$-dynamic neurones increases the sensitivity of primary endings to the velocity of stretch (Cheney and Preston, 1976). If the alpha-gamma coactivation hypothesis is correct even with respect to voluntary non-isometric contraction, it would be tempting to suggest that the observed systematic error in kinaesthetic matching (Figure 12) is due to different levels of fusimotor stimulation, and concomitant differential sensitivity of the spindles. When a spring is compressed, force increases linearly as long as the velocity of compression is constant, but it cannot be taken for granted that the sensitivity of the spindles increases linearly. Until more information is available, the relative role of the two types of muscle spindles in muscular kinaesthesia is impossible to determine.

### Impairment of sense of tension and kinaesthesia after localized lesions of the cerebral hemispheres in man

If there is a sense of tension and kinaesthesia from musculotendinous receptors, information about tension and muscular kinaesthesia must reach the cerebral cortex, and one would expect that the receipt and further processing of these signals might be impaired by lesions of the cerebral hemispheres.

To investigate this hypothesis, ninety-four patients with verified, unilateral and well-defined lesions of the cerebral
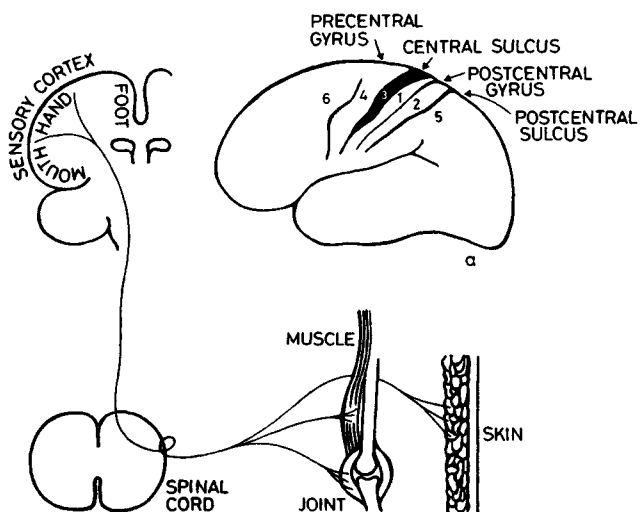


Figure 14. Schematic diagram of projection of somatosensory afferents to contralateral cerebral cortex. In (a) numbers refer to the cortical areas of motor (4 and 6) and sensory zones (3, 1, 2, and 5). The precise projection of somatosensory afferents in man is not known.

hemispheres were selected from among 750 patients undergoing craniotomy for cerebral disease. The selection criteria and methods for measurement of size, shape, and localization of damaged nervous tissue have been described in an earlier article (Roland, 1976). The exposed gyri and sulci were identified in every patient and the cortical and subcortical resection was mapped. For heuristic reasons, the individual lesions were transposed onto a standard brain map, but in a way designed to preserve the original distances from sulci and other landmarks. The resultant figures were constructed in accordance with the proportional system of Talairach et al. (1967). The brain was accordingly divided into subspaces, each having a coordinate of length, height, and depth. The distribution of lesions was such that every subspace was represented by one or more lesions. Patients were all examined for loss of sense of tension and akinaesthesia three months after the craniotomy.

The test used to evaluate the degree of impairment of the sense of tension was the above described discrimination of spring strength. It is generally believed that afferents from skin and joints project to the contralateral postcentral gyrus (Figure 14). This part of the cerebral cortex is of principal importance for the discrimination of complex somatosensory information (Ro-





Figure 16. Impairment of kinaesthesia after skin anaesthesia. Upper: the location of the horizontal sections. We found no single brain subspace in which the lesions induced a statistically significant decrease in discrimination of extent of voluntary movement. However, a group of patients had lesions involving a particular combination of brain subspaces, and these patients all had a statistically significant impairment of discrimination of extent of voluntary movement (p < 0.01). In each hemisphere there are two such combinations: one outlined by the heavy lines, the other marked with dots. These patients have a combined impairment of kinaesthetic signals from muscles as well as from joints. As the postcentral gyrus runs obliquely backwards medially from the brain surface, these lesions correspond well to destructions of this gyrus.
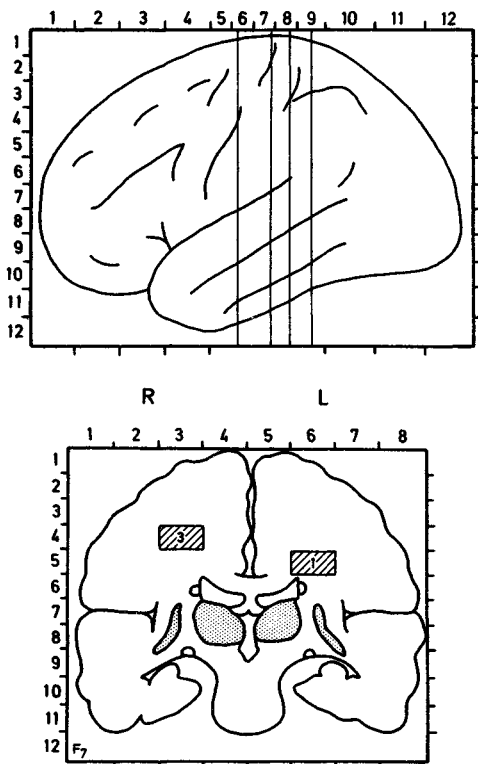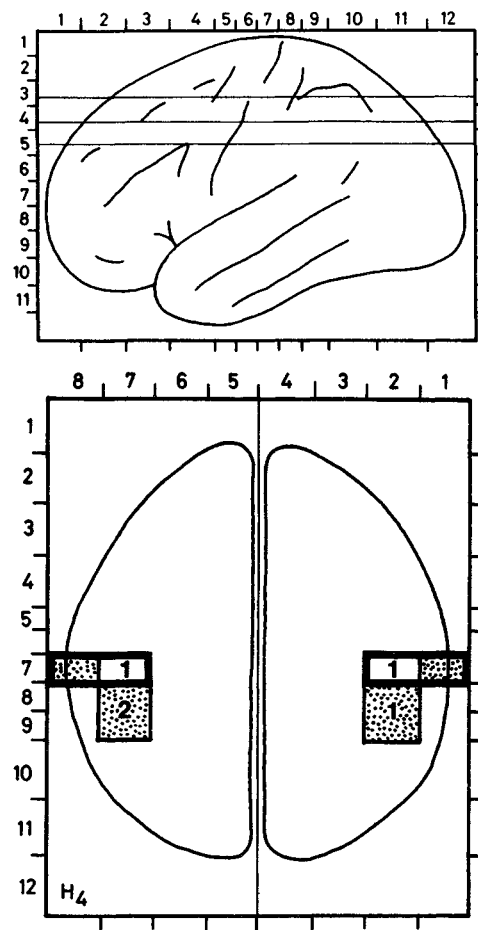


Figure 15. Impairment of sense of tension: locus of lesions in patients with statistically significant decrease in spring strength discrimination performance. Of ninety-four patients originally studied, forty-one volunteered for further spring strength discrimination tests with anaesthesia of skin and joints. Upper figure shows the division of the brain into subspaces modified after Talairach et al. (1967). For each brain subspace, mean discrimination capacity (see Roland, 1976) was computed for all patients with lesions involving that subspace. The mean value was then compared with that of a normal control group. Hatched areas mark those subspaces for which a statistically significant decrease in discrimination capacity was found (p < 0.01). The quantity in the hatched area shows number of patients with lesions at that locus. Lower figure: a frontal section of the brain is shown. F₇ designated the location of the section. All four patients marked in this section had an impairment in spring strength discrimination. It is evident that the lesions corresponding to the hatched subspaces destroy the depth or the projection to the middle third of the postcentral gyrus. Three of the patients had a severe paresis. No significant decrease in spring strength discrimination capacity could be found for lesions in the other brain subspaces.

land, 1976). A problem arises with lesions in man, because often these cannot be confined to a single strip of cortex, being the result of operations for diseased tissue, which does not respect the functional divisions of the brain. Because the motor cortex is situated just in front of the postcentral gyrus, the precentral gyrus often tends to be damaged concomitantly. The result of precentral gyral lesions is paresis.

Figure 15. shows the spring strength discrimination performance of patients with skin and joints anaesthetized. Four had an impaired sense of tension; three of these had severe paresis.

Although there was no correlation between degree of paresis and discrimination capacity, these results do not warrant any conclusion about the locus of lesions causing impairment of the sense of tension. As a certain amount of muscular tension is prerequisite for sufficient excitation of the tendon organs (so as to provide a viable range of afferent impulses for the cortical discriminator), it is not possible to state whether the impairment seen with lesions involving the cortex in the depth of the central sulcus is in fact due to destruction of the projection area for afferents from tension receptors or merely due to the paresis.

To test discrimination of extent of active movement, encapsulated springs with insertion cylinders (as described above) were
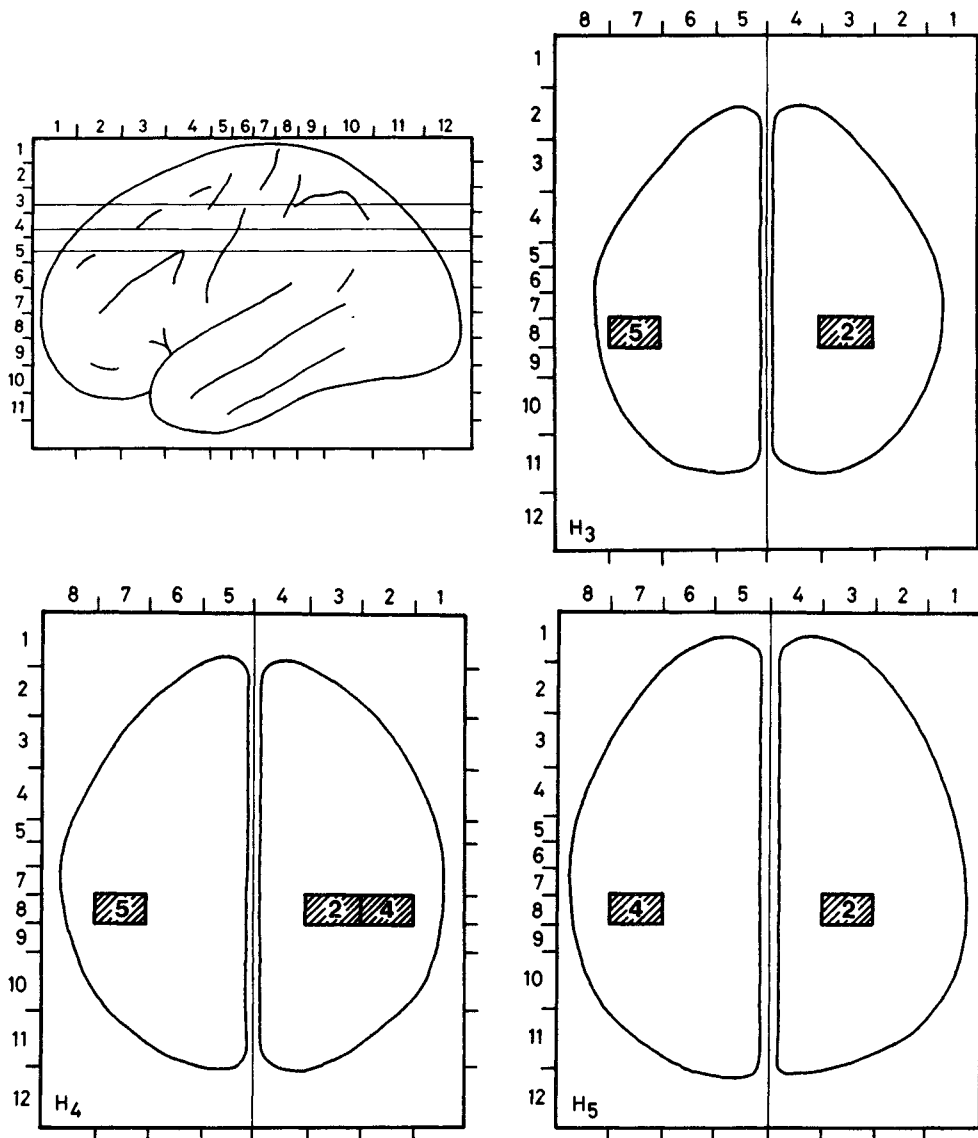
Figure 17. Impairment of kinaesthesia after anaesthesia of the skin and joints. Locus of lesions for patients with a statistically significant decrease in voluntary movement magnitude discrimination. Upper left shows the location of the horizontal sections H₃ – H₅. The lesions causing impairment in kinaesthesia now correspond to the depth of the central sulcus (Talairach et al., 1967).

used. Figure 16 displays the results of administering skin anaesthesia. These patients could utilize kinaesthetic information from neither muscles nor joints. When both skin and joints were anaesthetized, patients with lesions around the postcentral sulcus or the connections to this area also showed impairment (Figure 17). This last group of patients had probably relied on afferent information from joints in their previous discrimination.

These results may reflect a certain division of the projection areas for afferents carrying kinaesthetic information to the cortex such that projections from muscles dominate anteriorly around the depth of the central sulcus, projections from skin receptors dominate in an intermediate zone, and projections from joints are distributed mainly posteriorly, in the depth of the postcentral sulcus. The area in the depth of the central sulcus seems of special importance in the patients' ability to discriminate kinaesthetic information from muscles, because patients with lesions here were unable to use the kinaesthetic information from muscles when their joints were anaesthetized. It is however still possible that the different types of kinaesthetic information secondarily converge to other areas (area 5) eventually after callosal transfer (Duffy and Burchfiel, 1971); but, because the lesions were all unilateral, this question remains unsolved.

## Prior evidence for projection of afferents from muscles to the cerebral cortex

There is now increasing evidence from animal experiments that cortical projections exist from both group Ia and group II muscle afferents. Phillips, Powell, and Wiesendanger (1971) have shown that potentials with short latencies can be evoked from area 3a (Figure 18) in the depth of the central sulcus during stimulation of the (motor) branches of the deep radial or ulnar nerves of the baboon. These projections are strictly contralateral. Some of the neurons were excited by passive movements of the wrist and "it was found that brisk movements were the only effective stimuli." Some units responded to vibration and passive stretch of muscles and were clearly receiving signals from group Ia afferents. Although the stimulation techniques did not allow an evaluation of the projection of group Ib fibers, such projections were not excluded. Landgren and Silfvenius (1969) were further able to demonstrate the projection of group Ia as well as group Ib fibers from the hindlimb to the cerebral cortex in the cat. Hindlimb group II fibers were found to project to the region surrounding the group I projections. Finally, Hore, Preston, Durkovic, and Cheney (1976) elicited responses from neurons in
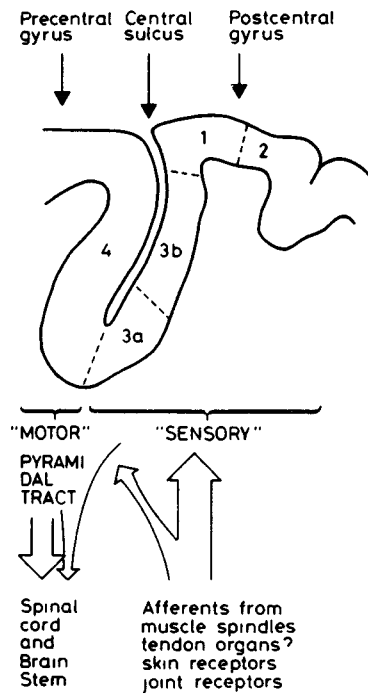
Figure 18. Diagram of anatomical division of cortex surrounding central sulcus in baboon (based partly on Phillips et al., 1971). The functional division between motor and sensory cortex is not rigid. Sensory afferents seem also to project to "motor" area 4, and neurones in area 3a seem to project to the anterior horn of the spinal cord.

area 3a and 4 in the baboon during linear stretches. Whereas the neurons in area 3a were found to have low sensitivity to passive movement, those located in area 4 had "high sensitivity equivalent to that of primary and secondary spindle afferents." They found, in addition, some units in area 3a that appeared to respond best to light taps on tendons but not to muscle stretch. Thus, whereas the projection of spindle afferents to the cerebral cortex in the depth of the central sulcus seems certain, the projection of tendon organ afferents has not yet been adequately demonstrated. If there is such a projection, the receptive areas are most probably the same as for spindle afferents, as these studies suggest.

From the studies of Mountcastle and Powell (1959; Powell and Mountcastle, 1959) it is known that joint afferents predominantly project to the contralateral area 2.

In light of the present experiments, there is anatomical and physiological support for the existence of a differential projection of fibers subserving muscular kinaesthesia and fibers subserving articular kinaesthesia. The present results are in accordance with these earlier findings inasmuch as lesions causing akinaesthesia were centered around the central and postcentral sulci, and by virtue of the apparent differential effects of rolandic lesions (causing muscular akinaesthesia) and more posterior lesions (causing articular akinaesthesia). But kinaesthetic discrimination is certainly not a function localized to a narrow strip of the cerebral cortex, and the impairment that has been found is probably also due to lesions that disconnect the anterior part of the parietal lobe from the rest of the brain. In this context, the effects of lesions in the contralateral superior parietal lobule (area 5?) may play an important role.

**Significance of sensory feedback of tension,
kinaesthesia, and feed-forward mechanisms
during voluntary muscular contractions**

What is the significance of the sense of tension and muscular kinaesthesia other than that it provides information in very spe-

cial situations, such as when subjects are judging the strengths of springs or the elasticity of objects? Does this feedback have any significance at all for the programming and execution of voluntary muscular contractions in general?

Taub, Berman and collaborators sectioned the dorsal roots (see Figure 1) in monkeys and thus prevented any information from skin, joints, and musculotendinous receptors from reaching the central nervous system. Even in the absence of vision, these monkeys were able to *learn* to grasp a manipulandum with a specified amount of force (Taub and Berman, 1966; 1968). From this and other experiments with such monkeys, they concluded that "once a motor program has been written into the central nervous system, the specified behaviour, having been initiated, can be performed without any reference to or guidance from the periphery. Moreover there does not appear to be any reason why the initiation, the trigger, cannot also be wholly central in nature" (Taub and Berman, 1968). It may be argued that successful performance of monkeys in such experiments was dependent upon prior feedback from musculotendinous receptors, which may in turn have contributed to the generation of the "motor programme." Later Taub, Perrella, and Barro (1972, 1973) extended these experiments, showing that newborn monkeys were able spontaneously to learn to walk and climb and could be shaped to perform precise hand-to-mouth movements even when they had been blinded at birth. In addition to these studies, which emphasize the role of feed-forward mechanisms in motor control and leave little room for afferent feedback to modify the programming of "voluntary" motor programs, there have been other studies stressing the automatic character of the activities usually called voluntary.

After removal of the entire cerebral cortex, mammals can move around spontaneously and (nonvisually) avoid obstacles appropriately (Ten Cate and van Herk, 1933). When the brain stem is transected at a high level, most mammals are still able to walk spontaneously (Hinsey et al., 1930). If the cut surface of the brain stem is stimulated electrically, the animal starts to walk and the physical parameters of the movements can be changed, such that at higher intensities the animal runs at a speed determined by stimulation intensity. At still higher intensities the run changes to a gallop (Shik et al., 1966). Even newborn kittens with transected spinal cords can walk with their hind-limbs in a treadmill, adapting their walking velocity to that of the treadmill (Grillner, 1973). It seems as if the motor system in mammals is organized in terms of a series of movement generators, each able to control the parameters of muscular contraction, and thereby the movement parameters (length, velocity, force, acceleration, time of start, and so on) in a more or less sophisticated way. (For a review, see Grillner, 1975.)

Against this background, a sense of tension and muscular kinaesthesia seem redundant. It has been suggested by Phillips (1969) and Evarts (1973) that the projection of spindle afferents to the cerebral cortex constitutes the afferent part of a transcortical servo-loop. It is therefore possible that the senses of tension and muscular kinaesthesia are simply signals from this afferent path that do not under normal circumstances intrude into consciousness but can do so if required (for example, in experiments like those reported here).

Pyramidal tract neurons have been considered to be the efferent part of the transcortical load-compensation reflex (Evarts, 1973; Evarts and Tanji, 1976; Tanji and Evarts, 1976). However, this may well be too simple a view, since it has recently been demonstrated that neurons in area 3a (Figure 18) independently project to the spinal cord close to the motoneurones (Coulter and Jones, 1977). It was originally the studies of Hammond (1955, 1956) that initiated the speculations about a long latency stretch reflex or a transcortical servo-loop. Hammond instructed S either to pull or release when the arm was suddenly extended by a velodyne motor. With latencies of about 50–60 msec a response appeared in S's force-time curve. This was neither a normal stretch reflex (response latency about 20 msec) nor the normal

reaction time to somatosensory stimulation (response latency 130–200 msec). However, when S was instructed to "let go," the response was absent or very much reduced. This experiment shows that commands to the motoneurones can be modified with short latencies dependent upon the intention or "set" of the subject. The afferent signals eliciting the response probably stem from musculotendinous receptors, but feedback from skin receptors and visual feedback can also modify this response (Marsden et al., 1977). Because of its short latency, this response is believed to be an automatism. In other words, with a short latency of about 50–80 msec kinaesthetic and tension feedback may change the commands to motoneurones but no S's intention or "set". The question is now whether sensory feedback of tension and muscular kinaesthesia can influence the programming of voluntary contractions. The latency for conscious receipt of tension signals may well be too great to subserve any conscious motor reprogramming during fast isolated contractions, but it is not excluded a priori that these signals could induce changes in the motor program during smooth and slower contractions. Evarts (1968) showed that the majority of pyramidal tract neurons he studied changed their firing correlatively with voluntary movement force or its time derivative. Since these changes occurred before muscular contraction, they cannot be explained as being induced via the transcortical servo-loop. The sense of tension, which probably carries information about both tension and its time derivative, is hence an excellent error signal for pyramidal tract neurons.

In Figure 19, the force time curve is shown for spring compression in the second observation interval (Figure 4) of a two-alternative discrimination of spring strength. In the first observation interval, S pressed a much weaker spring. The time derivative of force (dP/dt) seems to be adjusted three times during compression, the first with a latency of about 50–60 msec after the start of compression. Apparently the motor orders are reprogrammed under influence of some sensory feedback. Be-

cause skin and joints were anaesthetized and S was blindfolded, this feedback must be from musculotendinous receptors.

On the basis of time relations, voluntary movements are often divided into "ballistic" and "ramp" movements. Ballistic movements are fast movements with large initial acceleration and generated by a step force as in typewriting or piano-playing (see legend to Figure 19). Ramp movements are slower continuous voluntary movements in which force increases linearly with time or follows a smooth curve. Perhaps sensory feedback from musculotendinous receptors to the cerebral cortex sometimes causes reprogramming of the parameters of voluntary contraction. However, the latency for conscious detection of signals of tension and muscular kinaesthesia is most certainly too great to cause any conscious reprogramming during ballistic movements (Viviani and Terzuolo, 1973; Soechting, 1973). During ballistic movements, both the agonists and antagonists (Figure 2) contract (Wachholder and Altenburger, 1926; Dijkstra and van der Gon, 1973; Hallet, Shahani, and Young, 1975), but during smooth and slower (ramp-) movements only the agonists contract (Hallet et al., 1975). So if sensory feedback of tension and muscular kinaesthesia play any role in motor control, they would probably be restricted to these slower movements. Could it be that the principal importance of force information from the periphery is to update the cerebral cortex with data about the consequences of voluntary contractions? Since it is not possible to answer these last questions on the basis of the present experiments, they are addressed to those who will comment upon this article.

### Final summary and conclusions

Do we perceive sensations of movement and of muscular tension from musculotendinous receptors during voluntary contraction? Evidence from recent publications seems to be affirmative with respect to movement sensations, but the question of conscious tension information is more controversial. It has been suggested that some conscious feelings of expected extent of movement and muscular force accompany descending motor signals from the cerebral cortex at the initiation of a voluntary contraction. By this means, a subject could have a priori information from feed-forward signals about some of the parameters of voluntary contraction. Along with this view, it has been widely accepted that muscles are "insentient," and that signals from their receptors do not reach consciousness. This article describes a series of experiments designed to test the hypothesis of the existence of feed-forward and feedback of sensory information during voluntary muscular contractions in man.

In the first series of experiments, voluntary compression of springs and strain-gauge with thumb and index finger were investigated in healthy young subjects. Discrimination of spring strength was unaffected by anaesthesia of skin and joints. The fact that subjects had no visual or auditory cues during discrimination implies that tension (force) information is conscious. When the motor endplates in one arm were partially blocked by administration of gallamine, subjects with skin and joints of both hands anaesthetized could match the force output of the paretic hand with the other (non-paretic) hand. Under identical experimental conditions, subjects could discriminate spring strength and voluntary movement magnitude; they could also match the latter.

Since gallamine disturbs the normal relation between motor signals and force output, information concerning tension or force must be signalled by receptors in muscles and tendons. It was accordingly concluded that muscle receptors signal kinaesthetic information, and that these signals reach consciousness.

In other experiments, subjects, again with skin and joints anaesthetized in both hands, could with their right hand match the *effort* of their partially curarized left hand during compression of a strain-gauge. Apparently there is both a sensory
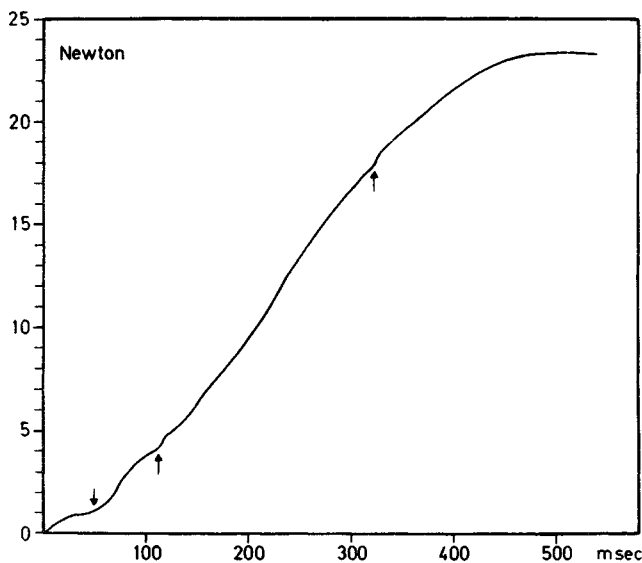


Figure 19. Force-time curve for compression of a spring with a strength of 53.93 N/cm. Just before this trial, S compressed a spring of strength 19.61 N/cm. Note that the acceleration at several points of the compression is close to zero. Arrows mark points of adjustment of the time derivative of force. The relation between force and time was obtained from a film of the discrimination with a highspeed camera (85.17 pictures per sec: Roland and Ladegaard-Pedersen, 1977). This is a ramp movement, probably composed of three or four different ramp functions (dp/dt), in contrast to a ballistic movement in which force almost instantly reaches its maximal value. It should be noted that the time origin in this figure does not correspond to onset of electromyographic activity. The command to "squeeze" this spring was given some 200 msec before any change in external force was registered.

feedback of tension and a memory for the amount of force signalled to lower motor centers.

In the next series of experiments, ninety-four patients with verified, localized, unilateral lesions of the cerebral hemispheres were investigated for akinaesthesia and impairment of sense of tension. Patients with impairment of sense of tension (defective discrimination of spring strength) were those with lesions in the depth of the sulcus centralis of the contralateral hemisphere. Unfortunately, it was not possible to decide with certainty whether this was due to a greatly reduced capacity for voluntary force or an impairment of the sense of tension per se.

Patients with akinaesthesia after induced skin anaesthesia all had lesions of the contralateral hemisphere below the post-central gyrus. These patients cannot utilize kinaesthetic information from either muscles or joints. When both skin and joints were anaesthetized, patients with lesions around the postcentral sulcus or the connections to this area showed impairment too. The possible existence of separate cortical projection areas for kinaesthetic signals from muscles and joint afferents is discussed. The implications of parallel feed-forward and feedback of tension during voluntary contractions is discussed with special reference of the learning of motor control.

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by **William D. Chapple**

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**Consciousness and the limitations of psychophysical approaches.** The role of sensory receptors in movement has a deceptive air of simplicity about it Roland's essay alternates between embracing this simplicity and acknowledging the underlying complexity of the problem On the one hand, his discussion of muscle spindles and tendon organs is oversimplified as an introduction to the kinds of psychophysical experiments he describes On the other hand, his discussion of the difficulties in interpreting the results of his experiments is detailed, leading us to ask the question of whether such experiments can tell us much that is useful about muscle spindles and consciousness

Consciousness is a slippery word for experimental scientists to grasp; Roland chooses an operational definition of it, a "capacity to perform discrimination    to be able upon verbal instruction, to distinguish between two physical inputs and make a decision about the respective magnitudes of one or more parameters " I have two reservations about such a definition First, it seems rather different from the definition provided by *Webster's Third New International Dictionary*, "intuitively perceived knowledge of something in one's inner self," and from that of other authors (Gelfan and Carter 1967 *op cit* ) Thus, muscle spindles may indeed provide a basis for discriminating between different spring strengths, but may not be recognized as a distinct perceptual entity of which we are aware Secondly, there is a tacit assumption that consciousness and the cerebral cortex are somehow equivalent In view of the difficulties in defining the state of consciousness, perhaps we should not try to associate a philosophical concept with an anatomical region too closely

Even if we accept Roland's operational definition, however, we encounter certain difficulties Experimentally he wishes to demonstrate that muscle spindles and Golgi tendon organs are used to discriminate between the amount of force necessary to compress one spring and another By using local anesthetics to rule out the contributions of skin and joint receptors, he argues that only the spindles and Golgi tendon organs are left with which to perform the discrimination However, it is really necessary to perform the control experiment of removing the spindles and tendon organs to show that the discrimination can no longer be performed Anesthetizing the finger does not rule out the possibility that cues from joint and skin receptors in the wrist and lower arm could be used as alternative sources of information during the discrimination task I recognize the difficulties of performing such a control, but techniques for disrupting the discrimination must be developed before any clear conclusions can even begin to be drawn from Roland's experiments

The difficulties in interpreting the experiments with gallamine, a curare analogue that weakens the force of contraction of the muscles, are well summarized by Roland Gallamine not only blocks neuromuscular connections between $\alpha$-motoneurons and extrafusal fibers but also blocks the $\gamma$-dynamics and $\gamma$-statics to different extents Thus the bias of the spindles is changed Moreover, since gallamine blocks slow extrafusal fibers more readily than fast extrafusal fibers, the balance of inhibition from the tendon organs will also be affected These changes make it difficult to evaluate the role of feedforward signals in these discrimination experiments Roland tests von Holst's (von Holst & Mittelstaedt 1950) efference copy model, that is that a copy of the motor program is subtracted from incoming sensory information to provide an error signal As the muscles are weakened with gallamine, so the error signal should increase But such a model assumes that the absolute value of the sensory information remains constant; that it is not related to the weakness produced by the gallamine This is to a varying and unknown extent not the case, for the spindles and tendon organs Moreover, it is possible that the "sense of effort" might alter the $\gamma$-driving of the spindles Thus, without much more detailed information about the spindles and their activity

it is difficult to draw any conclusions about the role of feed-forward signals in these experiments

Finally, with the direct demonstration in animal experiments that primaries, secondaries, and tendon organs project to the motor cortex (Oscarsson, and Rosen 1963; Murphy, Wong, and Kwan 1975 *op cit* , Hore, Preston, Burkovic, and Cheng 1976 *op cit* ) to activate cells that can produce contraction of the muscles from which they originate, the question must be asked whether psychophysical studies, with all their attendant ambiguities, can be used to answer questions such as Roland raises Psychophysical studies, it seems to me, can be validly used to describe accurately the behavior of a system and to exclude certain mechanisms from consideration But particularly in this area, they must be supplemented with electrophysiology Since we understand so little about the relationship between the complexities of proprioceptors and the control of movement at the physiological level, experimental approaches such as Roland's are predictably limited to only partial success We have too many possible mechanisms and too little understanding of how they fit together

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by **J. Dickinson**

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**The function of sensory feedback.** The evidence produced by Roland is persuasive and, with only minor reservations with respect to the use of gallamine which the author himself expresses, demands that we evaluate these results in the context of motor control theory It has been known for some time (Mountcastle, 1957) that joint receptors have direct projections to the cortex, and there is well-founded belief that such information reaches consciousness (Smith, 1969) Roland's evidence extends the sources from which movement characteristics may be perceived

If it is assumed that both musculo-tendinous and articular information is transmitted to consciousness, it is superficially difficult to account for the finding of Taub *et al* (1966 and 1968 *oper cit* ) that such feedback is essential for neither performance nor learning The explanation apparently preferred by Roland is that the afferents from musculo-tendinous sources constitute part of a transcortical feedback loop and do not enter consciousness under normal circumstances In promulgating such a hypothesis Roland may be devaluing the significance of his results The fact that acquisition of movements may occur in the absence of such feedback does not preclude the possibility that such feedback is normally used It could be argued that the process identified by Taub *et al* constituted a compensatory system in which specific force applications were learned on a trial-and-error basis with the feedback role taken over by an external reward procedure

From this perspective it may be argued that there exist two independent modes for acquisition of movement Where feedback is disrupted or where the skill in question is ballistic or requires rapid sequences of movement the learning of motor commands may be the predominant mode for acquisition Thus, studies such as those by Provins (1958 *op cit* ) and Laszlo (1967) demonstrated relatively little decrement in tapping tasks when proprioceptive feedback was eliminated It may also be argued that the motor command or motor-program mode is dominant in the control of well-learned movements in which, presumably, repeatedly accurate performance has led to the redundancy of feedback In this context one could cite the original studies by Lashley (1917) that showed accuracy in leg-positioning in the absence of peripheral feedback There does seem, however, to be good grounds for arguing that slow, delicate and novel movements may have recourse to a feedback-control-mode of acquisition Assuming the replicability of Roland's results, we are assured of the channels available for such a control system and the behavioral evidence supports the view For example, Laszlo and Bairstow (1971) showed disruption of performance of a novel task perfor-

mance following removal of feedback This disruption occurred even if some practice had been given on the task prior to feedback removal Correlational data also lend support to this contention Fleischman and Rich (1963) were able to demonstrate a positive relationship between proprioceptive sensitivity and performance in the later stages of acquiring a tracking skill Perhaps the significance of Roland's contribution is the identification of the mechanism by which all proprioceptors may contribute to the functioning of this feedback-control mode

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## by J. Duysens and G. Loeb

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*Precortical processing of somatosensory information* Between physical transduction and conscious perception, somatosensory information undergoes processing by at least three neurons At least two significant processes occur: information from receptors of similar and divergent modalities converges, and descending activity modulates both the quantity and the quality of the ascending information In considering how we might perceive the events described in this paper, let us consider first the information extracted by the physical transduction, and second, the information arriving at the primary somatosensory cortex, presumably our first level of conscious awareness of information derived from the events

*Receptor transduction* A complete description of the physical events accompanying a given behavioral task is virtually impossible; some change is effected in virtually every muscle, joint, skin surface, and metabolic and circulatory pathway in the body From this open-ended set, the psychophysical investigator faces the perilous task of identifying and monitoring or controlling all of the events which could conceivably be detectable by any type of receptor ending (many of which are poorly understood) and which could provide information significant to the task The following points illustrate this problem, but may reflect on such diverse aspects of research as experimental design, limitations imposed by reasonably brief descriptions of experimental procedure, and differences in the highly subjective estimation of "significant information "

1 Skin receptors Recently Gandevia and McCloskey (1977, *op cit* ; see also McCloskey, this *Commentary*) have provided evidence for a close interaction between exteroceptive and proprioceptive afferent inputs in the perception of heaviness in humans It is thus somewhat surprising that Roland found no deficit in the discrimination of spring strengths when he eliminated cutaneous input from the thumb and index fingers by local anaesthesia of the fingers To explain this discrepancy it is suggested that the elimination of cutaneous input may not have been complete enough in Roland's experiments The subjects had the three ulnar fingers maximally flexed during the spring discrimination tests This means that they must have pressed the tips of these fingers into the palm of their hand during the experiments Since one has a natural tendency to flex ulnar fingers in conjunction with the index finger it seems very likely that the pressure, exerted by the ulnar fingers against the palm of the hand, was a reasonably important clue to the strength of contraction of the index finger

This difficulty may be overcome by instructing the subjects to hold the ulnar fingers in extension However, even in that case one cannot be certain to have eliminated all cutaneous input since there is still another potential source of information from the skin, namely stretch of the skin on the dorsum of the hand In our own experiments on freely moving cats we have observed that slowly adapting skin receptors (Type II) react to minor skin stretches during small movements (Loeb, Bak, and Duysens, 1977) Information from skin stretch may have been minimal in the kinaesthetic discrimination experiments of Roland, since the amplitude of the movements, and presumably the related skin stretches, differed very little However, skin stretch of the dorsum of the hand may have been an important source of sensory information in the spring strength discrimination tests, where there probably was a considerable difference in the movement amplitude depending on the stiffness of the springs Perhaps this explains why simple anaesthesia of the index finger and thumb was not sufficient to induce a deficit in performance in the latter experiments while it was sufficient for the kinaesthetic discrimination tests

2 Muscle receptors Roland rightly pointed out that primary endings, secondary endings, and Golgi tendon organs could all signal force or tension Our own recordings from these afferents during normal movements of the cat indicate a close correlation between the EMG of a muscle and the firing rate of these afferents (Loeb and Duysens, unpublished observations) Tendon organs fired consistently with a fixed latency after the onset of EMG, and their discharge rate was in proportion to the amplitude of the EMG Many spindle primaries and secondaries were found to fire either in phase or out of phase with the EMG bursts of their parent muscle, depending on the type of movement and the type of muscle involved

In addition to the above mentioned receptors, however, one should not overlook the group III muscle afferents in relation to sense of tension and kinaesthesia Paintal (1960) and more recently Menze (personal communication) have found that some of the group III afferents are easily activated by contractions of their parent muscles Menze even found that some of these units fired in proportion to the force developed by the muscular contraction

3 Joint afferents Very little is known about the firing pattern of joint afferents during normal movements Recently, however, we have been able to record from a few of these afferents in the walking cat (Loeb, Bak, and Duysens, 1977) Firing in these afferents was not simply correlated with joint angle but apparently also signaled other factors such as the loading of the joint following footfall Hence it is not impossible that these receptors participate in "sense of tension" but their contribution may be limited since joint anaesthesia does not seem to affect the ability of subjects to discriminate spring strength

*Nerve network processing* It should be emphasized that the separation of afferent inputs in terms of their source is somewhat artificial in the context of normal movement Characteristically, there is already a large convergence of inputs from muscle, skin, and joints at the level of the spinal cord (Kolmodin, 1957; Lundberg, Malmgren, and Schomburg, 1975) At the cortical level, the importance of combined inputs from a number of different receptors has also become increasingly clear (Evarts and Tanji, 1976; Marsden, Merton, and Morton, 1972) Hence it may not be fruitful to try to link the sense of tension or kinaesthesia to one particular type of receptor

As to the relative contributions of the different sensory systems, we have frequently been impressed by the effectiveness of cutaneous input in reflexively changing the walking behavior of cats (Duysens and Pearson, 1976; Duysens and Stein, 1978) There too, however, it was found that skin and muscle afferents often act in functional unity (Pearson and Duysens, 1976; Duysens, 1977) as was also indicated by Gandevia and McCloskey (1977) and by the present experiments on kinaesthetic discrimination

The general conclusion one would like to draw from this paper is that we *can* consciously make use of information contained in the activity patterns of proprioceptive afferents Two hypotheses can be formulated to explain the apparent discrepancy with the opposite conclusion drawn by previous researchers

First, it may be that the information content influences our consciousness but that we have lost a specific sense of the modality of receptor from which it arises For example, if the proprioceptors combine with and modulate activity in the pathways which clearly ascend to consciousness (e g , cutaneous and possibly chemoreceptive), then a patient may be able to use the proprioceptive information for behavioral discrimination but still deny any sensation of muscle tension or length change when the surgically exposed tendon is pulled

Second, and more intriguing, it may be that our proprioceptive afferents

are gated into consciousness by the nature of the task being performed by the brain It has long been appreciated that we can selectively attend to auditory, cutaneous, and visual signals or ignore them almost at will It may be that the gating for the propriocpetive afferents is somewhat more rigid, with the requirement that the muscle be voluntarily activated before we can attend to its proprioceptive feedback This "efferent" requirement for the gate apparently exists for other sensory modalities and serves a useful function Consider the indeterminate nature of the muscle proprioceptor signals The meaning of the afferent activity is enormously changed by the conditions of muscle length, stiffness, and fusimotor activity obtaining at any given moment To attend to this activity in the absence of a consciously initiated state of musIce tone is akin to attending to the signals from the retina with the eyelids closed Both are difficult to do and not very instructive

Subtle differences in the instructions given to the subjects may lead to "yes" or "no" answers to questions that fail to address the complexities of describing sensations which cannot arise in the normally functioning system The difficulties that patients have in reporting the nature of "phantom-limb" sensations, neuroma pain, post-traumatic causalgia, and even the sensations from direct local electrical stimulation of the brain suggest that we need new psychophysical techniques to cope with this difficult but promising source of data

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## by P. Dyhre-Poulsen

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**Possible sources of discriminitive kinaesthetic information.** Normally we do not experience movement as a series of contractions in muscles We are not aware of the degree of contraction in each muscle although muscles and tendons are supplied with receptors sensitive to length and tension The aim of the study by Roland is to investigate whether information from these receptors reaches consciousness Roland first discusses different hypotheses about the control and perception of movement He defines consciousness operationally as the ability to discriminate between two stimuli, and defines the different senses involved in motor control in a concise and very useful way

Hypothetically we can derive information about our own executed force in two ways: either by monitoring output to alpha motoneurons (the "feedforward" or "corollary discharge" hypothesis), or by measuring force from peripheral receptors either in tendons, joints or skin Muscle spindles can be excluded in the last case since without "knowing" both gamma-motor activity and the activity in spindle afferents we cannot possibly measure either length or tension Thus the sense of tension or effort can only come from muscle spindles if a corollary discharge mechanism exists

Sense of effort apparently relies on a corollary discharge mechanism (Ro-

land and Ladegaard-Pedersen, 1977, Gandevia and McCloskey 1977 *op cit ;* see also McCloskey, this *Commentary*) Sense of tension, as measured in Roland's isometric force-matching experiment (Fig 8), may arise from the tendon organs However there is an increase in matching error during galamine induced paresis although the increase in error is not as big as expected from a corollary discharge theory Thus if tendon organs signal force, then they do it badly The ability to discriminate tension in the experiment may rely on receptors in skin and joints, which were not anaesthetized in this experiment During movement of thumb and index finger, the whole hand moves to form a stable base for the execution of the required movement The flexor digitorum longus muscle flexes other fingers concomitantly with the flexion of the index finger What may be recorded then is the force produced by these fingers and not the index finger It is thus possible that corollary discharge mechanisms take part in both sense of effort and sense of tension The very small impairment after selective disruption of afferent information in Roland's series of matching experiments indicates that subjects utilize redundant information from many sources. It would be very difficult to abolish information completely from all parts of the forearm except from one muscle and its tendon

The significance of sensory feedback during voluntary contraction remains unclear Movements may be controlled without peripheral feedback (Taub et al 1966 *op cit* ) and the response to unexpected disturbances during movement may be modified by changing the subjects' instructions (Marsden et al 1976) Even the stretch reflex may disappear if subjects are deceived (Laursen et al 1978) Programming of voluntary movement is thus important both in slow and fast movements Updating of the program presumably takes place after a certain time if the error is too big If updating is frequent it would be difficult to tell the difference between programmed and servo controlled movement The reprogramming should therefore take place as distally as possible Presumably the locus of simple programs is in the spinal cord

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## by H. -J. Freund

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**The role of extrapyramidal structures.** Roland's article provides a comprehensive survey of the relevant data concerning the functional role of afferent input in voluntary movements His own experiments demonstrate how much information can be obtained from human experiments and show that sense of effort, sense of tension, and kinaesthesia depend on inputs from muscle and tendon receptors Skin and joint receptors do not contribute to this information The contribution of feed-forward information from corollary discharges of motor command centers can also be ruled out on the basis of the end-plate blocking experiments It is therefore possible to conclude that conscious perception of the strength of a contraction or of other parameters of voluntary motor acts is based on messages from the contracting muscles

Roland's "psychophysical" conclusions – muscle action perceived via muscle and tendon receptors – have in my view a sound basis The question about the functional importance of this information for voluntary movement seems less clear The author suggests that "the principal importance of force information from the periphery is to update the central cortex with data about the consequences of voluntary contractions " Consequently, this information is regarded as more relevant for slower ramp movements than for ballistic movements

In my opinion, the functional role of muscle-tendon input for conscious perception of motor performances and for the generation of voluntary movements is different This assumption is based on clinical evidence from patients with well-defined lesions in different parts of the motor system and on experimental data from freely behaving monkeys From both we know that muscle-tendon information is not properly used when the cerebellum or the basal ganglia are impaired This is also true if the functional disturbance is transitory, by cooling; e g Brooks, *op cit* in Kelso's commentary ) What results is dysmetria, ataxia, or other forms of striking mismatches between intended and achieved movement On the other hand, lesions of the motor

cortex in man or monkey do not give rise to this type of dysfunction The characteristic disturbance after cerebellar lesions is that muscle-tendon information can obviously not be used properly for the elaboration of the motor command signals

It is therefore suggested that muscle-tendon input is much more crucial for normal voluntary innervation rather than merely for updating the motor cortex The elaboration of this information is mainly performed by the cerebellum and other extrapyramidal structures In addition, this information is important in the programming of ballistic movements These could not achieve their high level of accuracy without the motor programs taking into account all the information about muscle-tendon parameters immediately prior to a contraction A ballistic movement generator has to know whether the hand will approach the nose from the back or from the left shoulder, and whether this hand holds a glass of beer or a cigarette And a relevant part of this information comes from muscle-tendon receptors, as has been beautifully shown by Roland

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*The neural mechanisms subserving kinesthesia.* The proposition that afferent nerve fibres from muscles and tendons subserve the sense of limb position and movement is not a new one In the 19th century, controversy over the status of such afferent information was stimulated by common support for an alternative mechanism that was supposed to arise centrally rather than peripherally and to provoke sensation in relation to the effort to move rather than to the movement actually achieved Helmholtz (1866/1963) called this alternative the sense of innervation The flavour of the debate was often philosophical, with empiricists broadly ranged against idealists (cf Lewes, 1879), but scientifically it lost much of its interest with improved histological description of the receptors in muscles and tendons and the remarkable psychophysical work of Goldscheider (1889) on the ability of human subjects to detect positions and movements imposed passively on the limbs Sherrington (1900) gave the eventually dominant view that afferent activity from muscle and joint receptors subserves the 'muscular sense'

Modern controversy has resulted from the denial of a role for muscle afferents *per se* and from the attribution of position and movement sense entirely to afferents in the joint capsule (Merton, 1964; Mountcastle and Darian-Smith, 1968, *oper cit* ) Evidence contradicting this view was presented at length some years ago (Goodwin, McCloskey and Matthews, 1972, *op cit* ) and has accumulated since (see reviews by Goodwin, 1976; Matthews, 1977, and McCloskey, 1978, and this *Commentary*) Roland has extended this evidence to discrimination of spring compliances, a performance that requires accurate information about finger position and movement and yet can readily be executed after skin and joint anaesthesia No satisfactory estimate has yet been made of the relative contributions of skin and joint afferents to position and movement sense The properties of joint afferents make them surprisingly unlikely candidates for an important role (Clark and Burgess, 1975, *op cit* , discussion in Goodwin, 1976), whereas some slowly adapting skin mechanoreceptors are very sensitive to tangential forces on the skin, and so signal digit position (Knibestöl, 1975) Experimentally, selective block of skin afferents leaving joint afferents intact is likely to be difficult to achieve, and furthermore difficult to confirm, because the criteria for block (or otherwise) of joint afferents are uncertain while their function is likewise still in dispute Loss of peripheral nerve function in *tabes dorsalis* or diabetic neuropathy may lead to catastrophic damage to joints (Charcot or neuropathic joints) and it is tempting to suppose that the function of joint afferents may be to prevent such damage by signalling extremes of joint distortion rather than the normal joint angles required for position and movement sense

It is a general principle of sensory physiology that afferent activity must be evaluated in the light of motor activity (cf MacKay, 1973) It applies with particular force to proprioceptors because none of the known receptor types signal joint position or movement uncontaminated by the effects of extrafusal or intrafusal muscle contraction (see Fig 2 in Goodwin, 1976; Fig 3 in Roland, this issue) Hence it is interesting that gallamine paresis increases the distortion of position sense seen during compression of springs of varying compliance In Helmholtz's (1866/1963) concept of the sense of innervation, central representations of motor commands are generated as sensory equivalents, to be subtracted in some way from afferent signals Since efforts

to move a totally paralysed limb do not result in illusions of movement (Goodwin et al , 1972; McCloskey and Torda, 1975, *oper cit* ) and attempts to move a totally paralysed eye similarly fail to produce movement of visual images (Siebeck, 1954; Brindley et al , 1976) such a mechanism does not seem to operate for position information An alternative way in which motor commands might influence perception could be by somehow gating the afferent input; in the absence of an afferent input or change therein the gating effect might not reach consciousness Something of this sort must be supposed to account for the normal accuracy of position sense during active muscle contraction

The sense of increased effort that accompanies fatigue, paresis or total paralysis seems more likely to arise from motor commands having a certain sensory equivalence, although one that is quite unrelated to movement and position sense The critical evidence is that effort is experienced in trying to move a limb, sensation from which has been abolished by anoxia This sensory block can be achieved with the temporary persistence of conduction in motor fibres, which allows objective movement of a finger accompanied by a sensation of great effort and by the conviction that no movement has occurred (Goodwin et al , 1972) McCloskey, Ebeling & Goodwin (1974 *op cit* ) showed that increases or decreases in the subjective effort of muscle contraction influenced the estimation of weights and tensions by human subjects It was suggested that subjective effort is often used to estimate weights of lifted objects and that it may be in part made up of centripetal or motor commands However, it was also found, especially on changing the instructions to subjects, that there appeared to be a more objective sense of muscle tension that allowed the appropriate matching of forces exerted by fatigued and nonfatigued arms in the absence of feedback from skin receptors Golgi tendon organs are candidates for subserving this mechanism Roland has shown that in estimates of spring compliance using gallamine weakened muscles subjects do not make errors as large as might be expected from the increase in their sense of effort This may provide an interesting stimulus to determine the rules whereby, for different cases, subjects utilize cues from the effort of contraction on the one hand and from more objective peripheral estimates on the other Both mechanisms do appear to exist, and subject instruction will not alter this but will influence the ways in which they are used

The cerebral areas in which position, movement and muscle tension are analysed are poorly understood physiologically, although they can be tentatively identified as lying posterior to the central sulcus The recognition of muscle afferent projections to area 3a of the post-central gyrus has removed earlier difficulties about accepting muscle afferent contributions to perception Areas 3a and b together receive the densest direct projections from the ventrobasal thalamus (Jones and Powell, 1973), which suggests a primary sensory role for the muscle afferents in full accordance with the preceding discussion Roland's findings on patients with cortical lesions are useful in confirming those of Holmes (1927)

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## by **Ragnar Granit**

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*Breaking down open doors.* I think that Roland is breaking down open doors in wanting to prove that proprioceptive impulses can reach consciousness This was shown in excellent papers by von Frey (1914, 1915, *op cit*, 1917/18, and 1926) Roland mentions two of them, but one should also explain that von Frey obtained virtually the same results in studies on human subjects with resected joints, anesthetized joints as well as with severed skin nerves in the moving finger The experiments of Renqvist cited by Roland also seem to me conclusive for the existence of conscious proprioceptive information

The Brindley-Merton (1960) experiment on eye movements is, I think, nullified by the experiment of Skavenski (1971) showing that the position of the eye can be perceived in a darkroom when controlled movements are introduced *in a sensible manner*

Illusions, like those of Loeb (1890) and Charpentier (see Flowrnoy, 1894), cannot be understood at all on any perception-of-motor-innervation theory

In my book (1977) I have indicated my basic standpoint to be that the brain is sophisticated enough to perceive consciously whatever information it may need to perceive that way Normally we do not bother wasting consciousness on largely automatized motor acts, but create the correct situation, as in all the experiments that I have mentioned, and the brain is up to it! Conscious awareness is the supreme executive for purposive responses to the environment

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## by **Peter Grigg**

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*On the attribution of a functional role to joint afferent neurons.* The article deals with sensory phenomena that are mediated by muscle and tendon receptors Information about joint receptors is obtained only indirectly in that no effects were observed pursuant to their anesthesia There is discussion of joint afferents, however, and of the role they might play in kinaesthesis Although the paper does not deal directly with the properties of joint afferents, it is important that references to their properties, cited in an important paper, should reflect a current understanding of their role In that regard, joint afferent neurons have been consistently referred to in the paper as being detectors of joint angle This is a view that is not consistent with the current state of the literature, since most joint afferent neurons have been shown not to discharge at positions that joints commonly occupy

The works of Skoglund (1956 *op cit* ) and Boyd and Roberts (1953) are cited as examples that demonstrate that discharge in joint afferents can serve as a signal for joint angle However, Skoglund's findings of joint afferents that discharge at intermediate joint angles have not been confirmed (Burgess and Clark, 1969 *op cit* , Clark, 1975; Clark and Burgess, 1975 *op cit* , Grigg, 1975 *op cit* , Grigg, 1976) Boyd and Roberts (1953 *op cit* ) also

described knee joint afferents that discharged at intermediate joint angles Their results, however, can be attributed to tension in the quadriceps muscles under the conditions of their experiment (Grigg, 1975)

There seems to be no disagreement that most knee joint afferents discharge only at extreme joint angles, a finding that Skoglund (1956 *op cit* ) himself reports Rather, the question is the extent to which joint afferents can contribute to position sense at intermediate joint angles Clark and Burgess (1975 *op cit* ), in an exhaustive search of lateral, medial, and posterior articular nerves (LAN, MAN, and PAN) failed to find more than 1 5% of MAN afferents and 6 5% of PAN afferents that discharge at intermediate angles of the knee Further, of the PAN afferents that discharged at intermediate angles, 78% appeared from the popliteus muscle that were contained within the PAN Ferrell (1977) reported that there are on the average, four afferents in the PAN that discharge at intermediate angles Furthermore, the sense of joint position in the hip (Grigg, Finerman, and Riley, 1973) and finger (Cross and McCloskey, 1973 *op cit* ) have been shown not to be altered by capsulectomy and replacement of joint surfaces

The correct attribution of a role for joint afferents should incorporate the findings that joint afferents discharge (a) when the joint is rotated into an extreme displacement (Skoglund, 1956; Burgess and Clark, 1969; Clark and Burgess, 1975; Clark, 1975; Grigg, 1975; Millar, 1973 *oper cit* ) or (b) when capsular tension is increased by contractions of muscles inserting into the capsule (Grigg, 1975; Grigg, 1976; Millar, 1973), or (c) when pressure is applied to the joint capsule (Clark, 1975) In the case of the PAN, discharges in most afferents appear to be directly related to capsular tension (Grigg, 1975) Tension in the posterior capsule is developed in extreme extensions (Grigg, 1975; Lavigne, 1974), and may be increased by axial or abductive rotations, or by contractions of certain muscles In the case of the MAN, discharge in some afferents is observed with extreme rotations, although capsular pressure is the best stimulus for most afferents (Clark, 1975) These observations led Clark (1975) to suggest a role for joint afferents as mediators of "deep pressure" sensations

The properties of joint afferents recorded in freely moving, unanesthesized cats (Loeb, Bak, and Duysens, 1977 and this Commentary) fully confirm the findings cited above for knee joints and, if anything, stress the lack of a joint position signal in afferents Primate knee joint afferents (Grigg and Greenspan, 1977) have been shown to be virtually identical to those in cats

It should be pointed out that the above findings reflect, primarily, observations that have been made on knee and elbow (Millar, 1973) joints Findings from costovertebral (Godwin-Austen, 1969) and hip (Carli, Farabolline and Fontani, 1975) joints have indicated that full-range receptors exist in those joints Therefore, it may not be possible to produce a single statement about the general properties of joint afferents, across joints

In summary, joint afferent neurons may not be considered to be simple detectors of joint angles In knee and elbow joints, some information about joint angles is contained within the discharge of some afferents However, this information relates only to joint angles at and around the limits of movement of the joint where the capsule is stretched and is resisting further joint rotation Further a given discharge rate in an afferent can be diagnostic of several positions of the joint in different axes of movement In some neurons, any information about joint position is confounded by the effects of muscular tension Furthermore, since there is substantial hysteresis in the discharge of capsular afferents (Grigg and Greenspan, 1977; McCall, et al , 1974) any information about joint position is further confounded by the effects of the previous history of the sensory ending

I reiterate that this commentary is directed at the framework within which Roland's work is interpreted rather than at the work itself My purpose is to prevent the reader from forming either incorrect views or, worse yet, simplistic views of the role played by joint afferent neurons

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### by **Anthony M. Iannone**
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**What constitutes "proof" in the study of neural control of movement?** Roland's experimental evidence clearly demonstrates that his subjects can make distinctions between springs of different strengths when all sensory inputs from the sensing fingers have been blocked, and in the presence of partial paralysis from local application of gallamine From these data Roland infers that signals from the muscles and tendons reach consciousness and that this then leads to a "feed-forward" type of control of voluntary movements While his experimental approach seems sound, his conclusions go far beyond any his data would permit This paper raises in a general way the issues of what constitutes "proof" when one studies the nervous control of movement

In any attempt to study voluntary movement the following conditions must apply: (1) There must be a precise measurement of the rate and distance moved at each joint involved in the movement; (2) there must be EMG monitoring of the muscles involved on both sides of the involved joint so that anterior horn cell outputs are identified; and (3) sensory inputs must be correlated with the relevant stimuli (muscle contraction or stretch of receptors) and the critical control loops must be identified (e g , monosynaptic reflex vs polysynaptic or long loop via cerebellum or cortex)

This is being done in more and more laboratories devoted to the control of movement Thus, Evarts and Fromm (1977) have shown that cortical motor units in the monkey can be identified which, when used during small precise movements, respond to kinesthetic sensory stimuli These same units, when used in ballistic movements, do not then respond to sensory stimuli In short, different types of control systems, which presumably depend on different controls (e g , visual vs proprioceptive), and different types of movement (slow feedback-governed or fast ballistic type movements) will all affect the type of control system activated in the nervous system

The type of movement selected will place different conditions on the nervous system A rapid ballistic type movement very clearly requires the nervous system to make a prediction about the number of motor neurons that must be simultaneously activated in order to produce a force sufficient to accelerate the limb to a speed that will produce the antagonist movement necessary to decelerate the limb to a stop a the end point of the movement Often the motor discharge ceases before the limb has begun to move, and this obviously cannot be involved in a simple feedback system The antagonist muscle can be activated by stretch, but has been shown to contract even in the de-afferented limb (Polit & Bizzi, 1977) In these circumstances it is clear that the nervous system uses all of the relevant sensory inputs and a "go" signal, or may tie visual inputs into the jumps in motor outputs necessary for such responses as visual tracking tasks It would be preferable if the type of sensory input or probable mode of conversion into motor output were identified as precisely as possible

I object to the use of the term "feed-forward" if the nervous system is acting in a predictive manner "Ballistic" or "fast movement" is an accurate enough term for limb movements, while "saccade" describes the same movements in the eyes In all instances the movements are "all or none" and not influenced by feedback during the movement The implication that there are at least two types of motor control systems is strongly supported

The question of conscious appreciation of motor activity can only be studied in the human Libet (1965 and this Commentary) has demonstrated that sensation is perceived in human cortical sensory areas only after a stimulating electrode achieves a strength sufficient to activate systems that project away from the cortex Stimulation of cortical motorneurones is associated with sensation of movement only when enough stimulation has occurred to produce a minimal motor response One can presume that the active discharge of pyramidal or corticothalamic neurones is associated with a "sense of effort" perceived elsewhere in the brain

Roland is to be commended for a thorough and useful review of a very confusing literature

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**Changing views of feedforward and feedback in voluntary movement.** It seems abundantly clear from recent work that muscle receptors play a significant role in voluntary movement control and that the information they convey has access to consciousness (Kelso & Stelmach, 1976; Matthews, 1977, for reviews) Roland surveys a number of different psychophysical experiments using peripheral blocking techniques to support this viewpoint Roland's work is important in showing that sensations of movement and muscular tension may be perceived during voluntary contraction Its overall relevance to the role of sensory feedback in ongoing movement control is less clear, however In this commentary I wish to present briefly quite recent data concerning this issue and to discuss a mode of control not considered by Roland Rather than provide a critique of Roland's specific experiments – for he has done that quite well – my goal is to expand upon the notions that he has proposed, in the hope of gaining a richer perspective on the problem

First, some prefatory remarks upon the general reductionistic approach adopted by the author In attempting to isolate the behavioral significance of feedforward, joint, muscle, and cutaneous inputs in human beings, Roland is subject to the criticism that there may be considerable redundancy in the information provided by these processes Merely because one source of remaining information appears functionally significant following the removal of others does not necessarily imply that it is of major importance in *normal* voluntary movement Although Roland opts strongly for the conscious significance of muscular afferent mechanisms, we must exercise some caution concerning the methodology upon which this interpretation is based Nerve-blocking techniques are traditionally plagued with problems, a primary one being the lack of independent evidence that the blockade on sensory motor fibers has been completely selective (See, for example, the debate regarding the use of the ischemic nerve block in human movement control in Kelso, Stelmach, & Wanamaker, 1974, 1976; Laszlo & Bairstow, 1976) In fairness, however, it is difficult to imagine how one can approach the problem addressed by Roland without using intervention techniques

An important point to realize in any discussion of movement control is that the relative degree to which movements are dependent upon feed-forward and feedback appears to be a function of the *mode of response* Roland alludes to this issue when he emphasizes the inability of subjects to use feed-forward signals in his kinesthetic matching experiment where no a priori information about the distance to be moved is available There is evidence from studies of limb movement (Brooks, 1974) and eye movement (Bizzi, 1974) that monkeys use feed-forward mechanisms and are totally

impervious to peripheral feedback manipulations when advance information regarding the movement is available In contrast, during exploratory-type movements where no advance information is available, peripheral feedback mechanisms are required to regulate movement An analogous case occurs in recent studies on movement reproduction accuracy in human beings (Kelso, 1977) In one experiment, blindfolded subjects (Ss) were asked to define their own finger movements (preselected) into target areas when deprived of kinesthetic feedback from joint and cutaneous sources via a nerve block applied to the wrist No significant differences in reproduction error were found between normal and deprived feedback conditions These results were compared to a situation in which Ss moved to an experimenter-defined stop (constrained) Deprived feedback Ss were unable to detect the locus of the stop, a factor that led to a large deterioration in reproduction accuracy relative to normal constrained performance

It seems unlikely that muscular afferent mechanisms are responsible for differential performance under preselected and constrained conditions When preselected, planned movements were unexpectedly obstructed – a procedure designed to elevate the excitability in the firing of tendon organs and muscle spindles (Vallbo, 1971) – Ss failed to detect the obstruction Instead, they perceived that they had executed the movement as desired Thus, they reproduced the movement into the specified target sector in spite of the fact that no original criterion movement had ever been made I interpret this set of results to indicate that feed-forward signals conveying the expected consequences of intended movement are used under preselected conditions When peripheral inputs are unavailable, S relies on the internal signals as the principal reproduction cue In contrast, the data on constrained, exploratory movements reveal the requirement of peripheral feedback if accuracy is to result The important message seems to be this: Task requirements (predictive or exploratory) can affect the relative degree to which the motor control system utilizes feed-forward and sensory afferent information

Throughout his paper, Roland refers to feed-forward signals containing information about desired movement *magnitude* or *extent* There is recent evidence that this view may not be correct (Bizzi, Polit, & Morasso, 1976; Bizzi & Polit, in press; Kelso, 1977) Kelso (1977) had blindfolded Ss reproduce selected movement amplitudes (extent) and end positions (location) under normal and deprived feedback conditions Extent and location information were manipulated by altering reproduction-movement starting positions Location accuracy was unaffected by the removal of kinesthetic inputs, while distance accuracy significantly deteriorated in all Ss Precisely the opposite finding would have been predicted had S been relying on feed-forward signals coded in terms of extent or duration Studies on head (Bizzi, Polit, & Morasso, 1976) and limb movements (Bizzi & Polit, in press) in monkeys have revealed results analogous to the Kelso (1977) experiment Final position (location) was always correctly reached both in normal and deafferented monkeys in spite of constant or inertial load disturbances applied during movement Achievement of final position may be viewed as primarily dependent upon the recruitment pattern of alphamotoneurons, which in turn determines the particular length-tension relationship for relevant agonist and antagonist muscles involved in the activity The final resting state of the limb is thus reached when the tension on agonists and antagonists is equal and opposite Like a mass-spring system, the steady state or equilibrium position is determined only by the system parameters established prior to movement (Fel'dman, 1966), not by a read-out of proprioceptive signals Further, the feed-forward signals appear to contain intended *position* rather than extent as Roland and others (e g , Brooks, 1974; Taub, Goldberg, & Taub, 1975) suggest

What then can we conclude about the role of sensory feedback in volitional movement? Two recent types of evidence bear on this issue The first is from work by Evarts and Fromm (1977), who found that short-latency cortical responses to limb perturbations were evident during precisely controlled small movements but were greatly attenuated in rapid, ballistic movements In agreement with Roland, sensory feedback from muscular sources appears to be relatively more important during slower movements

Further insight into the role of sensory feedback is provided by Bizzi and Polit (in press), who have shown that successful termination of movement under deafferented conditions is dependent upon an established spatial relationship between the animal and the arm apparatus When the deafferented monkey was placed in an unusual postural setting, pointing accuracy was greatly diminished In contrast, intact monkeys compensated

quickly for altered spatial relationships, indicating that a major function of sensory feedback is to *update* and *adjust* learned motor patterns rather than to assist movement execution This view differs strongly from closed-loop models that have had a powerful influence in human motor behavior research (Adams, 1971; 1976) Here sensory feedback is continually compared against an internal standard of the movement for ongoing regulation Clearly, the continuing reassessment of the role of sensory feedback in voluntary movement augurs well for the development of an integrated theory that will be compatible with behavioral and neurophysiological data

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*by* **M. Levitt**
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*On the role of mental set in voluntary movement.* We are ostensibly considering two distinct domains of neurophysiology: somesthesis and voluntary movement Current interests focus upon the role of somesthesis in the regulation of voluntary movement, and here Roland has made outstanding contributions by means of his experimental analyses, literature review, and discussions Yet the theoretical problems are with us, and concepts are not always well defined, or appropriately employed

I believe it is somewhat unfortunate that at the outset Roland felt obliged to introduce the term "consciousness" because of the precedent established by earlier authors The difficulty here is the implication that somatic afferent or reafferent neural activity must necessarily provide a sensory content of consciousness (especially if that neural activity reaches the sensory cortex)

The conclusion that perception as well as sensorimotor regulation is *not* entirely dependent upon conscious sensory contents dates back at least as far as Helmholtz (Boring, 1950, pp 308–11) Indeed, Helmholtz spoke of unconscious inference To assert that discrimination is an index of consciousness begs the question Clearly, Roland is cognizant of this conceptual problem, for he later states, "It is therefore possible that the sense of tension and muscular kinaesthesis are simply signals from this afferent path that do not under normal circumstances intrude into consciousness but can do so if required (for example, in experiments like those reported here)" He then proceeds to suggest that voluntary movements and the successive judgments of movement parameters are based upon afferent or reafferent information that is stored in memory

Without intending to detract from Roland's contributions, I wish to suggest that the conceptualization of the issues might be clearer if we do not equate neural "information" with conscious sensation It is not necessary to assume that the neural "information" in question must give rise to a sensory content of consciousness The weakness of this assumption could be the basis for the negative findings in some prior investigations on the effects of direct stimulation of muscle receptors or their afferents

I would like to elaborate a little on this matter, using the example of position sense From studies of transformations of joint afferent information at the thalamic level, it has been suggested that position sense is encoded intensively (Mountcastle, Poggio, & Werner, 1963) That this is not obvious from introspection, and seems paradoxical, is indicated by those investigators Another viewpoint, suggested by Paillard and Brouchon (1968, pp 37–38), is that position of body parts has "local sign" with reference to body space They further suggest that muscle afferents might play a role in the assignment of local sign to body parts They then pose the rhetorical question, "What are the conscious counterparts of the 'local signs' of each conscious sensation?" (p 49) The suggestion is that there are none, other than an "awareness " Nonetheless, even these authors seem to assume that joint receptors provide the core sensation, the calibration of which arises from other receptors I submit that introspection does not reveal a sensation referrable to joint receptors any more than local sign can be considered a sensation I believe this might also be true in some of the other forms of "sensibility" that Roland discusses

Concerning discriminative performance we can raise theoretical questions, amenable to experimentation, without invoking the concept of sensation as a content of consciousness This is really what was done in Roland's experiments dealing with matching judgments of extent, force, or effort The theoretical questions pertain to those performances insofar as they are affected by blocking certain peripheral afferents, or neuromuscular junctions, or by instructions The question of whether or not these discriminative performances derive from conscious sensations is a separate theoretical issue

Additional comment on the subject of position sense is in order Roland prefers the term "statognosia" as a substitute for the familiar *sense of passive movement* or *sense of passive limb position* He then cites the report of Cross and McCloskey (1973 *op cit* ) as evidence that muscle afferents contribute to "kinaesthesia " But kinaesthesia was defined by Roland as "perception of change in the position of a limb due to muscular contraction" or active position sense Quite clearly, the report of Cross and McCloskey concerned the preservation of statognosia rather than kinaesthesia in patients after surgical removal of joints They offer their findings as evidence for the likely role of muscular and cutaneous receptors in position sense Similar conclusions are suggested by some unpublished observations made in my laboratory in collaboration with Janice Levitt

We had trained three monkeys to discriminate passive positions of the leg, that is, extensor positions after rotation of the knee joint Rate of limb movement was randomly varied, and vision was occluded Measured difference limens indicated precise sensibility In other animals, this ability was seriously impaired by homolateral thoracic spinal hemisections (Liebman & Levitt, 1973). Nonetheless, and to our astonishment, this ability was not at all affected by injections of large doses of local anesthetics into and around the knee joint capsule, or by surgically interrupting the posterior articular nerve Additional subcutaneous injections of local anesthetic at pressure points were of no avail Performance was impaired in one instance after extensive tenotomies, and articular anesthesia, at the knee; however, the limited passive mobility of the knee joint after tenotomies (due to surgical scars) was cause for cautious interpretation

A remarkable conclusion derives from the experiments of Roland that in-

volve manual compressions of a strain gauge In this situation, cutaneous and joint afferents were bilaterally blocked and the left hand was made gallamine paretic With their paretic left hands, Ss pressed the strain gauge to a degree announced by an auditory signal; then there was a matching trial with the right nonparetic hand (presumably in the absence of an auditory signal) The results obtained in this situation were found to depend upon S's mental set as determined by the particular task instructions When Ss were instructed to match forces, it was found that no systematic errors occurred; however, when Ss were instructed to match efforts, there resulted systematic errors of overestimation This latter result was taken to support the concept of a "sense of effort," whereas the former finding was interpreted in terms of a "sense of (musculotendinous) tension " In a subsequent discussion of related experiments by others, Roland suggests that whether performance is based upon the sense of tension or the sense of effort might depend upon "how Ss are instructed "

Apart from the matter of the validity of these concepts (senses of tension or effort), it must be admitted that the pronounced effect of instructions is quite significant; not only in the date, but also theoretically In the parlance of experimental psychology, such efforts are usually interpreted in the dynamic terms of mental set Historically (Boring, 1950, pp 147–49), the importance of mental set as a determinant of perceptual-motor performance in human reaction became recognized in the late 19th century These studies indicated that reaction times systematically depended upon whether Ss attended to the stimulus or to the response This was surely a difficult finding for classical psychophysics, but probably no more challenging than are the similar results that Roland deals with that concern simple voluntary movements

Furthermore, Roland discusses the studies of Hammond (1955, 1956, *op cit* ), in which it was found that a second component of the EMG response to perturbation was dependent upon the mental set of the Ss Indeed, this second component has been labelled "intended component" by Evarts and Tanji (1976 *op cit* ), and has been related by them to the "intended pyramidal tract neuron discharge " In those studies, the second or intended responses were determined by S's instructed mental set

Hence, pyramidal tract neuron discharges, EMG responses, sensorimotor reaction times, and systematic errors of voluntary movement are all determined by S's mental set Contemporary neurophysiology, striving to comprehend the elemental neural mechanisms of proprioception and motor control in the analytic terms of input and output, must acknowledge and contend with the pervasive dynamic central process that underlies mental sets Could it be that the circuitry of this process is in part congruent with the circuitry of the postulated transcortical servo loop, or that of corollary discharges? Perhaps neurobehavioral studies of "attention" (Velasco et al , 1975) or "anticipation" (Tanji & Evarts, 1976 *op cit* ) will shed light on these matters

In summary, the main point of my commentary is that voluntary movement and discriminative performance need not be conceptualized in terms of conscious sensations, or indeed the sense of this or that If we find that we must employ psychological concepts (and this is becoming increasingly apparent), evidence indicates that other concepts are more appropriate That evidence derives from psychological and neuropsychological observations, which implicate dynamic processes of "anticipation," "attention," "awareness," "intention," "purpose," and so forth

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## by B. Libet

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*What is conscious sensory experience, operationally?* My commentary is directed primarily to the question of whether the paper by Roland has demonstrated that tension information from muscle receptors does in fact "reach consciousness " Since the answer to this question depends on the criteria adopted to indicate a conscious response, I must briefly consider what operational definition of a conscious sensory experience may be acceptable

The case for an ability of muscle and tendon receptors to subserve discrimination of different tensions is well supported in Roland's work by several lines of effectively developed experimental evidence—in what one could say is a *tour-de-force* for an investigation in human subjects The conclusion that "muscle receptors signal kinesthetic information" seems justifiable But the further conclusion, "that these signals reach consciousness," is based on a serious conceptual confusion that must be clarified The confusion is immediately introduced by the kind of operational definition chosen to signify consciousness (The noun "consciousness" itself carries implications that are better avoided here; what is really meant is the process or event of "conscious experience ")

Conscious experience of sensory information is equated by Roland with the subject's ability to employ such information in making a successful discrimination between different degrees of applied tension and of movement magnitude In the experimental design, the subject (S) was asked to choose which of two springs was the stronger one This was a forced choice situation, in which S has to decide between two alternatives even if it should require guessing or hunches, etc S was not asked whether he subjectively felt a difference in tension; nor was S given the option of reporting that he felt no difference With this procedure, the successful discrimination between spring tensions by S is obviously an indicator that appropriate sensory information was *detected,* but it does not necessarily indicate that S was subjectively *aware* of the sensory information The distinction between a conscious sensory experience and other kinds of detection has been confronted by us in connection with our investigation of cortical activities that may uniquely subserve conscious experience (see Libet, 1966, 1973; Libet *et al*, 1972, 1975) There are many examples reported in which detection of a difference between sensory inputs is made unconsciously One of the most sophisticated is that in the work of Shevrin and Fritzler (1968), in which word associations by a subject can be modified by a visual stimulus difference of which S is completely unaware Another is the striking finding by Weiskrantz *et al* (1974) that an individual with a cortical lesion that prevented conscious vision for a part of the visual field, could nevertheless correctly detect the location and nature of some objects in that blind area when asked to do so in a quasi-forced choice manner

Conscious or subjective awareness of something can only be viewed in terms of direct introspective self-cognition It is experienced and known privately by each individual It is a primary phenomenon, whose nature cannot be defined in an *a priori* way by recourse to any other form of observation, whether molecular or behavioral (see Libet, 1966, 1973; Doty, 1975; Creutzfeld and Rager, in press) How, then, can one person investigate it scientifically in other persons? The premise that other individuals can and have experienced what each of us experiences subjectively and privately would have to be, and in fact is, commonly conceded and accepted by us We must then ask the subject an appropriate question about his subjective experience, a question that we are confident he understands and about which he can give us a report The essence of the question about a conscious experience of sensory input must be – what did you feel? Handled in this way, it turns out that conscious sensory experiences can be studied with the same kind of consistency and reliability as can other indicators of sensory detection (e g, Libet *et al*, 1964; Libet, 1973) However, relationships with sensory inputs and other variables obtained by this approach show certain striking differences from those obtained by study of other indicators of detection, and these very differences can provide important clues to neuronal processes uniquely associated with the "production" of a conscious experience (e g, Libet, 1965, 1973)

In Roland's investigation, the subject was asked to make a forced choice between two alternative spring tensions For the purpose of studying conscious sensory experience S might instead have been asked if he actually *felt* that one spring tension was stronger than the other, i e, without a guess

or hunch about there being a difference The primary concern would be with the subject's own introspective experience, regardless of a real difference between the two springs With such a concern S obviously might report that both springs felt the same to him, a possible report that is excluded in the forced choice approach Indeed, it is probably the difference in terms of the questions asked of the subjects that accounts for the difference between the conclusions drawn by Roland and by the earlier investigators quoted in the introduction concerning conscious sensory experience of muscle receptor inputs For example, Gelfan and Carter (1967, *op cit*) asked their Ss to report what they felt when their exposed tendons were pulled The negative reports by their Ss are valid indicators that changes in muscle length or tension were not consciously experienced It cannot be assumed that Gelfan and Carter's approach simply elicited responses having a cruder quantitative nature than those of Roland; their question to Ss elicited information that was qualitatively different from Roland's One can in fact argue, taking the two kinds of investigations together, that the discrimination elicited in Roland's experiments was made unconsciously by his Ss, without their actually subjectively feeling tension differences In another kind of study of an autogenic inhibitory role for tendon afferents, it was found that local anesthesia of the tendon could result in a remarkable increase in the level of a maximal voluntary effort, as judged by change in EMG (Libet *et al*, 1959) This change in capability for a voluntary action occurred without S's being aware of any difference in this capability, and appeared also to be independent of changes in conscious sensation in the vicinity of the tendon

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## by D. I. McCloskey

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*Sense of effort and sense of muscular tension.* Roland's studies demonstrate that normal people have both a sense of the outgoing voluntary motor commands that they employ and a sense of the intramuscular tensions that these commands produce His work is particularly valuable in measuring the acuity of the sense of muscular tension

I am concerned at the emphasis he places on this sense of muscular tension His subjects were carefully instructed that "although they might notice

that great effort was required . . it was not, in fact, their efforts that were of interest but the actual force produced." If both a sense of the motor command, or effort, and a sense of achieved tension exist, then the specific instruction to pay attention to the latter and to ignore the former can lead only to a demonstration that subjects "do not rely on feed-forward signals of force " This conclusion, however, applies only to the contrived conditions employed in his tests

If the instructions given are deliberately designed *not* to specify which sense should be heeded, then the performances of a subject will reveal which sense he normally relies upon Thus, for example, if a subject is asked to produce a tension or to lift a weight on the reference side, and then simply "to make the other side the same," he is free to select whichever sensation he likes to guide him He does *not* choose the sensation of muscular tension, but prefers to be guided by the magnitude of the voluntary effort he employs This is so when the relation between motor command and achieved muscular tension is disturbed by muscular fatigue (McCloskey et al , 1974; *op cit ;* see also Goodwin, this *Commentary*), by partial neuromuscular blockade (Gandevia and McCloskey, 1977a,b; *oper cit* ), by the inhibition of motoneurones through use of vibration to activate muscle spindles in antagonists of the contracting muscle (McCloskey, Ebeling and Goodwin, 1974; *op. cit* ), by the unilateral hypotonia of cerebellar disease (Holmes, 1917), or by simple motor "strokes" (Gandevia and McCloskey, 1977a; *op. cit* )

Roland makes the simple prediction that perceived signals of the motor command should "increase in proportion to the degree of paresis " The "expected error" lines on his Figures 8 and 9 are based on this prediction However, the prediction does little to assist analysis as it assumes (amongst other things) linear relations between command and achieved tension, and between the command signals and the sensations provided by their collaterals or "corollaries " Such assumptions cannot be made with any confidence. Moreover, as Roland concedes, the prediction ignores the contributions of muscle and other reflexes to normally achieved tension One further complication, which is not mentioned by Roland, arises in experiments using the neuromuscular blocker, gallamine Gallamine competes with the neuromuscular transmitter, acetylcholine, for receptor sites on the motor end-plates As only a portion of the motor units are recruited in any submaximal contraction, it follows that acetylcholine is constantly released onto the motor end-plates of only these motor units It is likely that these motor units (and only these) are selectively "unblocked" by this process If so, subjects would be making their submaximal contractions with normal muscles using normal efforts, while their infrequently made maximal contractions remain weakened by the gallamine Evidence that just such a process occurs has been documented elsewhere (Gandevia and McCloskey, 1977b; *op cit* )

Roland states that "it cannot be excluded that afferent signals from muscle spindles are the basis of the sense of effort " This is not so Vibration of the tendon of a muscle evokes an involuntary reflex -- the "tonic vibration reflex" (Hagbarth and Eklund, 1966; DeGail, Lance & Neilson, 1966) -- by exciting the muscle spindles of the vibrated muscle Such excitation does not cause a sensation of effort, or heaviness, as would be expected if the discharges of the spindles give rise to the sense of effort Instead, the "subject gets a feeling of relief or lessening of tension" (Hagbarth and Eklund, 1966) The involuntary contraction caused by vibration reduces the voluntary effort a subject must make to achieve a given tension, and the perceived muscular force is actually *reduced* during spindle activation (McCloskey, Ebeling and Goodwin, 1974; *op cit* )

Roland also suggests that the perception of effort may be, in fact, no more than the perception of the increases in heart rate and blood pressure that accompany efforts I know of no evidence that heart rate and blood pressure can be perceived as is claimed

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*by* **Julian Millar**
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**Lab strategy vs. life strategy.** I think Roland's is an important paper in that it presents evidence that may reconcile the two opposing views of how we judge the position and movements of our limbs in space (when we cannot see them) and how we judge the weight of objects Roland's arguments are persuasive, for he suggests that (as in many areas of psychology), the answer is not always either one strategy or the other, but that the strategy used by an individual depends on the particular task and particular instructions he is given

The first part of the paper, dealing with the effect of local anaesthetic block on finger joints, confirms earlier evidence (e g , Provins, 1958 *op cit ;* Browne, Lee and Ring, 1954) that this procedure severely impairs the appreciation of *passive* movements However, most joint movements we experience are either aided or opposed by our muscles and can be termed *active* The early papers cited above suggested that during active movements some source of information other than from joints was available to consciousness This "other" source has been suggested to be either a "sense of effort" (i e , monitoring the outflow from the forebrain, possibly via pyramidal tract collaterals to somatosensory cortex) or input from the muscle receptors

The fact that we are able accurately to discriminate the weight of handheld objects has always seemed to be powerful evidence that muscle receptors, in particular golgi tendon organs, can access consciousness, since the physical sensitivity and properties of these organs seem ideally suited for the appreciation of "weight " Accordingly, I was delighted to read Roland's report on the experiment with compressible springs, which seems to be fairly conclusive evidence that information from muscle receptors can reach consciousness

Many authors appear to equate "muscle receptors" with muscle spindle receptors There is certainly something unique about the central connections of spindle primary afferents, and it may well be that they do not reach consciousness (in this context the work of Swett and Bourassa [1967 *op. cit* ] is particularly compelling) However, golgi tendon organs interact with skin and joint receptors in the spinal cord (Lundberg, Malmgren, and Schomberg, 1975), and I agree with Roland that they are probably the receptors involved in the appreciation of the strength of springs in his experiments The experiments with gallamine are particularly pleasing in that they clearly demonstrate that a "sense of effort" explanation of the appreciation of weight or force can be ruled out in most cases, unless the subject is particularly instructed to use this means of cognitive assessment Roland's experiments do not tell us how we bias ourselves in normal life – whether to golgi feedback or "effort" feedforward, but the experiments suggest that feedback is much more accurate

The experiments are interesting also in that one can see (Fig 8) that with skin and joints anaesthetised, there is a great deal of uncertainty in matching weights, indicating that skin and joint afferents do normally combine with golgi organs to aid discrimination, although the latter may be able to function on their own

I found the section on the results of kinesthesia testing with brain-damaged patients less satisfactory The presentation was somewhat confusing, and the results did not seem to add materially to the points made in the first section The discussion was again very interesting, and if I have any criticism, it is that this is a very long paper, with an introduction and discussion that go far beyond the experiments I feel that the impact would have been greater if it had been split down, say into two research papers (one on the normal subjects, one on the patients) and a review

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**Musculotendinous receptors in conscious human behavior: experimental factors.** The stated purpose of the experiments described in this article is

two-fold: 1) to show that the musculotendinous receptors signal information to the cerebral cortex for use in conscious behavior, and 2) to show that nonsensory "feed-forward" information (efference copy and corollary discharge) resulting from the motor program itself is also available for conscious behavioral discriminations The clear demonstration of these goals is important for the understanding of the fundamental properties of the brain as well as for clinical applications Moreover, there are now available in the literature on invertebrate neurophysiology and behavior examples of motor programs, steering by afferents, and feed-forward mechanisms, some of which can potentially be understood on the level of individual, visually re-identifiable neurons (Kennedy & Davis, 1976)

The described experiments, however, have failed, in my opinion, to supply convincing evidence for either of the stated goals The reason for this lies in the nature of the experimental procedure itself that was used in all of the reported studies The experimental method requires the subjects to use the thumb and index finger to compress springs of different strengths or similar springs through different distances The remaining three fingers are maintained in a "maximally flexed" position Such movements of the thumb and index finger require the use of intrinsic muscles of the hand as well as the extrinsic muscles in the forearm The reported method of anesthesia deadens the skin of the thumb and index finger, their joints, and associated joints proximally to (and including) the carpometacarpal joint However, this procedure leaves the skin and joints of the remaining three fingers, the skin and joints of the palm and wrist, and the skin of the forearm sensitive Movements of the thumb and index finger can cause distortion of the palm; the three flexed fingers can be further coactivated along with movements of the thumb and index finger; movements of the tendons of the extrinsic muscles can be transmitted to the rest of the wrist and palm via the connective tissues and circular supporting retinaculum; the extrinsic muscles can move and distort the skin of the forearm These are only a few of the sources of pressure, skin and joint afferents, besides those of the thumb and index finger, that can supply information to the cerebral cortex for use in discriminative behavior Although these signals may be small, they nonetheless may be sufficient for accurate discriminations

Similar objections may be raised in all the studies In the experiments on the evidence for feed-forward signals, there is a further complication since the subjects were instructed to pay attention to their *efforts* rather than to the sense of tension While it is possible that there exists a central memory for motor orders, it is also possible that the observed discrimination behavior is related to a memory of sensory reafferents from the hand, the forearm and other body areas that are involved in the "effort" to perform the task and that activate receptors that are known to project to the cortex and are used in conscious behavior Finally, the lesion studies are subject to another objection inasmuch as they perforce have resulted from experimentally uncontrolled and relatively nonspecific damage, as already noted by the author

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by **Karl H. Pribram**

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*Movements and acts: distinguishing their neurophysiology* Roland has presented us with a review of a fascinating series of studies The ingenious use of curarized limbs in human subjects has provided a wealth of important information regarding voluntary movement in man Roland clearly differentiates sense of tension from sense of effort and shows that under the appropriate circumstances a subject can be aware of either or both He further shows that feedback is an essential ingredient of the organization of movement but that this feedback arrives too late to be of any concurrent use in any particular movement

Despite these very beautiful demonstrations and analyses there are some confusions in the paper that are worth comment The hope is that these comments will address the final question put by Roland: "Could it be that the principal importance of force information from the periphery is to update the cerebral cortex with data about the consequences of voluntary contraction?"

First some critique Roland uses discrimination as evidence of conscious awareness Although I believe that in the way Roland's experiments were accomplished, this is a reasonable assumption, it is by no means a necessary one Weiskrantz et al 's observations (1974) on "blind-sight" after selective removal of striate cortex with consequent hemianopia have shown that awareness and the ability to make discriminations instrumentally can be clearly dissociated

Second, Roland opposes feedback and feedforward mechanisms throughout his paper as if they were mutually exclusive Pribram (1971, Chap 5; 1976) has proposed a model of feedforward that is made up of connecting two or more feedback loops into a parallel process open loop system In describing the development of constancies, Ashby (1960) and McFarland (1971) have made somewhat similar proposals Thus, what needs to be demonstrated is not that feedbacks are unimportant but that two or more of them are operating in parallel P B C Matthews' (1964 *op cit* ) extensive review of the double gamma innervation of each muscle spindle as simultaneously providing "relatively independent control of the 'bias' and of the 'damping' of the servo loop" can be interpreted to furnish the requisite physiology for such a parallel process coupling of feedbacks (see Pribram, 1971, Fig 12-5) Feedforwards are thus part of the basic machinery of the motor process–not only because of the two types of gamma efferents but, by the alpha-gamma linkage, as Roland quotes Granit as stating: "the periphery itself is corollized by alpha-gamma linkage "

Finally, there is some evidence for believing that "the importance of force information from the periphery is to update the cerebral cortex with data about the *consequences* of voluntary contractions " Pribram et al (1956) performed a series of experiments on monkeys in which motor cortex had been extensively removed Careful cinematographic analysis of behavior in free situations and during problem solving showed that no individual muscle was paralyzed nor was any particular movement impaired Not even sequences of movements were altered unless the lesions extended medially into the cingulate cortex or forward into the engranular frontal cortex Despite this, skilled latch box performances were severely slowed and became clumsy These results were interpreted to indicate that the motor cortex encodes actions, not movements or muscles (though these are represented functionally and anatomically) Acts were defined as the *consequences* of movements The puzzle remained as to what these consequences consisted of, and how they could be cortically encoded Tentative answers to these questions were suggested by the experiments of Bernstein (1967), who filmed the path of joints while the subject was performing relatively repetitive acts and showed that these paths described wave forms Fourier analysis of the wave forms allowed reasonable predictions to be made of the subsequent course of the actions The possibility thus suggested itself that the motor cortex performs a similar frequency analysis, using the forces generated around joints as data (Pribram, 1971, Chap 13) To some considerable extent the results of Evarts' (1967) microelectrode experiment support this proposal

Roland's most interesting results, those he reviews and the additional ones noted above (and the more recent work of Bernstein's students – e g , Gel'fand et al [1971] and of Turvey and his group [1973 and this Commentary]) affirm the hierarchical nature of motor control Roland's contribution, I believe, is that he has shown that conscious awareness can tap this hierarchy at several levels and is not limited to some overall sense of effort presumably produced only by the operation of the highest level of interpretation

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*On intellectual compensation and deafferentation.* Data presented in Roland's paper indicate that human subjects can make accurate discriminations of the force required to compress springs of different stiffnesses in the absence of sensory feedback from skin and joints The author's conclusion, however, that there is no difference between normal subjects and those whose skin and joints were anesthetized is difficult to evaluate without more data Curve-fitting constants and correlation coefficients for the data presented in Figure 5 would have been useful in this regard From inspection of this figure it appears that thresholds were, in fact, slightly elevated in the anesthetized groups

The author goes on to address the question of whether these force discriminations, involving active movement of the fingers, are based upon central feedback of the neural activity initiating the movements ("sense of effort"), or upon the activity of musculotendinous receptors To modify the relationship between central discharge and the movement that it evokes, he paralyzed one hand of the subject with gallamine Under this condition there was no systematic error in force matching, but its overall accuracy decreased One aspect of the experimental design, however, makes this result difficult to interpret In subjects treated with gallamine the skin and joints of both hands were anesthetized, whereas in those not treated, only one hand was anesthetized Thus, one cannot determine the relative contributions of anesthesia of the reference arm, paralysis of the indicator arm, and any interaction between these factors, to the observed differences, or lack thereof Another reservation about the gallamine experiments concerns the fact that subjects were well aware from the instructions and from their own observations that the paralyzed hand was weaker than the other hand Is it not possible that discriminations were made using sense of effort as the major cue by compensating *intellectually* for the greater effort required by the paretic hand?

The author presents data indicating that human subjects can make discriminations based upon effort and discusses the evidence that at least some movements can be generated in the absence of feedback from any somatic structures The studies of Taub and collaborators are especially important in this regard Taub (1976) has recently shown that monkeys whose forelimbs were deafferented ⅔ of the way through gestation were similar in their spontaneous and conditioned movements to those deafferented at birth This study provides further evidence of the ability of the central nervous system to function autonomously in the performance of some voluntary movements This does not mean, however, that feedback from somatic structures, whether available to consciousness or not, is not used in the performance of movements in normal animals Closer examination of deafferented animals will probably reveal ways in which their movements, and their responses to externally applied perturbations of those movements, differ from those of normal animals For example, cats having one deafferented hindlimb recover the use of that limb for locomotion, but the posture of the limb never returns to normal (Goldberger and Murray, 1974)

As intriguing as the present experiments are in demonstrating the sensory capabilities of human subjects lacking afferent input from skin and joints, one hopes that they will be followed up by behavioral studies of animals in which the mechanical linkage between muscles and joints and the input from

selected nerves can be surgically interrupted Classical or operant conditioning techniques could be used to measure the animal's ability to make discriminations of muscle tension, joint rotation, etc Further, as pointed out by Matthews (1977), it is important that the contradiction between the two studies involving direct stimulation of tendons and muscles in human subjects (Gelfan and Carter, 1967; Matthews and Simmonds, 1974 *oper cit.*) be resolved by independent replication

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*The transmission of parameters by neural messages.* The questions posed by Roland in his paper are of great interest to students of motor control, but in assessing his contribution to providing answers it is necessary to note the way the terms in his argument change their meaning as the argument proceeds Consider, for example, the following two statements (which are not direct quotations): (1) Nerve impulses initiated at particular sense organs, e g , muscle spindles and tendon organs, can be traced to the cerebral cortex (2) A human subject is aware (conscious) of certain classifiable attributes, e g , spring stiffness, of test objects placed in his hand These statements belong to different realms of discourse and while it is convenient to suppose the statements to be related to one another, we need to be very careful about the significance of terms such as "signal" that might be used in either domain In Roland's paper, the argument appears to slide repeatedly from one domain to the other and back again This remark must not, however, be taken to imply any disparagement of this particular author since the phrases he manipulates are familiar items in the accepted currency of present-day neurophysiological debate

When discussing motor control in a context of servomechanisms it is usual, but not mandatory (Roberts, 1952, 1966b) to speak in terms of such physical variables as force, displacement, and their time-derivatives or ratios But these variables have no precise counterparts in the impulse traffic within the nervous system (Roberts, 1973) In the transduction process at any mechanoreceptor the generation of nerve impulses depends on dynamic as well as on static aspects of the stimulus (Roberts, 1966a), the relative proportions of these components differing for different receptors There is, however, no way in which the individual contributions can be deduced from the resulting impulse stream Effects attributable to displacement, to rate-of-change of displacement, and to the history of previous changes in displacement, are all combined into the single variable: the repetition interval between successive nerve impulses It is therefore misleading to state that a receptor signals *both* displacement and velocity The signal does not indicate the magnitude of either of these components, but only that of a combination including also some effects of adaptation The neural discharge from a receptor may be likened to the indication of a weighing machine where the weight of a basket of fruit does not indicate how many of the fruits are oranges and how many are apples or pears

Further complications arise if we wish to suppose the neural signals to be subject to arithmetical manipulation by analogue-computing elements as would be required for an error-driven servomechanism Even the notion of impulse-frequency itself needs rather careful definition where successive intervals are unequal (see Roberts, 1973) In a pathway that includes relays, any quantitative aspects of the neural signal must be profoundly modified during the passage of that signal through each relay because of the complexities involved in the convergence of excitatory and inhibitory synaptic events In consequence, a good deal of caution is appropriate in interpreting such statements as "force information reaches the cerebral cortex "

The experimental part of Roland's paper is concerned with tests of the effects on the discrimination of spring stiffness that are produced by various

types of sensory blockade Subjects are instructed to select the stronger of two springs after compressing them between finger and thumb The ability to discriminate is taken as evidence of consciousness It has been shown, however, that the responses to muscle stretch in the decerebrate cat are influenced by the compliance of the load presented to the muscle (Roberts, 1963) This implies some discriminative ability even in a reduced preparation deprived of any possibility of consciousness If the criterion is altered to require signs of concept recognition, this objection disappears without affecting the rest of the argument

For a linear spring, the force at a particular length depends on two parameters, slope and offset Only one of these, slope (= stiffness) is taken into account in the analysis Consideration is given to the force needed to accelerate the parts of the capsule containing the spring, but forces needed to move the fingers themselves are ignored, together with all the background motor activity that occurs in the arm, shoulder and trunk in association with a voluntary finger movement and which cannot be entirely eliminated by any routine of immobilization and support It is not realistic to treat the control of the arm and hand as identical to that of a mechanical grab attached to a rigid support

The author discusses the voluntary regulation of alpha and gamma motoneurones from the cerebral cortex but says nothing of the background activity contributed by the basal ganglia and cerebellum Some adjustments of postural fixation and of weight transfer can be expected to accompany any voluntary activity as a matter of course and the neural activity, both sensory and motor, associated with such adjustments must be presumed to play some part in our perceptual discriminations of the interaction between the body and its environment

The remarks made earlier about the relation between impulse traffic and physical parameters should be borne in mind when discussing the "efference copy" and the "reafference principle " When considering the possible feed-forward of movement parameters one meets the additional complication that the force developed by a motor unit is not uniquely determined by the activity pattern of its motoneurone but is also greatly dependent on the mechanical loading (Roberts, 1967) One also needs to take account of the nature of the task being performed, since different tasks call for different strategies of motor command (Roberts, 1976)

While it is reasonable to suppose that our experiences and our conclusions about external objects are in some way related to the activity of our nervous systems, we must not forget that this activity consists entirely of successions of activity-cycles in individual neurones Physicists' variables, such as force and length, are not directly represented Our conclusions about such abstract parameters are based upon recognition processes as elaborate as those involved in distinguishing the faces of our friends or the validity of a signature on a cheque What this paper serves to demonstrate is that we can continue to perform such recognition acts even in the face of considerable modifications to our sensory equipment We are familiar with extensions of the sensory base by the use of tools Here we see that some discriminations survive the restriction of the sensory base by particular kinds of anaesthetic blockade It is not necessary to accept the author's conclusion that the persistence of some discriminative ability in the conditions specified implies that "force information derived from musculo-tendinous receptors reaches consciousness "

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*Sensory feedback during eye movements reconsidered.* Roland's experiments and review of the literature call for a critical reconsideration of the significance of muscular feedback in the programming and execution of voluntary movements in man Research on oculomotor control adds to the list of experiments that must be considered Eye movements are particularly interesting because muscle load and eye position are in an essentially invariant relationship (cf Matin, 1972) Therefore, although muscle receptors could not indicate the position of limbs, which are continually subjected to varying loads, they could indicate eye position reliably

Until recently, eye movement experiments have been interpreted in favor of feed-forward models For example, Robinson (1964) and Stark (1971) fixed one eye of human subjects so that attempted saccades were transformed into isometric contractions Because there was no modulation of tension, it was concluded that muscular feedback was not available Similarly, Keller and Robinson (1971), recording from motoneurons in the abducens, failed to find a stretch reflex in extraocular muscles of rhesus monkeys Another observation, which is often cited in favor of feed-forward models, is the fact that humans have poor conscious sense of eye position (Brindley and Merton, 1960, *op cit ;* Irvine and Ludvigh, 1936) And finally, some perceptual illusions have been interpreted in favor of feed-forward explanations (cf MacKay, 1973; Skavenski, Haddad, and Steinman, 1972)

One of these can be observed by lightly pressing the side of your eye with your finger When the eye is moved by an external force in this manner, the world is seen to move in the direction opposite to that of the eye Another illusion of movement is seen when eye movements are mechanically restrained or inhibited by paralysis The first illusion is caused by the perceptual system failing to take into account passive eye movements; the second is caused by the perceptual system erroneously registering attempted eye movements Helmholtz (1866), and many others after him, have assumed that (a) muscle feedback is present but feed-forward is absent during passive movements and that (b) feed-forward is present but feedback is absent during inhibited eye movements Under these assumptions, the failure to take into account passive movements and the erroneous registration of inhibited eye movements indicate that the perceptual system monitors feed-forward signals

All these experiments and interpretations can be criticized as follows (cf Shebilske, 1977a):

(1) Experiments with isometric contraction are not conclusive since muscular feedback may not distinguish between uninhibited and isometric contractions, as Roland noted in his paper

(2) Experiments with monkeys must be interpreted cautiously since, as Roland pointed out, instruction-induced mental set is crucial in experiments that demonstrate the significance of feedback (cf. Skavenski and Steinman, 1970)

(3) Conclusions about conscious eye position must be reconsidered Skavenski (1972) showed that subjects can detect passive eye rotations as long as the external force is applied properly and subjects have the appropriate instructional set to maintain their eye position This ability is much poorer than the same subjects' ability to use muscular feedback to maintain their eye position in the dark, but this may be because of different task demands In addition, Skavenski and Steinman (1970) and Skavenski (1971) required subjects to match remembered eye positions in the dark By Roland's definition this is a "conscious" use of muscular feedback, and it was found to be very good

(4) Experiments with passive movements are inconclusive because gamma innervations are absent Consequently, afference from eye muscle spindles is substantially reduced (Bach-Y-Rita, 1972; Witteridge, 1959)

(5) Recent experiments on illusions of visual direction are contrary to feed-forward models and consistent with feedback explanations (cf Matin, 1976) For example, when eye movements are inhibited by *total* paralysis, the illusion of visual movement vanishes (Siebeck, 1954; Brindley et al , 1976) or is drastically changed (Stevens et al , 1976) Further, when a refixation eye movement terminates off target, perceived direction is determined by the actual eye position This is given by feedback, rather than by the intended eye position, which is given by feed-forward (Shebilske, 1976)

Thus, eye movement experiments are consistent with Roland's general thesis that feedback about tension and muscle length is sent from receptors in muscles and tendons to the cerebral cortex where it can be used for con-

scious discrimination and matching

My attempts to analyze the functional significance of muscular feedback have led me to study errors in registered eye position arising under conditions of eye and head position asymmetry (Shebilske, 1977a, 1977b; Shebilske and Fogelgren, 1977) When the eyes or limbs maintain asymmetric postures or asymmetric tensions, errors in registered positions develop, which in turn cause errors in various matching and discrimination tasks including judgments of weight and tension (cf. Ebenholtz, 1974; Hughes, 1958; Paap, 1975) Many possible physiological determinants could account for these effects Electrophysiological phenomena such as neuromuscular depression and facilitation have undetermined roles in normal synaptic integration. In addition, local intramuscular temperature related to circulation and metabolic levels has been implicated in neuromuscular variability, but its exact effects remain obscure (Hayes, 1975) Another possibility is post-tetanic potentiation, which is a long lasting increase in muscle responsiveness following repetitive stimulation Since maintained asymmetries are common in everyday situations, is it not possible that muscle responsiveness to motor signals is highly variable? If so, the conscious detection of muscular feedback may play a part in compensating for this neuromuscular variability

Roland's work sets the stage for an acute test of this hypothesis If gallamine, which was used to alter the relationship between motor signals and muscle force, were replaced in Roland's experiments by maintained asymmetric postures and tensions, the functional significance of the conscious detection of muscular feedback in everyday situations may be revealed

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**What muscle spindles and Golgi tendon organs could and could not signal to the brain.** That the left hand knows what the right hand does is achieved by a computation presumably requiring many kinds of information Probably no one would argue with this statement Controversy abounds, however, concerning the exact nature and sources of the data used by the cerebral computer.

Roland's study goes a long way in showing that the brain can do it, so to speak, on a shoestring budget of sensory input Partially paralyzed and with their sense organs in skin and joints inactivated, subjects could still perform several tasks of discrimination with remarkable accuracy Not all tasks were equally well done though, and therein may lie the main lesson

The expression "musculotendinous afferents" leaves it undetermined whether primary or secondary spindle endings, or Golgi tendon organs are responsible for a given effect But, in discussing his data the author imparts the impression that he believes that all three of the stretch receptors in muscle contribute to the conscious senses of active movement and of position

The study confirms that, with joints anaesthetised, there is no awareness of the bending of the fingers In other words, input from musculotendinous sense organs is insufficient for judging passive movement and position of the digits This in spite of the fact that when a finger is passively moved, and the subject refrains from active contraction, the spindles in his muscles vary their discharge rate Not so of the tendon organs, for they are insensitive to passive stretching, even though they briskly respond even to weak active contraction of extrafusal muscle Therefore, the tendon organs may be the ones enabling the same subjects, with joints anaesthetised, to judge the extent of active voluntary contraction

It is also significant that subjects with skin and joints anaesthetised, plus skeletal muscles partially paralyzed, could perform well in tasks where force was a simple function of path length They failed however when the extent of movement of the paralyzed hand had to match the non-paralyzed one, while the strength of the two springs differed In other words, they could not judge path length when force became a misleading clue If muscle spindles could inform the conscious subject about muscle length, then he should be able to adjust the extent of movement of the partially paralyzed fingers to those of the non-paralyzed ones.

This brings us to the central undecided issue of muscle spindle physiology. The extensive work of many investigators has provided us with accurate observations on the manner in which muscle spindles operate in the dissected, immobilized animal The remaining question is: to what use are these intriguing little organs put under ordinary, everyday circumstances? Basically, there are two possibilities, and both could not be true at the same time: either a spindle is the key sensor and guide element in a length-servo feedback loop, or it is a length-measuring device and velocity-gauge of variable gain The question could in principle be answered by recording the discharge of gamma efferent fibers during active movement in unanesthetized, unrestrained subjects If the output of gamma motoneurons sets the sensitivity or "bias" of a length- and velocity-meter (static gammas

for length, dynamic for velocity), then their output should remain constant, while alpha-discharge should vary according to the supraspinal commands received If, on the other hand, the fusimotor system is the governor of servo-controlled movement, then the output of gamma motoneurons should accordingly vary with the output of alpha motoneurons

Such an experiment could define the role of the muscle spindle in the processing of motor command It would not, of course, decide the question whether the information generated by the spindle ever reaches consciousness To the latter question Roland's results seem to give a negative answer As Roland correctly observes, the fact that impulses from spindle afferents are relayed to the cortex does not mean that they are consciously perceived For not all that is cortical is conscious, nor is all that is conscious, cortical

In sum, it would seem from this report that the discharge of Golgi's tendon organs furnishes the principal signal for the subjective awareness of the force of voluntary contraction The results also confirm the existence of "feed forward," or a true "sense of effort " A contribution by muscle spindle afferents to the conscious awareness of either movement or position of joints, or the path taken by a muscle during voluntary contraction, was not demonstrated In fact it is rather unlikely to exist

by **K.-H. Sontag**

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*Conscious and unconscious motor decisions.* Roland's article makes an up-to-date contribution to the question of origin and levels of motor programming In the discussion of voluntary movements the question arises whether voluntary movements are conscious, subconscious, or unconscious This question is a very important one in respect to purposeful voluntary movement or locomotion

The experiments presented, as well as the opinion of other authors, contradict the current notion of the exclusiveness of sensory feedback to subcortical centres There is experimental evidence from primates and cats that proprioceptive information on muscle activities does indeed reach the motor cortex

It is quite easy to test whether a man knows what movement he is making at a given moment If he were asked he would be able to refer to the accumulated muscular tension and muscular kinaesthesia This is a consciousness that is normally absent and unimportant Movements must be learned A sportsman's performance is optimal when he no longer thinks of the sequence of movements or no longer needs to remember them

The author cleverly demonstrates the problems of this subject and its experimental potential Even a reader who is familiar with the problems in question is fascinated by the theme But consciousness must not be confused with discrimination Discrimination does not mean consciousness It is possible to investigate the physical state by means of discrimination and to show whether sensory feedback impinges upon consciousness, but the fact that an individual discriminates does not mean that consciousness is the consequence of discrimination A man can be conscious of the sensory feedback if necessary, but that does not mean that voluntary movement (contractions) would always be practised consciously, although we know that afferent musculotendinous information does reach the cerebral cortex Conscious decisions are made only if changes are to occur In this context, sensory information is very important

Many fast working motor programs must be at our disposal If a man stumbles over an obstacle he will be conscious of the spinal motor reaction in terms of the well-known reflexes before he is aware of the situation itself In such cases sensory feedback fulfills two conditions: 1) triggering spinal motor reflexes and 2) providing information to the cerebral cortex milliseconds later The result would be increased attention But there is also a simultaneous interplay between sensory feedback, which impinges upon consciousness, spinal motor systems, and subcortical mechanisms when skillful, smooth movements are practiced This is also possible without any visual or auditory information

There is nothing exclusive in the hypotheses and experimental data presented and discussed here Conscious and unconscious motor decisions may obtain at different levels and be executed more unconsciously (or subconsciously) than consciously, most of them probably at spinal motor levels But that does not mean that man's motor programming normally works

without intact cortical centres At present we have no experimental means to demonstrate simultaneously the operation of the whole motor system, which may in turn integrate to various degrees with different motor systems in the cerebral cortex, subcortical structure, or spinal motor centres Sensory feedback takes part in both operations and controls

by **John Stein**

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*The interaction of motor and sensory signals in proprioception.* Seldom can one experiment have had such a dramatic effect on a field as the demonstration by Goodwin, McCloskey, and Matthews (1972) that vibration of arm muscles produces a powerful illusion of arm movement Since vibration predominantly excites primary muscle spindle afferents, their result implied that muscle spindle signals do after all affect consciousness Actually the prevailing view that muscle spindles were insentient (Merton, 1964) was already ripe for change, following new evidence that muscle spindles did in fact project to the cerebral cortex (Oscarsschn & Rosen, 1963; Phillips et al , 1971 *op cit* ) and that joint afferents, formerly ascribed the role of signalling limb position by themselves, were not usually able to supply enough information about joint angles, and so forth, to do the job (Burgess & Clark, 1969 *op cit* ) Moreover, greater understanding of the internal machinery of the muscle spindle has deprived the older argument, that the muscle spindle signal was just too complicated to be interpreted by the sensorium, of much of its force The description of the vibration illusion of limb movement therefore occurred at just the right time, and has naturally given rise to a host of new experiments Some of these simply reexamine and reinterpret old problems such as the alleged insensitivity of conscious humans to traction on their tendons (Matthews & Simmonds, 1974 *op cit* ) and the phenomena associated with phantom limbs But others have attacked the problems of position sense and kinaesthesia in rather more complicated situations in which both voluntary effort and sensory feedback contribute to the total perception The results of two different approaches of this sort, namely, investigating subjects' estimations of the heaviness of objects (Gandevia & McCloskey, 1977) and of the strength of springs (Roland, 1975 *op cit* ), have given rise to rather inconsistent results upon which others no doubt will comment I wish to attempt a reconciliation of these different views and in doing so to take up the challenge of Roland's last paragraph – to suggest that peripheral input to the cortex not only forms part of a feedback loop signalling position and movement of a limb in order to control its current state, but also is used in perfecting programmes for future movements

In the situations examined by McCloskey and by Roland, information from cutaneous, joint, muscle length, and tension receptors must be calibrated against some independent measure of the voluntary effort expended before its perceptual significance can be assessed When estimating the heaviness of objects, it appears that subjects prefer to rely more on their "sense of effort," whereas, when estimating the strength of springs, they rely more on tension feedback from the compressing muscles When judging whether and how far they have (actively) moved a finger, they require corroboration from peripheral receptors that their intended movement has in fact occurred Otherwise they judge that it has not (Goodwin et al , 1972) I do not think it need worry us that under these different circumstances different sources of information assume changed quantitative importance When one estimates the strength of a spring, the force exerted on contracting muscles by the spring is of cardinal importance That can be measured only by tension receptors within the muscle, though obviously their signal must be corrected for the amount of active tension developed by the muscle's own contraction However, when estimating the heaviness of an object, one is monitoring the active contraction just necessary to lift it against gravity The tension within the muscle is then less relevant Similarly, the voluntary effort applied to move a limb whose weight is known in advance is less important to the estimation of its final position than are receptor signals about the eventual lengths of its muscles and the position of its joints, and so forth

The changing weightings to be attached to different sources of information about limb movements presumably take place in an area of the CNS where all these signals converge Two most promising sites to investigate are the posterior part of the parietal lobe and the cerebellum In the superior parietal lobule (area 5), signals from cutaneous, joint, and muscle receptors converge and are powerfully modulated by the state of motor activity (Mountcastle et al , 1975) Posterior parietal lesions disturb position sense and

prevent monkeys and men from accurately discriminating between two weights, particularly if the subject is prevented from making active movements (Ruch et al , 1938) Chronic lesion experiments are difficult to interpret, however, as other parts of the cortex can often take over missing functions Reversible cooling of area 5 in trained monkeys has a much more dramatic effect (Stein, 1976) The monkey loses all ability to make palpatory movements controlled by somesthetic feedback whilst the hand ipsilateral to the cooler is virtually unaffected

The parietal lobe sends an important projection to the cerebellum via the pontine nucleus This organ also receives detailed information from cutaneous, joint, and muscle receptors in the moving limb Further, it receives a large input from the motor cortex and returns a major proportion of its total output back there Although the classical descriptions of cerebellar lesions do not include any deficits of passive sensation, seldom do clinical neurologists examine the active perceptions involving voluntary movement that we have been considering In fact, Holmes noted (1917) that cerebellar patients' judgments of heaviness were much impaired, but the questions of active position sense and of spring strength estimation have not been examined in human cerebellar lesion studies However, monkeys with cooling probes implanted in cerebellar nuclei cannot match the position of their arms to that of a visual target during cooling (Stein & Wattam-Bell, 1975) This may be interpreted to mean either that they do not know where their arms are or that they cannot control their movements properly

The burden of this commentary has been, therefore, to show that different amounts of interaction of various sources of information is essential for accurate appraisal of limb position, movement, heaviness, or spring strength The importance attributed to each source presumably depends upon experience of how successful a particular emphasis has been in the past for different estimations So the answer to Roland's challenge "Could it be that the principle importance of force information from the periphery is to update the cortex with data about the consequences of contraction?" is undoubtedly "Yes, it could " Such information can be used to choose the appropriate weighting, according to circumstances, to be given to tension versus muscle spindle, cutaneous, or motor outflow signals in order to adjust motor programmes in the light of experience As Roland points out, this would be particularly important for those fast "ballistic" movements where continuous feedback would be too slow to control the movement effectively

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## by **John K. Stevens**

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*The corollary discharge: is it a sense of position or a sense of space?* Roland has demonstrated with both his own data and data from others that sensory feedback during voluntary muscle movements can be used to sense both muscle tension and movement magnitude He has also demonstrated that these sensory inputs are consciously perceived He feels that there must also be a feed-forward or corollary discharge system for remembering effort; however, he leaves us with the impression that this system is not particularly important and that its "perceptibility" may be minimal He states that "the main weakness of the feed-forward hypothesis is the vagueness with which the mechanism is formulated What are the parameters encoded by the postulated signals?" He adds that this "vagueness makes empirical testing difficult "

The first purpose of my commentary is to crystallize the concept of a feed-forward system based on my own data from extraocular muscles (Stevens et al 1976) The second purpose of my commentary is to suggest a specific empirical experiment that will test for the presence of a feed-forward system in skeletal musculature This feed-forward concept has been called the corollary discharge by Sperry (1950, *op cit.*) and efference copy by Von Holst (1954, *op cit* ) I will use all these terms interchangeably throughout the commentary

Siebeck and Frey reported (1953) that total paralysis of the extraocular muscles via a neuromuscular blocking agent produced a strong sensation of total paralysis When an attempt was made to move the eye or any other muscle they reported that the sensation was that the muscle was simply immobile Siebeck and Frey reported no unusual visual perceptions during attempted eye movements We (Stevens et al 1976) decided to repeat the Siebeck studies since they appeared, at least on the surface, to contradict many other previous reports

We started by carrying out a series of experiments using low systemic doses of curare The results were dramatic, but very confusing All the subjects (three of the authors) reported diplopia, visual movements in the form of jerks and jumps, and errors in their ability to localize objects in space It was clear that if answers were to be obtained using this technique, total neuromuscular paralysis was a necessity I was the subject for those total paralysis experiments and can assure anyone who wishes to repeat them that the major perceptions were quite unambiguous – one felt like a solid piece of cement It was very much like being buried alive Not only was voluntary movement impossible, but one was painfully aware that it was impossible There were never any phantom perceptions of either limb movement or limb position This perception of paralysis or immobility was just as dramatic for the extraocular muscles Any attempt to move the eyes left or right was met with a sense of stark immobility These results appear to corroborate Siebeck and Frey (1953) However we found a number of additional perceptions not found by these authors, which have been described elsewhere (Stevens et al , 1976) and will be summarized below This sense of immobility is also consistent with Roland's argument that sensory feedback must be responsible for our sense of limb position and our sense effort Roland would, however, interpret my perception of my failure to execute motor commands as an indication of a memory or feed-forward system (i e , the corollary discharge) This sense of immobility (or effort) has in our view almost nothing to do with the corollary discharge Roland has not addressed himself to what we believe would be the major corollary discharge perception in a skeletal muscle system – the perception of egocentric space One must first make the distinction between felt position of the limb with respect to itself, and the perceived position of the limb in space This difference is not generally appreciated, but is, as we will demonstrate below, crucial to the understanding of the corollary discharge, at least in the extraocular muscle system To fully understand this difference and our final total paralysis result, I must briefly digress to some other related studies

During these total paralysis studies I was also the subject for a series of retrobulbar block experiments These studies used a local anesthetic as a blocking agent, leading to both a nerve and muscle block of efferent pathways as well as a neural block of all incoming sensory information We found, corroborating Kornmueller (1931), that one's ability to localize objects in space was totally lost This spatial confusion was very systematic and predictable With a fixed head and a monocular view we found pointing errors were always greater in the periphery than in the center field of view and that the errors were always in the direction of an attempted eye movement (i e , overshoots) An example has been illustrated in Figure 1 The subjective perception associated with these errors was not necessarily visual It was, at least to me, a new and previously unexperienced perception We arbitrarily called it "displacement" to distinguish it from the visual perception of movement Without actually touching an object this displacement was
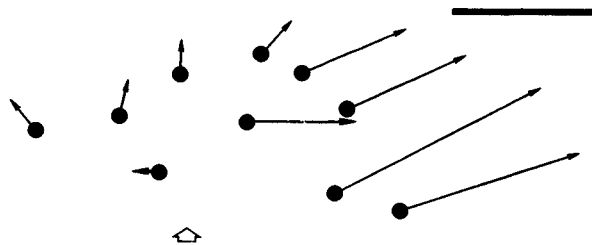
Figure 1. An example of the pointing overshoot errors associated with the retrobulbar block experiments. The subject (JKS) was seated and his head was fixed with a bite bar. An experimenter placed his finger on the table in front of the subject. The subject then attempted ballistically to touch the experimenter's finger. The right eye was paralyzed and the left eye was occluded. Each black circle represents a target point and the diameter of the circles represents the approximate error range for the normal subject. The black bar at the top of the figure corresponds to one foot, and the open arrow at the bottom is the subject. These same results were obtained under a wide variety of conditions (e.g., no bite bar, no visual feedback, etc.).

difficult to detect, particularly near center of view, yet the pointing overshoot seen in Figure 1 clearly indicates its presence In the periphery, however, where the errors were as large as 20 inches, it was much easier to detect without actually pointing I quickly learned to simply ask myself if I wanted to touch that object where would I reach If the object looked as if it were straight ahead, but I felt as if I would have to reach to the far right to touch it, I knew there was a displacement

We carried out a total of three retrobulbar block experiments and by the last study these strange, often confusing, sensations were old friends The misperception of space reported in these studies could have been due to a number of possible mechanisms It could not have been due to sensory feedback from the tested eye since the local anesthetic would have blocked not only motor outflow but also sensory feedback The fact that we had total motor paralysis within the muscle cone guarantees that the smaller sensory fibers would also have been blocked It is possible that sensory feedback from the contralateral working eye contributed to the misperception; however, this seemed unlikely For example, if one mechanically pushes an occluded eye, it seems to do absolutely nothing to the spatial perceptions of the contralateral unoccluded eye The final possible, and we felt most reasonable, explanation was that the spatial mislocalization was due to a corollary discharge If a corollary discharge were present, one would minimally expect the magnitude and the direction of the pointing errors to be correlated with the strength of the unsuccessful, extraocular muscle contraction One would also expect a greater strength of attempted extraocular muscle contraction for test points located in the peripheral visual fields than for points located in the central visual field Thus the pointing errors should be greater in the periphery than in the center, and the errors should always be in the direction of the attempted eye movement This is what we repeatedly found in all our retrobulbar block experiments (see Figure 1) It was clear however that the most direct demonstration of the existence of the corollary discharge would be to detect this displacement perception during total extraocular paralysis using a neuromuscular blocking agent

To this day the total paralysis experiments and their results are as clear in my mind as if they had taken place yesterday I had a tourniquet on my right arm to prevent its paralysis I had a scleral contact lens with a small mirror on a stalk placed on my unoccluded eye A beam of light was projected to the mirror and in turn to a screen This system was used to detect any possible eye movements during the experiment There were none To guarantee total paralysis we used twice the normal induction dose of succinylcholine All indications were that I was as paralyzed as one could ever hope to be As I tried unsuccessfully to look to the right I moved my index finger to indicate the attempt We had learned from our earlier experiments that it was very difficult to keep trying to move your eyes when they simply would not move Therefore I was verbally reminded with each attempted movement to try as hard as possible The perceptions were clear and quite unambiguous Again and again I would ask myself where would I reach if I wanted to touch the pattern projected on the screen, and again and again I felt that I would reach to

the right in spite of the fact that it appeared to be straight ahead I was unfortunately the only person who could be certain of these results; therefore, as one last check, we carried out a final total paralysis experiment (and I might add my last ever) Again I experienced the same perception of displacement during attempted eye movements The description here has necessarily been brief For more details the original paper should be consulted (Stevens et al 1976)

Our conclusions from these studies were simply that this perception we call displacement is not visual, certainly not something normally perceived as an isolated sense, was quite independent of our sense of muscle or eye position and must be due to a corollary discharge These experiments have of course one major weakness in that the most dramatic result depends entirely upon my subjective reports Fortunately, these same conclusions would be reached from a number of other sources and from a very simple experiment I will describe below

Weiskrantz et al (1974) have in a single subject dramatically demonstrated the non-visual character of our perception of space The subject had a portion of his primary visual cortex removed and upon testing the expected scotoma was found The subject reported no visual sensation whatsoever when a light was flashed within the scotoma However, when he was instructed to touch a light flashed in this same blind region he could localize it almost as well as you or I could have localized it Thus, the subject's normal "conscious" perceptions seem to be lost, yet he could certainly make use of the retinal information to perform visual tasks in space We might conclude, therefore, that the perception of visual space is not necessarily a visual perception

Skavenski (1972) has demonstrated that we have a non-visual sense of eye position and that it must be from retrobulbar sensory receptors He shows that if the eye is mechanically moved without superficial tactile stimulation not only can the subject detect the movement but he can compensate for the movement to maintain a fixed eye position The sensory receptors in the extraocular muscles must therefore be used to detect extraocular muscle position On the other hand it is very easy to demonstrate that this same sense of muscle position has nothing to do with spatial localization One can prove this with the simple experiment of mechanically displacing the eye (with a finger) and then ballistically reaching out to touch a point As you will discover, the point will be missed The obvious conclusion is that we must calculate our sense of space not from the sensory receptors, but from a corollary discharge One should not confuse the movement seen when the eye is mechanically relocated with our displacement perception The displacement is not perceived in this experiment until you actually see your hand

Given these results, the data from others presented above, our own retrobulbar block and total paralysis data, not to mention the hundreds of supporting papers published over the last century, we feel the following conclusions are warranted: The sense of extraocular muscle position is distinct from the perceived spatial position of the extraocular muscles The perception of the extraocular muscles' static or dynamic spatial position is not a visual perception The extraocular muscles' felt position is calculated from sensory information and the extraocular muscles' spatial position is calculated from a corollary discharge

It is rather simple to extrapolate from these conclusions concerning the extraocular muscles to skeletal muscle in general If all skeletal muscles were to operate in the same way as the extraocular muscles operate, one would predict that the sensory inflow would be used to calculate such things as felt position, tension, dynamic parameters associated with active movements, etc Furthermore, these would all be "consciously" perceived However, one would predict that the sense of where the limb is located in space would be calculated via an efference copy system Moreover, I would predict that the perception associated with this efference copy would be quite distinct from the sense of limb position Roland has in this review made a very convincing argument for the perception of sensory feedback and for its use in both static and dynamic position calculations The existence of a feed-forward system as I have suggested here has however not been directly tested I wish therefore to suggest a direct test for an efference copy system in skeletal muscle

McCloskey and Torda (1975, *op cit*) have selectively paralyzed the forearm muscles using D-tubocurarine and a tourniquet They found that subjects were "consciously" aware of their inability to move their fingers I would

agree with this result based on my own experience with similar experiments These authors however incorrectly conclude that this represents evidence against a corollary discharge. The correct test for the existence of a corollary discharge would be to ask the subjects to indicate with the normal hand the spatial location of the paralyzed fingers during an attempted, but unsuccessful, contraction If the subjects systematically mislocalize the paralyzed fingers, it is evidence for a corollary discharge system; if they correctly localize the paralyzed fingers, it is evidence against a corollary discharge system. It would also be important to try visual localization of the unseen, paralyzed hand

It is very clear that there are major differences between the extraocular muscles and all other skeletal muscles It is certainly possible that skeletal muscles do not have an efference copy system and that felt limb position and its perceived position in space are one and the same Until however, this is tested directly, I feel that no one is in a position to make any conclusions about the existence, perceptibility, or the importance of a general feed-forward system for all skeletal muscle

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## by C. Trevarthen

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**Cortical collaboration and consciousness.** Roland's experiments with a simple but effective device give impressive support to the view that receptors of changes in length and force in muscles can provide information to a subject about the strength of a squeeze applied by him to a small object held between index finger and thumb He has chosen an ideal system that permits separate elimination of inputs from joint and skin receptors or those from muscles

There are two quite distinct kinds of difficulty with this work One concerns the physiological details of the complex receptor and neuro-muscular mechanisms involved and the multiplicity of their presumed contribution in normal feedback control Pharmacological blocking of muscle contraction is complicated by partly differential effects of gallamine on individual efferent components, including those tuning the response of the muscle receptors directly This problem is adequately discussed but not fully resolved Allied to this is the question of how to refer representative effects, afferent, efferent, and coordinating, to anatomical components within the cerebral hemispheres The other kind of difficulty is not anatomical at all It is psychological and conceptual It concerns the definition of consciousness and the decision to regard an effect in a subject as a change in consciousness To explore this we need to go into the teleology of consciousness – what it is useful for This is not to deny the importance of muscle kinesthesia at many levels, conscious and unconscious

What kind of image or program must we assume to explain the efficiency and purposiveness of an intended movement? How much of the conditions for a movement of that reliability must be specified in the image? It must certainly take account of the inertial properties of the body as a mechanical system Then, if it is to be expressed as part of behavior in a resistant medium or structured field or environment containing objects to be used, it must also contain, or be able to build up quickly, a description of the kinds of effect arising from contact made with these externals, including mechanical effects in the elastic muscle tissues under varying degrees of tension Consciousness clearly has different roles for such different ways of taking the effects of movement into account It would appear to be most applicable to the second exteroceptive kind of data about the outside forms of "reality" that become goals or conditions for action of the brain

The hand is an organ of the highest voluntary capacities Roland's test, deceptively simple in *physical* description, cuts across the natural psychological functions of the hand in complex ways At least three different activities of different time course and different afference-related strategy are elicited by the instructions and controls of his three tests Moreover, the comparisons he asks for require monitoring in memory, that is, they require some form of retained image At another level, the uniformity of the movement patterns, on which the whole strategy of information uptake into the brain depends, must be controlled by very high speed as well as by lower speed feedback circuits to correct for errors or perturbations before they wreck or distort the act

On the anatomical side, we know that the cortex is not a seat of consciousness on its own It is naïve to consider that any signals arriving there must, by virtue of this fact, be incorporated into consciousness Moreover, the cortex attains the minimal requirements for sustaining a consciousness of goals and experiences in collaboration with other parts of the brain It seems to participate in partnerships with other brain mechanisms at all levels In the primates that use their hands most skillfully, including man of course, the large Betz cells of the motor cortex have direct (monosynaptic) projection to the motor neurons that move the hands (Kuypers, 1964) The Betz cell telodendria must intermingle in action with the immediate reflex effects of receptors governing the elementary contractile unit most directly Presumably they do so, not to command voluntary movements, as these are guided by slowly processed conscious images, but to make very fast adjustments to the basal figure of posture or displacement as Phillips (1969) has proposed, against which the effects of movement within consciousness are resolved They make the hand a servo-regulated organ of extraordinary stability and precise obedience However, most of the pyramidal cells of both motor and somatosensory cortices do not project directly They transmit effects to neurones one or many steps removed from the motor neurones of the anterior horns Some project more or less directly to the cerebellum, others to brainstem reticular cells Some modify the sensitivity of receptor structures in the muscles Where in this set of many parallel efferent pathways is the criterion for an effect that the movement has generated in consciousness?

Temporal or chronographic analysis appears to offer a partial answer The curve shown in Roland's Figure 19 is, in this connection, particularly interesting It has a small oscillation at the period of 18–20 / sec , then one at 3 / sec This is a very wide separation of resonances, indicative of two quite different levels of complexity in control Roland implies that the former very fast response may be a transcortical reflex, subconsciously correcting for a misapprehension about the strength of the spring The later fluctuation on the curve is more like a test of the "reality" or "nature" of the object that the subject has been asked by the experimenter to "know" and "report " There is a reaction time of about 200 milliseconds before the act is produced This is also at the level of effect in control that is relevant to "knowing" in the sense of "remembering " Presumably there was a prior long pause between the act of squeezing the second capsule and the utterance of the subject's judgment of comparative stiffness for the springs This utterance, too, would be a complex temporal pattern of movements with a preprogrammed goal of vocal effect and of meaning over a considerable background of subconscious rapid correction by "auditory" and "kinesthetic" channels

The confusion that bedevils this kind of discussion arises from the use of the same words, such as auditory, kinesthetic, touch, or articular, for a very wide range or complex hierarchy of functions Vision, input from the retina, enters into regulation of movements in a whole range of cerebral systems Some are almost (but never quite) reflexive Some, invading quite different brain circuits, involve imagination and semantic associations The lower-level processes of the midbrain visual system make some contribution to consciousness in man at the same time as they take care of "automatic" guidance of posture, progression, and orienting (Trevarthen & Sperry, 1973) Why should the kinesthetic receptor functions be different? No receptor system that picks up effects of doing things to objects in a discriminatory way can be safely assumed to have no say in consciousness Even vision and audition, which certainly feed consciousness, have reflex or automatic effects on motor contraction routines of transport or posture, keeping them balanced, on target, or in the desired trajectory by very fast adjustments (Lee, 1977) They are efficient proprioceptors Both audition and the detec-

tion of muscle force and extension, in collaboration with various skin pressure and deformation detectors and joint rotation sensors, can add vital information to vision about the substances, shapes, and mechanical structure of things being handled

I see no reason to doubt that leg muscle kinesthetic organs contribute to consciousness of the shape and consistency of things stepped on or kicked Obviously, the muscles of the fingers are potentially important as perceptors of things in the hand or of media against which the hand moves Physiologists, in classifying receptors by the forms of stimulus required to excite them, only begin the analysis of the processes of perception that transform the multiple excitations of any movement into awareness of what the subject, an integrated whole, is doing in relation to what kind of environment or object

The time it takes for a new conscious image to be formed after new information impinges on the receptors (at least 100 milliseconds) is long enough to invade circuits in every lobe of the brain This should not be forgotten when "locating" consciousness in an area of the cortex that receives a relatively direct afferent supply Vision is certainly not conscious in Area 17 It is hard, therefore, to feel confidence in proof from lesions that focalize on the primary projection area of the hand, except that such a finding does support the notion of cortical involvement in the tasks that the lesions selectively impair Unfortunately, the data Roland gives us on the lesions of his patients are insufficient to justify further speculation about where effects in muscle receptors concerning a squeezing effort are turned into consciousness of a movement or of an object's resilience

While the classical belief that kinesthesia from muscle receptors does not contribute to consciousness of objects is suspect on both teleological and neuroanatomical grounds, one may also doubt the other negative hypothesis, that corollary effects of motor neuron excitation are *not* contributing to sense of effort The brain is not a simple input-to-output device Nevertheless, the idea of feedforward is probably not a very apt one An image of pattern in the motor output cannot explain *detection* of object properties, nor can it claim on its own to explain constancies in perception because these, as Gibson (1966) has taught us, are also richly informed within the signals of afferent stimulation However, it is not a simple matter to rule out some corollary contribution to at least a baseline estimation of effort against which resistances, distortions, and perturbations can be detected by receptors The best example of a system using signals of an efference-copy type as background information for analysis of the afference still appears to be the oculomoter system, in spite of rich and precise feedback from vision itself in most situations where sight is being explored by these movements (Bizzi et al , 1976; Mohler & Wurtz, 1976) Do not phantom limbs seem to move? Do they ever seem to move according to the subject's will? If so, then some feedforward (or sideways) would seem to be indicated for awareness mediated by the arm or hand

Use of the muscle receptors to perceive attributes of objects seized in the hand depends upon precise regulation of the muscle state and detection of any changes in it that are due to innervation It seems likely that a central record of the figure of efferent excitation to the muscle would be a useful, even necessary component of these background data even if it makes no contribution directly to consciousness of external objects I do not believe that Roland's tests are appropriate to rule out this component

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*by* **E. G. Walsh**
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*Sensing springiness.* In these days of big science it is gratifying that it is still possible to obtain interesting results in physiology and neurology using simple and inexpensive methods in well-designed experiments Roland is accordingly to be congratulated

I was investigating the positional sensitivity of the terminal phalanx of the ring finger when Gandevia and McCloskey's paper (1976 *op cit* ) appeared The terminal phalanx can be positioned so that the muscle cannot pull on the joint I found the joint sensitivity then much poorer than under conditions when the muscle could pull As the findings were essentially the same as those of Gandevia and McCloskey, on the middle finger, I am not proposing to carry mine to formal publication

Roland's work leads to the conclusion that muscle sense contributes to kinaesthesia and that the motor reafference too may be significant

Goodwin, McCloskey and Matthews (1972 *op cit* ) came to similar conclusions Their methods were different insofar as they activated muscle spindles by vibration and were interested principally in the sense of position

I am not aware of the stiffness of springs having been investigated previously Recently I have been using printed motors to study limb control These devices produce a torque that corresponds with the current supplied to them

By introducing abrupt perturbation it is possible to see if the stretch reflex is working (Walsh, 1976) and this method has been used too by Merton and his colleagues *(oper cit )* It would thus be possible to design an experiment on spring stiffness discrimination in which one could tell whether or not the muscle servo was working

I have used printed motors too in servo systems Fitted with a potentiometer to register shaft position, it is possible to introduce negative position feedback, and the effect then is to mimic a spring Furthermore the stiffness of the spring is determined by the gain of the feedback loop Such a system could lead to a sensory test more versatile than is possible by the use of mechanical springs for the degree of springiness can be made continuously variable over a wide range Furthermore, the springiness could be induced for restricted periods and the potentiometer could simultaneously record movement on a chart recorder

I think the method used by the author to record motion is inelegant To plot a graph (Fig 19) from many frames of a cine camera must be cumbersome compared with the use of a transducer and recorder, and must have severely restricted the handling of data – a kymograph would have been better!

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*by* **M. J. Wells**
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*Invertebrate stretch receptors, and consciousness.* Roland has given us a very clear exposition of the 'sensory feedback' and 'efference copy' positions in relation to the fine control of voluntary movements, and I shall certainly recommend his article to students as an introduction to the problems that it covers The people I teach are zoologists and as such (and assuming for the moment that he has proved his case – his experiments seem very convincing to one who knows nothing of the pharmacology of gallamine block and must take them at their face value) will be particularly interested in the implications of his work for an understanding of animal behaviour

The point here is that *all* animals so far examined have proved, on careful examination, to have stretch receptors in their muscles; many in addition have receptors in their tendons, in series with the stretch receptors Only a few animals, those with jointed skeletons (notably the arthropods, but also perhaps some echinoderms and polychaetes) have additional sense organs in or around their joints that could be capable of yielding information about the magnitude of movements made, and about positions achieved, independently of muscular tension

Pringle (1963) has discussed the situation with regard to arthropods, where the array of proprioceptive sense organs falls into two distinct categories, analogous to our own contact and joint receptors on the one hand, and to muscle spindles and tendon stretch receptors on the other

A variety of observations, ranging from the behaviour of bees in mazes to the ability of hermit crabs to pick out shells of suitable depth and aperture,

show that arthropods can measure the relative position of parts of their own bodies with considerable accuracy They can, moreover, learn from these proprioceptive inputs, so they are, by Roland's definition, 'conscious' of what they are doing Arthropods, happily, wear their contact and joint angle receptors on the outside of their exoskeletons, where it is possible to destroy them without much damaging the rest of the animal Abilities that depend upon a recognition of posture, or movements made, are then lost, despite the continued existence of muscle and tendon stretch receptors (see, for examples, Markl [1966a, b] Kinosita and Okajima [1968]) The implication is clearly that information from stretch receptors is *not* available in these cases

It is arguable, of course, that one would hardly expect a crab or an ant to reveal a capacity to substitute stretch receptor information following sudden elimination of its 'preferred' source of conscious proprioceptive input Our testing methods are too crude and the fine points of the animal's behaviour certainly elude us – after all, it has taken several generations of physiologists to develop sufficiently sophisticated techniques to determine whether *we* are aware of stretch receptor inputs Nobody has yet tried to carry out the sort of long term experiments that would be needed to check whether arthropods can eventually adapt to using internal sources of proprioceptive information when their externally placed proprioceptors have been eliminated

The shock of trying to reorganise responses in relation to an unfamiliar set of inputs cannot, in any case, be the explanation of the failure of soft-bodied animals to behave in ways indicative of a sense of movement and bodily position Unlike the arthropods, the soft-bodied animals (worms and molluscs, and a host of others) never behave in ways that would suggest that they can measure the magnitude of a movement made Soft-bodies animals never build regular structures – to create a spider's web or a honeycomb, an animal must be able to measure distances with some accuracy Soft-bodied animals are, in general, unable to learn images on a basis of kinaesthetic information alone; they must apparently always have some outside stimulus with respect to which they can orient – compare the maze learning literature for arthropods and other invertebrates The latter almost certainly cannot learn to make discriminations based on measurements of the sizes or shapes or weights of objects that they encounter (Wells 1977)

This last series of incapacities would remain undemonstrated but for a further happy accident of evolution, which has produced one type of intelligent soft-bodied animal, the octopus *Octopus* learns many things very rapidly – visual and tactile discriminations that appear quite difficult even to ourselves are regularly mastered within a few tens of trials – and as a result we probably know more about the perceptual world of an octopus than that of any other invertebrate, and indeed of most vertebrates *Octopus* has stretch receptors in its muscles, but seems incapable of using the information that these provide when it learns to discriminate Textures can be recognised by touch, but shapes (which would require some assessment of the bends in the arms, or the relative positions in space of the suckers) cannot Tastes can be distinguished, but the animals do not learn to discriminate between objects that differ only in weight (although the muscles of the arms quite obviously increase tensions to support additional loads)

Electrophysiological results and the effects of brain lesions on the control of movement all suggest that octopuses use stretch receptor information locally, for the adjustment of muscular output There is no evidence that this category of proprioceptive input even penetrates to levels of the cephalopod brain concerned with learning (Wells 1978)

A variety of experiments with invertebrate animals (gathered, be it said, for the most part in much less sophisticated experiments than Roland's) thus suggests that the capacity to recognise stretch receptor inputs may be a purely vertebrate, or possibly even solely a primate thing It may be developed significantly only in animals like ourselves that need every scrap of sensory information available because of the very elaborate tasks that we consciously perform with our hands For a zoologist the interest of Roland's paper is that is does seem to swing the balance in an old controversy firmly in a direction that indicates that at least one sort of animal *can* use stretch receptor information in the regulation of voluntary movements What is possible in man is, arguably, possible in other creatures and suggests that it would be worth a very critical re-examination of the evidence against the use of stretch receptors in other organisms

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*by* **Mario Wiesendanger**
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*Toward contextual instead of either/or thinking* The experiments described by Roland are interesting in that they provide evidence for the notion that proprioceptive afferents contribute to the correction of ongoing movements The latencies of the earliest adjustments suggest (but of course do not prove) that the pathway is complex, perhaps involving the motor cortex in the manner proposed by Phillips Such studies, as valuable as they may be, remain speculative in many points A particular difficulty is one of semantics: the author does not define what he means by "reprogramming." Is reflex adjustment of an ongoing program also a kind of reprogramming? Where are the borderlines between reflexes, triggered actions, automatisms, voluntary adjustments? In my opinion, an operational definition of a reflex (versus a triggered action or voluntary adjustment) would be provided by a positive observed relationship between magnitude of input (perturbation) and magnitude of output (correction)

A second point I would like to raise is the question of "mutilation experiments" (deafferentation, decortication, decerebration, spinalization, blinding, etc ) "which emphasize the role of feed-forward mechanisms in motor control and leave little room for afferent feedback to modify the programming of 'voluntary' motor programs " The author also refers to experiments that have revealed the "automatic character" of walking and galloping I think that one cannot emphasize enough that demonstration of, say, locomotion in a deafferented or spinal animal does *not* at all prove that proprioceptive (or other) feedback is not used normally Most of these experiments have been performed without use of the operational "perturbation" paradigm described above Whether or not feedback is used may change from moment to moment, depending on the *strategy* of the motor behavior (performance in a standardized operant conditioning situation, or in a free behavioral situation, etc )

From these considerations I would like to propose that in future research of this kind the questions should not be feed-forward versus feedback, segmental versus long-loop, reflex versus voluntary My contention is that all these possibilities exist; some of the more interesting and testable questions would be: in what context does reflex adjustment dominate open-loop control (or vice versa, see, for instance, Grimby & Hannerz, 1976; Freyschuss & Knutsson, 1971); in what context may a transcortical adjustment be of more importance than segmental adjustment (and vice versa), and so forth We are perhaps thinking too much in "either-or" terms

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# Author's Response

*by* **P. E. Roland**

### The cerebral cortex and conscious kinaesthetic and tensional information

**Non-metaphysical sensory feedback during voluntary movement** (replies to commentators **Chapple, Iannone, Libet, Pri-**

bram, **Roberts, Sontag, & Wells**). Unless one is a very good sailor, one should always steer clear of storm centers. One of the most stormy centers in neuroscience is the concept of consciousness. Since not all experimentalists are materialists, the consciousness concept has often tended to generate more heat than light. Unfortunately, earlier authors have posed the problem about sensory feedback from muscular receptors in terms of whether or not this reaches consciousness, without specifying what they were taking to be the content of this concept. Every scientist who wants to use this term ought clearly to assume the burden of defining what he means by consciousness or being conscious. The clinician, who is often confronted with the problem of deciding whether a patient is conscious or unconscious, is not able to do this unless he defines a set of operational criteria that he takes to constitute the distinctive marks of being conscious. Consciousness is regarded as an extension of certain functions that the patient can or cannot perform (Jouvet, 1974). The state of being conscious is thus wisely attached to praxis.

In my article I select from among the many relevant, distinctive marks of the state of consciousness the capacity to discriminate and to match two physical inputs. However, conscious experience of sensory information is not thereby *equated* with these capacities. It is, of course, still possible to define consciousness in a nonoperational way, but unless one is a metaphysician, there is still no alternative to specifying the relation between the state of being conscious and the physical world. So far, physical descriptions of events within and outside the nervous system have been the most successful and unambiguous methods of description.

As the reported investigations were designed to evaluate the quantitative contributions of muscle and tendon receptors to kinaesthesia and a putative sense of tension, introspective analysis could not be employed. Moreover, introspective analyses are of limited interest in sensory physiology since the value of subjective reports obviously depends on factors such as S's vocabulary and the preciseness with which he can express himself. Whether or not S is able to express verbally the character of his sensations is not pertinent to the present discussion. Indeed, some of the patients with cerebral lesions had total expressive aphasia and yet could discriminate spring strength and movement magnitude within the range of normal performance.

In the type of psychophysical study reported, there is no uncertainty as to the physical parameters to be discriminated; however, no direct conclusions concerning the relation between the physical parameters and impulse traffic in the sensory pathways can be drawn. This limitation does not appear critical so long as input is appropriately decoded centrally and performance correctly covaries with the relevant physical parameters.

It has been objected that, although Ss can discriminate normally when inputs from skin and joints have been excluded, they may not be *aware* of the character of the remaining input as kinaesthetic or force information. Other commentators urge that the original force signal (i.e., that set up by the tendon organs) may be distorted, transformed, or otherwise changed under the influence of information (or lack thereof) from other sources during transmission from spinal cord to cerebral cortex; or simply it may be that the impulses in the Golgi tendon afferents may already have lost their force information content and "may be likened to the indication of a weighing machine where the weight of a basket of fruit does not indicate how many of the fruit are oranges and how many are apples or pears."

These arguments apply to different modes of description or "different realms of discourse" (**Roberts**). Although both psychophysical experiments and studies of nerve impulses are defined in relation to the physical world, the transfer functions for the respective operations of the organism are not the same: The partitioning of the system studied is quite different when impulse traffic is studied at various loci on the route from periphery to cortex versus when the physical stimulus is studied in relation to a specified binary output indicating greater or lesser spring stiffness.

Consider the following (thought) experiment (refer to article Figure 1): Suppose the forearm is cut at the elbow and the exact motor-firing pattern is recorded from all motor nerves at their central end. Suppose further that this pattern is transferred to a computer that selects the exact afferent counterpart of the impulse pattern and transfers this to all relevant sensory nerves. If we now ask S to discriminate spring stiffness (the characteristics of different springs are easily simulated by computer), we would expect the outcome of this experiment to be very much the same as that actually exhibited by normal Ss. Presumably no one would object that the psychometric curves would differ from previous force discrimination curves, although there are no mechanical forces or tensions in the system, only nerve impulses. Is such an armless subject still discriminating force? If not, then what *is* he discriminating?

Stimulus detection and discrimination are not the same (Roland, 1976 *op. cit.*). That these two functions can be instrumentally dissociated (**Pribram**) should consequently present no mystery. A "mystery" arises only if it is claimed that normal detection is prerequisite to normal discrimination. Otherwise, it is hard to accept that if a person cannot detect normally, then his discriminations must be made unconsciously (**Libet**). The paper of Weiskrantz et al. (1974) is mentioned in this context. Their patient had a left-sided hemianopia on "conventional perimetric testing" but was able to discriminate large horizontal bars from vertical ones in the left visual field. This discriminative ability was severely impaired, however, and no attempts were made to control eye saccades or to occlude the right visual field. This patient was undoubtedly conscious, and when stimuli were well above the discriminatory limen the corresponding signals did, by my definition, reach consciousness, because he was able, upon *verbal* instruction, to distinguish between two physical inputs and to make a decision about the respective magnitudes of one or more parameters. It is hard, therefore, to feel the weight of statements about "discriminations made unconsciously" or the absence of conscious vision in this patient – unless one either takes conventional perimetric testing or S's verbalizations of his understanding of his sensory processes as overall indices of conscious sensory experience. [Note that, by my definition, discrimination is not possible in a decerebrate cat (**Roberts**) or an arthropod (**Wells**).]

**The role of cortex in discrimination** (replies to commentators **Chapple, Goodwin, Libet, Millar, Mpitsos, Roberts, & Trevarthen**). That the integrity of the cerebral cortex is important for normal sensory discrimination is well documented (Head & Holmes, 1911, Holmes, 1927 *op. cit.*; Corkin et al., 1970; Roland, 1976 *op. cit.*). With respect to the visual field, the paper of Weiskrantz et al. (1974) provides further support for this conception. The integrity of the postcentral gyrus is especially necessary to discriminate most somaesthetic information normally (Corkin et al., 1970; Roland, 1976). In these latter two studies the extent of cortical damage was evaluated very carefully, and as identical anatomical methods were employed in the present study, commentator **Mpitsos** is encouraged to consult these works.

To my knowledge, kinaesthetic discrimination, in the sense that I have defined it, has not been previously studied in patients with focal damage to the cerebral hemispheres (**Goodwin**), not even by Holmes (1927 *op. cit.*). Lesions near the contralateral central and postcentral sulcus impair spring strength and kinaesthetic discrimination. This implies that the lesion interferes with the information transmission necessary to perform the discrimination and nothing more. If one were to try to evaluate the nature of this information transmission block, one would have to perform control studies involving discrimination of other types of information (e.g., visual and auditory, as has indeed been done) to see whether the discrimination defect is limited to somaesthetic information, and perhaps even to a special type of

somaesthetic information. These patients can discriminate visual, auditory, and even some kinds of somatosensory stimuli normally. Now, if (1) the patient's muscular power is sufficient to produce an acceptable stimulus consisting of force and amplitude of movement at the peripheral end (e.g., compressing the spring), (2) there are no other sources than the receptors in muscles and tendon organs able to transduce the stimuli and transmit these messages by way of their afferents, and (3) it is no longer possible to discriminate the stimuli because of localized cortical damage, then it is reasonable to infer that under normal discrimination conditions, these messages do reach the cortex.

Nothing has been said yet about the conscious awareness or unawareness of these messages or signals. No attempt at "locating consciousness in an area of cortex that receives direct afferent supply" (**Trevarthen**) has ever issued from my pen. To infer *that* from my data and presentation, one would have to draw upon a new type of syllogism. Consider the following premises: (1) One of the distinctive marks of consciousness is the capacity to perform discrimination; (2) a lesion in the postcentral gyrus causes an impairment in kinaesthetic discrimination. *Ergo* consciousness is located in the postcentral gyrus. Another application of the Trevarthen syllogism could be this: (1) Among the distinctive marks of consciousness is normal sexual behavior; (2) pinealectomy reduces the time spent on sexual activities in the spring time. *Ergo* consciousness is located in the pineal body!

**The purpose of the presentation** (replies to commentators **Goodwin, Granit, Iannone, Kelso, Stevens, & Travarthen**). The purpose of the study was to support the hypothesis that receptors in muscles and tendons signal kinaesthetic and force information to the cerebral cortex and that this information reaches consciousness. To do this it was also necessary to investigate whether another type of mechanism, independent of sensory information, could yield the information necessary to perform the discriminations. That is why the corollary discharge hypothesis was formulated as a feed-forward mechanism signaling information about force, position, and amplitude of active movement. The aim was neither to study control of voluntary movement in general, nor to study the overall role of sensory feedback in motor control. The fact that some kind of feed-forward mechanism or memory for motor commands, it was found, does seem to exist, may have served to open a door to investigators who did not previously believe in such a mechanism (**Granit**). Because the main purpose was to provide evidence for sensory feedback from the above-mentioned receptors, the description of this feedback outweighed the description of the sense of effort and of feed-forward mechanisms during voluntary movement. This does not mean that the feed-forward mechanisms are less important than feedback; neither does it mean that feed-forward signals are signals of force, position, or movement amplitude. Likewise, the relative importance of afferents from skin and joints for statognosia and kinaesthesia was not evaluated or discussed since these receptors were anaesthetized, and recent good reviews exist (cf. **Goodwin**).

**The question of whether information from other sources was properly excluded by our experimental procedures** (replies to commentators **Chapple, Duysens & Loeb, Dyhre-Poulsen, Goodwin, Iannone, Kelso, McCloskey, Mpitsos, & Walsh**). It was not by chance that we chose movements of the index finger as our experimental response. The flexor digitorum profundus flexes the index finger in the interphalangeal and metacarpal joints. The part of the flexor that acts on the index finger is a separate muscle, often with its own nerve (Davies and Davies, 1962). In the flexion of the metacarpal joint, this muscle is assisted by the flexor digitorum superficialis, the first lumbrical and the first dorsal and palmar interosseous muscle, which together with the extensor indicis stabilizes the movement. The tendon from the flexor digitorum superficialis to the index finger

belongs to the radial part of the deep muscle fibers, and passes the wrist joint at a deeper level, together with the tendon to the fifth finger. In this way the index finger (like the thumb) is moved by several separate and selectively active muscles; due to this anatomical arrangement it is possible to flex the index finger selectively without any concomitant movements of the three ulnar fingers.

When the three ulnar fingers are maximally flexed the force exerted by the index finger during the flexion bears no relation to the pressure exerted by them against the palm. This can easily be tested with a strain gauge positioned against the ulnar fingers during the compression of a spring. The force-matching or force-discrimination results cannot, therefore, be explained by the assumption that Ss monitored the force or the pressure against the palm from these fingers.

Another reason why we had Ss flex the three ulnar fingers maximally was to prevent them from flexing the third finger concomitantly with the index finger in the kinaesthetic discrimination tests in order to monitor the amplitude of movement. During maximal voluntary compression with the index finger, Ss use not only the above-mentioned muscles but also accessory muscles in the forearm, upper arm, and sometimes the shoulder. During gallamine blockade, forearm muscles were equally well paralyzed, because the cuff was placed on the upper arm. It might be hypothesized, as **Dyhre-Poulsen** remarks, that Ss monitor force in the shoulder muscles as a cue for their sense of effort. If this were the case, then their estimate of effort should be more accurate in trials with maximum or near maximum voluntary force. This was not the case ($p < 0.2$, t test between trials of subjective effort matching with 80–100 percent of maximum voluntary force, compared to trials of effort matching with 0–40 percent of maximum voluntary force; see also **Goodwin**). It is of course not possible for Ss to use the force exerted by the shoulder or upper-arm muscles as a cue for the sense of tension during gallamine-induced paresis.

We had to undertake the cumbersome technique of making a high-speed motion picture of the discrimination tasks in order to evaluate the movement of joints and the stretching and deformation of the skin both prior to external motion of the spring and during the compression (**Walsh**); this problem is of course not compensated by the monitoring of the EMG. The maximum movement amplitude in spring compression is 27.5 mm (Roland and Ladegaard-Pedersen, 1977 *op. cit.*). Close inspection of the film reveals that the stretching of the skin on the dorsum of the hand is less than 4 percent when the spring is maximally compressed. In the force discrimination trials, there were usually no detectable differences in skin stretching. Moreover, stretching of the skin of the dorsum of the hand and fingers is unlikely to have played a role because these skin receptors would have been excited in much the same way with the fingers passively pressed against the object (the test for anaesthesia sufficiency) as during active compression. In the experiments reported, the skin was sufficiently anesthetized because the force level used to determine anesthesia sufficiency (force per unit area) was more than 10 times the highest discrimination limit (in terms of newtons).

Again, inspection of the film reveals that the joints which were distorted, stretched, or moved under the compression of weak and strong springs were the interphalangeal joints of the first and second finger, the metacarpal joints of these fingers, and the carpometacarpal joint (Roland and Ladegaard-Pedersen, 1977 *op. cit.*) These joints were fully anesthetized. It is, therefore, hardly possible that information from the remaining unanesthetized joints (the interphalangeal and carpometacarpal joints of the three ulnar fingers) provided any useful information during spring and strain-gauge compression. That the receptors in the radio-carpal joint and the distal radio-ulnar joint should provide information for the discrimination is unlikely since none of the muscles acting on the thumb or index finger enter or originate from the capsule of these joints.

Still, with these sources of information excluded, **Duysens & Loeb** suggest that receptors in muscles other than spindle and tendon receptors may have signaled the force information to the sensorium. The role of Pacinian corpuscles and group III afferents is difficult to evaluate and only sparse data are available. Paintal (1960, *op. cit.*) found no relation between the firing of group III afferents and force accumulated during muscle twitch. It would be interesting to know the exact relation between impulse frequency and muscular force in Menze's experiments (*op. cit.*, Duysens & Loeb). As far as the Pacinian corpuscles are concerned, those near the joints were probably anesthetized; those in the fassiae could, of course, theoretically signal some information, but whether their firing frequency is correlated with the force developed during muscle twitch is, to my knowledge, still unresolved.

The lignocaine used for skin anesthesia selectively blocked sensory fibers at the base of the fingers because these nerves contain no muscular efferents (see **Kelso**). The efficiency of the lignocaine block was tested several times during the procedures with stimuli relevant to the task. So far as we could see from the film, there should be no tangential forces on the skin (Roland and Ladegaard-Pedersen, 1977, p. 674, *op. cit.*).

In sum, we think that the experimental procedures and the control experiments have excluded relevant information from receptors outside the muscles and tendons.

**McCloskey** suspects that there might be uneven decurization during gallamine block and has provided some data to support this (Gandevia & McCloskey, 1977c). He further suggests that this could explain the precise matching of isometric force by our subjects. This is unlikely, however, since we tested maximum voluntary force on every third trial during the matching experiment. One can accordingly infer that the entire range of motor units was recruited, hence no motor units should be expected to be selectively unblocked by repetitive matching with the gallamine paretic arm. Clearly, S's performance during voluntary effort matching is very different from performance during isometric force matching. When Ss are asked to match their efforts in muscular contraction, it turns out that effort increases roughly in proportion to degree of gallamine induced paresis. This means that the effect of the muscle servo is small. However, as mentioned before, because of the complex interference with alpha-gamma coactivation it might be unwarranted to infer that this mechanism works the same way during normal conditions.

**Some clarification of the results** (replies to commentators **Pubols & Somjen**). **Pubols** wrongly interprets Fig. 5 as showing a slightly elevated threshold for spring-strength discrimination in the anesthetized group. The figure clearly shows that there are no statistically significant differences between the regression lines at a reasonable confidence limit. (The curve-fitting constants may be obtained from Roland and Ladegaard-Pedersen, 1977, p. 677, *op. cit.*) Thus, there are no spring-strength discrimination performance differences between normals and Ss with sensory information restricted to receptors in the muscles and tendons.

By contrast, there is a slight elevation of kinaesthetic discrimination limits when the skin is anesthetized (Figure 10). This means that skin receptors probably assist in yielding kinaesthetic information.

**Somjen** remarks that Ss paralyzed with gallamine could not judge path length when force became a misleading cue; he also raises the question whether information from muscle spindles reaches consciousness at all, as well as whether Ss with joints and skin anesthetized did, indeed, use the force signal as a cue to judge the extent of their active voluntary movements. From Figure 12 it can be seen that, if Ss had been monitoring the actual force directly, errors would have been at least twice as great. However, the muscle spindles are certainly not very accurate kinaesthetic recorders. Perhaps the best argument for a signaling of kinaesthetic information to cortex and to conscious-

ness is that patients with lesions outside the postcentral gyrus exhibit discrimination performance not significantly different from that of normals, whereas patients with lesions in the postcentral area (and the peripheral information restricted to receptors in muscles and tendons) have severely impaired kinaesthetic discrimination.

**The receptors responsible for kinaesthesia and sense of tension** (replies to **Duysens & Loeb, Goodwin, Grigg, Levitt, & Somjen**). The results do not permit pinpointing the receptors responsible for the tension information. However, it would require some rather elaborate hypotheses to support a view that the primary or secondary endings contribute significantly to tension information during gallamine blockade of the end plates. Under normal circumstances, tendon receptors cannot signal position. They are probably only force receptors. The Golgi tendon organs have a much lower threshold for active muscular contraction than for passive stretch. This might be one of the explanations for the discrepancies between these results and those of Gelfan and Carter (1967, *op. cit.*).

The recent experiments on the firing of joint afferents during movement (see **Grigg**) leave us with an apparent paradox, because these receptors seem to be poor at signaling joint position and angular velocity; the muscular receptors likewise seem to record kinaesthesia with a considerable error, depending on the loads opposing the voluntary muscular contractions. Kinaesthesia should thus not be expected to be a very accurate sense. Perhaps the results of Loeb and Duysens (1977, see **Duysens & Loeb**) provide a solution to this paradox, as the information from skin, joints, and spindles already seems to converge at a spinal level.

**The role of feedback and feed-forward during voluntary contraction** (replies to **Chapple, Dickinson, Duysens & Loeb, Freund, Shebilske, Stein, Stevens, & Trevarthen**). Under the experimental constraints described, the sensory information from the peripheral receptors is somewhat artificial. From the data presented, it is not possible to determine the significance of feedback from muscular and tendinous receptors and of motor memory. Many of the commentators have provided very elegant hypotheses about this point. However, I agree with **Chapple** that we as yet understand so little about the relationship between the complexities of proprioceptors and the control of movement at the physiological level, that, although I certainly ought to make my position clear on this issue, my answer can only consist of speculations. I think that sensory feedback from tension receptors is of primary importance only during the learning of new motor skills. In this context I should like to draw attention to the connection from the postcentral gyrus to the supplementary motor area. The latter receives direct afferents from areas 3, 2, 1, and 5 as well as from the superior parietal lobule (Pandya and Kuypers, 1969; Jones and Powell, 1969, 1970; Pandya and Vignolo, 1971). There is some recent evidence that the supplementary motor area is involved in the planning of complex motor sequences and that a motor program can be changed here under the influence of somaesthetic information (Roland et al., 1977, *op. cit.*).

Most probably the sensory information from muscle spindles and tendon organs is normally restricted to subcortical parts of the motor system (e.g., the cerebellum), but it is indeed an interesting hypothesis that our proprioceptive information could be gated into consciousness by the nature of the task being performed by the brain (**Duysens & Loeb**).

**Stevens** makes some interesting observations concerning his personal experiences during gallamine blockade of the eye muscles. These are in agreement with my own experience when personally pretesting the effects of gallamine. The dosage I received was smaller than that necessary to induce full paralysis of the finger muscles, but I can corroborate the inability to locate points in extrapersonal space. I am not sure, however, that this

phenomenon should be explained as primarily a disorder of orientation in extrapersonal space. There is another explanation: gallamine clearly interferes with the reliability of muscle spindles as kinesthetic recorders. An additional observation is that extrapersonal spatial operations with the limbs activate the superior parietal lobule (Roland et al., 1977) while saccades to points in the visual field do not; neither does tracing a moving object with the eyes (Melamed & Larsen, 1977). Thus, the patterns of cortical activation are quite different for eye movements and limb movements, which probably means that the organization of information about relations in extrapersonal space likewise differs.

My article is not meant to emphasize the role of feedback mechanisms at the expense of feedforward information. Clearly, Figures 8 and 9 indicate that man has feedforward information *as well as* feedback during voluntary movement. It is meaningless to state which type of information a subject "normally" relies on because this may obviously vary from task to task.

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