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THE HOFFMANN REFLEX: A MEANS OF ASSESSING SPINAL REFLEX EXCITABILITY AND ITS DESCENDING CONTROL IN MAN

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1. Introduction

1.1. HISTORICAL ASPECTS

Electrical stimulation of the posterior tibial nerve in the popliteal fossa evokes a contraction of the calf muscles. This was shown first by Piper (1912) and then clearly described by Hoffmann (1918, 1922), who demonstrated that the response observed consisted in a short-latency and/or in a delayed activation of the motor units of the triceps surae muscle. The former was due to direct activation of the axons of the alpha-motoneurones and had a latency of about 5 msec; the latter, indirect response was reflex in origin, had a latency of about 35 msec (for the normal range of variation of the M-H interval see Visser *et al.*, 1983) and could be evoked in isolation, i.e. without evoking the direct response, having a threshold below that for motor fibres (Fig. 1). Earlier arguments in favour of the reflex nature of the late response are to be found in a review by Hoffmann (1934). The reflex-elicited contraction of the calf muscles was due to activation of group Ia fibres from spindles, and became called Hoffmann-reflex, or "H"-reflex (Magladery and McDougal, 1950), whereas the direct motor response was called "M"-response. Tábořiková and Sax (1968) demonstrated by collision technique that the percentage of soleus motoneurones activated by a maximal stimulation of the Ia fibres ranges from 24 to 100, with a usual value around 50%. The slower fibres within the soleus muscle are mainly responsible for the reflex evoked twitch (Buchtal and Schmalbruch, 1970).

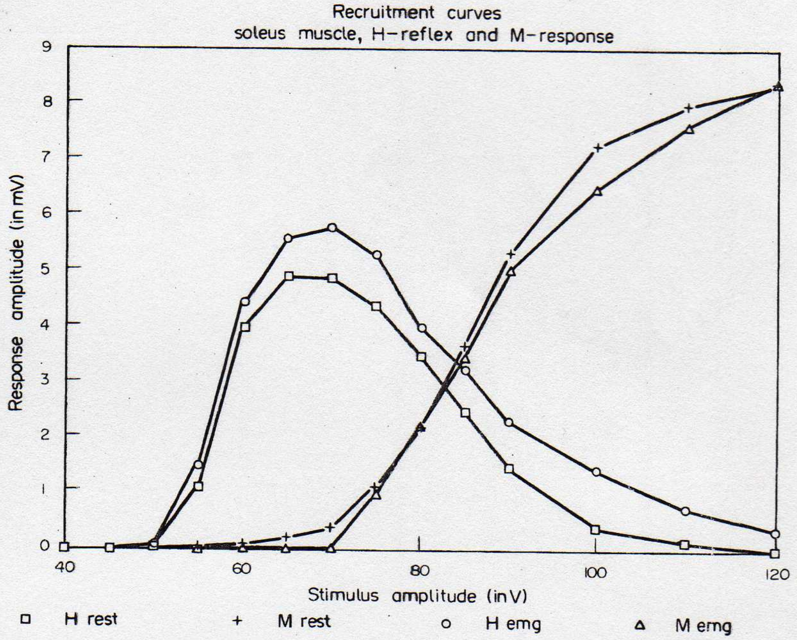
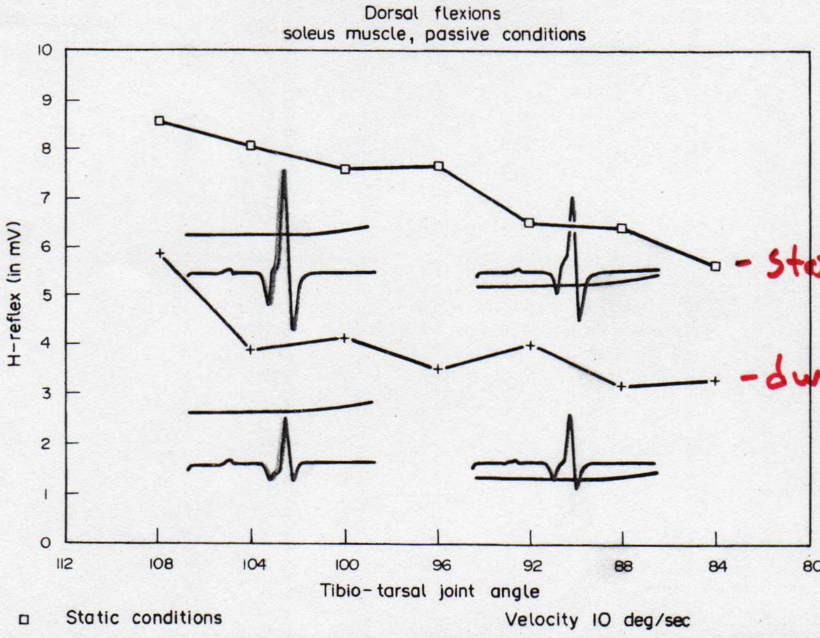


FIG. 1. Recruitment curves of H-reflex of soleus muscle. Ordinate: absolute amplitudes of H-reflex and M-response (each point mean of five measurements). Abscissa: intensity of stimulus delivered to posterior tibial nerve in popliteal fossa. Low amplitude stimuli evoke H-reflexes with minimal or no M-responses, owing to low threshold of Ia afferent fibres. High amplitude stimuli excite both Ia fibres and alpha-motoneurones: their antidromic activation prevents the appearance of H-reflex. Two experimental conditions are shown: the responses were obtained in a sitting subject, at rest and during slight voluntary innervation of soleus muscle. Increased motoneurones excitability in the latter case is indicated by higher amplitude of H-reflex, other things being equal. (Courtesy of Dr Nardone.)

The history of this reflex and of its investigation in the first half of this century, and of the scientific quarelles about its nature, has been beautifully summarized by Paillard in the introduction to his doctoral thesis (Paillard, 1955). In the early 50s, Magladery and colleagues (1951a,b, 1952) in Baltimore and Paillard in Paris explored systematically this reflex arc and confirmed many of Hoffmann's findings. They laid down the basis for the subsequent widespread use of this technique in the study of the excitability of the motoneurones in various conditions, in health and disease. Many studies have been done since then, in fact, and quite a few review articles have been published, among them those of Rushworth (1964), Delwaide (1971) and Kimura (1983); recent reviews reporting the evolutions of the investigations carried out in single laboratories are published in the book, *Motor Control Mechanisms in Health and Disease*, edited by Desmedt (1983), and will be quoted later in the appropriate sections.

1.2. METHODOLOGICAL CONSIDERATIONS

The utility of the H-reflex, as a means of studying stimulus-induced and/or task-related changes in human motoneurones excitability, rests on the use of an accurate technique for eliciting and recording the muscle response. As previously emphasized by Rushworth (1964), much of Paillard's meticulous technique and many of his warnings have been ignored by subsequent workers. From a purely technical point of view, poor conclusions can be drawn by wrong placement of stimulating electrodes (Simon, 1962), by inappropriate choice of stimulus parameters as duration and repetition rate (Paillard, 1955; Ishikawa *et al.*, 1966; Cook, 1968), by the recording (surface) electrodes picking up the electrical activity of muscles other than the one under study, by uncontrolled postural changes of the upper extremities (Delwaide *et al.*, 1977), by variations in muscle geometry or in foot position. In fact, dorsiflexion of the ankle or triceps stretch have an inhibitory



- static

- during dynamic phase moving 10°/sec

FIG. 2. Effect of passive dorsiflexion on the H-reflex of soleus muscle. Ordinate: absolute amplitude of H-reflex (at rest and at a tibio-tarsal joint angle of 110 degrees). Abscissa: tibio-tarsal joint angles. Squares correspond to reflexes evoked in static conditions, i.e. at least 10 sec following changes in foot position. Crosses indicate reflexes evoked during dynamic passive dorsal flexions at a velocity of 10 deg/sec. Each point is the mean of five measurements. In the insets are shown sample recordings (upper beams position, lower beams H-reflexes) obtained in static (upper traces) and dynamic (lower traces) conditions; position is 104 and 92 degrees on the left and right respectively. (Romano' and Schieppati, unpublished results.)

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effect on the motoneurone pool of the soleus muscle (Fig. 2) (Mark *et al.*, 1968; Herman, 1969; Delwaide, 1971, 1973; Gerilovsky *et al.*, 1977; Gottlieb and Agarwal, 1978; Robinson *et al.*, 1982; Davies and Lader, 1983; Burke *et al.*, 1983). Furthermore, modulations in the excitability of the H-reflex can also be induced by changes in head position (see Section 4.2). The reader is referred to the papers of Hugon (1973a) and Brunia *et al.* (1973b) for technical details and a thorough discussion of the correct methodology for eliciting the H-reflex.

Conclusions about increases or decreases in the excitability of the motoneurones tested by the H-reflex must take into account that the degree to which the H-reflex is facilitated or inhibited under various conditions, or following diverse stimulation procedures, is correlated with the amplitude of the H-reflex that is taken as control (Clare and Landau, 1964; Gassel and Diamantopoulos, 1964; Meinck, 1980). Moreover, changes in H-reflex magnitude are induced by variations in the baseline EMG activity (Fig. 1) (Hoffmann, 1934; Paillard, 1955; Magladery *et al.*, 1951; Gottlieb *et al.*, 1970; Gottlieb and Agarwal, 1971, 1976; Iles, 1977; Upton *et al.*, 1971; Deschuytere *et al.*, 1976, in the hand and forearm muscles), and these variations interact with those linked to the intensity of the stimulus used (Verrier, 1985).

1.3. THE EXCITABILITY CYCLE OF THE H-REFLEX

The H-reflex amplitude is a measure of the excitability of the motoneurones, and consequently may change in various conditions as a function of segmental and supraspinal influences playing upon them. Other things being equal, it is of interest to investigate the time-course of the recovery to control values of the excitability of the motoneurones immediately after their own reflex discharge: a measure of the speed and shape of this recovery may disclose to what extent tonic influences related to the state, and possibly altered in pathological conditions affect motoneurones' excitability. These questions have

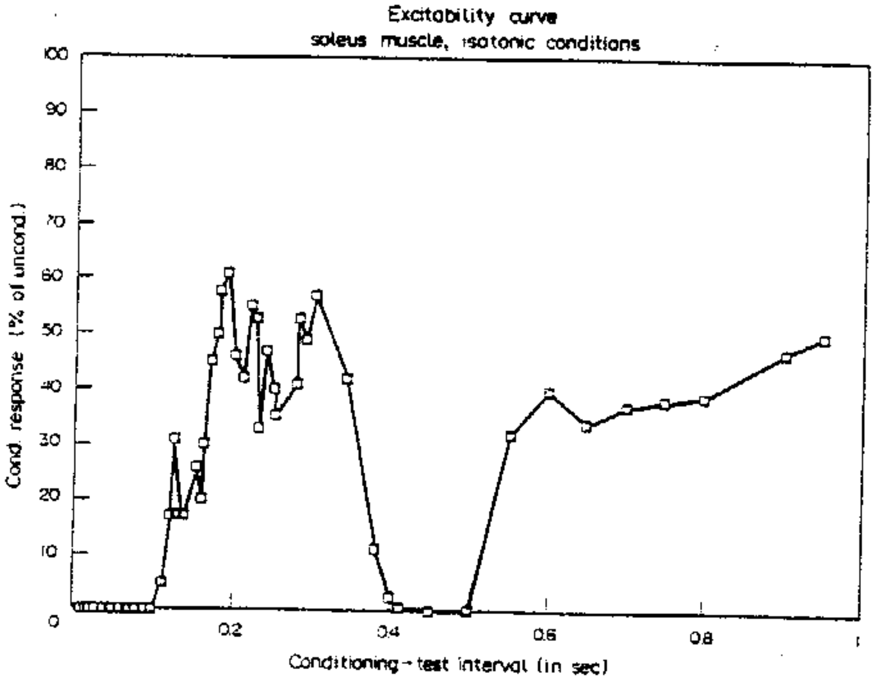

FIG. 3. Excitability curve of H-reflex. Ordinate: amplitude of reflex in percent of its control value (half-maximal). Abscissa: time-interval elapsing from conditioning stimulus (evoking the control reflex) and test stimulus (of equal intensity). The data were obtained in a sitting subject at rest, whose soleus muscle contracted in isotonic conditions. In this subject the depression following phase IV was particularly large, and the reflex recovered to control values onlly at conditioning-test intervals longer than 7 sec. (Courtesy of Dr Di Francesco.)

been addressed by using the technique of conditioning a H-reflex (test) stimulus with another H-reflex stimulus, of equal or of different characteristics (Schenk, 1951; Magladery *et al.*, 1951b, 1952; Paillard, 1955; Delwaide, 1971). In normal subjects, the time-course of the excitability cycle consists of an early facilitation during the initial 3 to 20 msec from the conditioning stimulus (Paillard's phase II) (for the origin of this phase see Pierrot-Deseilligny *et al.*, 1976), an early depression occurring from 10 to 50 msec (phase III), and a secondary facilitation between 100 and 400 msec (phase IV); this gives way to a depression lasting up to the time of complete recovery to control values (at conditioning-test intervals larger than 1 sec) (Fig. 3). The shape of the recovery curve is highly stable within each subject (Crayton and King, 1981), although left–right differences may be associated with handedness (Tan, 1985a,b). It is non-linear, and various mathematical procedures have been proposed in order to quantify the relevant parameters and allow comparison between curves obtained from different subjects (or patients, see for instance Yap, 1967) and/or in different experimental situations (Johnson *et al.*, 1974; Hayes *et al.*, 1979).

The causes of the particular time-course of the recovery curve are not firmly established. Tábořiková and Sax (1969) used conditioning stimuli below the motor threshold to avoid changes in the excitability of the motoneurones linked to reafferences from the moving leg, but could still evoke in some subjects a facilitation in the 100–300 msec interval, thus pointing to a long-loop mechanism called into action by the Ia afferent discharge (Tábořiková *et al.*, 1966; Tábořiková, 1973). Cutaneous afferences have been also considered among the mechanisms accounting for the intercurrent facilitation of the H-reflex, possibly through a supraspinal loop (Gassel, 1970, 1973; Katz *et al.*, 1977; Robinson *et al.*, 1979). Sabbahi and De Luca (1981) demonstrated that anaesthesia in various skin areas of the lower limb could anticipate the interval at which the conditioned H-reflex starts to recover. When the conditioning stimulus evokes a twitch, the rebound discharge of muscle afferents during relaxation of the muscle certainly contributes to the facilitation of the motoneurones (Lieberson and Paillard, 1963; Diamantopoulos and Zander Olsen, 1967), since this phenomenon is also present in spinal cord injured patients.

Muscle relaxation may be followed (in isotonic conditions) by passive foot dorsiflexion, which in turn may have an inhibitory effect on the reflex excitability (see Section 1.2). On the other hand, that both peripheral and supraspinal (transcortical) loops are travelled by impulses evoked in the low-threshold muscular afferents by the conditioning stimulus was suggested by Decandia *et al.* (1974), and by Hayes and Clarke (1978), who found "late reflexes" when the H-reflex was evoked during the preparatory period of a voluntary plantar flexion. The same is definitely demonstrated by studies performed in monkeys with various controlled lesions (Chofflon *et al.*, 1982; Rüegg and Chofflon, 1983).

Other methods of studying supraspinal loops have been those of conditioning the H-reflex by a stimulus evoking an H-reflex in the contralateral leg (Masland, 1972; Robinson *et al.*, 1979), and of studying the changes in phase IV facilitation induced during a preparatory period prior to a reaction-time task (Sullivan, 1980; Semjen and Bonnet, 1982).

1.4. H-REFLEXES IN MUSCLES OTHER THAN THE SOLEUS

Although the technique of evoking the H-reflex in the soleus muscle is the one most commonly used, owing to the easy accessibility of the posterior tibial nerve and the selectivity of stimulation, an equivalent of the H-reflex can be evoked also in other muscles of the body. As early as in the late 50s, Pinelli and Valle (1960) evoked an H-reflex in the muscle flexor digitorum brevis, and Johns *et al.* (1957) indicated the possibility of evoking the H-reflex in the hypothenar muscles, a manoeuvre that is consistently successful only in very young children (Thomas and Lambert, 1960; Hodes *et al.*, 1962). In older patients the reflex may reappear, as in subjects affected by central nervous system disorders (Hodes *et al.*, 1962; Ioku, 1984). For that matter, in phenylketonuria, French *et al.* (1961) elicited H-reflexes in peroneal muscles from stimulation of the lateral peroneal nerve, but this reflex was absent in normal control children, as it is usually in adults. Well identifiable H-reflexes can be obtained from the muscle extensor digitorum brevis in the foot of normal men (Willer, 1975; Dehen *et al.*, 1976; Willer and Dehen, 1977), from the quadriceps muscle

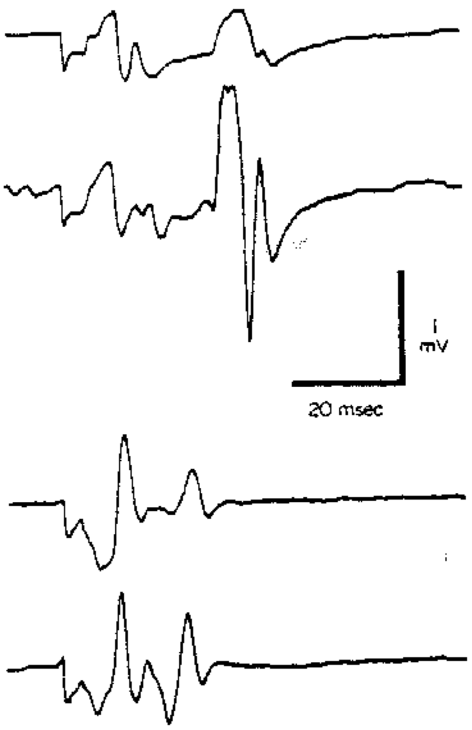

FIG. 4. Examples of M-responses and H-reflexes evoked in the muscles tibialis anterior (upper panel) and flexor carpi ulnaris (lower panel). In both cases upper beams refer to resting conditions, and lower beams to slight voluntary innervation of the muscles.

(Gassel, 1963; Mongia, 1972; Bathien and Guiheunec, 1974; Guiheunec and Ginet, 1974; Bergmans *et al.*, 1978; Kudina, 1981; Pierrot-Deseilligny *et al.*, 1981b; Aiello *et al.*, 1983b), from the forearm flexor muscles (Fig. 4) (Deschuytere and Rosselle, 1974; see Deschuytere *et al.*, 1983), and from the masseter muscle (Godaux and Desmedt, 1975). In selected cases or during voluntary innervation of muscle, H-reflexes can be evoked also in other muscle groups, as the pretibial muscles (Fig. 4) (Upton *et al.*, 1971; Deschuytere and Rosselle, 1971; Pierrot-Deseilligny and Bussel, 1973; Pierrot-Deseilligny *et al.*, 1981a; Schieppati and Crenna, 1985; Davies, 1985) and thenar muscles (Stanley, 1978; Deuschl *et al.*, 1985), the wrist extensors (Day *et al.*, 1984; Cavallari *et al.*, 1985) and occasionally in the abductor pollicis muscle (McComas *et al.*, 1970; Person and Kozina, 1978). When investigating muscles other than those in which the H-reflex is easily elicitable, one has to bear in mind that from many skeletal muscles a late response can be recorded on high intensity stimulation of its motor nerve, with approximately the same latency of the H-reflex. This is the F-wave, and is most probably due to a centrifugal discharge of some motoneurones initiated by antidromic volleys in their axons (for a recent review on the F-wave see Shahani, 1985).

2. Motoneurone Vs Reflex Arc Excitability

2.1. A Monosynaptic Reflex?

Following Hoffmann's (1922) and Hoffmann and Keller's (1928) claim that the electrically evoked reflex was a monosynaptic reflex, Magladery *et al.* (1951a) confirmed by intrathecally recordings of action potentials from both dorsal and ventral spinal roots in man that spinal transmission was sufficiently rapid to be compatible with a direct monosynaptic pathway. The constant latency of the electrical muscle response also led Paillard (1955) to admit the monosynaptic nature of the H-reflex. Since these observations were paralleled by similar findings in cat experiments (Lloyd, 1943, 1946), it became obvious that the H-reflex occupied a two-neurone arc, and as such it could be used as the background against which either facilitatory or inhibitory influences could be measured. Recent researches, however, have pointed to the possibility that oligosynaptic as well as monosynaptic pathways are activated by the incoming volley elicited by the electrical stimulation of tibial nerve. In fact it is known from animal experiments that Ia afferents impinge onto motoneurones both directly and through spinal interneurones, some of which may also be inhibitory (Fetz *et al.*, 1979; Hultborn *et al.*, 1975; Hultborn and Wigström, 1980; Jankowska *et al.*, 1981a,b; Schomburg and Behrends, 1978; Watt *et al.*, 1976; see Pierrot-Deseilligny and Mazières, 1984a). On the other hand, it has been demonstrated in man that the experimental conditions are far from permitting a selective stimulation of Ia afferent fibres: the induced afferent volley is contaminated by afferent activity from the Ib fibres of the triceps surae, because the threshold of these fibres is very close to that of the Ia fibres in man (Pierrot-Deseilligny *et al.*, 1981b; Fukushima *et al.*, 1982), by afferent activity (both Ia and Ib) from the small muscles of the foot, and from cutaneous fibres from the heel and the sole (Burke *et al.*, 1983). Owing to the short distance separating the popliteal fossa from the spinal cord, and the very narrow range of conduction velocities within which Ib and large cutaneous fibres are situated, discernible effects may be expected to have some influence on the motoneurones within less than 1 to 3 msec after the Ia facilitatory effect. In conclusion, primary afferent fibres from the spindles *can* affect motoneurones also through oligosynaptic pathways, and other afferent fibres activated by the stimulation procedure, known to oligosynaptically influence the motoneurones, can as well exert their effect.

These considerations are important in the light of the time necessary for the Ia afferent volley to drive the motoneurones to threshold: if they would discharge within, say, less than 1 msec from the arrival of the afferent volley, every other input impingeing upon them immediately after that time, i.e. during the action potential would produce no effect. However, it appears that the Ia-induced EPSP has a finite rise time, so allowing enough time for other stimulus-induced inputs in addition to the monosynaptic one, to exert some effect through oligosynaptic pathways before the time at which the motoneurones would reach threshold (Burke *et al.*, 1984; see Burke, 1985). As far as the H-reflex is concerned, the EPSP rise time appears to be very short, probably less than 2 msec; this would allow postsynaptic temporal summation only to a limited extent.

The consequences of these findings are however very relevant as to the widely held opinion that the H-reflex and the T-response are remarkably similar in their central pathways and essentially involve the same afferent input. In fact, with that idea in mind, many authors started using the comparison between the amplitudes of the H- and T-reflexes as a tool of testing the gamma system (see Krishna Murthy, 1978), in spite of ample evidences of differences in the synchronization of the afferent volley (Diamantopoulos and Gassel, 1965, Gassel and Diamantopoulos, 1966; Herman, 1969; Burke *et al.*, 1983; Abbruzzese *et al.*, 1985). The rationale, partly supported by cats' experiments (Matthews and Rushworth, 1957) was that with little or no gamma drive a tap to the tendon would give rise to a sluggish response in Ia afferents owing to low spindle endings sensitivity, and vice versa. A comparison with the electrically induced H-reflex (the stimulus bypasses the receptors) would therefore give an idea of hypo- or hyperactivity of the gamma system (Hoffmann, 1951; Paillard, 1955).

The T-response elicited during the Jendrassik manoeuvre, which consists in squeezing a hand grip, was considered an example of a method to test the "gamma drive", both in physiological (Bishop *et al.*, 1968a,b) or pathological conditions (Buller and Dornhorst, 1957; Dietrichson, 1971; see Delwaide *et al.*, 1980). As a matter of fact, however, the reinforcement also potentiates the H-reflex (Landau and Clare, 1964a,b; Bussel *et al.*, 1978), and, what's more, no proof has been found in cats that selective activation of the fusimotor system increases the amplitude of a tap-evoked reflex contraction (Morgan *et al.*, 1984). On the other hand, ample evidences have accumulated recently against the identity of the two reflex responses (Burke, 1985; Van Boxtel, 1986), preventing any conclusion to be drawn about the gamma drive as the sole factor responsible for dissociations between the two reflexes (Gassel, 1973; Burke, 1983; Delwaide, 1985).

2.2. PRESYNAPTIC INHIBITION OF THE REFLEX ARC

In the preceding section new results were reported, that do not allow us any more to consider the electrically or mechanically induced reflex contraction in the soleus muscle, and presumably also in other muscles, exclusively as a monosynaptic reflex. The evidences seriously point to the possibility that the amplitude of the T-response, and to a lesser extent, of the H-reflex, be determined not only by the motoneurones' excitability *per se*, but also, at least in part, by the activation of spinal interneuronal systems, onto which the various afferences evoked by the stimulation procedure may impinge. The study of what these interneurones are, and how they eventually contribute to the build up of the recorded muscle response has not yet been undertaken. The results of such an investigation will be of the utmost interest, since it is probable that the afferences to these interneurones may find them in different states of excitability depending on their control by descending or segmental inputs. And, not necessarily the same descending or segmental pathways impinge onto both the MNs and the INs.

Apart from these considerations, there is another well known mechanism that can act on the reflex arc to alter its input/output ratio, even in the case of a two-neurone arc, without operating onto the MN itself (Fig. 5): it is the presynaptic inhibition of the afferent fibres, a mechanism thoroughly studied in cats (Eccles *et al.*, 1962; Schmidt, 1971). By changing the level of "tonic" presynaptic inhibition, the effectiveness of the electrically evoked afferent input may actually be changed and alter in turn the number of discharging motor units, in spite of constant excitability of the motoneurones.

The most dramatic effect which has been explained by postulating a presynaptic inhibitory mechanism is the inhibition of the H-reflex and the tendon jerk by peripheral vibration applied to the tendon or belly of the examined muscles or of nearby muscles (Lance, 1965; Gail *et al.*, 1966; Rushworth and Young, 1966; Marsden *et al.*, 1969;

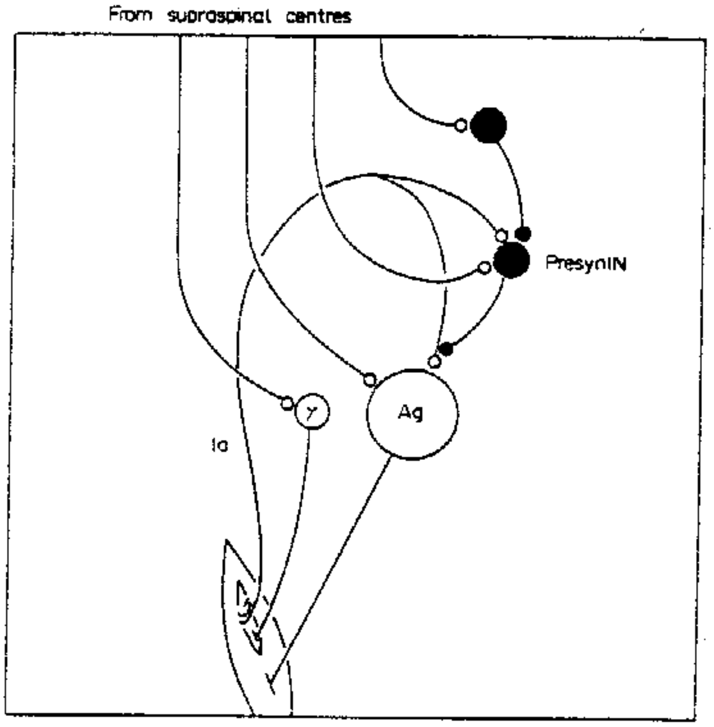

FIG. 5. Schematic diagram showing neuronal network referred to in the text (in this and in the following diagrams black neurones are inhibitory). Alpha- and gamma-motoneurones innervate extra and intrafusal muscle fibres. Ia afferent fibres impinge onto both the alpha-motoneurone and the interneurone responsible for the (presynaptic) inhibition of the Ia-alpha motoneurone synapse. Along with fibres from supraspinal centres directed to alpha- and gamma-motoneurones, fibres are shown exerting excitatory or inhibitory (through a spinal interneurone) effects on the interneurone mediating presynaptic inhibition.

Delwaide, 1969, 1971; Deschuytere *et al.*, 1976). The idea is that vibration, known to activate the primary endings of the muscle spindles (see Matthews, 1972, in the cat; Delwaide, 1973; Dindar and Verrier, 1973; Burke *et al.*, 1976, in man), activates a central inhibitory process involving spinal interneurones (Besson and Rivot, 1973; Solodkin *et al.*, 1984) and acting through depolarization of the terminals of the Ia afferent fibres themselves, as demonstrated in cats by Gillies *et al.* (1969) and Barnes and Pompeiano (1970). It is worth noting that when vibration is applied to the soleus muscle a tonic contraction (tonic vibration reflex, TVR) may ensue, whereas when it is shifted anywhere in the leg, the soleus H-reflex inhibition appears alone (Rushworth and Young, 1966). Another important fact is that the inhibition is operative at the terminals of Ia fibres on spinal motoneurones, but may be absent on the spinal pathways mediating late muscle responses (Van Boxtel, 1979b), or on the central projections of muscle afferents to supraspinal centers (Hendrie and Lee, 1978; see however Dietz *et al.*, 1984).

There are reasons to believe that a "tonic" presynaptic inhibition exists on the Ia afferents' terminals, and that it may be different from muscle to muscle: the difficulty in evoking a H-reflex in the pretibial muscles in adult humans has been explained by the presence of a high level of presynaptic inhibition (Delwaide, 1973; Person and Kozhina, 1978) specifically acting on the Ia terminal impingeing onto the pretibial motoneurones (Kudina, 1980). A mechanism of presynaptic modulation of Ia input, rather than a general increase of motoneuronal excitability, has been recently proposed as the factor responsible for the increase in soleus H-reflex occurring during a Jendrassik manoeuvre (Dowman and Wolpow, 1985).

Persuasive evidence that such a mechanism was indeed responsible for reducing the power of the afferent input in man had to await for long time (Morin *et al.*, 1984) since the description of the inhibitory effects. Previous work already yielded strong suggestions that the reduction in amplitude of the H-reflex was not attributable to a decrease of the afferent volley, recorded from the sciatic nerve, due to occlusion in Ia fibres from vibration-induced activity (Lance *et al.*, 1968; Gillies *et al.*, 1970). In addition, the considerations that the inhibition is present even when vibration induces a reflex contraction in the muscle, i.e. when motoneurones are postsynaptically facilitated (Lance *et al.*, 1973), that inhibition still persists, albeit reduced, when a voluntary plantar torque is exerted by the subjects (Iles and Roberts, 1981), and the finding that the excitability of the motoneurones to other inputs was unchanged during vibratory inhibition (Delwaide, 1973), all point to at least a "pre-motoneuronal" gating of the afferent input.

The effectiveness of the presynaptic inhibition appears to be amenable to adaptive plastic changes, as recently suggested by Wolpow *et al.* (1985a,b). Their results in monkeys show in fact that the animals can change in the long run the amplitude of their H-reflex (in either direction), when confronted with a task requiring that variation.

3. State-Related Changes in the H-Reflex

It is worth remembering that variations in the H-reflex amplitude can depend, often in an unpredictable way, on the state of awareness of the subject or, in general, on the mental state: the H-reflex increases during alertness (Bathien and Hugelin, 1969) at least as far as high levels of attention are reached (Bathien, 1971; Bathien and Morin, 1972). Its amplitude is related to the percentage of alpha rhythm in the ongoing electroencephalogram (Van Boxtel, 1976) bearing instead no correlation with the phase of the alpha rhythm itself (Van Boxtel, 1979a). Task demands can induce variations in the H-reflex related to the particular characteristics of the mental effort required by the task itself (Brunia, 1971; Brunia *et al.*, 1973; Honore *et al.*, 1983; Grillon and Zarifian, 1985) (see Section 6).

The old remark that monosynaptic reflex decreases during sleep (Tuttle, 1924) has been confirmed by recent investigations on the H-reflex. It has been shown in fact that the H-reflex significantly decreases in the early stages of sleep, and is abolished during REM sleep (Paillard, 1959; Hodes and Gribetz, 1962a,b; Hodes and Dement, 1964; Coquery *et al.*, 1965; Hishikawa *et al.*, 1965; Pivik and Dement, 1970; Mayer and Mosser, 1973). This decrease in excitability of the motoneurones is confirmed by a slow recovery of excitability (Mayer and Mosser, 1969) and by the absence of the secondary facilitation between 100 and 300 msec in the H-reflex recovery curve (see Section 1.3) during slow wave sleep (Pivik and Mercier, 1979). This finding has been explained on the basis of absence of gamma-drive induced facilitation during sleep, rather than by the presence of active inhibition, as foreseen by Hoffmann (1934). Supraspinal inhibitory mechanisms are probably also involved, though, since an auditory stimulus that induces H-reflex facilitation during wakefulness, provokes during slow wave sleep phasic loss of muscle tone and H-reflex complete inhibition (Cirignotta *et al.*, 1983) (for the facilitation induced on the H-reflex of awake subjects by a strong tone see Rossignol and Melville-Jones, 1976; Rudell and Eberle, 1985). It is interesting to note that absence of pyramids, cortico-spinal tracts and cerebellar vermis do not prevent changes in reflex amplitude in the transition from wakefulness to sleep (Hodes and Gribetz, 1963). On the contrary, the decrease in H-reflex amplitude occurring during REM sleep is prevented by a cord lesion involving the descending pathways coursing along the anterior funiculi, or by a brain stem lesion extending into the central portion of the medulla (Shimizu *et al.*, 1966).

4. Reflex Effects from Distant Sources

4.1. EFFECTS FROM CUTANEOUS AFFERENCES

Early investigations of Hagbarth (1960), Bathien and Hugon (1964), Hugon and Bathien (1967), Gassel and Ott (1970) and Castaigne *et al.* (1973) have demonstrated that afferences from the skin affect the excitability of the soleus motoneurones, as tested by the H-reflex (see Hugon, 1973b; Pierrot-Deseilligny *et al.*, 1973a). The results show a long-latency facilitation of the H-reflex on tactile conditioning stimulation, that may have a non-reciprocal distribution (Delwaide *et al.*, 1981) and be superimposed on a phase of decreased excitability in the case of painful stimulation. Owing to the long-latency of the facilitatory effect, the hypothesis has been put foward that a long-loop is activated by the conditioning stimulation. Non-segmental effects are indeed present: when the cutaneous stimulation is not applied to the skin of the lower limb, but to sites cranial to the buttock, a facilitation is present at a latency not different from that occurring on sural or saphenous nerve stimulation (Gassel and Ott, 1973; Meinck, 1976; Piesiur-Strehlow and Meinck, 1980). Delwaide and Crenna (1983) have reviewed the issue, contributing original results in favour of a long-loop facilitation of lower limb H-reflexes, possibly travelling through a supraspinal center (Delwaide and Crenna, 1984). Segmental pathways, however, do certainly contribute to the observed effect, since in patients with complete spinal cord lesion a late facilitation of the soleus H-reflex is still elicitable on sural nerve stimulation (Lebizec *et al.*, 1983). Meinck and Piesiur-Strehlow (1981) presented convincing evidence that, in normal subjects, late cutaneous effects from ipsi- and contralateral arms on the H-reflex of the soleus muscle might be mediated by propriospinal pathways.

That cutaneous afferences may have segmental, short-latency effects is evident from experiments aimed at investigating the interactions between exteroceptive and proprioceptive afferences. Pierot-Deseilligny *et al.* (1981b) showed in fact that stimulation of the skin of the sole or of the toes does not in itself affect the excitability of the motoneurones to the muscles of the ipsilateral lower limb, but it able to depress the Ib reflex pathway to the quadriceps muscle. Analogous experiments have been performed on the upper limb: again, it has been shown that cutaneous stimulation *per se* does not exert short-latency effects on the H-reflex of the wrist flexor muscles, but is able to increase facilitation obtained by conditioning the reflex with a low-threshold (Ib) volley from the antagonist muscles (Cavallari *et al.*, 1985).

4.2. VESTIBULAR AND NECK RECEPTOR INFLUENCES

The inputs from the vestibular system provide a vertical reference against which inputs from other sensory systems are confronted (see Nashner, 1983). H-reflex studies on the spinal effects of vestibular stimulation in man are relatively few, at variance with the bulk of information that comes from animal studies (see Schwindt, 1981; Chan, 1983). Unilateral vestibular neurotomy is able to depress the ipsilaterally and enhance the contralaterally evoked soleus H-reflexes in baboons (Lacour *et al.*, 1976). In man, the H-reflex technique has been used by Chan and Kearney (1982) who, by rotating subjects along the sagittal plane with the head fixed in respect with the body, showed that the H-reflex reached a minimum when the head was near the vertical position, whereas it could increase as a function of tilt in the sagittal plane. Opposite results have been found by Aiello *et al.* (1983) in normal subjects; as a further clue that the observed effects were actually of vestibular origin they gave evidence of a lack of H-reflex modulation in a labyrinthine defective patient. This controversy over the influence of static tilt on soleus motoneurones' excitability in man does not appear to be solved to date (Chan and Kearney, 1984). Artefacts in the measurement of monosynaptic reflex may depend on unpredictable shifts in impedance of the stimulating electrodes, on shift of the soft tissues of the calf with respect to the recording electrodes, or on the great intersubject and intrasubject variability, as suggested by Myklebust *et al.* (1984).

For the time being, static vestibular influences on the H-reflex must be considered with a word of caution, because they may not be potent in normal subjects, although dynamic short-latency EMG responses of the leg muscles are indeed present, e.g. during sudden falls (Melvill Jones and Watt, 1971; Greenwood and Hopkins, 1976; 1977). In fact, changes in the tendon jerk and in the H-reflex have been studied during free fall in humans. During fall, a facilitation of the reflexes occurs in the calf muscles about 80 msec from onset of fall, i.e. some 40 msec prior to the onset of their contraction; the pathways involved, however, remain to be investigated in detail, as the latency of the effect is longer than one would expect in the case of a direct vestibulo-spinal effect. Technical artefacts may have contributed to previously reported findings, obtained in experiments in which the vestibular effect was observed on the T-response (Matthews and Whiteside, 1960). Baboon studies have confirmed that normal vestibular function is essential for the appearance of a short-latency facilitation of the H-reflex evoked at the onset of a free fall (Lacour *et al.*, 1978; see Lacour *et al.*, 1983).

Vestibular caloric or electrical stimulation, activating the receptors of the semicircular canals, also induces facilitatory effects on the soleus motoneurones excitability, as tested by the H-reflex and tendon jerk (Delwaide and Delbecq, 1973; Delwaide, 1977). The time-course of the facilitation shows a peak at about 80 msec and then decays monotonically. The larger effects on the T-response as compared to the H-reflex led these authors to postulate an effect largely mediated through the gamma-system, a conclusion also drawn by Benson (1959) by using rotatory stimulation. The possibility of a presynaptic disinhibition was also considered (critical considerations about the use of the H/T ratio in judging about gamma bias are reported in Section 2.1). Unfortunately no proof could be obtained that the effects observed were exclusively mediated by vestibular receptors (Delwaide and Juprelle, 1977).

Space experiments have been performed to investigate the possibility of a otolith-modulated motoneuronal sensitivity, by conditioning the H-reflex with a brief unexpected linear acceleration delivered at various times prior to, during, or following a period of microgravity (Reschke *et al.*, 1984). An early potentiation of the H-reflex after the drop was present before flight but seemed to vanish around one week after take off. Instead, this peak showed a huge increase in amplitude when the experiments were repeated after landing. These results are in favour of the existence of adaptive mechanisms in the dynamic vestibulo-spinal reflexes in conditions of altered gravity.

The role that the neck receptors play in the production of tonic reflexes has been addressed only sporadically in systematic studies, although every investigator points to the importance of avoiding changes in head position during elicitation of the H-reflex. The findings of Hayes and Sullivan (1976) show an increase in the H-reflex (and T-response) of the right soleus muscle induced by voluntarily rotating the head to the right, whereas a rotation to the left induces a decrease in the reflex. Recently, Traccis *et al.* (1985) found similar results in a different, controlled experimental condition: a slight facilitation in the H-reflex is induced when the body is rotated to the left in respect with the head, and a slight inhibition is observed in the opposite situation. Further investigations are needed, in which the relationships in space between head and body be changed along different planes.

5. The H-Reflex during Locomotion

Evidence that spinal reflexes may play a role in locomotion was obtained in humans by Dietz *et al.* (1979; see Dietz and Noth, 1983). Their results suggest that spinal stretch reflex assists triceps surae contraction during the stance phase of running. Subsequently, the reflex excitability of the triceps surae motoneurones was tested by means of the H-reflex technique by Garret *et al.* (1981). They showed that during the swing phase the reflex is markedly reduced, while it is enhanced during stance; its excitability increases from the beginning to the end of the stance phase, to fall sharply again at the end of the stance (Garrett *et al.*, 1984). Similar results have been obtained by Capaday and Stein (1985, 1986) and by Crenna and Frigo (1985a). All groups went through considerable effort in trying to overcome the problem represented by changes in position of the stimulating electrode during the step cycle. The values of the H-reflex was determined by using stimulus voltages which produced similar M-responses during each phase of the cycle. Alternatively, the H-reflex obtained during gait, accompanied by a certain M wave, was confronted with what would have been produced at rest by a stimulus evoking that particular M-response. Their conclusions emphasize that the excitability of the soleus motoneurones is not only function of their general state of excitation, as indicated by the level of electromyographic activity, but might in addition be dependent on premotoneuronal (possibly presynaptic) mechanisms called into action by the central generator. For that matter, it is worth recalling that the soleus H-reflex excitability is lower during the stance phase of gait than during a contraction of the soleus muscle of similar characteristics, voluntarily performed: this fact has been ascribed to differences at the spinal cord level under the two conditions, and in particular to an increase of presynaptic inhibition of Ia fibres during gait (Morin *et al.*, 1982). Any interpretation of the changes in H-reflex observed during the walking cycle must take into account both the decrease in the H-reflex (without changes in the M-response) induced by passive stretch of the triceps surae (see Section 1.2.), and the simultaneous activity of antagonist or distant muscles, that is able to affect soleus motoneurones (Delwaide *et al.*, 1976; Pierrot-Deseilligny *et al.*, 1981b; Falconer and Winter, 1985; Yang and Winter, 1985).

The question of how the transmission in spinal pathways can assist locomotion has been also addressed by the Pierrot-Deseilligny group (see Pierrot-Deseilligny, 1983). They found that, in contrast to spinal cat, in man group I effects from ankle muscles onto synergistic or antagonistic muscles are weak or absent; on the other hand, the group I projections from ankle muscles to quadriceps muscle, either absent or negligible in the cat, are potent in man (Pierrot-Deseilligny *et al.*, 1981a). The latter are such that conditioning stimulation to the gastrocnemius nerve evokes a short-latency facilitation (Ia in origin) followed by an inhibition (Ib in origin) of the H-reflex evoked in the quadriceps muscle; opposite effects are obtained on stimulating the nerve to pretibial muscles. Interestingly enough, the Ib inhibition from the ankle extensor to the knee extensor muscles disappears when a cutaneous stimulation (sural nerve) precedes the conditioning stimulation (Pierrot-Deseilligny *et al.*, 1981b) (see Section 4.1). In accord with the hypothesis that cutaneous effects might assist bipedal gait in man, a facilitation in the Ib reflex pathway in the same quadriceps muscle could be demonstrated, when the conditioning skin stimulation was shifted to the contralateral foot sole (Bergego *et al.*, 1981). The functional significance of this arrangement is summarized by Pierrot-Deseilligny (1985). In brief, it is assumed that during the stance phase in which the quadriceps supports the body weight, a great Ia and Ib barrage originates from the ankle extensors undergoing a lengthening contraction; the net effect of this discharge on the quadriceps motoneurones would be excitatory, owing to the fact that contact of the foot with the ground is able to depress their Ib-induced inhibition. Recently, Brooke and McIlroy (1985) demonstrated that, during pedalling a cycle ergometer, low-intensity stimulation of posterior tibial nerve, in addition to producing a H-reflex in the triceps surae muscles, increased the EMG of the quadriceps (heteronymous synergist) at a monosynaptic latency. The reverse is also true: stimulating in the femoral nerve and recording from the triceps surae muscles disclosed a short latency effect on the EMG; this confirms and extends the notion that short-latency pathways are open between extensors of the knee and ankle during locomotor synergism in man.

6. Modulation of H-Reflex Excitability and Voluntary Movement

6.1. RECIPROCAL INHIBITORY LINKAGE BETWEEN ANTAGONIST MUSCLES

The finding that a voluntary contraction of the pretibial muscles decreases the amplitude of the reflex evoked in the triceps surae is an old one (Hoffmann, 1918; Paillard, 1955). It is in keeping with the essence of Sherrington's principle of reciprocal innervation, namely that during contraction of the agonist muscles the antagonists do not behave passively, but are actively inhibited by central nervous mechanisms (Sherrington, 1947). In cats, electrical stimulation of agonist Ia afferent fibres (Lloyd, 1946) induces inhibition of the motoneurones to the antagonist muscles, with a central delay compatible with a disynaptic linkage (Araki *et al.*, 1960). The interneurones responsible for this effect have received much attention since then; the many convergences they receive from diverse descending and afferent systems (see Baldissera *et al.*, 1981) led Eccles and Lundberg (1958) to consider them important integrative centers in the control of the inhibition of the antagonists, when the agonists are activated. In man, reciprocal inhibitory effects compatible in time with the activation of a disynaptic arc are exerted by a conditioning low-threshold electrical stimulation of the nerve to the antagonist, and are recorded as a

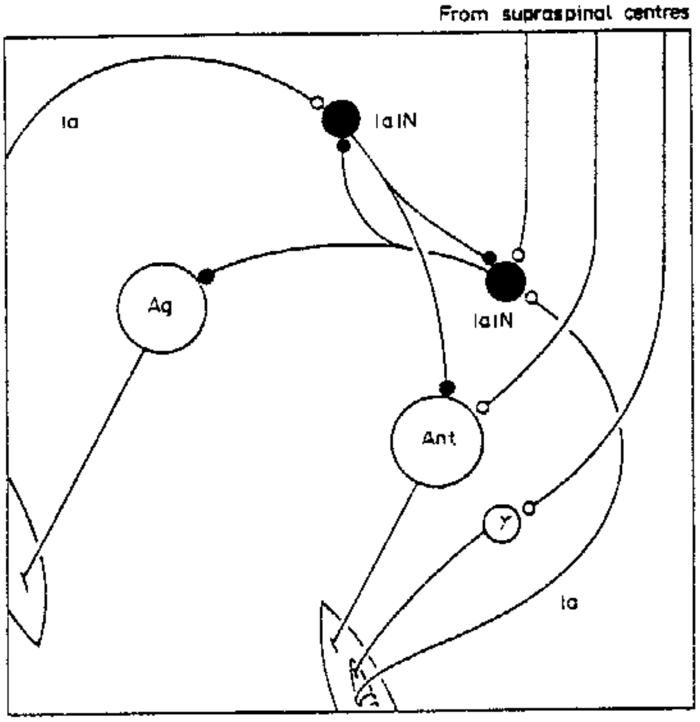

Fig. 6. Diagram showing presumed neuronal connections responsible for reciprocal inhibition. Two alpha-motoneurones are shown: that on the left (e.g. agonist) is target of postsynaptic reciprocal inhibition induced by activation of antagonist muscle. The descending command impinges both onto the alpha- and gamma-motoneurones of antagonist muscle, and onto the "corresponding" Ia interneurone, whose discharge is enhanced by the reafferent discharge through the gamma-loop. The reciprocal connections between Ia inhibitory interneurones allow descending modulation of their excitability.

decrease in the test H-reflex of the agonist muscle. The muscles whose H-reflex is most easily affected by the reciprocal inhibition are the flexor muscles of the wrist, when the conditioning stimulation is applied to the radial nerve in the spiral groove (Day *et al.*, 1981, 1982, 1983; Baldissera *et al.*, 1983; Day and Rothwell, 1983). Occasionally, when the H-reflex can be evoked in the wrist extensor muscles, a reciprocal inhibitory effect on stimulation of the median nerve can be observed (Day *et al.*, 1984). The inhibition of the flexor muscles' H-reflex can be very powerful, reducing the reflex to 20% of the (half-maximal) controls. Day *et al.* (1984) obtained results consistent with the existence of a spatial facilitation from descending and peripheral sources acting on the presumed spinal Ia interneurones mediating the reciprocal inhibition. Rothwell *et al.* (1984) studied the effect of cortical stimulation in man, and demonstrated that a corticospinal volley able to induce a large increase in the H-reflex of the forearm flexor muscles, also caused a decrease in the reciprocal inhibition induced onto the same H-reflex by stimulation of Ia afferences from the antagonist muscle. This result can be interpreted on the light of known neural connections in the cat and monkey (Schwindt, 1981; Baldissera *et al.*, 1981): the corticospinal tract impinges onto agonist alpha-motoneurones and "corresponding" Ia interneurones, which in turn inhibit both the antagonist alpha-motoneurones and the antagonist ("opposite") Ia inhibitory interneurones (Fig. 6). A functional role of these pathways is suggested by the possibility for a voluntary command to appropriately modulate the transmission in the Ia inhibitory pathway from extensor to flexor muscles in the human forearm prior to or during a willed movement (Day *et al.*, 1983, 1984; Cavallari *et al.*, 1984; see Pierrot-Deseilligny and Mazières, 1984b).

In spite of the early difficulties in finding any large reciprocal inhibitory effect on the leg muscles in normal prone and relaxed men (Mizuno *et al.*, 1971), conditioning stimulation of the peroneal nerve has been used extensively to modulate the soleus H-reflex excitability during the last decade. Tanaka (1972, 1974) showed that a short-latency inhibition of the soleus H-reflex could be induced by peroneal stimulation provided that

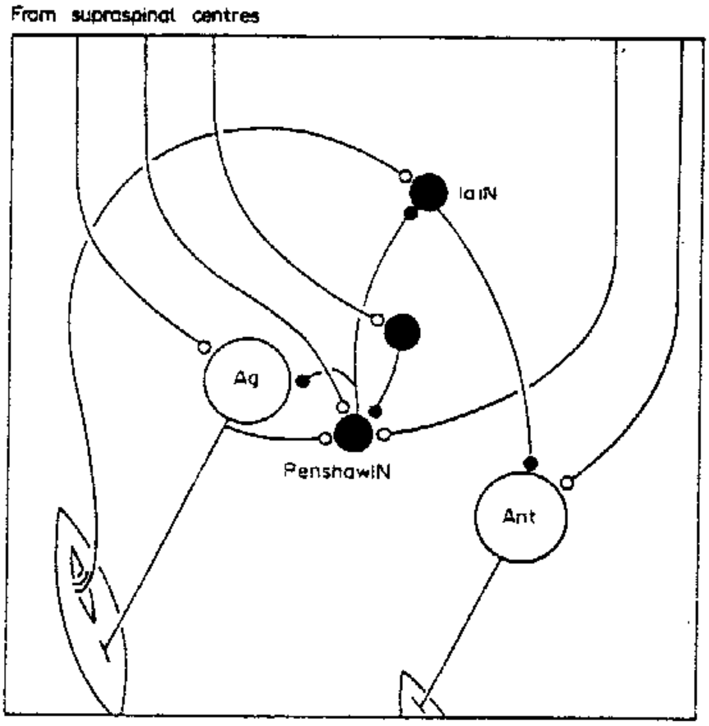

FIG. 7. Diagram showing presumed neuronal connections responsible for recurrent inhibition. It is indicated that descending command to agonist can either enhance or decrease (through an inhibitory interneurone) the excitability of the Renshaw cell. A pathway is also shown through which a Renshaw interneurone might be activated along with the antagonist motoneurone. The Renshaw cell, in turn, can exert inhibitory effects onto both the alpha-motoneurone and the corresponding Ia interneurone.

spasticity in which great variability among subjects has instead been found (Chaco *et al.*, 1984; Delwaide, 1985a). The search for changes in Renshaw inhibition in parkinsonian patients was also unsuccessful (Delwaide, 1985b).

6.3. EXCITABILITY OF THE REFLEX ARC PRIOR TO AND AT THE ONSET OF A MUSCLE CONTRACTION

Changes in excitability in the soleus motor pool occur prior to a voluntary muscle contraction. This has been shown for many years, although the mechanisms responsible, and the functional purpose of this phenomenon are not yet completely elucidated. Variations in the H-reflex preceding the movement may be related to the movement *per se*, or be connected with the preparation to move. Therefore, the experimental paradigm employed by the various authors must be considered: a voluntary plantar flexion is required in response to an imperative signal, but the latter can be delivered unpredictably to the subject, or else be preceded by a warning signal, so that a fixed foreperiod is created.

In the absence of a fixed foreperiod, the H-reflex of the future agonist undergoes an increase in amplitude well before the arrival of the response signal (Kots, 1977; Schieppati *et al.*, 1986). This facilitation is presumably linked to the expectancy of the signal, that requires to contract the triceps surea as rapidly as possible. It is only in part dependent on the general increase in reflex excitability occurring prior to a voluntary contraction (even of a remote muscle) in both legs; in fact it is significantly higher in the future agonist than in the contralateral muscle (Kots, 1977).

When the H-reflex is tested during a fixed foreperiod, i.e. in the time interval of constant duration comprised between a warning signal and the response signal, the changes in spinal excitability behave in a different way. The warning signal may be followed by a small and short-lasting facilitation of the H-reflexes of both legs, and this is probably a sign of general non-specific arousal, as mentioned above (Réquin and Paillard, 1971; Brunia and Vuister, 1979). Thereafter, as the expected response signal comes closer, the H-reflex in the non-involved leg remains facilitated, whereas that in the future agonist drops towards its control value (Brunia and Vuister, 1979; Sullivan, 1980), or even shows a slight degree of inhibition (Coquery and Coulmance, 1971; Pierrot-Deseilligny *et al.*, 1971; Réquin *et al.*, 1977; Hayes and Clarke, 1978; Gerilovsky *et al.*, 1983). The depression of the H-reflex is larger than that of the T-response evoked in the same conditions (Réquin and Paillard, 1971); the latter response normally shows no shift from its control value (Bonnet, 1981), in spite of the presence of a facilitation of the T-response in the non-involved leg (Brunia, 1983). This phenomenon has been considered a negative component of the preparatory process, a sort of active suspension of the execution of the response, whose function might be that of a protection of the agonist motor pool from undesirable influences. It has been suggested that the mechanism responsible for this selective disfacilitation is a presynaptic inhibition of the Ia afferences of the agonist muscle (Réquin *et al.*, 1977; Brunia, 1984; Brunia *et al.*, 1985). In this connection it is relevant to mention that the activity of the gamma motoneurones, at least as deduced from the discharge in the spindle afferences, is not changed during the foreperiod (Gerilovsky *et al.*, 1983).

The H-reflex evoked after the response signal increases sharply above its prior value, be the signal preceded by a fixed foreperiod or not. This facilitation is specific to the future agonist (Michie *et al.*, 1975; Kots, 1977; Eichenberger and Rüegg, 1984), and precedes the movement-related electromyogram by 50–80 msec, according to various reports in the literature (Coquery and Coulmance, 1971; Pierrot-Deseilligny *et al.*, 1971; Michie *et al.*, 1976; Kots, 1977; Person and Kudina, 1978; Eichenberger and Rüegg, 1984). In this laboratory we found that premovement H-reflex facilitation has an average duration of about 40 msec (Schieppati *et al.*, 1986). This figure was obtained by referring in time the amplitude of the H-reflex to the onset of the elecromyographic activity of the contralateral soleus muscle, the experimental procedure requiring a reaction-time bilateral plantar flexion. In this way the measurements are not affected by possible interactions between the reflex discharge elicited by the stimulus and the beginning of the voluntary electromyogram. In fact, it has been shown that the H-reflex, evoked just prior to the movement, delays to a significant extent (about 20 msec) the onset of the electromyogram in the same muscle, owing to the refractoriness of its motoneurones. By subtracting the 40-msec period of increased excitability from the reaction-time, it results that about 80 msec elapse from the response signal to the beginning of the facilitation. This is exactly the same period of time elapsing between the response signal and the beginning of the "pre-terminal inhibition" of the H-reflex that occurs in the situation in which the required task is to relax a tonic contraction of the soleus muscle on arrival of the response signal (Fig. 10) (see Section 6.4).

Pierrot-Deseilligny and Bussel (1973) made a comparison of the changes in motor pool excitability occurring at the onset of a voluntary contraction or of a reflexively-induced contraction of the pretibial muscles in man. They noted that, for the same level of electromyographic activity, the H-reflex amplitude was consistently higher in the former case than in the latter. Therefore, a spinal mechanism different from that of a postsynaptic facilitation of the motoneurones most probably contributes to the premovement facilitation (see also Gottlieb *et al.*, 1970). There is a general agreement among all the authors quoted above on the possibility that a mechanism of presynaptic disinhibition is responsible for the observed facilitation of the H-reflex occurring prior to the onset of voluntary contraction, and in the early phase of a dynamic plantar effort. A possible functional role of this mechanism is discussed in the following section, on the light of the phenomena observed in the opposite situation, i.e. at the end of a voluntary contraction.

6.4. CONTROL OF THE REFLEX EXCITABILITY OF THE MOTONEURONES DURING AND AFTER VOLUNTARY MUSCLE RELAXATION. FACTS AND HYPOTHESES

When an agonist muscle relaxes from a previous contraction, its motoneurones become the target of an autogenetic Ia afferent discharge started by the relaxation; this is true both

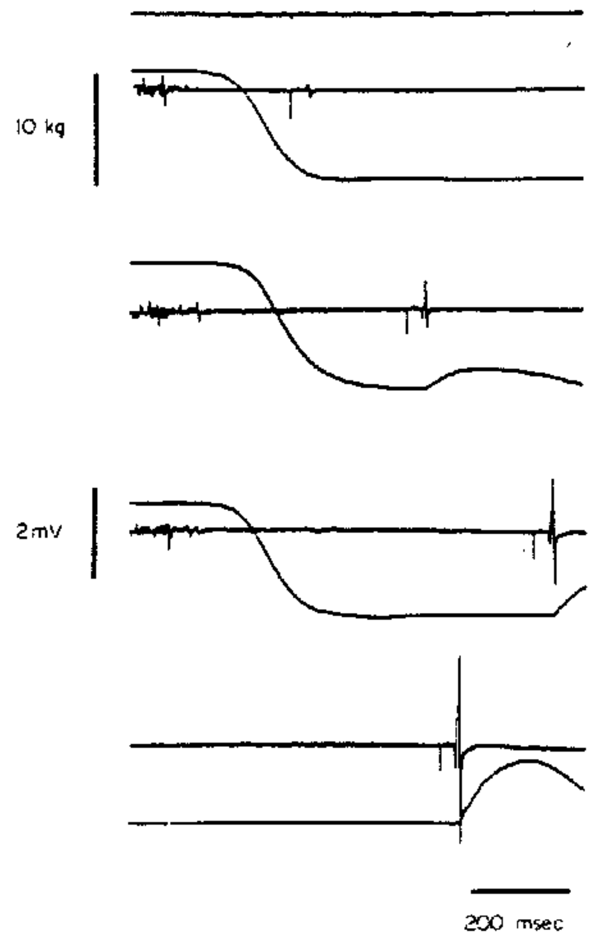

Fig. 8. H-reflex inhibition accompanying rapid voluntary muscle relaxations in isometric conditions, in a normal subject. The recordings show H-reflexes elicited (from top) during relaxation, and about 400, 700 msec and 10 sec (control) after termination of the electromyogram. No electrical activity was present in the pretibial muscles (uppermost beam).

in the case of a reflexly evoked twitch (Burg *et al.*, 1973; Szumski *et al.*, 1974; Vallbo, 1973; Wallin *et al.*, 1973) or of a voluntarily performed graded contraction (Vallbo, 1970; Burke *et al.*, 1978; Hulliger and Vallbo, 1979; Schieber and Thach, 1980; Vallbo and Hulliger, 1981; Roll and Vedel, 1982). Moreover, the faster the velocity of relaxation, the higher must be the excitation coming from the periphery, as evidenced for instance by the amplitude of the electromyographic burst following the silent period (Schieppati and Crenna, 1979). A question therefore arises: how can the CNS cope with this unwanted feed-back excitation, occurring just when the intended behaviour demands motoneurones' derecruitment? The excitability of the motoneurones to the soleus muscle during this particular task has been recently studied by means of an H-reflex technique, and found to be depressed (Schieppati and Crenna, 1984), in agreement with early observations of Paillard (1955), Hufschmidt (1962), Gottlieb and Agarwal (1972, 1973), and Enoka *et al.* (1980). The results were gathered in various experimental situations, to allow an investigation of the role that known spinal mechanisms might possibly play in the supraspinal control of motor termination. They were the following: (1) the amplitude of the soleus H-reflex is strikingly reduced during and following voluntary termination of contraction (Fig. 8); (2) this happens both during isometric and isotonic muscle relaxations, and the phenomenon is limited to the relaxing muscle (e.g. the H-reflex of the contralateral muscle is not affected); (3) the depression of the reflex excitability precedes the termination of the electromyogram of the relaxing muscle: in fact, the H-reflex decreases below the resting values in spite of the persistence of electromyographic activity; (4) the time-course of its subsequent recovery to control values is very much similar to that of the recovery from the reflex depression induced by a preceding tonic vibration of the

Achilles tendon (see Section 2.2); (5) the decrease in excitability of the soleus motor pool is not affected by any intercurrent contraction of the antagonist muscle, that might unpredictably occur after the end of the soleus electromyographic activity (Herman and Mayer, 1969; Herman, 1970). Experiments aimed at testing Ia reciprocal inhibition have indicated that an inhibition of less than 2% of the motoneurone pool could be explained by this mechanism; on the contrary, it appeared that the inhibition normally induced on the H-reflex of the soleus muscle by a descending command to contract the antagonist (see Section 6.1) was diminished when evoked just after relaxation, as if the command to release would produce a block of the normal functioning of the reciprocal inhibitory pathway. An increase in recurrent postsynaptic inhibition to the soleus motoneurones was also excluded, at least as far as rapid releases were concerned (Schieppati and Crenna, 1985). Any role for influences from articular receptors appears unlikely because the H-reflex is reduced to very low amplitudes far in advance of recordable mechanical changes in the muscle or joint (Nardone and Schieppati, 1985; Schieppati *et al.*, 1986). That the inhibition of the soleus H-reflex actually precedes changes in the muscle force is important in the light of the effects induced on the motoneurones by the Ib afferences from tendon organs (Pierrot-Deseilligny *et al.*, 1979, 1982; Fournier *et al.*, 1983, 1984; Heckman *et al.*, 1984). Besides, cutaneous afferences are certainly not activated during the first part of the muscle relaxation, either, and this fact is also relevant because cutaneous afferences do affect motoneurones' excitability, both directly and through their effects on the Ib reflex pathways to the motoneurones (see Section 4.1).

These considerations led to the conclusion that a presynaptic inhibition of the Ia afferent fibres originating from the spindles of the relaxing muscle is the main mechanism

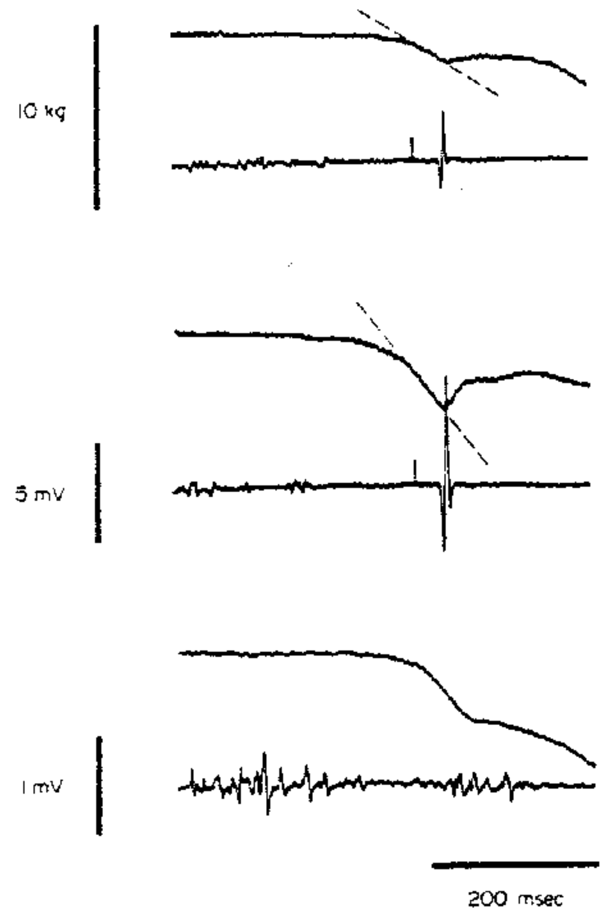

FIG. 9. Force decay (upper beams) and EMG (lower beams) after rapid voluntary termination of muscle contraction in a spastic patient. Contrary to normal subjects, H-reflex excitability is not depressed in this phase, it rather appears to be affected by the velocity of muscle lengthening (although of a small extent, such as in isometric conditions). The reflex excitability leads, in unstimulated relaxations (bottom traces) to clonus-like EMG and force decay.

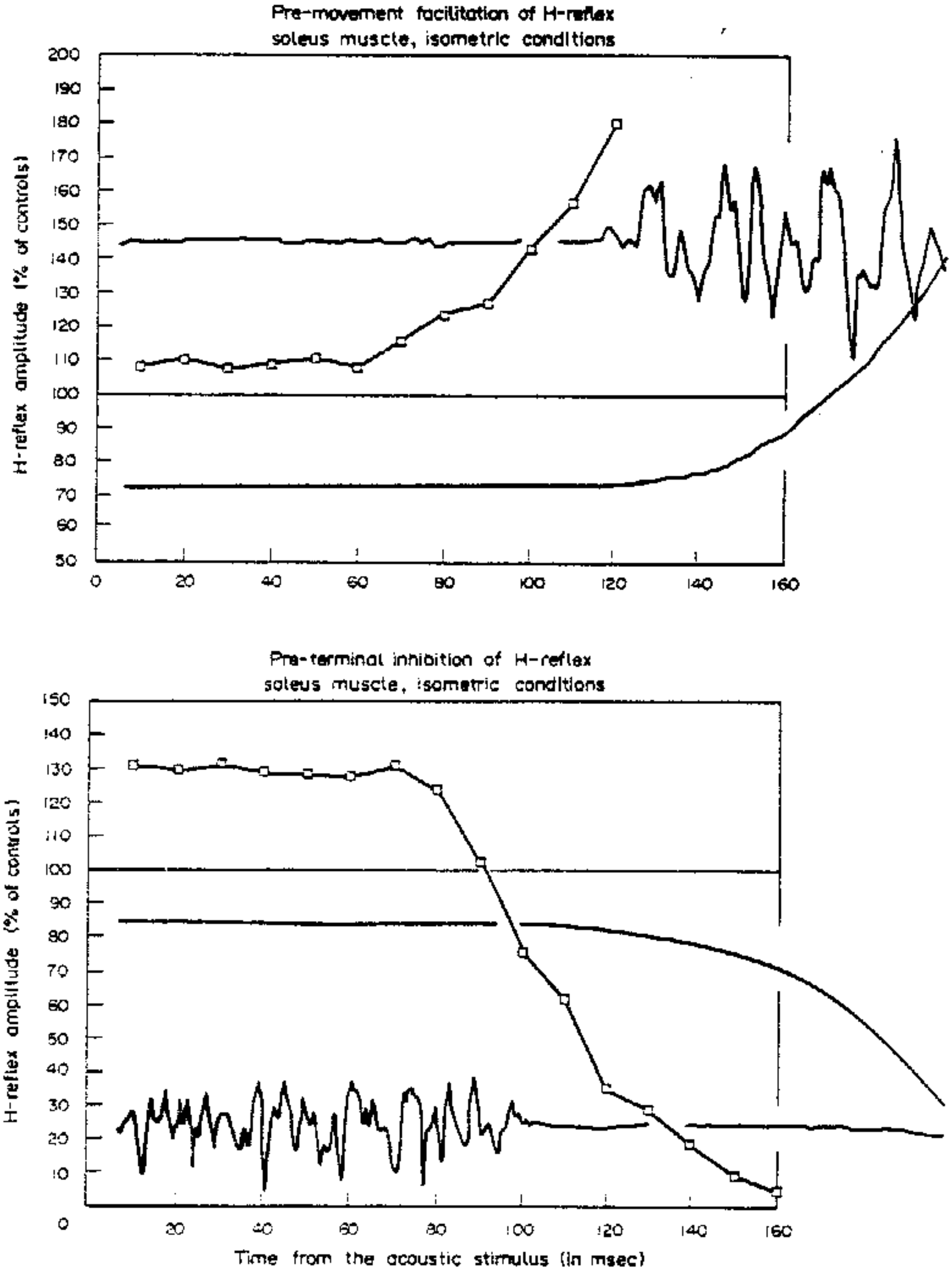

FIG. 10. Time-relationship between premovement facilitation (top) and preterminal inhibition (bottom) of soleus H-reflex, as occurring during rapid voluntary muscle contractions or relaxations, respectively. Each point in the graphs is the grand mean of average values from five subjects. Included in the picture are recordings of EMG and force obtained in the corresponding situations. Graphs and recordings are arbitrarily aligned along the same time-base, starting from the reaction-time signal. It is shown that modulations of H-reflex excitability (in opposite directions) occur nearly simultaneously in the two conditions, notwithstanding later onset of EMG with respect to its earlier termination. On the other hand, thanks to the phase lead in the soleus electrical activity, the time-course of force increase matches exactly that of force decrease.

responsible for the H-reflex inhibition, and that it is actively brought into play in parallel with the withdrawal of the descending activation of the motoneurones. This mechanism would therefore serve the purpose of gating unwanted excitation coming from the spindles of the relaxing (and therefore lengthening) muscle: its presumed absence appears quite disturbing in spastics (Fig. 9) (Szumski *et al.*, 1974; Schieppati *et al.*, 1985; Crenna and Frigo, 1985b). In spastic patients, in fact, the H-reflex is not inhibited at the end of a voluntary contraction, but its amplitude is higher than at rest during the contraction, as expected, and recovers to control values in a manner roughly proportional to the involuntary, clonus-like electromyographic activity which persists for a while in the after period, probably sustained by the lengthening in the relaxing muscle (Fig. 9). As a further impairment in muscle relaxation in spastics, one has to account the delay in voluntarily terminating the EMG, as measured in an acoustic reaction time situation (Schieppati *et al.*, 1985). In normal subjects, in fact, the time elapsing from a reaction command to the end of the soleus electromyogram is very short, and in particular it is shorter than the time necessary for the electromyogram to begin, in the corresponding reaction-time situation (Schieppati *et al.*, 1986) (Fig. 10).

The hypothesis is therefore put forward that a kind of inverse servo-loop assistance is performed during muscle relaxation, whereby presynaptic inhibition contributes to early motoneurones derecruitment, in addition to prevent reflex autogenetic excitation. That action would be in keeping with the notion of the essential role played by the discharge in the Ia afferences in the opposite situation, i.e. in maintaining electromyographic activity in a voluntarily contracting muscle (Angel *et al.*, 1965; Hagbarth *et al.*, 1970; Wallin *et al.*, 1973; Hugon *et al.*, 1982). Besides, it is safe to say that a mechanical advantage of this prompt motoneurones derecruitment would be to equalize the time-course of force decay to that of force onset in the opposite condition, i.e. at the beginning of a rapid contraction, owing to the fact that in a muscle the time to peak force is considerably shorter than the relaxation phase (Fig. 10).

Preliminary observations further indicate that the extent of the presumed presynaptic gating is proportional to the velocity of isotonic muscle relaxation, in a tracking task (Romano' and Schieppati, 1986): in this case the mechanism appears again to take into account the mechanical properties of muscle. In fact, a contracting muscle, owing to its in-series elastic properties, develops additional force during a *lengthening* contraction than during a contraction in which it is allowed to shorten, as described by the force/velocity diagram, the extra force being proportional to the velocity of stretch (Katz, 1939; Abbott *et al.*, 1951; Cavagna *et al.*, 1968). Therefore, when the relaxing soleus muscle has to resist a constant load, a conflicting situation would ensue whereby both the muscle mechanical properties and the spindle reafference are leading to the development of more force than required. In this view, a controlled decrease in force of the relaxing muscle can only occur if the motoneurones discharge is damped proportionally to the velocity of lengthening. On the other hand, the results indicate as well that the H-reflex is larger during an isotonic *shortening* contraction than would be predicted for the same level of motoneurone activation (as monitored by the electromyographic activity) occurring when the soleus muscle opposes in static conditions an equal flexor load. Also this finding is in keeping with the hypothesis of a controlled change in the gain of the servo assistance mechanism, whereby the central nervous symtem "anticipates", by removal of tonic presynaptic inhibition, the disadvantageous consequences of the mechanical properties of muscle shortening: in this case both the force/velocity and the force/length relationships might be compensated for by monosynaptic reflex "ignition" (Granit, 1979). Remember that a facilitation of the soleus H-reflex, occurring prior to a voluntary plantar flexion of the foot, has been repeatedly demonstrated, and attributed by many authors to removal of presynaptic inhibition by the descending command to move (Gottlieb *et al.*, 1970; Coquery and Coulmance, 1971; Pierrot-Deseilligny *et al.*, 1971; Michie *et al.*, 1976; Kots, 1977; Person and Kudina, 1978; Hayes and Clarke, 1978; Sullivan, 1980; Eichenberger and Rüegg, 1984; Schieppati *et al.*, 1985). Pierrot-Deseilligny and Bussel (1973) and Morin *et al.* (1982) already demonstrated that the facilitation of the soleus H-reflex at the onset of a voluntary movement far exceeds that observed at the onset of a soleus contraction induced by a polysynaptic reflex or occurring during the stance phase of human gait. It appears relevant in this regard that the alternative possibility of an anticipation in the discharge of the fusimotor as compared to the skeletomotor neurones has not been demonstrated, although carefully searched for (Westerman *et al.*, 1981; Gerilovksy *et al.*, 1983).

7. Conclusions

For a long time our knowledge on the spinal reflexes, their organization and functional role has relied on animal studies, although human experiments, carefully done in controlled conditions, have been performed for many decades. Looking back to the history of both scientific efforts, one gets the impression that they followed parallel routes, whose connections were banned by various considerations: human reflex studies would help mainly in identifying normative values against which to compare findings in patients, they could hardly penetrate physiological mechanisms because the system could not be split into parts to be systematically analyzed, and so on. Few far sighted scientists and their pupils prevented a definitive break up in the field of reflex studies, and lay out the bases for a fruitful integration, whose outcome has been already, and will be, of great value for both physiology and clinical neurology. Thus, spinal cord neurons and circuits in man have now become a matter of detailed investigation, and their functional organization has resulted understandably on the basis of the principles of animal physiology; in addition, a whole new range of possibilities has opened, i.e. the observation of the changes in excitability of these neurons, and of the modulation of the gain of the reflex pathways along which they are interposed, under the influence of voluntary descending commands. Investigations on the Hoffmann reflex and of the modulation in its excitability, therefore, represent a worthwhile endeavour, to be achieved with diverse working hypotheses in mind, and by means of combined techniques: we are still living the period of excitement in which we have more questions than answers.

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