Stretch and H Reflexes in Triceps Surae Are Similar During Tonic and Rhythmic Contractions in High Decerebrate Cats

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Misiaszek, J. E., S. J. De Serres, R. B. Stein, W. Jiang, and K. G. Pearson. Stretch and H reflexes in triceps surae are similar during tonic and rhythmic contractions in high decerebrate cats. J. Neurophysiol. 83: 1941–1950, 2000. During locomotion in decerebrate and spinal cats the group Ia afferents from hind leg muscles are depolarized rhythmically. An earlier study concluded that this locomotor-related primary afferent depolarization (PAD) does not contribute to modulation of monosynaptic reflex pathways during locomotion. This finding indicated that the neural network generating the locomotor rhythm, the central pattern generator (CPG), does not presynaptically inhibit monosynaptic reflexes. In this investigation we tested this prediction in decerebrate cats by measuring the magnitude of reflexes evoked in ankle extensor muscles during periods of tonic contractions and during sequences of rhythmic contractions. The latter occurred when the animal was induced to walk on a treadmill. At the similar levels of activity in the soleus muscle there was no significant difference in the magnitude of the soleus H reflex in these two behavioral situations. Similar results were obtained for reflexes evoked by brief stretches of the soleus muscle. We also examined the reflexes evoked by ramp-and-hold stretches during periods of rhythmic and tonic activity of the isolated medial gastrocnemius (MG) muscle. At similar levels of background activity, the reflexes evoked in the MG muscle were the same during rhythmic and tonic contractions. Our failure to observe a reduction in the magnitude of H reflexes and stretch reflexes during rhythmic contractions, compared with reflexes evoked at the same level of background activity during tonic contractions, is consistent with the notion that the CPG for stepping does not presynaptically inhibit monosynaptic reflexes during the extension phase of locomotor activity. Our results indicate that presynaptic inhibition of the monosynaptic reflex associated with normal locomotion in cats or humans arises from sources other than the extensor burst generating system of the central pattern generator.

INTRODUCTION

Spinal segmental reflexes can be modulated in a task- and phase-dependent manner (Rossignol 1996). A good example of phase-dependent modulation is the variation of the H reflex in the soleus muscle during walking in humans (Capaday and Stein 1986, 1987; Crenna and Frigo 1987; Edamura et al. 1991; Simonsen and Dyhre-Poulsen 1999; Simonsen et al. 1995) and cats (Akazawa et al. 1982; Duenas et al. 1990; Misiaszek and Pearson 1997). In general, the soleus H reflex is large during stance and small or absent during swing. Much of the modulation during walking can be attributed to variation in the locomotor drive potentials that produce the normal ebb and flow of excitability in the motoneurons (Shefchyk et al. 1984). However, the amplitude of the H reflex does not always parallel the background excitability of the motoneuronal pool as judged by the magnitude of the ongoing electromyographic (EMG) activity (Capaday and Stein 1987; Edamura et al. 1991; Simonsen et al. 1995). This observation has led to the conclusion that presynaptic inhibition contributes significantly to the modulation of the H reflex during walking (Stein and Capaday 1988).

Presynaptic inhibition also regulates the soleus H reflex in a task-dependent manner. For instance, Capaday and Stein (1986) reported that the magnitude of the human soleus H reflex was decreased during walking compared with standing at similar levels of EMG activity in the soleus muscle. The origin of the increase in presynaptic inhibition of group Ia afferents during walking has not yet been firmly established. One possibility is that it arises from descending command signals involved in initiating walking. A preliminary study in decerebrate cats reported tonic inhibition of group Ia afferents during fictive locomotion evoked by stimulation of the mesencephalic locomotor region (Gosgnach et al. 1998). Another possibility is that the group Ia afferents are presynaptically inhibited by signals arising from the spinal interneuronal network generating the locomotor rhythm, that is from the central pattern generator (CPG). The terminals of group Ia afferents from ankle extensors are depolarized phasically during fictive locomotion in spinal cats (Gossard et al. 1991) but, as yet, these centrally generated depolarizations have not been linked to a reduction in the strength of synaptic transmission from Ia afferents to motoneurons (Gossard 1996). Finally, phasic sensory feedback from peripheral receptors in the stepping legs may contribute to presynaptic inhibition of the soleus H reflex during walking. A number of studies in humans, cats, and dogs have demonstrated a reduction in H reflexes in response to either imposed leg movements or stretch of extensor muscles (Misiaszek and Pearson 1997; see review by Brooke et al. 1997).

This investigation focuses on the issue of whether the CPG for stepping presynaptically inhibits the proprioeceptive reflexes in ankle extensor muscles during the extension phase of locomotor activity. We used the method introduced by Capaday and Stein (1987) for assessing presynaptic inhibition of monosynaptic reflexes during different tasks. This method involves the comparison of reflex responses evoked during rhythmic contractions with those during tonic contractions at similar levels of background activity (see also Capaday and Stein 1989 for a theoretical analysis of this method). We predicted that if the CPG does presynaptically inhibit monosynaptic reflexes in the ankle extensor muscles then the soleus H reflex would be...
smaller during rhythmic contractions associated with walking than during tonic contractions between periods of walking. The only other study to directly address this issue concluded that the stepping CPG does not presynaptically inhibit monosynaptic transmission from group Ia afferents to motoneurons (Gossard 1996). Simultaneous recordings from the terminals of group Ia afferents and identified motoneurons failed to show that CPG-related primary afferent depolarization (PAD) reduced the magnitude of the monosynaptic EPSPs. However, only a small number of pairs were recorded for ankle extensor muscles (n = 2) and it is conceivable that the absence of an inhibitory effect in these cases does not reflect the properties of the larger population of afferents and motoneurons.

We examined the magnitudes of reflexes evoked by brief stretches and by ramp-and-hold stretches in the two behavioral situations. The initial rationale for studying stretch reflexes was to determine whether more naturally evoked reflex responses that depend on transmission in the monosynaptic group Ia to motoneuron pathway might also differ during rhythmic and tonic contractions of the ankle extensor muscles. Sinkjaer et al. (1996) reported that the amplitude of the soleus stretch reflex is not reduced during walking, compared with standing with matched background activity, in humans. This was contrary to the previously reported reduction in soleus H reflex amplitude during walking, compared with standing (Capaday and Stein 1986), suggesting the H reflex is not always an accurate reflection of the state of the stretch reflex pathway. It was also hoped that a comparison of H reflex responses and stretch reflex responses would provide information on differences in the fusimotor regulation of muscle spindles during tonic and rhythmic contractions in addition to information on presynaptic inhibition of stretch reflex pathways.

Preliminary accounts of portions of this work have appeared in abstracts (De Serres et al. 1996; Pearson et al. 1998).

METHODS

General preparation

A total of 13 adult cats (2.2–3.8 kg) were used in these experiments. Approval for the procedures was granted by the University of Alberta Health Sciences Laboratory Animal Welfare Committee.

The cats were anesthetized with halothane, which was delivered with 95% O2-5% CO2. Continued administration of the anesthetic was achieved through a tracheal cannula. Both carotid arteries were ligated and one artery was also cannulated proximally to monitor blood pressure. A jugular vein was cannulated to allow the administration of fluids and drugs. During the dissection the body temperature of the animal was maintained with the use of a heating pad. After this initial procedure, the right hind leg was prepared to allow measurements of H reflexes and/or stretch reflexes in the triceps surae muscles (see Preparation of the right hind leg).

The animal was placed above a treadmill and the head secured in a stereotaxic holder. The right hind leg was immobilized via clamps attached to the knee and paw and a steel flange fixed between the iliac crests. The hip, knee, and ankle joints were set at 90°. A temperature probe was placed close to the ankle extensor muscles and radiant heat was used to maintain a temperature of 37°C. The animal was decerebrated by transecting the brainstem at a 50° angle rostral to the superior colliculi. The anesthetic was discontinued after decerebration and a bolus (2–5 ml) of 5% dextrose solution, plasma volume expander (Dextran) was administered if the blood pressure fell below 60 mmHg. In most animals (10 of 13) spontaneous bouts of locomotion occurred within 1 h of the decerebration and locomotor activity lasted up to 3 h. Stepping of the three free limbs was accompanied by in-phase rhythmic contraction of the triceps surae muscle of the fixed limb. In the three animals which locomotor activity was not elicited after decerebration, the spinal cord was transected at T12 and locomotor activity of the hind legs was elicited by the intravenous administration of clomidone (100–500 μg/kg) and stimulation of the perineum. In all preparations, periods of spontaneous tonic activity were observed before or after the bouts of locomotion.

Preparation of the right hind leg

In all animals the following nerves were transected in the right hind leg: femoral, obturator, sartorius, hamstrings, lateral gastrocnemius, distal tibial, and common peroneal. In nine animals the nerves to medial and lateral gastrocnemius muscles were also transected leaving only the soleus and proximal hip muscle innervated. These animals were used to measure H reflexes and stretch reflexes in the soleus muscle. In five other animals the nerve to lateral gastrocnemius and soleus muscles were cut leaving only the medial gastrocnemius (MG) and proximal hip muscles innervated. These animals were used to measure stretch reflexes in the MG muscle. The triceps surae muscles were attached to a muscle puller via the detached distal bone fragment of the calcaneum. The length of the triceps surae was set to the muscle length achieved when the knee and ankle were fixed at 90°.

To evoke H reflexes in the soleus muscle, a bipolar cuff electrode was placed around the tibial nerve at the popliteal fossa. We chose to stimulate the tibial nerve rather than the dissected nerves to the triceps surae to minimize potential damage to the nerves. A similar cuff electrode was placed around the sciatic nerve to record the afferent volley produced by the stimulus. The stimulus was a 0.2-ms square-wave pulse (Grass S88 stimulator) at an intensity ranging from 1.2 to 1.5 times threshold for the afferent volley. The stimulus intensity was always below the threshold for the M wave. At this stimulus strength the H reflex was below maximum (see Misiaszek and Pearson 1997).

Stimulus threshold was checked throughout an experiment to ensure stability of the stimulus strength. The sciatic volley was analyzed post hoc to assure consistency of the applied stimulus. Stimuli were delivered to the tibial nerve at a constant rate (1.5–2 Hz) during periods of tonic contraction and rhythmic locomotor activity.

Stretch reflexes were evoked in either the SOL or MG muscles (depending on the initial dissection, see above) by either briefly stretching the muscle (0.3 mm amplitude, <10 ms total duration) or applying a ramp-and-hold stretch (50 ms rise time, 200 ms plateau, 3 mm amplitude). The brief stretches were delivered at a rate of 0.7 Hz and the ramp-and-hold stretches were initiated 150 ms after the beginning of extensor bursts during locomotor activity and at a rate of ~0.5 Hz during tonic activity.

A pair of Teflon-coated, stainless steel wires (Cooner Wire, AS632, bared at the ends) were implanted into the belly of the muscle to record EMG activity from SOL or MG. Routinely, EMGs were recorded from the ipsilateral iliopsoas and contralateral MG muscles to monitor the quality of locomotor activity.

Data acquisition and analysis

The EMGs and sciatic electroneurogram (ENG) were amplified and filtered (30–10,000 Hz band-pass, Grass P511) before storage to a magnetic tape (VHS, Vetter 4000A PCM recording unit). The length output from the muscle puller and a stimulus marker were also stored. The data were later digitized offline using an Axotape data acquisition system (Axon Instruments) and stored to disk. The H reflex data were digitized at a sampling rate of 3kHz. Stretch reflex data were digitized at 500 Hz. The sciatic ENG was sampled at 10 kHz. At this time, the raw EMG signal and a rectified and filtered version were stored.

The peak-to-peak amplitude of the H reflex was measured from the raw EMG signal along with the background EMG activity which was averaged from the rectified EMG for 30 ms before stimulus onset (Fig. 1A). From the data obtained during the phasic contractions, only...
The amplitude of the tonic stretch reflex evoked by a ramp-and-hold stretch was measured as the increase in the average rectified EMG for a 100-ms period beginning 100 ms after the onset of the stretch, which is 50 ms into the plateau period. This averaging period was chosen to exclude the phasic component of the stretch reflex. The reflex response during maintained contractions was determined by subtracting the background activity (averaged over a period of 100 ms immediately preceding the stretch) from the total EMG averaged over the 100 ms period during the plateau phase of the stretch (see Fig. 1C, top). The reflex response during rhythmic contractions was determined by subtracting the average activity of the EMG bursts without stretches (Fig. 1C, bottom). A minimum of 10 trials was used to obtain the average burst used for subtraction. We attribute the reflexes evoked during the plateau phase of the stretch as arising from group I afferents because no excitatory influences from triceps group II afferents on extensor burst generation has been observed (Guertin et al. 1995; Whelan et al. 1995).

**RESULTS**

*H reflexes are similar during tonic and rhythmic contractions of soleus muscle*

Five animals provided data for the comparison of H reflex amplitudes in the soleus muscle during tonic and rhythmic contractions of the muscle in decerebrate animals. Figure 2A shows typical raw data collected during rhythmic and tonic contractions of the soleus muscle in one of these animals. It is apparent that the amplitude of the H reflex is quite variable and during rhythmic contractions it was only elicited during the bursts of activity in the soleus muscle. This is shown more clearly in the plots in Fig. 2B. The H reflex amplitude is plotted in the upper panel and the associated background EMG activity is shown in the lower panel of this figure. These data are similar to those previously described by Akazawa et al. (1982). Because we were primarily interested in comparing H reflex amplitudes at different levels of background EMG, data obtained during the silent periods in the SOL EMG were not included in our quantitative analysis.

Figure 3A shows a plot of the amplitude of individual H reflexes sampled from a single decerebrate animal during tonic activity (♦) and rhythmic activity (○). In this animal it is apparent that the magnitude of the H reflex increased with increasing background EMG levels at low levels of EMG activity. The data points for the tonic and rhythmic contractions are quite scattered yet the two data sets overlap exten-
sively indicating that there is no difference in the H reflexes elicited during tonic and rhythmic contractions. Data similar to those shown in Fig. 3A were obtained in two other decerebrate animals. In the remaining two decerebrate animals, however, there was only a very weak dependency of H reflex amplitude on background EMG. Even so, there was also extensive overlap of the data sets for the tonic and rhythmic contractions.

To more objectively assess a potential difference in reflex amplitude elicited during the two contraction types, individual samples from the animals in which the H reflex increased with increasing background EMG were submitted to an ANOVA. This initial quantitative analysis was restricted to these animals because Capaday and Stein (1986, 1987) demonstrated in humans that H reflexes are most sensitive to task-dependent influences at low levels of background EMG. The H reflexes sampled during low levels of background EMG activity were binned before being submitted for analysis (see METHODS). The results of this analysis are summarized in Fig. 3B. The histograms in Fig. 3B display the group average H reflex amplitudes for the rhythmic (open) and tonic (filled) contractions for each bin level of background EMG. The mean H reflex amplitude during rhythmic contractions was slightly larger than the mean H reflex amplitude during tonic contractions for each of the bins. However, the ANOVA did not detect a main effect due to contraction type ($F_{1,10} = 0.3, P > 0.05$). In addition, no significant differences in reflex amplitude could be detected between tonic and rhythmic contractions compared within individual animals (Student’s t-test, $P > 0.05$).

A similar ANOVA was carried out to compare the amplitudes of the H reflexes in the two animals in which the H reflexes were relatively independent of background EMG, along with the data with a background EMG $>40\%$ max for the three animals in the previous analysis. On average, the amplitude of the H reflex was slightly larger during rhythmic contractions ($56.8 \pm 16.7$ (SD) % max], compared with tonic contractions ($30.3 \pm 16.7$ % max). This slight increase during rhythmic contractions was significant as detected by the ANOVA ($F_{1,4} = 17.26, P < 0.001$). Four of the five animals showed a modest increase in H reflex amplitude during rhythmic contractions. The fifth animal showed a slight decrease in amplitude during rhythmic contractions. None of the differences in individual animals were significant (Student’s t-tests, $P > 0.05$).

In the three additional animals that failed to step after decerebration, we compared the SOL H reflexes during tonic contractions in the decerebrate state with those evoked during rhythmic contractions in the same animal after spinalization and the admin-
administration of clonidine. Figure 4A shows individual data points sampled during both contraction types from one animal. It is clear that H reflex amplitude is related to background EMG during both types of contraction and that there is no obvious difference in the amplitude of the H reflexes evoked during tonic and rhythmic contractions. However, binning and averaging the data from all three animals showed that the amplitude of the H reflex was larger during rhythmic contractions in the spinal animal than during tonic contractions in the decerebrate animal (Fig. 4B). An ANOVA indicated that this increase in H reflex amplitude during rhythmic activity was significant ($F_{1,10} = 17.07$, $P < 0.005$). Moreover, Student’s t-tests performed on the data for individual animals showed that all three animals had significantly ($P < 0.05$) larger amplitude H reflexes during rhythmic contractions than during tonic.

**Stretch reflexes are similar during rhythmic and tonic contractions**

As with the H reflex, the amplitude of the stretch reflex evoked by a brief stretch of the soleus muscle was modulated over a cycle of locomotor activity (Fig. 5). The amplitude of this reflex tends to be large during periods of SOL activity and mostly absent during periods of SOL inactivity. As with the previous analysis of the H reflex data, only reflexes elicited during periods of SOL activity were considered in the comparison with reflexes elicited during tonic periods of activity.

Figure 6 shows scatter plots of the amplitude of the reflex evoked by a brief stretch of SOL versus background EMG for four animals. In all four animals there was considerable scatter of the data but all showed that the magnitude of the reflex decreased with increasing background EMG. This relationship was similar for reflexes sampled both during tonic and rhythmic contractions of SOL. A least-squares linear regression analysis did not reveal any obvious difference in the relationship between reflex amplitude and background EMG during both types of contractions for any of the animals. We did not pursue further statistical analysis of the data because the samples obtained during the rhythmic contractions either tended to be too few to allow for binning (cats A and D in Fig. 6) or were biased to high background EMG levels (cats B and C in Fig. 6).

Unlike the reflexes evoked by stimulation of the tibial nerve
and by brief stretches of SOL, the reflex evoked by a ramp-and-hold stretch of either MG or SOL was elicited at only one point in the step cycle beginning 100 ms after the onset of muscle contraction. Consequently, there was usually not a large range of background EMG levels for the ramp-and-hold reflexes sampled during rhythmic contractions. Nevertheless over this limited range of background EMG, the amplitude of the reflex was similar during tonic and rhythmic contractions (Fig. 7). Figure 7A shows a short sequence of rhythmic activity in a decerebrate animal when reflexes were evoked by ramp-and-hold stretches of MG every second cycle, along with a short sequence of tonic activity. The data relating reflex magnitude to background EMG for this animal during rhythmic contractions are plotted in Fig. 7B together with data obtained during tonic contractions of MG. There was no obvious difference in reflex amplitude between the tonic and rhythmic contraction paradigms for this animal and three other animals. In the one remaining animal the reflexes evoked during rhythmic contractions were ~20% larger than those evoked during tonic contractions ($t = 2.55, P = 0.012$). Overall, an analysis of the group average data did not show a significant difference in reflex amplitude during tonic and rhythmic contractions ($F_{1,3} = 0.47, P = 0.54$). The mean amplitudes of the reflexes evoked by ramp-and-hold stretches during tonic and rhythmic contractions are summarized in Fig. 7C. The slightly larger reflex amplitude during the rhythmic contractions shown in Fig. 7C is the result of the data from the one animal that showed a significant increase in reflex magnitude during rhythmic contractions.

In one animal we also recorded the reflexes evoked by ramp-and-hold of SOL. Again no significant difference was found in the reflex during tonic and rhythmic contractions ($t = 0.028, P = 0.98$).

**DISCUSSION**

The main finding of this investigation was that the magnitude of H reflexes and stretch reflexes in the ankle extensor muscles of decerebrate cats were the same during tonic and rhythmic contractions, the latter being associated with walking. The fact that these reflexes were similar at the same level of background activity in the two behavioral states indicates that transmission in the monosynaptic pathways from group Ia afferents to ankle extensor motoneurons was not presynaptically inhibited by the system generating the extension phase of locomotor activity (see Capaday and Stein 1986, 1987 for explanation of method). In other words, the spinal central pattern generator (CPG), when active, did not presynaptically influence transmission in the monosynaptic pathways during extensor activity. This conclusion is consistent with an earlier finding by Gossard (1996) that locomotor-related primary afferent depolarization in group Ia afferents does not suppress
monosynaptic excitatory postsynaptic potentials in motoneurons innervating ankle muscles.

Our conclusion that the CPG does not suppress reflex transmission from group Ia afferents during the extension phase is based largely on the absence of any reduction in the H reflex in the soleus muscle during walking (Figs. 3 and 4). It is important to consider the reliability of H reflex measurements for assessing the level of presynaptic inhibition in group Ia afferents. Our assumption is that a reduction in H reflex amplitude will be seen if the Ia afferents that lead to the reflex activation of the motoneurons are presynaptically inhibited. One possibility is that with the relatively high levels of background EMG activity in SOL, and consequently relatively high levels of motoneuron excitability, reductions in the amplitude of the excitatory postsynaptic potentials might not be sufficient to alter the probability of generating action potentials in the motoneurons. In a previous study we showed that the modulation of the SOL H reflex that is produced with sinusoidal stretch of quadriceps can be blocked if the background activation of SOL is high and the stimulus intensity to evoke the H reflex is also high (see Fig. 5 in Misiaszek and Pearson 1997). However, if the stimulus intensity used to elicit the H reflex was below threshold for the M wave, modulation of the H reflex occurred even at the highest levels of background activity. Using lower stimulus intensities, we were able to demonstrate that the soleus H reflex is suppressed during stance phase if the quadriceps muscles are stretched, indicating that presynaptic inhibition of the afferent volley is detectable with this method. Consequently, in this study we used stimulus strengths below threshold for the M wave. In addition, in our quantitative analysis we focused on reflexes evoked at low levels of background activity in preparations in which there was a positive relationship between H reflex amplitude and background EMG (Figs. 3 and 4). Under these conditions the H-reflex was clearly not saturated. Another indication that the afferent volley was not large enough to mask any presynaptic inhibition was the fact that the response brief stretches were not reduced during rhythmic contractions compared with tonic contractions. It is unlikely that the brief stretches were sufficient to maximally activate the Ia afferents. Thus these reflexes would be more susceptible to the influence of presynaptic inhibition but none of our data indicated that presynaptic inhibition generated by the CPG affected the amplitude of these reflexes.

Comparison of H reflexes and reflexes evoked by brief muscle stretches

Both the H reflex and the reflex evoked by brief stretches of SOL are mediated largely via the monosynaptic pathway from
group Ia afferents to the homonymous motoneuron pool. It is not surprising therefore that the magnitude of these two reflexes was modulated in a qualitatively similar manner during rhythmic contractions of the muscle (Figs. 2 and 5). A more interesting issue is the basis for the difference in the relationship between reflex amplitude and background EMG. The H reflex tends to increase in amplitude with increasing background EMG both for tonic and rhythmic contractions (Fig. 3) whereas the reflexes elicited by brief stretches decrease with increasing background EMG (Fig. 6). One factor that might underlie this difference is the pattern of activation of the motoneurons in response to the synchronous activation of the Ia afferents (H reflex) and to the asynchronous activation of the Ia afferents (brief stretches). This difference has been proposed to be the basis for the differences in the characteristics of H reflexes and stretch reflexes in humans (Morita et al. 1998; Sinkjaer et al. 1996). However, we believe this is unlikely to be an important factor in our experiments on the cat. Although the afferent volleys with brief stretch would undoubtedly be less synchronous than the volleys evoked by tibial nerve stimulation, the dispersal of action potentials in each volley must have been fairly low because a clear reflex was evoked at a latency only slightly greater than the H reflex (Fig. 1). A far more likely reason for the different characteristics of the H reflex and the reflex produced by brief stretches is a difference in the magnitude of the afferent volley. With tibial nerve stimulation the afferent volleys remained constant at all levels of background EMG, whereas the volleys elicited by brief muscle stretches were probably influenced by the level of muscle contraction. With high levels of contraction of the extrafusal muscle fibers the muscle spindles could have been unloaded, thus reducing the effectiveness of the mechanical stimulus to activate the group Ia afferents. This explanation would be consistent with our finding of a decline in the reflexes evoked by brief stretches with increasing background EMG (Fig. 6) and the large reflexes evoked near the beginning of the extensor bursts. A third factor that could be involved in reducing the magnitude of the stretch reflex with increase background EMG is a modification of the fusimotor input to the spindles. It is well known that an increase in static fusimotor input reduces the dynamic sensitivity of primary spindle endings (Hunt 1990). However, this reduction occurs primarily for phasic responses produced by relatively slow stretches and not to brief stretches. Thus we believe that alterations in fusimotor drive is an unlikely explanation for the decline in stretch reflex amplitude with increasing background EMG.

**Comparison with other studies in walking cats**

Two previous studies have examined stretch reflexes in ankle extensor muscles during tonic and rhythmic contractions in decerebrate cats (Akazawa et al. 1982; Bennett et al. 1996b). Both reported a qualitative difference in characteristics in stretch reflexes from the soleus muscle for the two contractile states. Akazawa et al. (1982) found that the reflex contractions evoked by a brief stretch increased with increasing background
force during rhythmic contractions but decreased with increasing background force for tonic contractions. Our data are consistent with the latter observation (Fig. 6) but not with the former. We are unable to explain adequately this discrepancy but one factor is that the positive relationship reported by Akazawa et al. for rhythmic contractions depends to a large extent on the inclusion of reflexes evoked during the flexion phase (zero background force). In our experiments we only examined reflexes evoked during the extension phase. In the study by Bennett et al. (1996b) the gain of the stretch reflexes evoked by 5-Hz sinusoidal stretches of the soleus muscle was measured during tonic contractions in a decerebrate cat and during rhythmic contractions after spinalization and the administration of clonidine intravenously. The finding relevant to the present investigation was that at low background forces the gain of the stretch reflex was smaller during rhythmic contractions. Our result of an absence of any difference in H reflexes and stretch reflexes over a wide range of background EMGs appears at odds with this finding. This difference in the two studies might arise from a number of factors. First, it could be a result of the use of different preparations for measuring stretch reflexes during rhythmic and tonic contractions. In an earlier study Bennett et al. (1996a) reported that clonidine decreased or even eliminated resting fusimotor drive to many muscle spindles, at least in the resting state. Thus it is likely that the sensitivity of the muscle spindles to the sinusoidal stretches used by Bennett et al. was lower during the rhythmic contractions in the spinal cats than it was during tonic contractions in the decerebrate cats, explaining the lower stretch reflex gain during rhythmic contractions. Because we failed to observe any reduction in H reflexes during rhythmic contractions using the same two preparations (Fig. 4) it seems unlikely that the reduced gain during rhythmic contractions reported by Bennett et al. was caused by modification of transmission in the spinal cord. Another possible reason for the apparent difference between our results and those of Bennett et al. was the method of analysis. Bennett et al. binned and averaged the individual reflex responses and, for rhythmic contractions, included data from the flexor phase of the locomotor cycle in the bins representing low background forces. Inclusion of data from the flexion phase occurred because small background forces persisted for some time after the termination of extensor activity. The effect of this additional data in the averages would reduce the magnitude of the averaged reflex response because reflexes are either not evoked or very small during the flexion phase. Thus we conclude that the difference between our results with those of Bennett et al. is likely a result of a combination of a different method of analysis and the use of different preparations for the comparison of reflexes during tonic and rhythmic contractions.

One of the implications of our data are that locomotor-related PAD in group Ia afferents does not result in presynaptic inhibition of reflex transmission during the extension phase of walking in decerebrate cats. This finding is consistent with the direct observation that locomotor-related PAD does not reduce monosynaptic EPSPs during spontaneous fictive locomotion (Gossard 1996). However, in another study on decerebrate cats, Duenas and Rudomin (1988) concluded that group Ia afferents receive tonic PAD during locomotion in addition to the locomotor-related PAD. This conclusion is supported by a recent study by Gosgnach et al. (1998) who reported a tonic inhibition of the monosynaptic reflex in ankle extensor motoneurons that during fictive locomotion evoked electrical stimulation of the mesencephalic locomotor region. An unresolved issue is whether the tonic inhibition of the monosynaptic reflex reported in these two studies is a result of the activation of the CPG per se or whether it is caused by activating descending pathways by the electrical stimulation of the mesencephalic locomotor region. Our results, and those of Gossard (1996), would suggest that the latter is the case. We cannot rule out the possibility that in our preparation a similar tonic suppression of Ia input is present during both rhythmic and tonic contractions. If so, such tonic suppression is not related to rhythmic activation of the CPG, but might be related to a general state of arousal required for such rhythmic activity.

Functional relevance

From the results of this study and those of Gossard (1996), it appears that in the decerebrate cat the activation of the CPG for locomotion does not provide presynaptic inhibition to the Ia afferent pathway generating monosynaptic reflexes in ankle extensor muscles. Can this conclusion be extended to the intact, behaving animal? The only study to investigate the triceps surae monosynaptic reflex in the intact, walking animal (Duenas et al. 1990) showed that the reflex was modulated over a cycle of locomotion in a manner similar to the decerebrate (thalamic) preparation. The monosynaptic reflex is largest during extension phase. Unfortunately, no comparison of reflex amplitude between different tasks was made in the intact animal.

In the study by Duenas et al. (1990) it was shown that the amplitude of the monosynaptic reflex in ankle extensors did not always parallel the level of background EMG activity during walking in the intact animal. These authors indicated that this was evidence for presynaptic contributions to the regulation of the reflex pathway during the stance phase. Because our study and the study by Gossard (1996) indicate that this presynaptic inhibition is not derived from the CPG, it presumable comes from other sources. One possibility is from the command system initiating and maintaining locomotion (Gosgnach et al. 1998). Another is from afferent signals generated by the moving limbs. It is well documented that stimulation of some peripheral nerves depolarizes heteronymous primary afferents and presynaptically inhibits monosynaptic reflexes (Schmidt 1971). Furthermore, Gossard (1996) has demonstrated that sensory-evoked primary afferent depolarization leads to presynaptic inhibition of the monosynaptic reflex pathways during fictive locomotion in decerebrate cats and Misiazek and Pearson (1997) recently have found that stretching the quadriceps muscles inhibits the soleus H reflex without suppressing the ongoing soleus EMG during walking in decerebrate cats.

In conclusion, our results do not preclude that presynaptic inhibition is associated with normal walking in cats or humans (see INTRODUCTION), but they do suggest that any presynaptic inhibition observed during the activity of ankle extensor muscles arises from sources other than the extensor burst generating system of the central pattern generator.

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