# Kinesthetic Information and Sensorimotor Functions

# for the Control of Limb Movement

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## Abstract

We reviewed the literature on the peripheral sources of kinesthetic information and some relevant sensorimotor functions in the central nervous system. Human movement is thought to be controlled by a hybrid control system consisting of closed-loop and open-loop control mechanisms, in reference to kinesthetic information available from various sensory receptors. Kinesthetic information about limb position and movement is believed to be available primarily from muscle and tendon receptors, with cutaneous and joint receptors supplementarily subserving to sense limb position and movement. On receiving kinesthetic signals available from sensory receptors, spinal segmental mechanisms are responsible for either facilitating or inhibiting the activity of the motoneurones of agonist and antagonist muscles used in limb movements. These facilitatory and inhibitory actions in the spinal segmental systems can be examined by measuring the H-reflex (Hoffmann, 1918), with several careful considerations being needed when using the H-reflex technique. Sensory information is sent to the central nervous system via spinal ascending pathways, and is processed in cortical and subcortical sensorimotor systems. The cortical and subcortical systems make movement plans and prepare motor commands to be sent to the spinal segmental systems. The cortical motor system is believed to send a copy of the motor commands (efference copy), in advance of the planned movement to be actually executed, to cortical sensory areas as well. This efference copy sent to the sensory areas is thought to subserve to effectively evaluate the kinesthetic information available, via spinal pathways, from the execution of the movement. Various human movements,

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such as limb joint movements, are thus executed with various sensorimotor neural network systems being activated.    To further understand the mechanisms underlying human movement we should fully take into account the various neural levels of sensorimotor functions in relation to the specific neural and behavioural conditions of the movement to be examined.


# Introduction

The question of how our various movements are accurately controlled has been investigated since the late nineteenth century (Leuba, 1909; Woodworth, 1899).    However, systematic attempts to understand human motor behaviour did not commence until the 1960s ( e. g., Adams & Dijkstra, 1966; Posner, 1967).    The most popular conceptualization for understanding human motor performance since the post-1960 period has been based on the notion that humans are processors of information, in the same way as modern computers are.    In fact, cognitive psychologists borrowed the term "information-processing" from computer scientists (Klatzky, 1980).    Implicit in the information-processing notion is the idea that information to guide movement is available both in the environment and in the body itself.    This perceptual information is received by the individual through a number of receptors, put into various storage (memory) systems, and sequentially processed in the central nervous system of the individual (Marteniuk, 1976; Schmidt, 1988).    Numerous questions have been raised in relation to these various information-processing stages, such as what kind of information is available from both outside and inside the individual, how it is received, processed, stored and retained, and how it is utilised for action (Posner, 1986; Stelmach, 1982).

Based on the notion of information-processing, human motor behaviour and movement are frequently viewed as being controlled by a kind of hybrid control system, involving the integration of two different fundamental modes of control, closed-loop and open-loop control (Glencross, 1977; Schmidt, 1988; Summers, 1981).    In this review, we first briefly consider these control systems (i. e., closed-loop and open-loop control) in relation to the utilisation of peripheral feedback information.    We then deal with a specific issue regarding peripheral sources of kinesthetic information which could contribute to the control of limb movement.    Following this examination, we discuss the issues of spinal and central sensorimotor functions for motor control and the notion of corollary discharges or efference copy, which relate to an effective

evaluation of sensory feedback information by the central nervous system.


## Control Systems and Peripheral Feedback Information

Closed-loop control, upon which Adams (1971) based his theory of motor learning, involves several information-processing stages. These stages include detecting errors by comparing response-produced feedback to certain references stored in the central nervous system, determining the nature of the correction required, and executing the correction. This control model emphasises the utilisation of feedback information as a means of attaining the correct movement (Sage, 1984; Schmidt, 1988, for reviews). Potential sources of the sensory information needed to subserve this mode of movement control will be examined as a primary concern in this review article.

Open-loop control, in contrast, is not assumed to be dependent upon feedback functions, but is based rather on the generation of a series of movement instructions, in the form of a motor program (Henry & Rogers, 1960), structured prior to the initiation of the movement. Powerful evidence for motor programs has been gained through studies on deafferented humans and monkeys (e. g., Bizzi, Polit, & Morasso, 1976; Lashley, 1917), and through studies of human motor control under sensory deprivation by the nerve compression technique (Laszlo, 1966; Laszlo & Bairstow, 1971a, 1971b), which studies have shown that skilled movements can be performed in the absence of sensory feedback.

The main point of divergence for the two control models (i. e., closed-loop and open-loop control mechanisms) relates to the necessity of using peripheral feedback information. One of the strongest criticisms of the closed-loop model of motor control has related to the need for sufficient time for the performer to consciously process the available feedback information. Since conscious error detection and its correction during an ongoing movement generally requires about 150 to 200 msec to complete, the closed-loop control model does not seem to be able to explain well the control of fast or ballistic movements (Schmidt, 1988). Thus, slow and fast movements may be controlled differently, especially with respect to the utilisation of feedback information. Self-paced slow limb movement is controlled mainly by the closed-loop control system. The role of peripheral feedback information is therefore crucial for the control of this kind of movement.

However, nonconscious reflexive closed-loop mechanisms are also involved

in the nervous system: the monosynaptic reflex loop with a latency of about 30-50 msec (Dewhurst, 1967; Evarts, 1973), the long-loop or transcortical reflex with a latency of some 50-80 msec (Evarts, 1973; Evarts & Fromm, 1981; Evarts & Tanji, 1974; Hammond, 1956; Lee & Tatton, 1975, 1978; Marsden, Merton, Morton, & Adam, 1978; Matsunami, 1984), and the conscious closed-loop mechanisms mentioned above (with latencies in the order of simple reaction time). In addition, Crago, Houk, and Hasan (1976) have proposed the existence of a fourth kind of response mechanism termed triggered reactions, of which the latency is about 80 to 120 msec (Schmidt, 1988). The muscle activity in this mechanism is thought to be triggered by afferent inputs from various receptors (other than those in muscle and tendon), for example, those in the skin (Johansson & Westling, 1984).

Both the closed-loop and open-loop control modes may contain nonconscious reflexive mechanisms. Keele (1982) has suggested that a motor program is a hierarchical structure of action proceeding from general goals to specific selections of muscles. He has stated that, "Much of the learning is concentrated at higher levels in the hierarchy that specify the general sequence of action. Lower levels are free for alternative specification such as speed or arm. Final details may partly be taken care of by innate reflex patterns" (p. 180). Likewise, Glencross (1977) has emphasised the importance of an interaction between peripheral feedback and motor programs in the control mechanisms. Also, Russell (1976) has suggested that at a "micro" level in closed-loop control, corrective movements must be determined predictively, or preprogrammed with a short duration.

Although the closed-loop and open-loop control mechanisms are quite different, particularly in their dependence upon conscious feedback requiring long processing time, overall control systems of human motor behaviour undoubtedly involve both control modes acting at different levels of the motor system. For example, open-loop systems often include some embedded feedback loops (Schmidt, 1988), and closed-loop systems, which involve conscious mechanisms of information processing, may well mimic open-loop control through their use of programmed corrective movements (Russell, 1976).

## Peripheral Sources of Kinesthetic Information

*Kinesthesis*

Kinesthesis is thought of as a sensory modality associated with joint position and movement (Burgess, Wei, Clark, & Simon, 1982). Other kinds of sensory information, such as vision, audition, and information arising from the vestibular apparatus, are also believed to be important in the control of movement. Traditionally, vision and audition have been regarded as essential modalities for providing information about the nature of the environment, being called exteroceptive information. In the absence of visual and auditory information, kinesthesis is thought of as an important sensory modality for motor control and learning (Sage,1984).

The term, kinesthesis, has been used synonymously with the term, proprioception, which was originally coined by Sherrington (1906, cited in Sage, 1984, and Schmidt, 1988) to refer to the perception of movement of the body and its orientation in space (see Schmidt, 1988). According to Marteniuk (1976), kinesthesis is a part of proprioception and is defined much more specifically as movement information arising primarily from the joint afferents and muscle spindle afferents. More strictly, Smith (1969) has attempted to limit the term, kinesthesis, to mean information from the joint receptors.

However, others have used the term more liberally. Gibson (1966) argued that kinesthesis should be considered to mean information about action, irrespective of the sensory modalities involved, and he suggested that stretch and pressure signals from the skin should also be involved. Furthermore, Gibson himself, and, more recently, Lee (1978, 1980; Lee & Young, 1985), have argued that vision is not only an exteroceptive sense, which provides information about the spatial structure of the environment, but that it is also a proprioceptive sense, which provides information about the position and movement of a performer's limbs and body in relation to the environment. Lee (1978) termed such a union of exteroceptive and proprioceptive information "exproprioceptive". Smyth and Marriott (1982) have also suggested that visual information about arm position, at least during the performance of an ongoing ball-catching movement, is essential in calibrating the kinesthetic information arising from the arms and this contention has recently been confirmed by a number of researchers (Davids, 1988; Diggles, Grabiner, & Garhammer, 1987; Fischman & Schneider, 1985; Populin, Rose, & Heath, 1990; Rosengren, Pick, & Hofsten, 1988). Fischman and Schneider (1985) suggest that vision may serve to tune up other perceptual systems. Thus, vision is now thought of as both a powerful source and as a calibrator of kinesthetic information.

Clark and Horch (1986) also used the term, kinesthesis, in a somewhat broad sense to include awareness of the positions and movements of the limbs

and other body parts, including sensations arising from contractions of the muscles, but excluding sensations arising from the visual, auditory, and vestibular systems.  The vestibular apparatus provides information about movements of the head, and is important in balance and in responses for which the individual requires information about forces and acceleration applied to the head (Schmidt, 1988).

Since the present review focuses primarily on peripheral information for the control of limb movements in the absence of visual information, it would be appropriate to define kinesthesis as that sense which is responsible for the discrimination of the position and movement of a limb, based on information provided from systems other than vision, audition (Marteniuk, 1976; Sage, 1984), and the vestibular apparatus (Walsh, 1980).

Although considerable confusion still exists with regard to the exact role that each receptor type plays in kinesthesis (Clark & Horch, 1986; McCloskey, Cross, Honner, & Potter, 1983; Moberg, 1983; Sage, 1984), each of the sensory receptors for kinesthesis is structurally different and responds to different types of stimuli.  Each of the receptors may contribute to a different extent to total kinesthetic perception.  Relevant studies of the characteristics of different receptors such as joint, muscle and tendon, and cutaneous receptors, are reviewed in the sections that follow.

*Joint Receptors*

Until the studies of Burgess and Clark (1969a, 1969b), it was generally believed that joint receptors were the ideal position sensors.  Physiological studies on the knee joint of the cat had shown that the joint receptors had appropriate sensory properties to signal joint movement and position (Andrew & Dodt, 1953; Boyd & Roberts, 1953).  Different joint receptors had been found to be active at different ranges of joint movement from 15 to 30 degrees, with these ranges overlapped to cover the whole range of joint movement (Skoglund, 1956).  However, Burgess and Clark (1969a) examined the responses of the receptors over the whole range of joint angles and, by minimising sampling bias, showed that steady firing at intermediate angles between full extension and full flexion occurred for only 4 of 209 joint receptors, while 140 of the sampled receptors fired at both full extension and full flexion.  Thus, they found no evidence to support the earlier study of Skoglund (1956), which now appears to have artificially exaggerated the number of receptors firing at intermediate angles.  Further, Clark and Burgess (1975) have indicated that joint receptors are not appropriate for signalling steady-state joint angles

over most of the working range, but rather reliably signal only joint positions at the extremes of flexion and extension.   Studies performed on subjects after prosthetic surgery (Cross & McCloskey, 1973; Grigg, Finerman, & Riley, 1973; Kelso, Holt, & Flatt, 1980) have shown that total replacement of joints causes only minimum reduction of kinesthetic function, suggesting that joint receptors alone do not subserve position sense (Goodwin, 1976; Goodwin, McCloskey, & Matthews, 1972b; Kelso, 1978; McCloskey, 1978).   Recently, Sage (1984) has suggested that, "The receptors may be capable of signalling information on the velocity and acceleration of joint movement, or even the forces generated by muscles acting at the joint, rather than steady-state-joint angulation or position" (p. 180).   In fact, Clark (1975) has shown that many joint receptors respond only upon forceful hyperextension of the joint.   Grigg (1975, 1976) has also suggested that the responses of joint receptors correlate best with torque applied to the joint, rather than with joint position.   Thus, joint receptors may have an entirely protective function to prevent the hyperextension of the joint during a vigorous movement (Clark & Horch, 1986), rather than having an essential position sensing function for motor control.

However, for some joints such as the hip, the joint receptors have recently been found to provide appropriate signals throughout the full range of movement (Carli, Farabollini, Fontani, & Meucci, 1979).   Ferrell (1980) found that the receptors in the cat knee joint responded significantly to midrange joint angles.   A more recent study (Swash, 1986) also shows abnormality of the sense of movement and of motor control after partial meniscectomy of the human knee joint, suggesting that joint receptors may play a role in movement sensation that is more complex than simply contributing to the static sense of position.   These findings imply the possibility of the joint receptors making some contribution to position and movement sense, although their major role seems to be in joint protection.

*Muscle and Tendon Receptors*

In the 1950s and 1960s many physiological studies (e. g., those of Rose & Mountcastle, 1959) emphasised the role of the joint receptors rather than the muscle receptors in kinesthesis.   Gelfan and Carter (1967), for example, stretched the muscles of subjects who were undergoing operations by pulling on their exposed tendons.   As none of the subjects experienced any sensation referable to the muscles, the researchers concluded that there was no muscle sense.   However, Matthews and Simmonds (1974) found that patients could sense the stretch of an exposed muscle, and this result was corroborated by

McCloskey et al. (1983), but not by Moberg (1983). Clark and Horch (1986) have stated that, "The reasons for these differences remain obscure, but for such differences to still exist underscores the difficulty in getting answers to seemingly simple, straightforward questions about kinesthesia" (p. 13-15).

Complete revision of the role of muscle and joint receptors in kinesthesis was made by Eklund (1972), and also Goodwin, McCloskey, and Matthews (1972a, 1972c, 1972d), using studies in which mechanical vibration was applied to muscle tendons (Eklund & Hagbarth, 1965, 1966; Hagbarth & Eklund, 1969; Marsden, Meadows, & Hodgson, 1969). Eklund (1972) examined the position sense of the knee joint and Goodwin et al. (1972a, 1972c, 1972d) examined this in the elbow joint, both used a paradigm which required subjects to indicate, with the other limb and in the absence of visual information, the perceived position of the vibrated limb. These studies were consistent in their findings that mechanical vibration applied to the muscle tendons induced errors in the perception of joint position and produced illusions of joint movement in the direction that would have occurred had the vibrated muscle been stretched. These findings suggest that receptors in muscles may be used to judge limb position, and that thereby they contribute actively to kinesthesis.

Burke, Hagbarth, Löfstedt, & Wallin (1976) have indicated that the discharge rate of the muscle spindle is strongly related to the frequency (or subharmonics of the frequency) of induced vibration, suggesting that these proprioceptors could be responsible for the illusion of movement evoked by such a mechanical vibration. Further, Craske (1977) has shown that subjects felt as if their hands were extended beyond their maximum operating range when the flexor muscle of the wrist was vibrated during passive extension of the hand to its anatomical limit. This suggests that the mechanism of position sense must involve processes of extrapolation taking place within the central nervous system.

A number of studies (Burke et al., 1978; Burke, Hagbarth, & Skuse, 1978; Clark, Matthews, & Muir, 1979; Juta, Van Beekum, & Van Der Gon, 1979) have also examined the relationship between mechanical vibration and muscle spindle activity or illusions of movement. Collectively, these studies suggest that the central nervous system may monitor muscle afferent activity for the lengthening (antagonist) muscle (Capaday & Cooke, 1981; Roll & Vedel, 1982). More recent studies (Gregory, McIntyre, & Proske, 1986; Gregory & Proske, 1988; Rogers, Bendrups, & Lewis, 1985; Sitting, Van Der Gon, Gielen, 1985a, 1985b) have corroborated such a viewpoint, arguing that mechanical vibration may distort the Ia afferent information from the muscle spindle, and that it

is such distortion that leads to a misperception of limb position.   Thus, it
has been suggested that the muscle spindle is strongly related to the perception
of limb position and velocity (Kelso, 1978; Kelso et al., 1980).   Recent work
has also shown that the tendon receptors can respond to forces of less than
0.1g (Houk & Henneman, 1967), and thus the current view of tendon receptors
is that they are very sensitive to the active tension of a muscle (Crago, Houk,
& Rymer, 1982).   In the light of these physiological findings, it seems reason-
able to expect that the afferent information from muscle receptors is impor-
tant for the accurate execution of limb movements.

## Cutaneous Receptors

At present, the role of cutaneous receptors in movement control remains
unclear (Clark & Horch, 1986).   However, since a joint movement involves
stretching and distorting the skin around the joint, it might be reasonable to
expect that the cutaneous receptors may play a role in kinesthesis.   Recent
studies suggest that these receptors may be more important than has tradi-
tionally been believed (Sage, 1984).   According to Sherrick and Cholewiak
(1986), there are at least a dozen different receptor types in the skin, and the
majority respond and signal the velocity or acceleration of rapid skin defor-
mation or hair displacement.   Only two receptor types show a slowly adapting
response, and continue to discharge if deformation of the skin is maintained.
Knibestöl (1975) reported that one of the slow adapting receptors (called type
SA-II) in human fingers was able to signal joint angle over a wide range, and
he suggested that the SA-II receptors in the skin contributed kinesthetic
information about joint position.   However, a recent study using the technique
of microstimulation, which can activate identified single nerve fibres from the
various cutaneous receptors, has shown that SA-II receptors do not elicit any
sensation when activated in isolation (Vallbo, Olsson, Westberg, & Clark, 1984),
and, as yet, no one has reported any kinesthetic sensations arising from the
stimulation of cutaneous receptors (Clark & Horch, 1986).   Further, Clark,
Burgess, and Chapin (1983) have found that anesthetizing a fingertip impairs
subjects' ability to sense slow joint movements (anesthetizing the thumb
diminishes their ability to detect slow displacements of the index finger), while
anesthetic injected into the joint results in no impairment.   Based on these
findings, Clark and his co-workers (Clark et al., 1983; Clark, Burgess, Chapin,
& Lipscomb, 1985) have suggested that cutaneous receptors in the fingers may
provide the central nervous system with some kind of supportive or facili-
tatory input to supplement position and movement signals derived from other

sources, particularly muscle receptors, but that, in the main, the cutaneous receptors play, at most, only a minor role in kinesthesis.

## Spinal Sensorimotor Functions and Supraspinal Control

Several types of afferent information ascending from the joint, muscle, tendon, and cutaneous receptors described in the previous section are believed to activate the spinal reflex mechanisms. These mechanisms are also affected by supraspinal descending motor commands. As a typical example of such sensorimotor functions in spinal reflex mechanisms, reciprocal Ia inhibition is considered to be one of the most important neural mechanisms responsible for natural, smooth limb movement. In this section we will briefly refer to the spinal mechanisms of reciprocal Ia inhibition and to the supraspinal influences on these mechanisms.

The phenomenon that a voluntary contraction of the pretibial muscle attenuates the amplitude of the H-reflex (Hoffmann, 1918) evoked in the triceps surae (i.e., the antagonist of the pretibial muscle) has frequently been observed (e. g., Paillard, 1955). In cats, electrical stimulation applied to Ia afferent fibres of an agonist muscle has been reported (Lloyd, 1946) to induce inhibitory effects on the motoneurone of the antagonist muscle, with a central latency (i. e., a latency measured within a spinal segment) of almost 0 msec. This latency was later interpreted by Araki, Eccles, and Ito (1960) to mean a central delay (about 0.8 msec) via disynaptic linkage (i. e., via an interneurone) between the Ia afferent fibre and motoneurone. Since the study by Araki et al., interneurones mediating this kind of inhibition occurring at spinal segments have been extensively investigated in the spinal cord of the cat (see Hultborn, 1972). In short, the interneurones within a spinal segment are believed to receive various signals from both the supraspinal and spinal segmental systems, and are therefore considered to play an important role, as integrative centres, in reciprocal innervation (see Baldissera, Hultborn, & Illert, 1981; Rothwell, Day, Berardelli, & Marsden, 1984).

In humans, reciprocal Ia inhibition (which occurs in time with the activation of a disynaptic circuit) has been examined in experiments with a specific paradigm in which low-intensity electrical stimulation (as a conditioning stimulus) is applied to agonist Ia afferent fibres for activating a disynaptic circuit (i. e., for inducing the reciprocal Ia inhibition) and a subsequent test-stimulation is applied, with a short latency, to the Ia fibres of the antagonist

muscles to evoke an H-reflex.   In such a paradigm, the amplitude of the H-reflex is expected to decrease as the activation level of the reciprocal Ia inhibition increases (by increasing the intensity of the conditioning stimulation).   Tanaka (1972, 1974), by applying conditioning stimulation to the peroneal nerve (which innervates the pretibial muscle, which is the antagonist of the soleus), has shown that the soleus H-reflex is subject to an inhibitory effect, showing a typical effect of reciprocal Ia inhibition.   Tanaka also found that the pretibial H-reflex was inhibited by applying conditioning stimulation to the tibial nerve, which innervates the soleus muscle.   Pierrot-Deseilligny, Morin, Bergego, and Tankov (1981) showed slightly different results for the depression of the soleus H-reflex (e. g., shorter latency and duration than those reported by Tanaka), although in general, they corroborated Tanaka's findings on the relationship between the reflexive effects of the conditioning and test stimulation.

Reciprocal inhibition has also been examined in the search for supraspinal influences on the spinal inhibitory effect, with a voluntary contraction being used in experiments for producing descending motor commands.   Simoyama and Tanaka (1974; Tanaka, 1980, 1983) have shown that depression of the soleus H-reflex (i. e., reciprocal inhibition on the antagonist muscle) begins to occur at about 70 to 80 msec prior to the onset of a voluntary contraction of the pretibial (agonist) muscle.   This suggests that the supraspinal systems may influence reciprocal inhibitory action on the motoneurone of the antagonist muscle prior to the actual voluntary contraction of the agonist muscle occurring.   However, the preceding depression of the H-reflex appearing prior to the voluntary contraction is found only under conditions of artificial activation of the Ia afferent fibre derived from the agonist muscle (i. e., conditions in which the conditioning stimulation is provided to the peroneal nerve, which innervates the pretibial muscle).   Under conditions in which no conditioning stimulation is provided, depression of the soleus H-reflex has been shown to commence at 100 msec *after* the onset of voluntary contraction.   In contrast, some studies (e. g., Pierrot-Deseilligny, Lacert, & Cathala, 1971) have shown that depression of the soleus H-reflex appears at about 50 msec *prior to* the EMG onset of the pretibial muscle, under the same conditions (i. e., with no conditioning stimulation being provided).   Such a discrepancy between the results of these previous studies has since been suggested by Kagamihara and Tanaka (1985) to probably depend on the methodologies used in each study. Kagamihara and Tanaka concluded, on the basis of their experimental findings, that reciprocal Ia inhibition was likely to occur at almost the same time

as onset of agonist muscle activity, but was probably very weak in its inhibitory influence on the antagonist muscle.   The inhibitory effect on the antagonist muscle can therefore be easily cancelled by changing the conditions of the antagonist muscle per se, as when the antagonist muscle is slightly stretched and when a relatively strong test stimulation is applied on the antagonist muscle.

Kasai and Komiyama (1988) have recently reported that depression of the soleus H-reflex begins at about 40 msec prior to the onset of the voluntary contraction of the pretibial muscle under conditions in which there is no conditioning stimulation (i. e., without artificial activation of the Ia afferent fibre of the pretibial muscle).   When conditioning stimulation is applied to the Ia afferent fibre of the pretibial muscle, depression of the soleus H-reflex begins to occur at about 80 msec prior to the onset of voluntary contraction of this muscle.   More importantly, this depression of the soleus H-reflex begins to occur at the same time as *facilitation* of the H-reflex tested in the pretibial (agonist) muscle per se begins to appear.   This means that descending motor commands facilitate the excitability of the $\alpha$-motoneurone in the agonist (i. e., pretibial) muscle and, at the same time, this supraspinal influence (i. e., the descending motor commands), in all probability, begins to gradually activate the Ia inhibitory interneurone up to the subliminal fringe in advance of the pretibial EMG onset.   This preceding supraspinal influence may cause an inhibitory effect on the antagonist (soleus) $\alpha$-motoneurone about 40 to 50 msec prior to the EMG onset of voluntary foot dorsiflexion (Kasai & Komiyama, 1988; Pierrot-Deseilligny et al., 1971).   Likewise, activation of the reciprocal inhibitory effect on the H-reflex of the forearm flexor has also been shown to occur prior to voluntary wrist extension (Day & Rothwell, 1983).

The supraspinal influence is likely to subserve the activation of the Ia inhibitory interneurone at a subliminal excitation level in advance of the agonist muscle contraction.   On the agonist muscle contraction being initiated, a large number of excitatory inputs is provided from the actual muscle contraction, via $\gamma$-driven Ia afferent fibres, to the Ia inhibitory interneurone, thereby resulting in the excitation level of the Ia inhibitory interneurone being saturated beyond its discharge threshold (Shindo, Harayama, Kondo, Yanagisawa, & Tanaka, 1984).   This notion is consistent with the earlier findings of Morin and Pierrot-Deseilligny (1977), who have examined, using an ischemic technique for blocking Ia afferent pathways, the role of Ia afferent inputs in the inhibition of the soleus motoneurone during voluntary contrac-

tion of the tibialis anterior muscle.

Some methodological problems have recently been suggested to remain regarding the examination of inhibitory effects in terms of the H-reflex. Several studies (Crone, Hultborn, & Jespersen, 1985; Iles, 1986) have reported that reciprocal Ia inhibition assessed by depression of the soleus H-reflex appears to vary irregularly during tonic voluntary dorsiflexion of the foot, even with the contraction level being kept constant. During voluntary tonic dorsiflexion, Ia afferent inputs from the pretibial muscle are likely to vary necessarily according to the function of the " $\alpha$- $\gamma$ linkage". Further consideration of the role of the " $\alpha$- $\gamma$ linkage" has therefore been suggested as being needed for investigating the issue of reciprocal inhibition.

Crone, Hultborn, Mazières, Morin, Nielsen, & Pierrot-Deseilligny ( 1990 ) have recently examined the effects of the amplitude of test stimulation[1],which is used for inducing the H-reflex in a test muscle, with a constant conditioning stimulation being applied either to the test muscle per se (under these conditions the H-reflex should increase in amplitude, since the conditioning stimulation is applied to facilitate the H-reflex as a monosynaptic reflex) or to the antagonist muscle of the test muscle (under these conditions the conditioning stimulation is used to activate inhibitory effects on the H-reflex of the antagonist muscle). The extent of either the inhibitory or excitatory effect on the H-reflex is shown to differ for the different amplitudes of the test stimulation used for inducing H-reflexes. Remember that the conditioning stimulation is kept at a constant intensity for all test stimulation conditions. Selection of the amplitude of test stimulation for inducing the H-reflex may therefore be an important, and indeed, is probably one of the most crucial, methodological factors involved when the H-reflex technique is used as a more quantitative tool for investigating spatial facilitation in spinal sensorimotor functions in humans at a premotoneuronal level.


## Central Sensorimotor Functions and Monitoring of Efference

*General Sensorimotor Functions in the Brain*

It has been clearly demonstrated that a number of specific areas of the brain and central nervous system are directly involved in the control of

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[1] The amplitude of the test stimulation is usually determined at a constant level so that the amplitude of the H-reflex can be a function of the intensity of the conditioning stimulation.

voluntary movement (e. g., Allen & Tsukahara, 1974). It has been suggested that the motor cortex is the final relay to output motor commands to the spinal neurones, which we referred to in the previous section. The motor cortex is also the summing point: various inputs converge in the motor cortex from other cortical areas such as the somatosensory and prefrontal cortex, and also from subcortical areas such as the cerebellum and basal ganglia (see Allen & Tsukahara, 1974; Bloom & Lazerson, 1988; Kubota, 1984a; Mizuno, 1984; Sage, 1984). The somatosensory cortex receives afferent inputs from muscle, tendon, and cutaneous receptors (Oscarsson & Rosén, 1963; Phillips, Powell, & Wiesendanger, 1971; Zarzecki, Shinoda, & Asanuma, 1978), and conveys signals to the motor cortex (Zarzecki et al., 1978), completing a feedback loop believed to be required for movements requiring fine control (Evarts & Fromm, 1981; Lee & Tatton, 1978; Marsden et al., 1978; Matsunami, 1984). The prefrontal cortex is involved in the analysis of sensory information and the initiation of voluntary movement, and the major function of this area of the cortex appears to be to establish the spatial and temporal structure for an action, so that the intended goal-directed behaviour may be accomplished (see Kubota, 1984b). These cortical areas are linked with subcortical areas such as the basal ganglia and cerebellum, which are believed to play an important role in the initiation and execution of voluntary movement (see Mizuno, 1984).

The basal ganglia receive inputs mainly from the motor, somatosensory, and prefrontal areas of the cerebral cortex. Their major output is directed, via the thalamus, to the prefrontal and premotor cortex, but they do not act directly upon the motor cortex controlling distal musculature (see DeLong & Georgopoulos, 1981; Greer, 1984; Yoshida, 1984). On these anatomical grounds, it has been suggested that the basal ganglia may integrate the inputs from various cerebral areas and transmit them to the frontal association areas, participating in the initiation (and also execution) of more complex motor behaviour rather than distal motor function (DeLong & Georgopoulos, 1981).

The cerebellum receives two broad classes of input; proprioceptive information from both the somatosensory receptors and the vestibular apparatus, and projections from various areas of the cerebral cortex (see Greer, 1984; Mizuno, 1984). A significant role of the cerebellar output is believed to lie in regulating postural adjustments, locomotion, and many reflexive movements (Brooks & Thach, 1981; Sage, 1984). It has also been suggested that the cerebellum may integrate and transform inputs from the frontal association

areas into the motor and premotor areas. It is therefore believed that the cerebellum is involved in the preprogramming and initiation of intended movement, acting in parallel with the basal ganglia (Mizuno, 1984). Furthermore, two different viewpoints have been proposed regarding the global (ultimate) function of the cerebellum: the cerebellum can be thought of either as a central regulating system capable of implementing motor coordination, or as the seat of the acquisition and retention of newly acquired motor skills (see Llinas, 1981).

*Monitoring of Efference: Effective Evaluation of Kinesthetic Information*

In the area of motor control and memory, some studies (e. g., Adams, 1971; Laabs, 1973) have emphasised the importance of peripheral sources of information, while some have emphasised central sources of information. Jones (1974) has stressed the role of the central monitoring of efferent commands to the muscles as the necessary and sufficient information on which the short-term retention of limb movements may be based. Likewise, Kelso (1977a, 1977b) has also emphasised the role of efferent information and planning processes prior to the initiation of an intended movement. These studies emphasising central sources have often referred to the notion of corollary discharge (Sperry, 1950) or efference copy (von Holst, 1954).

The notion of corollary discharge hypothesises that a copy of the efferent command signals which are sent to the muscles is also sent to various perceptual centres, where it has a direct influence on perception (see Clark & Horch, 1986). Similarly, efference copy involves a copy of the efferent command signals being directed to a lower, comparator system, whose function it is to generate a difference signal between this input and the sensory input derived from the movement itself. This difference signal is then believed to be sent both to the perceptual centres to influence perception, and to the motor command centre to modify motor (efferent) commands. Although the original notions of corollary discharge and efference copy were quite different, these terms have often been used interchangeably in the literature (Clark & Horch, 1986; McCloskey, 1981). A major function of corollary discharge or efference copy may be to influence the central processing of kinesthetic signals arising from the muscle receptors. In this way, corollary discharge or efference copy may be responsible for the perception of muscular force or effort, and for the estimation of the heaviness of objects to be lifted (Matthews, 1982; McCloskey, 1981). Movement errors may be detected and corrected by using corollary discharge or efference copy, as these provide some information about what is

about to happen in the movement or about the intended movement character-
istics (Schmidt, 1988).

Strong neurological evidence has been reported for the notion of corollary
discharge or efference copy (seeEvarts, 1974, 1981; Nishihira, Araki, & Ishihara,
1987; Sakata, 1984; Woolsey, 1958). For example, a number of neurones in
the parietal association cortex (which is recognised as a sensory centre) have
been shown to be activated prior to the onset of muscular activity during
active forelimb movement in the monkey (Mountcastle, Lynch, Georgopoulos,
Sakata, & Acuna, 1975; Soso & Fetz, 1980), and yet these same neurones are
not activated with passive movements (Soso & Fetz, 1980). Moreover, these
parietal neurones fire with a short delay (about 60 msec) from the onset of
discharges in the motor cortex, suggesting that this activity in selected parietal
neurones may represent corollary discharge from the motor cortex (Kalaska,
Caminiti, & Georgopoulos, 1983).

## Summary and Conclusions

We reviewed the literature concerning the role of peripheral sources of
kinesthetic information and some relevant sensorimotor functions in the
peripheral, or spinal, and central nervous systems. We first discussed
overall control systems, such as the closed-loop and open-loop types, in
relation to the utilisation of sensory feedback information. We then exam-
ined sensory receptors, such as joint, muscle and tendon, and cutaneous
receptors, and the relevant spinal and supraspinal sensorimotor functions, in
reference to both reciprocal inhibition at the spinal level and the H-reflex
(Hoffmann, 1918). Finally, we discussed central sensorimotor functions and
the function of efference monitoring, which relates to effective evaluation of
kinesthetic information.

As stated above, control systems are thought to consist of the closed-loop
and open-loop control mechanisms. Although the use of peripheral feedback
information is generally thought of as a characteristic feature of the closed-
loop rather than the open-loop system, unconscious, reflexive closed-loop
mechanisms, such as monosynaptic reflexes, transcortical or long-loop
reflexes, and triggered reactions, are believed to be embedded in both control
systems. These two control systems are thought to be integrated into a
hybrid system which controls commonly observed human motor behaviour.
Peripheral information regarding movement is very influential in the accurate

control of movements.

Sensory receptors, such as those in the joints, muscles and tendons, and those in the skin, mediate peripheral kinesthetic information in the absence of vision and audition; these receptors have frequently been examined to see which of them are primarily responsible for kinesthesis.　Until the end of the 1960s joint receptors had been thought of as the sources most responsible for kinesthetic information (e. g., Skoglund, 1956), with muscle receptors making no contribution to kinesthesis.　However, a complete revision of the respective roles of joint and muscle receptors in kinesthesis has been made since the early 1970s.　A number of studies at that time used mechanical vibration applied to muscles (e. g., Eklund, 1972; Goodwin et al., 1972a, 1972c, 1972d), and their results led to the now accepted notion that muscle and tendon receptors play a crucial role in monitoring limb movements.　Cutaneous receptors are also believed to contribute to sensing joint movements, with, at most, only a minor role in kinesthesis, supplementing the position and movement signals derived from muscle receptors.

Sensory signals derived from these various sensory receptors are conveyed to spinal segments.　Spinal interneurones are thought of as an integrative centre for receiving both the afferent inputs from sensory receptors and the descending motor commands from supraspinal sensorimotor systems.　In particular, Ia afferent inputs from muscle spindles of an agonist muscle to Ia inhibitory interneurones play an important role in providing inhibitory effects on the antagonist muscle, resulting in natural, smooth limb movement in which the agonist muscle contracts, with the antagonist being inhibited from contracting.　The neural circuit responsible for such reciprocal Ia inhibition has been examined by testing the amplitude of the H-reflex evoked on the antagonist muscle, with a conditioning stimulation being applied to the Ia afferent nerve of the agonist muscle to activate Ia afferent signals from this muscle. Furthermore, the effect of descending motor commands from supraspinal systems upon the inhibitory action of the antagonist muscle has also been examined by using the H-reflex.　Motor commands descending from supraspinal systems to cause agonist contraction have been shown not only to facilitate agonist $\alpha$-motoneurones, but also to inhibit antagonist $\alpha$-motoneurones.　Such facilitatory and inhibitory actions have been shown to occur on a time-course of 70 to 80 msec prior to the onset of the actual agonist contraction.　Spinal sensorimotor functions, particularly the integrative functions of interneurones, are believed to be quite important for the execution of natural, smooth limb movements.

Kinesthetic information derived from peripheral sensory receptors is sent to the spinal sensorimotor systems, where reflexive actions that enable smooth limb movements are likely to occur, and is also sent to the central (supraspinal) nervous system via spinal ascending pathways.   In the central nervous system, various cortical areas such as the motor cortex, somatosensory areas, and prefrontal cortex, are linked to each other and also to subcortical areas such as cerebellum and basal ganglia, forming a neural network for sensing position and movement and for planning and controlling movement.

The motor cortex is the summing point of various cortical and subcortical inputs and is also the final relay to output motor commands to spinal neurones (e. g., Allen & Tsukahara, 1974).   Furthermore, the motor cortex is believed to output a copy of efferent command signals (which are sent to the muscles) to the perceptual centres.   This notion has been developed as the corollary discharge (Sperry, 1950) or efference copy (von Holst, 1954) hypothesis, with much supporting neurophysiological evidence being reported.   Corollary discharges or efference copy sent to the sensory areas is assumed to be compared with actual sensory inputs (i. e., kinesthetic feedback signals) available from the execution of the movement itself.   This comparison generates a difference signal between the copy of efferent signals and actual afferent signals and, with this difference signal, the ongoing movement is rapidly corrected.   Monitoring of efference is therefore believed to play an important role in sensing limb position/movement and in producing accurate limb movements.

In conclusion, various human movements, such as limb joint movements, are executed by the necessary activation of various sensorimotor neural network systems, such as sensory receptors, spinal segmental systems, and the brain, with facilitatory and inhibitory actions being activated in these systems. To further understand the neural and behavioural mechanisms underlying human movement, we should fully take into account these peripheral and central sensorimotor functions at various neural levels, in relation to the neural and behavioural conditions of the specific movement to be examined.

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