

Amplitude Modulation of the Soleus H-Reflex in the Human During Walking and Standing

C. Capaday and R. B. Stein

Department of Physiology, University of Alberta, Edmonton, Alberta T6G 2H7, Canada

Experiments were done to determine the amplitude of the monosynaptically mediated H-reflex of the soleus muscle at various phases of the step cycle, using a computer-based analysis procedure. In all subjects tested the amplitude of the H-reflex was strongly modulated in amplitude during the walking cycle and was highest during the stance phase. In many subjects the peak reflex amplitude occurred at about the same time as the peak soleus electromyographic (EMG) activity, but in others it occurred earlier. The form of the reflex variation (i.e., envelope of H-reflex amplitude versus phase in cycle) during the step cycle could also be quite different from that of the EMG produced during stepping. At an equal stimulus strength and EMG level, the H-reflex was always much larger, up to $3.5\times$, during steadily maintained contractions while standing than during walking.

The large reflexes when subjects were standing are consistent with the control of position required to maintain a stable posture in this task. Similarly, the reflexes during walking are greatest during the stance phase, when they will assist in maintaining the upright position of the body against gravity. The reflexes are smallest during the swing phase when they would oppose ankle flexion. However, since the reflex amplitude is task-dependent (i.e., greater during standing than during walking at the same EMG and stimulus levels) and is not always closely related to the EMG produced during a given task such as walking, the strong modulation of H-reflex during walking is not simply a passive consequence of the α -motoneuron excitation level. Rather, it depends on central mechanisms in addition to those that modify α -motoneuron excitation.

It was reported recently that the stretch reflex of the soleus muscle was strongly modulated in amplitude during the walking cycle of the mesencephalic cat (Akazawa et al., 1982). Moreover, the modulation of the amplitude of the stretch reflex was not simply a function of the level of activity in the soleus muscle. This demonstration depended on comparing reflexes obtained during locomotion to those obtained during similar levels of tonic activity that occur spontaneously in the mesencephalic cat. Therefore, it is possible that the efficacy of the synaptic transmission between the Ia afferents and the motoneurons may be modulated by central neural mechanisms independently of the level of motoneuronal activity (Akazawa et al., 1982). However, because the study used a reduced preparation and relied on spontaneous changes of activity, the utilization and functional value of such a modulation during voluntary activity remains unknown.

Does a functional modulation of the stretch reflex occur in normal human subjects, and if so, what is its origin? Surpris-

ingly, these questions have been the subject of only brief reports (Capaday and Stein, 1985; Garrett et al., 1984; Morin et al., 1982). Walking and standing were chosen to investigate these questions in more detail, because the stretch reflex is of functional value in both tasks (Dietz et al., 1979, 1980; Nashner, 1976) and may be used to a different extent in each. Walking requires a certain amount of compliance (Houk, 1976), whereas standing may require a more rigid control of ankle position. In principle, a modulation of the amplitude of the stretch reflex can be produced by a shift of reflex threshold, i.e., the curve relating reflex output to stimulus input is shifted along the abscissa without changing its slope (Crago et al., 1976; Houk, 1976, 1979) or by a change in reflex sensitivity that would change the slope of the input-output relation. These two possibilities may result from quite different neural mechanisms.

There are obvious technical difficulties in applying, during walking, perturbations that would stretch a muscle group of a normally moving limb. However, Akazawa et al. (1982) found that in the mesencephalic walking cat the amplitude of the H-reflex and the stretch reflex were modulated in essentially the same way. It was also found in this preparation, that during spontaneous states of tonic contractions the amplitude of the H-reflex paralleled that of the stretch reflex (Akazawa et al., 1982; see also Aldridge and Stein, 1982). Furthermore, while the H-reflex and the stretch reflex are not identical (Burke, 1983; Burke et al., 1984), both depend in large part on the synaptic connections between the Ia muscle afferents and the α -motoneurons. Therefore, the amplitude of the H-reflex and the stretch reflex may have similar temporal profiles during the course of a movement of postural state, although the extent of facilitation or depression of each reflex may not be exactly the same. To the extent that the H-reflex is less dependent on the peripheral effects of the fusimotor system on muscle spindles, it should provide a better measure of any change in synaptic efficacy between the muscle afferents and the α -motoneurons. There is, however, a problem in maintaining a constant electrical stimulus to the tibial nerve at all phases of the step cycle, but this can be minimized (see Materials and Methods).

In this paper we show that the H-reflex is deeply modulated during walking in humans and that this modulation is dependent on central mechanisms, of which the level of α -motoneuron excitation is only one component. The modulation is accompanied by changes in both reflex sensitivity and reflex threshold.

Materials and Methods

Experimental procedures

H-reflexes were obtained from six human subjects during level walking on a treadmill at a comfortable speed (0.6–0.8 m/sec). The average cycle time was about 1.4 sec/step. A silver disk stimulus electrode (diameter of active area, 0.7 cm) was placed over the tibial nerve in the popliteal fossa, fastened to the skin with adhesive tape, and secured by a Velcro strap around the leg. The stimulus ground electrode was placed either above the patella or above the popliteal fossa. Care was taken in the

Received July 8, 1985; revised Oct. 10, 1985; accepted Nov. 21, 1985.

This research was supported by a grant from the Medical Research Council of Canada to R. B. Stein. We thank Dr. K. G. Pearson for his helpful comments on the manuscript.

Correspondence should be addressed to R. B. Stein at the above address.

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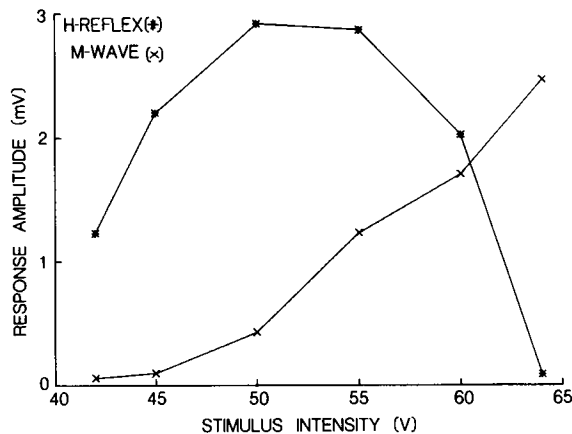


Figure 1. H-reflex and M-wave amplitude recorded from the soleus muscle as a function of the intensity of the stimuli applied to the tibial nerve. Note the range in which the H-reflex amplitude is relatively constant in spite of a large variation of M-wave amplitude.

placement of electrodes to avoid restricting normal movement of the knee joint. Similar surface electrodes were placed over the soleus and tibialis anterior (TA) muscles to record the electromyographic (EMG) activity. The tibial nerve was electrically stimulated in a pseudorandom sequence at a strength that elicited both an M-wave (direct stimulation of α -motoneuron axons) and an H-wave (reflex response to stimulation of Ia muscle afferents). The minimum interstimulus interval was 400 msec and the maximum was 2 sec. Although some H-reflex depression can occur at interstimulus intervals in the lower part of this range (Taborikova and Sax, 1969), these rather short intervals were used to minimize fatigue in the walking subjects during the course of prolonged experiments. Moreover, any potential effects of the interstimulus interval were minimized by randomizing the intervals and by averaging the individual responses (described further below).

The EMG signals of the soleus and TA muscles were amplified, high-pass filtered (10 Hz RC filter), and recorded on FM magnetic tape along with the stimulus marker. The data were later analyzed on a computer. Because of changes in distance between the nerve and the stimulating electrode during walking, the effective stimulus strength (current density) was not constant throughout the walking cycle. However, by repeating the experiment at several stimulus intensities and using the M-wave as a measure of the effective stimulus strength, H-reflexes occurring at various phases of the step cycle could be compared at equal stimulus intensities. Moreover, the data were selected from a range in which the H-reflex was relatively independent of the stimulus strength (Fig. 1); this range was similar during walking and standing. A further problem is that the size of the EMG response to a constant electrical stimulus to the muscle nerve may vary significantly at different muscle lengths (Inman et al., 1952). However, both M- and H-waves are affected in the same way, so maintaining a constant M-wave should largely overcome this problem.

It may be argued that a stronger stimulus is required to produce the same M-wave when the muscle is active. However, the relative refractory period of human nerves is between 4–5 msec, whereas the highest discharge rates of soleus motor units is between 10–15 spikes/sec (i.e., one spike every 60–100 msec). Therefore, only a small fraction of motor units will be refractory at any time and the procedure of matching the amplitudes of M-waves as a measure of stimulus strength is justified. In fact, an essentially maximal M-wave can be obtained even during a maximum voluntary contraction.

In a second series of experiments, subjects were instructed to maintain tonic contractions of the soleus muscle at various levels while standing. To increase the level of the contraction, subjects shifted progressively more of their body weight onto the leg used for experimentation and went onto their toes. During these maintained tonic contractions, electrical stimuli were applied to the tibial nerve in the same pseudorandom sequence as during walking. The whole range of maintainable voluntary activity of the soleus was investigated.

Data analysis

The data were analyzed on a digital computer as follows. The EMG activity of the TA muscle was full-wave rectified, low-pass filtered (20

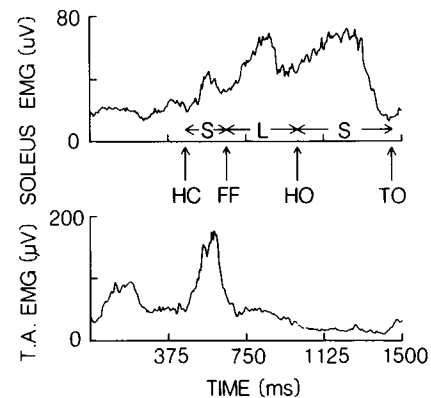


Figure 2. Full-wave rectified, filtered, and averaged ($n = 100$) EMG activity of the soleus and TA muscles of the ankle during walking. The EMG during individual steps was superimposed on a videotaped image of the walking subject, so that the EMG could be correlated with various kinematic features of the step cycle, which are indicated by arrows (further details in text). Abbreviations: heel contact, HC; foot flat on the ground, FF; heel off, HO; toe off, TO; muscle shortening, S; muscle lengthening, L. The background EMG level of 10–20 μ V is mainly attributable to amplifier noise and perhaps some DC offset in the rectifier circuit.

Hz RC filter), Paynter filtered (3 Hz cutoff), and then passed through a Schmitt trigger to generate a pulse that served as a step marker. An EMG signal was preferred as a step marker because fitting shoes with heel contacts or strain gauges could affect the walking. The large and randomly occurring stimulus-evoked EMG in the soleus made this signal unusable as a step marker, so the EMG activity of the antagonist (TA) was therefore used.

The computer used the latency between a step marker and a stimulus marker to determine in which of 16 possible intervals (or phases of the step cycle) the stimulus occurred. A detailed description of the analysis procedure can be found in Akazawa et al. (1982). Responses occurring in the same phase of the step cycle were averaged together. The duration of each average was 76.8 msec from the time of stimulation, which was sufficient to include the M-wave and H-reflex. The amplitude of the H-reflex as a function of the phase in the step cycle (16 phases) was thus obtained. As explained above, H-reflexes occurring at various phases of the step cycle were grouped for comparison by matching the amplitude of the M-wave.

The peak-to-peak amplitude of the H-reflex obtained in each of the 16 phases of the step cycle was plotted against the mean level of EMG activity in each of the phases. These results were compared to those obtained during steadily maintained contractions.

In a few experiments, walking subjects were videotaped. Using a special-effects generator, the full-wave rectified and smoothed EMG activity of the soleus and TA muscles during walking was superimposed in real-time on the videotape of the walking subject. Thus, the EMG activity could be directly compared to changes in ankle angle, and hence changes in soleus muscle length (see Fig. 2).

Results

EMG activity of soleus and TA during walking

The full-wave rectified, RC-filtered, and averaged ($n = 100$) EMG activity of an ankle extensor, soleus, and an ankle flexor, TA, during walking are shown in Figure 2 (see also Fig. 4D). In this experiment, the subject was videotaped during walking, and the various step markers commonly used in human locomotion studies were correlated with the EMG activity of the soleus and TA muscles. The EMG activity of soleus usually began before the heel touched the ground (heel contact = HC), increased during most of the stance phase, and terminated abruptly just before the toes were lifted off the ground (TO). After heel contact, the soleus muscle shortens (S) until the foot is flat on the ground (FF); it then lengthens (L) until the heel comes off the ground (HO); finally, it shortens (S) between HO and TO. The length

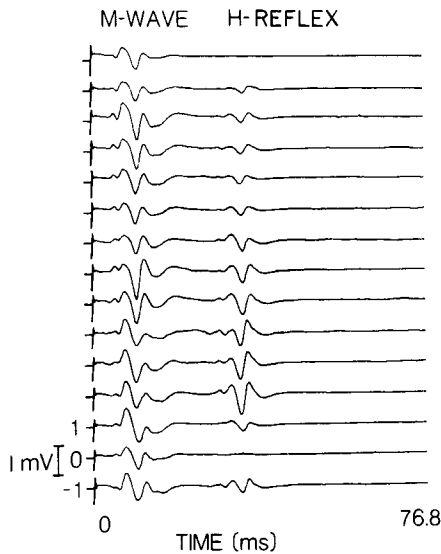


Figure 3. M-wave and H-reflex responses to tibial nerve stimulation at various phases of the step cycle. The topmost trace represents the response of the soleus in the first phase of the step cycle (i.e., the average of 14 responses occurring in the first 94 msec after the step marker, which was set for this subject at about the time of ankle dorsiflexion). Subsequent traces are responses that occurred progressively later in the step cycle. The third trace from the bottom occurs at about the time of TO.

changes of TA during this period are, of course, in the opposite direction.

The TA EMG activity consisted of two prominent bursts. The first burst (Fig. 2) was associated with the ankle dorsiflexion, which occurs late in the swing phase. The second, usually larger burst began at about the same time as HC and continued until about the time the foot was flat on the ground. Since the soleus muscle was also active during this time, HC was followed by considerable cocontraction of these two antagonistic muscles.

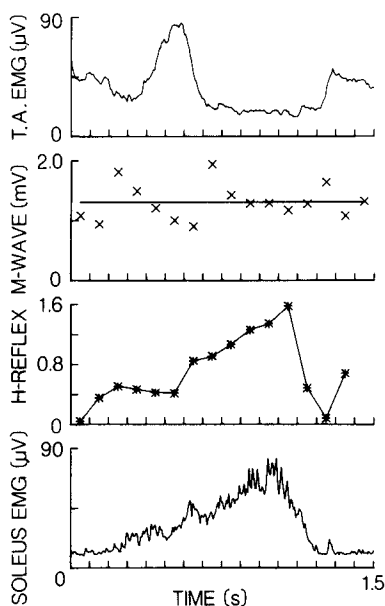


Figure 4. Amplitude of the H-reflex as a function of the phase, or time, in the step cycle. The amplitude of the M-wave (mean = 1.31 mV, SD = 0.31) in the various phases of the step cycle is also shown, as well as the EMG activity of soleus and TA muscles.

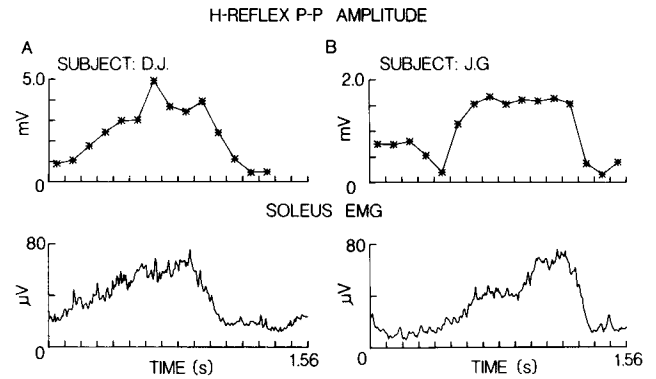


Figure 5. Other examples of H-reflex amplitude as a function of the phase in the step cycle. In each case the corresponding soleus EMG activity is also shown for comparison. Details are given in the text.

Amplitude modulation of the soleus H-reflex during walking

The amplitude of the soleus H-reflex in each of the phases of the step cycle of one subject is shown in Figure 3. The first phase in this example occurs at about the time of HC, and the period of analysis (1.5 sec) occupies approximately one step cycle. Each of the traces in Figure 3 was selected as described under Materials and Methods. The reader should note that despite a relatively constant amplitude of the M-wave (mean = 1.31 mV, SD = 0.31), the H-reflex was strongly modulated throughout the cycle. The H-reflex was small at the time of foot contact but increased rapidly to a maximum value and then decreased very abruptly after TO.

In Figure 4 the peak-to-peak (P-P) amplitude of the H-reflex was plotted against the phase in the step cycle. The P-P amplitude of the M-wave was also plotted against the phase in the step cycle. The average ($n = 70$) rectified and filtered EMG activities of the soleus and TA are also shown in Figure 4. In this example, the amplitude of the soleus H-reflex covaries directly with the EMG activity in this muscle.

In the example shown in Figure 4, the amplitude of the soleus H-reflex is closely related to the EMG activity of the muscle. However, such a close correlation between the EMG activity and the reflex amplitude was observed in only three of the six subjects. In the other three subjects, the soleus H-reflex amplitude was strongly modulated in amplitude, but the variation was not as closely correlated with the EMG activity of the muscle. Two such examples are shown in Figure 5. In Figure 5A the peak reflex amplitude occurs prior to the peak EMG level. Another example is shown in Figure 5B, in which the reflex amplitude is not closely related to the EMG activity, being high throughout the stance phase. In this and other subjects, the peak reflex amplitude attained during walking was not the maximum possible (see following section). Therefore, the broad, relatively flat reflex peak seen in Figure 5B is not due to a saturation phenomenon.

It seems unlikely that the observed pattern of amplitude modulation of the H-reflex during the walking cycle was due to changes in the refractoriness of the Ia-afferent fibers. There are two phases in the walking cycle in which the Ia-afferents discharge at high frequency, and hence where these afferents may show the greatest degree of refractoriness. During the swing phase the soleus is stretched by the ankle dorsiflexion and the Ia-afferents consequently discharge at high frequency (Prochazka et al., 1976). The same afferents also discharge at high frequency during the stance phase when the soleus is stretched between FF and HO as the body rotates over the ankles (Prochazka et al., 1976). However, during stance the H-reflex is relatively high, whereas during swing it is low. The H-reflex is also low in the period between HC and FF, when the soleus is

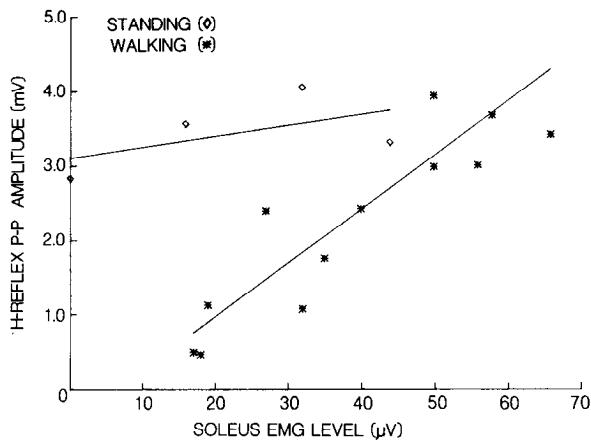


Figure 6. Soleus H-reflex amplitude during walking (*) and standing (\diamond) as a function of EMG level. Note the marked difference in the slopes ($m = 0.075$ walking, $m = 0.015$ standing) and y -intercepts ($b = -0.54$ walking, $b = 3.1$ standing) of the straight lines, which were computed to minimize the mean-square errors.

both actively contracting and shortening, and therefore the discharge rate of the Ia-afferents is relatively low, and so too their degree of refractoriness. Therefore, if changes in the degree of refractoriness were the only factor contributing to the observed amplitude modulation of the H-reflex, the H-reflex should be high during low refractoriness (e.g., between HC and FF) and low during high refractoriness (e.g., between FF and HO), but exactly the opposite was observed. In summary, changes in the degree of refractoriness of the Ia-afferents may influence the magnitude but not the pattern of the observed amplitude modulation of the H-reflex during walking.

Comparing H-reflexes in tonic contractions and walking

The amplitude of the H-reflex, obtained while the subject was standing and steadily maintaining contractions of the soleus muscle at various levels, was compared with that obtained during walking. The subject relied on a chart recorder display of the rectified and smoothed soleus EMG activity to maintain a steady contraction at the required level for a period of about 20–30 sec. The amplitude of the H-reflexes obtained in one subject during steadily maintained contractions is plotted in Figure 6 as a function of the mean level of the soleus EMG activity. The amplitude of the H-reflex obtained in the same subject during walking is also plotted in Fig. 6 as a function of the mean EMG level (i.e., the mean EMG level during the phase in which the reflex occurred). It can be seen that the amplitude of the reflex was larger during maintained contractions (referred to as standing, below) than during walking, and that the difference was greatest during low-level activity. In this example, the slope of the best-fitting straight line, in the least-squares sense, was $0.015 \text{ mV}/\mu\text{V}$ ($\text{SE} = 0.016$) for standing and $0.075 \text{ mV}/\mu\text{V}$ ($\text{SE} = 0.012$) for walking; thus, there was a highly statistically significant difference between the slopes in the two conditions. Of particular interest is the large amplitude of the H-reflex at “zero” EMG level (y -intercept), which will be referred to as “quiet” standing. Thus, the reflex sensitivity (i.e., the slope of the line relating H-reflex amplitude to EMG level) and the reflex threshold (x -intercept) were lower during standing than during walking. Both effects (i.e., decrease in sensitivity and threshold) were observed in the four subjects tested.

In the example of Figure 6, the mean value of the M-wave was 1.25 mV ($\text{SD} = 0.16$) during walking and 1.23 mV ($\text{SD} = 0.09$) during the isometric contractions. Therefore, the difference in the amplitude of the H-reflex between the two conditions was not due to the stimulus strength. Moreover, the data were

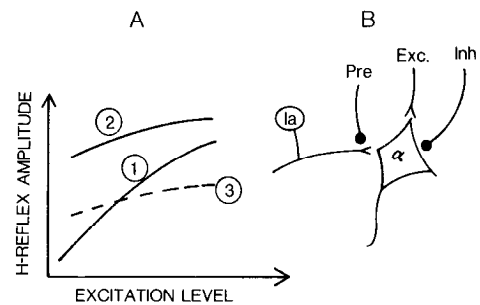


Figure 7. A, Expected relation between the H-reflex amplitude and the level of α -motoneuron excitation for different combinations of excitatory, inhibitory, and presynaptic inputs to the motoneurons (B). Further explanation in Discussion.

taken from a range in which the H-reflex was relatively independent of the stimulus strength (see Materials and Methods).

A potential problem in comparing EMG levels during walking and standing is that the EMG activity recorded by the soleus electrodes may include a component (due to cross-talk) from the other ankle extensors, medial and lateral gastrocnemius. For example, if, as in the cat (Walmsley et al., 1978), the human soleus is predominantly, if not exclusively, active during standing and the gastrocnemius becomes more active during walking, then the H-reflexes recorded during walking would thus appear smaller than those recorded during standing because the activity level of the soleus is in fact less than that indicated by the recording electrodes. However, the recording electrodes were placed over the soleus muscle just above the insertion of the gastrocnemius into the Achilles tendon, a site where soleus EMG activity can be selectively recorded (Hugon, 1973). Second, the largest difference between the H-reflexes elicited during walking and standing occurs at the lowest levels of activity, where a fast-twitch muscle like the gastrocnemius is least active, and therefore the effects of cross-talk, if any, are least significant.

Discussion

The major new findings reported here are the strong modulation of the H-reflex during locomotion in normal human subjects and the difference between the modulation of this reflex during walking and standing. Clearly, the modulation of the reflex is not simply a passive consequence of the excitation level of α -motoneurons, but depends on central mechanisms, of which the level of α -motoneuron excitation is only one component. The change in the slope and x -intercept of the curve in the two states is also important, because it means that the sensitivity of the reflex as well as its threshold can be changed. Some authors have suggested that only the reflex threshold could be changed by central commands (Crago et al., 1976; Feldman and Orlovsky, 1972; Houk, 1976). Possible neural mechanisms underlying these reflex changes and their functional implications for the two types of motor activities studied will be dealt with, in turn, in the following sections.

Neural mechanisms

The neural mechanisms by which the modulation of the H-reflex is brought about during walking and standing are difficult to determine in human experiments, but some suggestions are illustrated in the schematic diagram of Figure 7. The H-reflex increases more or less in parallel with the level of EMG activity (curve 1, Fig. 7A). If the same mechanisms are used as in the cat, α -motoneurons are depolarized by a combination of added excitation (Exc. in Fig. 7B) and decreased postsynaptic inhibition (Inh.), such that the resistance of the cell body is little affected (Shefchyk et al., 1984). The EPSP from primary muscle spindle receptors (group Ia fibers) is then relatively constant at all phases of the cycle (Shefchyk et al., 1984), and the size of

the H-reflex will therefore reflect the percentage of voluntarily activated α -motoneurons.

The much larger H-reflex in quiet standing could arise if weak excitatory inputs are active and inhibitory inputs are inactive, or greatly decreased compared to the levels during walking. Therefore, the size of the EPSP would be large during quiet standing because less shunting would be produced by inhibitory inputs. However, the EPSP would decrease in size with increasing excitation, because of the additional conductance produced by more excitatory inputs (i.e., decreased resistance). Therefore, as the number of active motoneurons increases with increasing excitation, the H-reflex would increase more slowly during standing (curve 2, Fig. 7A) than during walking (curve 1, Fig. 7A).

Morin et al. (1982) suggested that the differences between the two states might arise from presynaptic inhibition (Pre. in Fig. 7B). This mechanism would reduce the Ia EPSP by a constant factor at all levels of excitation, without affecting postsynaptic conductance, and therefore produce a proportional reduction in the H-reflex (compare the dashed curve 3 in Fig. 7A with the solid curve 2). Clearly, if walking and standing are compared at only one level of excitation, presynaptic inhibition can appear to be an explanation for the results. Morin et al. (1982) used only one level of excitation and so did not anticipate the change in slope. One could, of course, postulate that the level of presynaptic inhibition is also tied to the level of EMG in just the right way to produce the observed change in shape between curves 1 and 2, but the postsynaptic mechanisms suggested above are far simpler to envisage. These suggestions should also be directly testable by intracellular recording from α -motoneurons in paralyzed decerebrate cats during fictive walking and tonic states with comparable levels of α -motoneuron excitation. Once data are obtained from these experiments, a mathematical model of how motoneurons are controlled in various types of motor activities may be formulated.

Another possible explanation for the difference between the amplitude of the H-reflex during walking and standing is that EPSPs during walking are smaller than during standing because the high-frequency discharge of the Ia-afferents during walking results in a depression of transmitter release and hence smaller EPSPs (Curtis and Eccles, 1960). However, if the depression lasted throughout the step cycle, it would be functionally equivalent to presynaptic inhibition, which cannot explain our results (see above). If the depression occurred only when the afferents were firing fastest, it would have an effect analogous to that of refractoriness, which was also ruled out as an explanation of the results (see Results). In conclusion, while changes in the amplitude of the EPSPs due to this well-known depression phenomenon may have occurred, postsynaptic factors such as those described above must also be considered.

Functional implications

The large difference in the y -intercepts (Fig. 6) of the H-reflex versus EMG curves between walking and standing is functionally important. During standing, most of the body weight is supported by the skeleton, so the activity of the leg and other muscles during quiet standing is minimal (Basmajian, 1967). The large value of the H-reflex during quiet standing implies that even a small body sway will result in a relatively large stretch reflex in the soleus, which will tend to counteract the sway. Thus, the large reflexes when the subjects were standing are consistent with the control of ankle angle and hence body position in this task. However, a comparably large stretch reflex during the swing phase of walking, where the EMG activity of the soleus is also minimal, would impede ankle dorsiflexion and would therefore be inappropriate. As discussed in the introduction, the stretch reflex of a muscle will be much more influenced by fusimotor effects than will the H-reflex and, possibly

because of the temporal dispersion of the afferent volley (Burke, 1983), also by the state of certain spinal interneurons (e.g., Ib interneurons and Renshaw cells). However, at least in the mesencephalic walking cat, peripheral fusimotor effects add to and reinforce the modulation produced centrally (Murphy et al., 1984; Taylor et al., 1985), and both the stretch reflex and the H-reflex are modulated in essentially the same way (Akazawa et al., 1983).

Foot contact with the ground (HC) occurred during cocontraction of the ankle flexors and extensors, at a time when the amplitude of the H-reflex was relatively low. Therefore, the reflex was not adjusted to help overcome the loading of the foot at the time of HC. Indeed, it has been suggested that the stretch reflex would occur too late to contribute force to counteract the increased loading at the time of foot contact (Grillner, 1972; Melvill Jones and Watt, 1971; but see Stuart et al., 1973). The sudden impact and loading of the foot at the time of HC is compensated by a stiffening of the ankle resulting from a cocontraction of the ankle flexors and extensors that may be preprogrammed (Engberg and Lundberg, 1969).

The H-reflex increased rapidly to a maximum value during stance and then abruptly decreased to a low value after TO. The highest values of the stretch reflex during walking are therefore timed to resist the stretch of the ankle extensors while the foot is flat on the ground and the body rotates over this fixed support and to assist the "push-off" phase (i.e., the ankle extension late in the stance phase). This extends the finding of Dietz and his collaborators, who showed that the stretch reflex of the triceps surae contributes significantly to the tension required for the push-off phase of running (Dietz et al., 1979). Thus, the stretch reflex amplitude appears to be appropriately adjusted in each phase of the step cycle to the requirements of locomotion.

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