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978-0-521-19258-3 — The Circuitry of the Human Spinal Cord
Spinal and Corticospinal Mechanisms of Movement
Emmanuel Pierrot-Deseilligny , David Burke
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1

General Methodology

Whatever the spinal, motor cortical or descending pathway investigated, its activation produces changes in the excitability of spinal motoneurones, 'the final common path' in the motor system. Whenever the output measure is a muscle action potential, the excitability of the motoneurone pool will determine if and to what extent changes taking place at cerebral level are manifest: it is unsafe to assume that any conditioning manoeuvre acts solely at cortical level and does not have direct or indirect influences on spinal motoneurones. A prerequisite for any investigation of changes in spinal or corticospinal pathways controlling movement in humans is therefore to be able to assess changes in motoneurone excitability quantitatively, using valid reproducible methods. Several non-invasive methods have been developed, and these are considered in this chapter with their advantages and disadvantages. Because all are indirect, it is desirable to obtain congruent results with different techniques relying on different principles. All may be and many have been used in studies on patients, but here the methodology should be simple and rapid.

H Reflex and Tendon Jerk

The 'monosynaptic reflex' was the first technique available to investigate spinal pathways in animals and humans. Its principle is based on the apparent simplicity of the monosynaptic projection of Ia afferents to homonymous motoneurones, but subsequent studies have shown that the reflex is not as simple as was initially thought, particularly in humans.

Initial Studies

Animal Studies

The monosynaptic reflex was described as a tool for investigating changes in excitability of the motoneurone pool (Renshaw, 1940). When used as a *test reflex*, the monosynaptic reflex allows one to assess the effect on the motoneurone pool of *conditioning* volleys in peripheral afferents or descending tracts. During the 1940s and early 1950s this method was used to reveal important features of the input to spinal motoneurones. Intracellular recordings later allowed more detailed analysis of the synaptic input to motoneurones in animals, but this greater precision did not change the main conclusions that had emerged from the experiments using the monosynaptic reflex. This suggests that monosynaptic testing can give reliable results.

Human Studies

Percutaneous electrical stimulation of the posterior tibial nerve (PTN) produces a synchronised response in the soleus muscle (Hoffmann, 1918), known as the Hoffmann reflex or H reflex (Magladery & McDougal, 1950). Magladery *et al.* (1951a) showed that the first motoneurones discharging in the H reflex do so at a latency consistent with a monosynaptic pathway (see p. 67). The H reflex is the equivalent of the monosynaptic reflex in animal studies (Paillard, 1955), and has become the main tool in many motor control investigations and

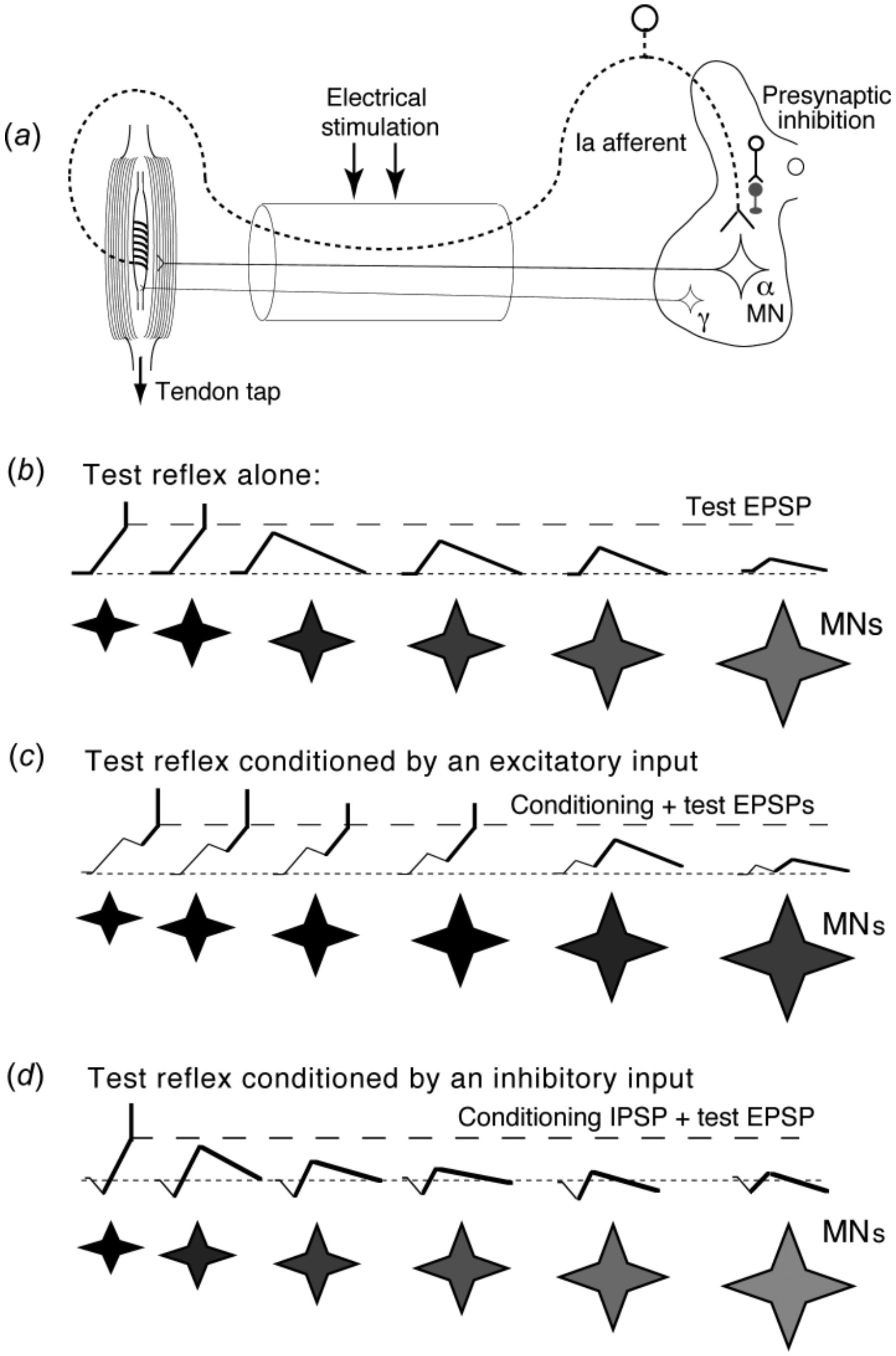

Fig. 1.1. *Sketch of the pathway and principles of the monosynaptic reflex*. (*a*) Sketch of the pathway: Ia afferents from muscle spindle primary endings (dotted line) have monosynaptic projections to α motoneurones (MNs) innervating the corresponding muscle. The H reflex is produced by electrical stimulation of Ia afferents, and bypasses muscle spindles. The tendon jerk is elicited by a tap that stretches muscle

diagnostic studies performed on human subjects (for reviews, see e.g., Schieppati, 1987; Pierrot-Deseilligny & Mazevet, 2000; Knikou, 2008).

Underlying Principles

The Monosynaptic Reflex Arc

Pathway

The motor unit, i.e., a motoneurone and the muscle fibres it innervates, constitutes the basic building block of motor output and is the efferent arm of the pathway. Ia fibres from muscle spindle primary endings have monosynaptic excitatory projections to motoneurones innervating the muscle from which the afferents emanate (homonymous projections, Fig. 1.1(*a*)). This pathway is also used in the tendon jerk. The H reflex is produced by electrical stimulation of Ia afferents which have a lower electrical threshold than α motor axons, particularly for stimuli of relatively long duration (see p. 6).

H Reflex, Tendon Jerk and SLSR

These reflexes are all dependent on monosynaptic excitation from homonymous Ia afferents. However, their afferent volleys differ in many respects: (i) the electrically induced afferent volley for the H reflex bypasses muscle spindles and produces a single synchronous volley in group Ia and Ib afferents; (ii) the tendon tap produces a highly dynamic stretch, which activates mainly muscle spindle primary endings and elicits a prolonged discharge in Ia afferents and other sensitive mechanoreceptors from many sources (cf. Chapter 3); (iii) the short-latency stretch reflex (SLSR) is overlapped by a medium-latency response due to a group II volley from muscle spindle secondary endings (p. 261). In addition to the different composition of these afferent volleys, their Ia component is differently sensitive to presynaptic inhibition (pp. 307–308).

Orderly Recruitment of Motoneurones

Fig. 1.1(*b*) shows that, in the cat, the size of the test Ia excitatory post-synaptic potential (EPSP) evoked in individual motoneurones by a given afferent volley is larger in small motoneurones supplying slow motor units than in large motoneurones supplying fast units. As a result, motoneurones are recruited in an orderly sequence by the Ia input, from the smallest to the largest, according to Henneman's size principle (see Henneman & Mendell, 1981). Motoneurones contributing to the human H reflex are recruited in a similar orderly sequence from slow to fast motor units (Buchthal & Schmalbruch, 1970). This orderly recruitment of motoneurones is preserved when they receive a variety of excitatory and inhibitory inputs (though not all, see pp. 16–17).

Principles of the Monosynaptic Reflex Method

In the control situation, the test Ia volley elicited by stimulation of constant intensity causes some motoneurones

Fig. 1.1. (*cont*)

spindles. It therefore also depends on the sensitivity to stretch of primary endings, and this is controlled by the activity of γ efferents (but the two reflexes cannot be compared to estimate the level of γ activity, see pp. 114–115). The pathway of presynaptic inhibition of Ia terminals (see Chapter 8) is represented. (*b*)–(*d*) Principles of the monosynaptic reflex. (*b*) Orderly recruitment of motoneurones (MNs) by a given Ia input: the size of the monosynaptic Ia excitatory post-synaptic potential (EPSP; upper row) decreases as MN size increases (lower row). The dotted horizontal lines indicate the resting level of motoneurone excitability. The interrupted horizontal lines represent the threshold for discharge of the MNs. Only the smallest MNs (black) are fired by the test Ia volley, and the excitability of subliminally excited MNs decreases from the smallest to the largest (as indicated by the decreasing tone of grey). (*c*) Facilitation by an excitatory input. There is summation of the conditioning EPSP (thin lines) and the test EPSP (thick lines). As a result, MNs which had just failed to discharge in the control reflex are raised to firing threshold and the size of the reflex is increased. (*d*) Inhibition by an inhibitory input. There is summation of the conditioning inhibitory post-synaptic potential (IPSP; thin line) and of the test EPSP (the test EPSP is also reduced by changes in the membrane conductance, see pp. 18–19). As a result, MNs which had just been recruited in the control reflex cannot be discharged, and the size of the reflex is reduced. The excitability of the MNs in the subliminal fringe of excitation (grey MNs in (*b*)) is also modified by the conditioning input in (*c*), (*d*). Adapted from Pierrot-Deseilligny & Mazevet (2000) ((*b*)-(*d*)), with permission.

to discharge producing the control test reflex and creates EPSPs in other motoneurones which thereby become subliminally excited (black and grey motoneurones, respectively, in Fig. 1.1(*b*)). If the motoneurone pool is now facilitated by a subthreshold conditioning volley, motoneurones that had just failed to fire in the control reflex will discharge when the conditioning and test EPSPs summate (Fig. 1.1(*c*)). The size of the test reflex will increase. By contrast, if motoneurones receive conditioning inhibitory post-synaptic potentials (IPSPs), the same test Ia volley will not be able to discharge the motoneurones that had been recruited last into the control reflex, and the size of the test reflex will be decreased (Fig. 1.1(*d*)). The method allows one to distinguish between: (i) conditioning stimuli without effect on the excitability of motoneurones; (ii) those which evoke only subliminal excitation of the motoneurones when applied alone; (iii) and those which inhibit motoneurones. A variant of the method involves merely comparing the amplitude of the reflex in two situations (e.g., 'natural reciprocal inhibition' of the reflex with respect to rest during voluntary contraction of the antagonistic muscle, p. 194).

Basic Methodology

In most healthy subjects *at rest*, H reflexes can usually be recorded only from soleus, quadriceps and flexor carpi radialis (FCR) (see Pierrot-Deseilligny & Mazevet, 2000). However, when a weak voluntary contraction is used to potentiate the reflex by raising motoneurone excitability close to firing threshold and by suppressing Ib inhibition, H reflexes can be recorded from virtually all limb muscles, if the parent nerve is accessible to electrical stimulation (p. 67).

General Experimental Arrangement

Subject's Posture

The subject should be comfortably seated in an armchair with the examined limb loosely fixed in a position avoiding stretch of the test muscle (see Burke *et al.* 1999). Thus, the lower limb is commonly explored with the hip semi-flexed (120°), the knee slightly flexed (160°) and the ankle at 110° plantar flexion. The upper limb is explored with the shoulder in slight abduction (60°), the elbow semi-flexed (110°), and the forearm pronated and supported by the arm of the chair. In patients, recordings can be performed supine. However, the H reflex modulation observed after activation of some spinal pathways in normal seated subjects disappears when they are transferred supine (Knikou, 2006).

Awareness

Because H reflexes increase with alerting stimuli, they should be recorded in a quiet room, and the influence of the mental effort involved in a difficult motor task should be taken into account (Brunia, 1971). Conversely, the H reflex decreases during the early stages of sleep and is abolished during REM sleep (Hodes & Dement, 1964).

Recording the H Reflex

Recording

Reflexes generally appear in the electromyogram (EMG) as triphasic waveforms (Fig. 1.2(*e*)–(*f*)), reflecting the fact that input grid 1 (often called the 'active electrode') is usually not over the motor point, particularly with soleus.

(i) Bipolar surface electrodes are commonly placed 1.5–2 cm apart over the corresponding muscle belly. For the quadriceps the best place is on the anterior aspect of the thigh, 5–10 cm above the patella. In the forearm, a selective voluntary contraction can be used as a first step to focus the reflex response on the desired motoneurone pool, because during the contraction the reflex discharge can be obtained at lower threshold in the contracting muscle.

(ii) Monopolar recordings, with an 'active' electrode over the mid-belly of the muscle and a 'remote' electrode over its tendon, have been recommended to minimise the effects of changes in geometry of the muscle during voluntary contraction (Gerilovsky *et al.*, 1989). However, these changes are adequately taken into account if the reflex is expressed as a percentage of the maximal M wave ('M_{max}', p. 7) measured under the same conditions. In addition, the more distant the 'remote' electrode

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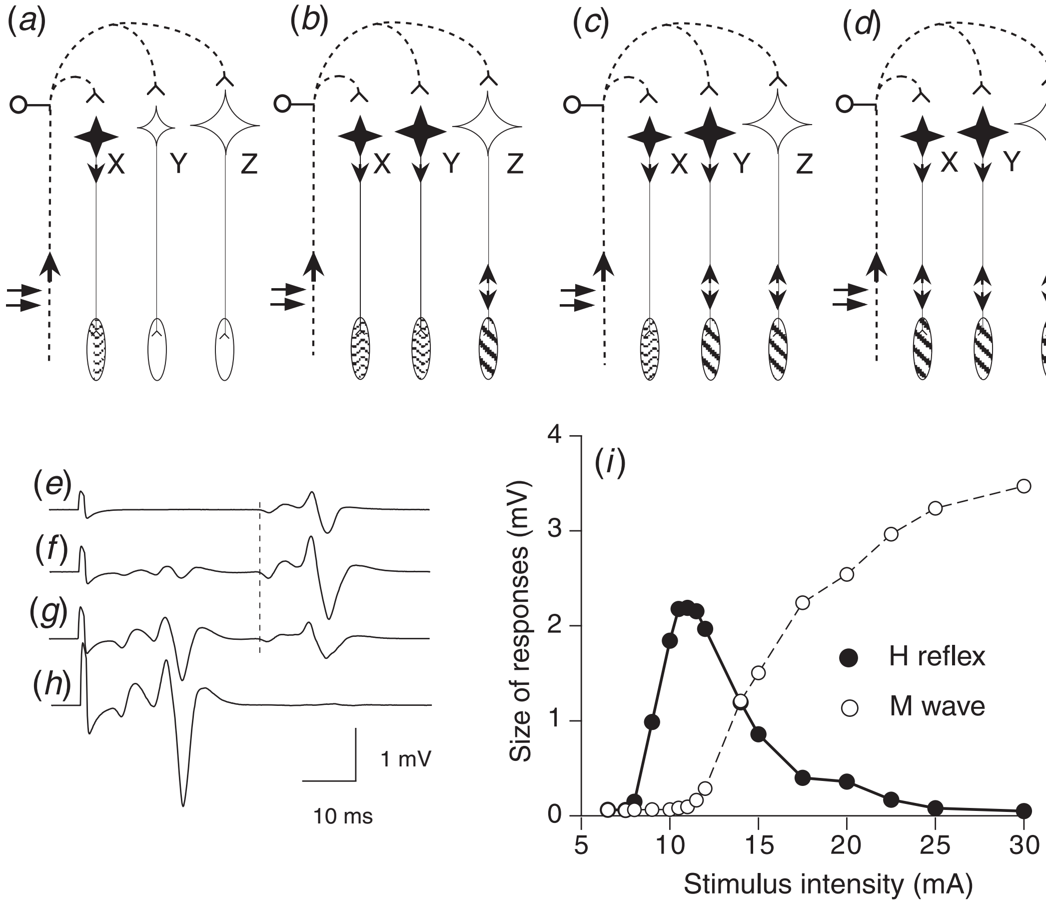

Fig. 1.2. *Recruitment curve of the H and M waves in the soleus*. Sample electromyographic (EMG) responses are shown in (*e*)–(*h*) and sketches of the corresponding volleys in Ia afferents (dotted lines) and motor axons (continuous lines) in (*a*)–(*d*) when the stimulus intensity is progressively increased. MNs discharged by the Ia volley are black, muscle fibres activated by the H reflex are speckled and those activated by the M wave are hatched. (*a*) and (*e*) Stimulation (at 9 mA) activates only Ia afferents and causes MN 'X' to fire in the H reflex. (*b*) and (*f*) Stronger stimulation (12 mA) activates more Ia afferents and this causes MNs 'X' and 'Y' to fire in the H reflex, which increases in size. It also elicits a motor volley in the axon of MN 'Z' and an M wave appears in the EMG. The antidromic motor volley in MN 'Z' does not collide with the reflex response, because this MN does not contribute to the reflex. (*c*) and (*g*) Even stronger stimulation (15 mA) causes MNs 'X' and 'Y' to fire in the H reflex and elicits a motor volley in the axon of MNs 'Z' and 'Y'. As a result, an M wave appears in the muscle fibres innervated by MN 'Y'. The antidromic motor volley collides with and eliminates the reflex volley in the axon of MN 'Y', and the H reflex decreases. (*d*) and(*h*) Yet stronger stimulation (30 mA) produces M_{max}, and the H reflex is eliminated by collision with the antidromic motor volley. Note that collision between the antidromic volley and the reflex discharge will also prevent antidromic invasion of those reflexly activated motoneurones, so that F waves cannot occur in them. The vertical dashed line in (*e*)–(*g*) indicates the latency of the H reflex. (*i*) The amplitude of the H reflex (●) and of the M wave (○) are plotted against stimulus intensity. Adapted from Pierrot-Deseilligny & Mazevet (2000), with permission.

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the less likely is the recorded activity to come from only the muscle underlying the ‘active’ electrode.

Measurement

(i) Reflex latency is measured to the first deflection of the H wave from baseline, regardless of polarity (see the vertical dashed line in Fig. 1.2(*e*)–(*g*)).
(ii) In practice it makes little difference whether the amplitude or the surface area of the reflex is assessed or whether amplitude is measured for the negative phase only or from negative peak to the following positive peak. Whichever way the H reflex is measured, the same method should be used for ‘M_{max}’, and the amplitude of the H reflex must be expressed as a percentage of M_{max}.

Cross-talk

Pick up of the EMG potentials from an adjacent muscle can occur if there is spread of the electrical stimulus to another nerve (with the H reflex), or of the mechanical stimulus to another muscle (with the tendon jerk) (see Hutton *et al.* 1988). Even if this does not occur, it can still be difficult to be certain that a surface-recorded EMG potential comes from the underlying muscle rather than a synergist (e.g., responses elicited in the FCR and finger flexors after median nerve stimulation). A simple way of ensuring that a response is truly reflex and that it originates from the desired muscle is to check that it increases during a selective voluntary contraction of that muscle.

Stimulation to Elicit the H Reflex

H reflexes are produced by percutaneous electrical stimulation of Ia afferents in the parent nerve. The technique is now well codified (see Pierrot-Deseilligny & Mazevet, 2000).

Duration of the Stimulus

The diameter of Ia afferents is probably slightly greater than that of α motor axons and their rheobasic threshold is lower, such that it is generally possible, particularly in soleus, to evoke an H reflex with stimuli below motor threshold (1 × MT). The strength-duration curves for motor axons and Ia afferents differ and, as a result, the optimal stimulus duration for eliciting the H reflex is long (1 ms; Paillard, 1955). The stimulus intensity for the threshold H reflex then approaches rheobase for low-threshold Ia afferents, approximately 50% of rheobase for motor axons (Lin *et al.* 2002). Stimuli of 1 ms duration result in larger H reflexes when the M wave is <5% M_{max}, smaller M wave at H_{max} and a lower H reflex threshold than stimuli of 0.05 ms (Lagerquist & Collins, 2008). The effects of the differences in strength-duration properties are greater than they might at first appear, because it takes only one motor axon to produce a detectable M wave, but many afferents are required to produce a detectable H reflex.

Uni- and Bi-polar Stimulation

The best method for ensuring that Ia afferents are excited at lower threshold than motor axons involves placing the cathode over the nerve and the anode on the opposite side of the limb, so that current passes transversely through the nerve. The soleus and quadriceps H reflexes are commonly evoked by monopolar stimulation of the PTN (cathode in the popliteal fossa, anode on the anterior aspect of the knee) and the femoral nerve (cathode in the femoral triangle, anode on the posterior aspect of the thigh), respectively. However, in areas where there are many nerves, bipolar stimulation may avoid stimulus encroachment upon other nerves or other branches of the same nerve: the median nerve (supplying the FCR) is so stimulated at the elbow, the deep peroneal nerve (DPN supplying the tibialis anterior [TA]) at the fibular neck and the sciatic nerve (supplying the hamstrings) at the posterior aspect of the thigh. In general, the cathode should then be placed over the nerve with anode distal (or lateral) to avoid the possibility of anodal block.

Frequency of Stimulation

Because of homosynaptic depression (HD, see p. 87), there is reflex attenuation as stimulus rate is increased above 0.1 Hz. Although this attenuation requires at least 10 s to subside completely, its effects are sufficiently small after 3–4 s to allow testing at 0.2–0.3 Hz. Use of these frequencies constitutes a compromise between reflex depression and the necessity to collect

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a large number of responses because of reflex variability and fluctuating attention. During a background contraction of the tested muscle, the attenuation with increasing stimulus repetition rate is reduced or even abolished, and stimulus rates of 2–3 Hz are often optimal (p. 89).

Magnetic Stimulation

The H reflex may also be evoked by magnetic stimulation of the parent nerve (or nerve root) and appears with the same latency as with electrical stimulation (Zhu *et al.* 1992). One advantage of magnetic stimulation is the ease with which an H reflex can be elicited from deep nerves which are difficult to access with percutaneous electrical stimulation. However, because of the extreme brevity (~0.05 ms) of the effective stimulus produced by magnetic stimulation, the threshold for the H reflex is then usually higher than that for the M wave (see above).

H and M Recruitment Curve

The Recruitment Curve

As the intensity of an electrical stimulus to the PTN is increased, there is initially a progressive increase in amplitude of the soleus reflex due to the stronger Ia afferent volley (Fig. 1.2(*a*) and (*e*), (*b*) and (*f*)). When the stimulus exceeds motor threshold, the short-latency direct motor response (M wave) appears in the EMG due to stimulation of motor axons ((*b*) and (*f*)). Further increases in the intensity of the test stimulus cause the M wave to increase and the H reflex to decrease ((*c*) and (*g*)). Finally, when the direct motor response is maximal, the reflex response is completely suppressed ((*d*) and (*h*)). This is because the antidromic motor volley set up in motor axons collides with and eliminates the H reflex response (Hoffmann, 1922; Fig. 1.2(*d*)). Note that, when it first appears in the EMG, the M response involves axons of the largest motoneurones (e.g., MN ‘Z’ in Fig. 1.2(*b*) and (*f*)), which have a high threshold for recruitment by Ia volleys. Because they are not activated in the reflex, stimulation of these motor axons does not interfere with the reflex response. The variations of the H and M responses with the test stimulus intensity can be plotted as the recruitment curve of Fig. 1.2(*i*). Because of the orderly recruitment of motoneurones (p. 3), the sensitivity of the reflex to facilitation and inhibition depends on the last motoneurones recruited by the test volley.

Maximal M Wave (M_{max})

M_{max} is evoked by the stimulation of all motor axons and provides an estimate of the response of the entire motoneurone pool. This estimate is actually an overestimate, because the necessarily strong stimulus will produce EMG activity in all muscles innervated by the stimulated nerve. Accordingly, M_{max} following median nerve stimulation at the elbow comes from the FCR, finger flexors and pronator teres. Ignoring this issue, M_{max} should always be measured in the same experiment with the same recording electrode placement because: (i) comparing it with the reflex response provides an (admittedly flawed) estimate of the proportion of the motoneurone pool discharging in the reflex; (ii) expressing the reflex as a percentage of M_{max} enables one to control for changes in muscle geometry due to changes in muscle length or contraction; (iii) expressing the test reflex as a percentage of M_{max} allows the investigator to be sure that the test reflex remains within the ‘linear’ range of the input/output relationship for the motoneurone pool (see pp. 15–16).

Descending Limb of the Recruitment Curve

Because electrical stimulation will first activate motor axons of large diameter from high-threshold motoneurones, on the descending limb of the recruitment curve, the reflex response seen in the EMG will be produced by small motoneurones (those first recruited into the H reflex, p. 3), for which the collision in motor axons has not taken place. The faster motor units in the H reflex were last recruited into the reflex and their discharge is thus particularly sensitive to excitation and inhibition. However, with these motoneurones the reflex discharge is more likely to be eliminated by collision with the antidromic motor volley (Fig. 1.2(*c*) and (*g*)) (see Pierrot-Deseilligny & Mazevet, 2000).

Monitoring the Stability of the Stimulation Conditions

Small M wave. If the H reflex is recorded during a manoeuvre that can alter the stimulating conditions

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(e.g., muscle contraction or gait), it is necessary to ensure that changes in the test H reflex are not due to a change in the position of the stimulating electrode. The reproducibility of the M wave can be used to monitor the stability of the stimulation. To that end, stimulation should be adjusted to produce a small M wave in addition to the H reflex. If there is need for a test response without a M wave, stability can be monitored by alternating the test stimulus with a stimulus evoking a M wave through the same electrode. Changes not exceeding ± 10% of the recorded M wave (not ± 10% of M_{max}) are then recommended.

Limitations: (i) During experiments involving a contraction of the tested muscle, there will be changes in axonal excitability unrelated to stability of the stimulating conditions (Vagg *et al.* 1998), and there will inevitably be some variability in the M wave from trial to trial. (ii) A further complication is that, even at rest, M_{max} (and consequently the small control M wave) may decrease in size during long experiments (1–3 hours) (Crone *et al.* 1999), though this finding has not been reproduced by others (P. McNulty & D. Burke, unpublished data). Either way, it is necessary to monitor the amplitude of M_{max} repeatedly during the course of long experiments.

Recruitment Curves in Other Muscles

The recruitment curves for the quadriceps and FCR H reflexes are similar. However, the thresholds of the M and H responses of these muscles are generally closer than in soleus.

Tendon Jerk

With proximal muscles, the H reflex may be difficult to record at rest without the M wave, and it then appears merged into the end of the M wave. It may therefore be convenient to test the excitability of these motoneurone pools using tendon reflexes evoked by an electromagnetic hammer that produces reproducible transient tendon percussion. Use of the tendon jerk introduces two complications:

Delay Due to the Tendon Tap

The tendon tap introduces a delay due to the time required for receptor activation and supplementary peripheral afferent conduction time. An estimate of the *central* delay of the effect of a conditioning volley on a test tendon jerk may be obtained by comparing the first interstimulus interval (ISI) at which this effect occurs to the first ISI at which a heteronymous monosynaptic Ia volley delivered to the same ('conditioning') nerve facilitates the tested motoneurones (see Mazevet & Pierrot-Deseilligny, 1994).

Fusimotor Drive

Theoretically at least, the amplitude of the reflex response produced by tendon percussion depends on the sensitivity of muscle spindle primary endings in the tested muscle and on the level of γ drive directed to them (Fig. 1.1(*a*)). However, differences in the behaviour of the H reflex and the tendon jerk cannot be used as a measure of γ drive to the muscle because H and tendon jerk reflexes differ in several other respects (pp. 114–115).

Random Alternation of Control and Conditioned Reflexes

In most investigations, the monosynaptic reflex is used as a test reflex to assess the effect of conditioning volleys on the motoneurone pool. The size of the reflex is compared in the absence (control reflex) and in the presence (conditioned reflex) of the conditioning volley. Control and conditioned reflexes should be randomly alternated, because: (i) this avoids the possibility of the subject voluntarily or involuntarily predicting the reflex sequence; and (ii) regular alternation produces erroneously large results (Fournier *et al.* 1984), possibly due to HD (see Pierrot-Deseilligny & Mazevet, 2000).

Time Resolution of the Method

It is essential to estimate the central delay of an effect to characterise the neural pathway activated by a conditioning stimulus as mono-, di-, or poly-synaptic. This can be done by comparing the earliest conditioning-test interval at which the test reflex is modified with the interval when the conditioning and test volleys would arrive simultaneously at spinal level: the more synapses involved, the greater the difference between these two values. However, the H reflex method underestimates

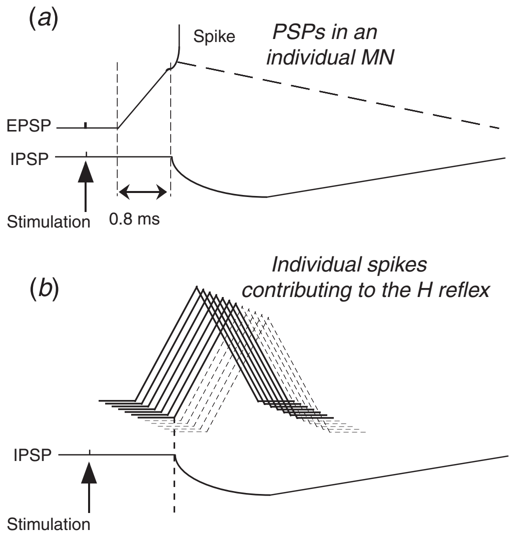

Fig. 1.3. *Inhibition of the monosynaptic reflex by a disynaptic IPSP*. (*a*) Post-synaptic potentials (PSPs) in a motoneurone (MN): when volleys eliciting a monosynaptic Ia excitatory post-synaptic potential (EPSP) and a disynaptic (IPSP) enter the spinal cord simultaneously, the rise time of the EPSP in individual MNs allows the spike in the last recruited MNs to be inhibited by the IPSP, even though the latter does not begin until 0.5–1.0 ms after the beginning of the EPSP (because it must traverse an interneurone). Adapted from Matthews (1972), with permission. (*b*) MNs contributing to the H reflex do not discharge simultaneously in the test reflex. Thus, a disynaptic inhibitory post-synaptic potential (IPSP) elicited by a conditioning volley entering the spinal cord at the same time as the test monosynaptic Ia volley may inhibit the last spikes (thin interrupted lines) contributing to the monosynaptic reflex discharge, while the first spikes (thick continuous lines) are not modified, as described in the cat by Araki *et al.* (1960).

the true central delay: e.g., with reciprocal Ia inhibition, the earliest conditioning-test interval with inhibition corresponds to the simultaneous arrival of the two volleys at spinal level, even though an extra 0.8 ms is required for the interneurone interposed in the pathway (pp. 184–185). This is due to two reasons (Fig. 1.3).

EPSPs in Individual Motoneurones

The rise time of the test Ia EPSP is sufficiently long that the discharge of the last recruited motoneurones evoked by the monosynaptic input will not occur before the arrival of a disynaptic IPSP. This is so even though the synaptic delay at the interneurone results in an IPSP with an onset 0.5–1.0 ms later than the beginning of the monosynaptic EPSP (see Matthews, 1972; Fig. 1.3(*a*)). Moreover, an EPSP elicited by a conditioning volley entering the spinal cord after the test volley may summate with the decay phase of the test Ia EPSP and cause the motoneurone to discharge at a ‘too early’ ISI.

Dispersed Discharge of Motoneurones in the Reflex

In the cat there is 0.5 ms between the firing of the first and last recruited motoneurones contributing to the monosynaptic reflex (Araki *et al.* 1960). In human subjects, where the afferent pathway is longer and the conduction velocity (CV) of Ia afferents slower, this interval has been estimated at 1.5 ms for the quadriceps H reflex (Fournier *et al.* 1986) and ~2 ms for the soleus H reflex (Burke *et al.* 1984). Fig. 1.3(*b*) shows that, because of the desynchronisation at spinal level, the last individual spikes contributing to the monosynaptic test reflex discharge can be inhibited by a disynaptic IPSP elicited by a conditioning volley entering the spinal cord at the same time as the monosynaptic test volley. All things being equal, the axons of earlier-recruited motoneurones will have slower conduction times to the muscle, so that the onset of the compound EMG potential will be determined by the higher-threshold units despite their later discharge. This is not so with the tendon jerk, and as a result the reflex potential is only slightly broader than that for the H reflex (Burke *et al.* 1984).

Recovery Cycle of the H Reflex

The recovery cycle of the H reflex investigates the time course of the changes in the H reflex after a conditioning reflex for conditioning-test intervals up to 1–2 s. Such studies were in vogue in the 1950–1960s (Magladery *et al.* 1951b; Paillard, 1955). However, such long recovery cycles are no longer used, because too many overlapping and uncontrollable phenomena are responsible for the changes: HD (p. 87), presynaptic inhibition of Ia terminals activated by the conditioning volley (p. 304), afterhyperpolarisation and recurrent inhibition of motoneurones (p. 147), muscle spindle receptor unloading and Golgi tendon organ activation

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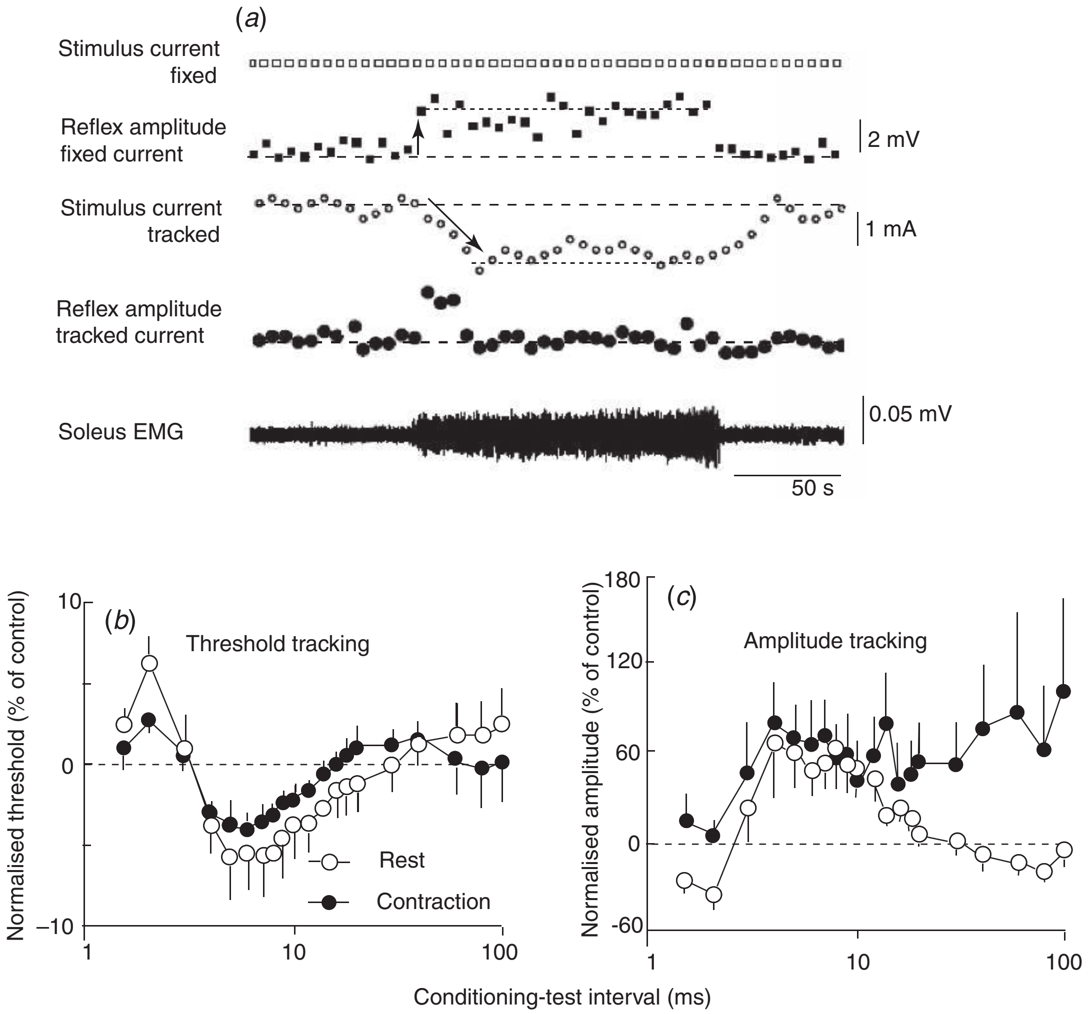

Fig. 1.4. *Threshold tracking of the H reflex*. Panel (*a*) shows H reflex recordings before, during and after a weak voluntary contraction of soleus, using conventional 'amplitude tracking' (upper two traces, fixed stimulus, changing H reflex amplitude) and 'threshold tracking' (stimulus current in trace 3 necessary to maintain an H reflex of constant amplitude in trace 4). The arrows emphasise that the reflex change is detected immediately with amplitude tracking but more slowly with threshold tracking, as the computer reduces the stimulus to the correct level (and this is the reason why the reflex amplitude in those trials exceeds the target level). (*b*), (*c*) The soleus H reflex was conditioned by a weak stimulus to the posterior tibial nerve (PTN; 65% of the unconditioned test stimulus, subthreshold for the H reflex during contraction). The data show the deviation from the unconditioned value (horizontal dotted line), using threshold tracking (*b*) and amplitude tracking (*c*) at rest (○) and during tonic soleus voluntary contractions (●), plotted against the conditioning-test interval. (*b*) The intensity of the test stimulus was altered to keep the test H reflex constant: an increase in excitability would therefore require less current. (*c*) The test stimulus was constant: an increase in excitability would therefore increase the amplitude of the test H reflex. Note the logarithmic scale for the X-axes. Mean data + SEM for six subjects ((*b*), (*c*)). Adapted from McNulty *et al.* (*J Neurophysiol*. 2008, Am Physiol Soc, used with permission) (*a*), Chan *et al.* (2002) ((*b*), (*c*)), with permission.