Functional Coupling of Motor Units Is Modulated During Walking in Human Subjects


Department of Electronics, University of York, York YO10 5DD, United Kingdom; 2Bioengineering Unit, University of Strathclyde, Glasgow G4 0NW, United Kingdom; and 3Division of Neurophysiology, Department of Medical Physiology, The Panum Institute, University of Copenhagen, 2200 Copenhagen N., Denmark

Submitted 24 May 2002; accepted in final form 15 October 2002

Halliday, D. M., B. A. Conway, I.O.D. Christensen, N. L. Hansen, N. P. Petersen, and J. B. Nielsen. Functional coupling of motor units is modulated during walking in human subjects. J Neurophysiol 89: 960–968, 2003; 10.1152/jn.00844.2002. Time- and frequency-domain analysis of the coupling between pairs of electromyograms (EMG) recorded from leg muscles was investigated during walking in healthy human subjects. For two independent surface EMG signals from the tibialis anterior (TA) muscle, coupling estimated from coherence measurements was observed at frequencies ≤50 Hz, with identifiable peaks occurring in two frequency bands ranging approximately from 8 to 15 and 15 to 20 Hz. The coherence between TA recordings was greatest toward the end of swing, reduced in early swing, and largely absent in midswing. In time-domain estimates constructed from paired TA EMG recordings, a short-lasting central peak indicative of motor-unit synchronization was observed. This feature of motor-unit coupling was also reduced in midswing. In paired recordings made among triceps surae, quadriceps, and hamstring muscles, a similar pattern of correlation to that for paired TA recordings was observed. However, no significant coupling was observed in recordings for which one EMG recording was made from an ankle flexor/extensor muscle and the other from a knee extensor/flexor muscle. These results demonstrate that for TA a modulation exists in the functional coupling of motor units recruited during swing. The data also indicate that human motoneurons belonging to different muscles are only weakly coupled during walking. This absence of widespread short-term synchronization between the activities of muscles of the leg may provide a basis for the highly adaptive nature of human gait patterns.

INTRODUCTION

The recruitment of motor units within a single muscle and the coactivation of synergist motor pools during locomotion in vertebrates is generally considered to result from synaptic activity in a central pattern generator. Consequently, all models of rhythmic locomotor activity that are based on a centrally generated locomotor drive imply that synchronization resulting from a common presynaptic drive to groups of motoneurons exists and that this synchronization plays a role in shaping the temporal relationships that characterize locomotor behavior. Studying the organization of synchronization between the activities of motor units during locomotion may therefore provide an insight into the organization of the neural pathways that sustain the locomotor drive.

In principle, two forms of synchronization can be predicted to co-exist during locomotion. One is synchronization reflecting the time course of the activity envelopes of repeating locomotor cycles. In human locomotion, this form of synchronization is recognizable as broad peaks in cross-correlograms constructed from electromyograms (EMGs) of different leg muscles (see Grasso et al. 1998; Hansen et al. 2001). The features of this form of correlation reveal the temporal relationships within the muscle synergies that operate during different forms of gait (e.g., forward vs. backward walking). However, the correlation structure itself is closely related to the duration of the locomotor cycle and the EMG burst profiles, thereby providing little information on the organization of the synaptic drive to motor pools arising from locomotor generating circuits. Of potentially more interest in identifying features of the synaptic drive during locomotion is synchronization that couples the discharges of populations of motor units over short time scales. Referred to as short-term synchronization, and extensively studied using time- and/or frequency-domain methods (see Farmer et al. 1997 for review), this type of synchronization has only recently been studied during human locomotion (Hansen et al. 2001). Based on a time-domain analysis of the complete step cycle Hansen et al. (2001) showed that motor-unit synchronization was restricted to activity in single motor pools and between the activities of close agonist muscle groups acting on a common joint. This result suggests that during human walking, the control of individual muscle groups is driven by networks with a restricted divergence of common projections. However, because the analysis was based on the entire step cycle, any modulation of the synchronization within the EMG bursts or the presence of significant secondary features relating to the frequency content of the common drive cannot be easily resolved. Furthermore, the results reported by Hansen et al. (2001) appear to be at variance with coherence studies in the cat where widespread broadband coupling between the activities of coactive muscle groups acting across the hip, knee, and ankle are reported to exist during fictive walking and scratching (Hamm and Mc-
Curdy 1995, 1999, 2001; Trank et al. 1998). Although species differences may contribute to these discrepancies, the use of different analytical methods may also be a factor. It was therefore the aim of this study to apply a joint time- and frequency-domain analysis of motor-unit synchronization within and between coactivated motor pools during human walking to explore if any modulation of short-term synchronization occurs in human stepping and to determine if any features of the common presynaptic drive to motor pools could be exposed through the use of coherence analysis.

**METHODS**

**Experimental methods**

Experiments were successfully performed on 10 of 17 healthy subjects, aged 21–41 yr, 8 women and 9 men, in accordance with the Helsinki declaration. The local ethics committee approved all experimental protocols (J. No. KF 01-05598), and all subjects provided informed written consent prior to participation. Data from seven subjects were rejected due to cross-talk between nearby EMG recordings.

Paired bipolar surface EMG recordings (Ag-AgCl electrodes; 1 cm² recording area; 2 cm between poles) were made from two sites over the tibialis anterior (TA) muscle separated by a minimum distance of 10 cm during treadmill walking at 4 km/h. In addition, paired recordings were made from the following muscle combinations: soleus (SOL); medial gastrocnemius (MG), SOL: lateral gastrocnemius (LG), MG:LG, SOL: vastus lateralis (VL), MG:VL, LG:VL, TA: VL, TA:biceps femoris (BF), BF:VL, BF: semimembranosus, and VL: quadiceps vastus medialis (VM). For each combination, similar bipolar electrodes as used for the TA recordings were placed over the belly of the respective muscles. The EMG signals were amplified (5,000–10,000), filtered (1–1000 Hz), and stored as waveforms on a computer for later analysis. All subjects wore a heel switch that was used to provide the precise time of heel contact during each step cycle. All data were sampled at 2,000 Hz.

For each recording session, subjects were required to maintain treadmill walking for a minimum of 5 min at a constant speed of 4 km/h. All subjects had previous experience of treadmill walking and were given no additional instruction. The treadmill was started and stopped by a member of the research team.

**Analytical methods**

The analysis is based on a unified framework, which allows the correlation structure between the paired EMG signals to be characterized as a function of time and frequency (Halliday et al. 1995). The EMG signals, after full-wave rectification, are assumed to be realizations of stationary zero mean time series, which we denote by \( x \) and \( y \). Power spectra are estimated using a periodogram approach, where the discrete Fourier transform is constructed from short sections of data taken at a fixed offset time with respect to a trigger point (heel strike) in each step cycle. Estimates of the spectra are constructed by averaging periodograms across all step cycles. Changes in the correlation structure over different phases of the step cycle are assessed by changing the offset time to the start of each segment. A segment length of 200 ms is used for part of the present data (Figs. 1 and 2). Thus if the burst duration of TA was close to 600 ms, the analysis would be based on three consecutive segments. We use \( f_x(\omega) \) and \( f_y(\omega) \) to represent the power spectra of processes \( x \) and \( y \), respectively. The cross-spectrum between \( x \) and \( y \) is denoted by \( f_{xy}(\omega) \) and is estimated in a similar manner.

In the frequency domain, the correlation between the EMG signals is assessed through coherence functions (Brillinger 1981; Halliday et al. 1995; Rosenberg et al. 1989). The coherence function between the two rectified EMG signals is defined at frequency \( \lambda \) as

\[
|R_{xy}(\lambda)|^2 = \frac{|f_{xy}(\lambda)|^2}{f_x(\lambda)f_y(\lambda)} \quad (1)
\]

Coherence functions provide normative measures of linear association on a scale from 0 to 1. For the present data, the coherence provides a measure, at each Fourier frequency \( \lambda \), of the fraction of the activity in one surface EMG signal that can be predicted by the activity in the second surface EMG signal. In this way, the coherence is used to quantify the strength and frequency of rhythmic synaptic inputs, which are distributed across the motoneuron pool (Farmer et al. 1993).

In the time domain, estimates of the cumulant density function are used to characterize the correlation between the two rectified surface EMG signals. The cumulant density function, denoted by \( q_{xy}(u) \), is defined as the inverse Fourier transform of the cross-spectrum

\[
q_{xy}(u) = \int_{-\infty}^{\infty} f_{xy}(\lambda)e^{iu\lambda} d\lambda \quad (2)
\]

For two uncorrelated signals, the cumulant has an expected value of zero, deviations from this indicate a correlation between the two EMG signals at a particular time lag, \( u \). In the present experiments, which are exploring aspects of the common drive to motoneuron pools during locomotion, the dominant feature in cumulant density estimates is the central peak around zero lag, reflecting the presence of common synaptic input. Rhythmic inputs will induce symmetrical oscillatory components in the cumulant (Perkel et al. 1967), the frequency and strength of these components can be quantified from the corresponding coherence estimates. Cumulant density functions are analogous to cross-correlation functions often used to quantify spike train data and have a similar interpretation (Halliday et al. 1995).

To summarize the correlation structure across subjects, estimates of pooled coherence and pooled cumulant density functions are used. Pooled coherence and cumulant functions provide a single measure, which summarizes the correlation structure across several data sets (Amjad et al. 1997). Pooled coherence estimates, like individual coherence estimates, provide a normative measure of measures of linear association on a scale from 0 to 1 (Halliday and Rosenberg 2000). Pooled cumulant density estimates provide a measure of time-domain correlation across subjects. The interpretation of pooled estimates is similar to those for individual records except any inferences related to the population as a whole. In the pooled case, the time-dependent aspect of the analysis, using short segments at varying offset times relative to the heel trigger, provides a measure of how the correlation structure across subjects changes (in an average sense) during the step cycle.

Pooled coherence estimates can be considered as a weighted average of individual coherence estimates. Full details on the construction of pooled coherence estimates and the setting of confidence limits can be found in Amjad et al. (1997). In a pooled coherence study of paired motor-unit recordings from forearm muscles, Halliday et al. (1999) found that pooled coherence estimates were not affected by motor-unit firing rate but were reflecting the presence of task related of common rhythmic modulation of motoneuronal activity. A similar interpretation is placed on the present data.

**RESULTS**

Figure 1 shows data obtained from one subject walking at 4 km/h. This record consists of 380 steps made in 500 s (0.76 steps/s). An event triggered average of the rectified EMG indicates that the TA muscle was active during swing for a period from 550 ms prior to heel strike until 100 ms after heel strike (Fig. 1A). For subsequent spectral analysis, this period of
activity was divided into three nonoverlapping segments each lasting 200 ms corresponding to early, mid, and late swing for each step cycle (Fig. 1A) and encapsulating the dual burst nature of TA activation at this speed of walking. Coherence and cumulant estimates between the two EMG recordings for these three segments are shown in Fig. 1, B–G. A feature of using 200-ms segmented data are a loss of frequency resolution <5 Hz. Accordingly, coherence <5 Hz is not represented in the analysis. Based on this approach, our analysis failed to reveal any coherence between EMG records >50 Hz. However, significant coherence was observed at frequencies <50 Hz and accordingly all coherence plots illustrated in this report focus on this frequency range. As illustrated in Fig. 1, the TA/TA coherence consist of a significant low-frequency component (<8 Hz) present in early (Fig. 1B) and late (Fig. 1D) swing together with peaks of coherence arising between 8–15 Hz and 15–20 Hz. During mid-swing, coherence magnitude between 8 and 20 Hz appears reduced (Fig. 1C). A small broad peak close to 30 Hz can also be observed. Comparative cumulant estimates obtained for early and late swing show a narrow
primary central peak (Fig. 1, E and G), which appears to be absent in midswing (Fig. 1F).

The 8- to 15- and 15- to 20-Hz rhythmic components highlighted in the coherence estimates (Fig. 1, B and C) were evident as secondary features appearing on each side of the central peak in the cumulant (Fig. 1, E and G). The complex nature of these oscillations are indicative of rhythmic effects in different frequency bands, e.g., in Fig. 1G an oscillation of ~56 ms (~18 Hz) can be identified, in addition to oscillations with a longer periodicity reflecting lower frequencies. The 56-ms oscillation is consistent with the 15- to 20-Hz peak featured in the coherence (Fig. 1D). The secondary features seen in early and late swing were not present in the cumulant estimate for mid swing (Fig. 1F) nor were they represented in the equivalent coherence estimate from this subject.

To study the consistency of these findings across subjects, a pooled spectral analysis was undertaken using records obtained from all subjects. The mean step frequency for these records was 0.85 ± 0.09 (SD) steps/s. To characterize changes over time in the EMG-EMG correlation, the pooled analysis was based on the three 200-ms nonoverlapping segments obtained from each step cycle as depicted in Fig. 1A. The result of the pooled analysis is illustrated in Fig. 2, and shows similar findings to those obtained for the individual subject illustrated in Fig. 1. The pooled frequency-domain analysis (Fig. 2, A, C, and E) highlights that during walking coherence is restricted to frequencies <50 Hz and that the principal features comprise a low-frequency coherence <8 Hz and several peaks occurring at higher frequencies. In early swing, a single peak is present between 8 and 20 Hz, whereas during mid and late swing, two separate peaks occur in this frequency range. The coherence in the 8- to 20-Hz range during mid-swing is reduced in magnitude when compared with the similar feature seen in late swing. In addition, the pooled analysis suggests that significant and maintained coherence close to 30 Hz exists between TA recordings throughout the entire swing phase. The corresponding time-domain estimates for the pooled data are shown in Fig. 2, B, D, and F, these all have a central peak, indicating the synchronizing effect of the common synaptic input and have additional oscillatory side bands highlighting the rhythmic components present in the coherence estimates.

Thus the picture that emerges from the application of time and frequency measures of correlation to human treadmill locomotion is that a significant component of the synaptic drive that couples the activity of the TA motoneuronal pool is modulated during swing. This modulation is characterized by a reduction in the strength of common synaptic inputs during mid-swing and the existence of distinct rhythmic components within the 8- to 15- and 15- to 20-Hz frequency bands during early and late swing.

In addition to the study of synchronization within a single motor pool, the extent of synchronization between independent muscle groups was examined by analyzing the relationships between the EMG activities in a range of lower limb flexor and extensor muscles. Figure 3 shows data from a single subject walking at 4 km/h. Pair-wise EMG recordings were made from surface electrodes placed over the TA, soleus, MG, LG, and Q muscles. Figure 3A shows the EMG pattern associated with the gait cycle from these muscles. The coherence and cumulant is shown for paired TA recordings in Fig. 3, B and C. In this figure, the analysis on TA was based on the whole period of EMG activity, in which the TA muscle was active (~600 ms). Accordingly coherence estimates below ~2 Hz are not represented in the figure. Consistent with previous figures there was clear coherence in the 8- to 20-Hz frequency band and a central peak in the cumulant with no coherence evident at frequencies >50 Hz.

To analyze correlations between different muscles, periods of coactivity occurring within the independent EMG bursts were used as the basis for time- and frequency-domain analyses. During the stance phase of the gait cycle, a 300-ms period of coactivity is evident in the EMG activity recorded from the three triceps surae muscles. This period was therefore used to determine the segments of EMG activity for cumulant and coherence estimates among these three muscles. Only data for MG and soleus are shown (Fig. 3, D and E) as essentially similar findings were obtained for the other combinations (i.e., LG-Sol and MG-LG). Similar to paired recordings from the TA muscle, coherence was observed <8 Hz, between 8 and 20 Hz, and close to 30 Hz. The magnitude of the coherence between triceps surae muscles is, however, smaller than that seen in the case of the single motor pool coupling identified in the analysis of TA EMG records. Time-domain estimates of coupling between triceps surae motor pools also reveal the presence of a central peak in each of the cumulants estimated. However, once again this central peak was smaller than the equivalent features observed for the paired TA recordings.

The quadriceps and soleus EMG activity overlapped for a period of 200 ms in early stance, but as seen from Fig. 3, F and G, there was no significant coherence >5 Hz or any central peak observable in the cumulant. This result, as can be seen from Fig. 3, H and I, was similar to that seen between TA and quadriceps where a 200-ms period of coactivity during late swing existed.

Similar findings were made when data from different muscles recorded from all 10 subjects was subjected to a pooled analysis. Figure 4, A and B, shows the coherence and cumulant for the paired EMG recordings from the TA muscle, and these provide a comparison against which estimates calculated from pairs of independent muscles can be made. In the case of TA, the coherence in the 8- to 20-Hz frequency band and the central peak in the cumulant are evident (the calculations were made for the same segment as in Fig. 3). There was also a small central peak in the cumulant and weak coherence in the 8- to 20-Hz frequency band for paired recordings from the triceps surae muscles in the stance phase (Fig. 4, C–H). This was also the case for paired recordings from the lateral and medial head of the quadriceps muscle (Fig. 4, Q–R) as well as paired recordings from the hamstring muscles (Fig. 4, S and T). However, note that in these thigh muscle pairings the size of the central peak in the cumulant centered at 0 ms (Fig. 4, R and T) and the corresponding coherence (Fig. 4, Q and S) estimates between 8 and 20 Hz are small in comparison to the results from synergist muscles acting on the ankle (Fig. 4, C–H). For all other combinations, no coherence >10 Hz or a clear central peak of synchronization could be observed (Fig. 4, I–P), suggesting that processes generating the features seen within the TA motor pool and between some pairs of muscle groups is restricted.
DISCUSSION

This study reports the results of a combined time and frequency domain analysis of the pattern of synchronization evident in the activity of different lower limb muscles during human locomotion.

The interpretation of the analysis performed in this study depends on the requirement that segmentation of the EMG data overcomes the lack of stationarity in locomotor data and that each EMG record is free from contamination by cross-talk. We will initially address these two issues in turn.

By analyzing data in short segments, data can be considered to display local stationarity and thereby satisfy an important criterion for time series analysis. However, segment length is inversely related to the lowest frequency that can be resolved using Fourier-based methods. Thus the determination of an appropriate segment length in this study is a compromise between the need for stationarity, the maintenance of low-frequency resolution in spectral estimates and the EMG burst duration. In locomotor data, the periodicity of the gait cycle dominates the low-frequency spectral components (<8 Hz) of

![Graphs showing pooled coherence and cumulant calculated from all subjects during walking at 4 km/h.](http://jn.physiology.org/)

As shown in Fig. 1, the TA EMG signals were divided into three 200-ms segments corresponding to early, mid, and late swing in all 8 subjects. A, C, and E: the pooled coherence for the 8 subjects calculated for early, mid, and late swing, respectively. B, D, and F: the corresponding cumulants. Due to the long record length represented in this figure, the upper 95% confidence limit for the coherence estimate (based on the assumption of independence) is <0.01, the line indicating this value has merged with the abscissa in the coherence plots.
EMG records, and therefore segmentation will primarily influence spectral features that reflect the frequency profile of the envelope of repeating EMG bursts. The minimum segment length used in this study is 200 ms and, given the desire to examine short-term synchronization within locomotor bursts, we consider that the cut-off in low-frequency resolution that this incurs (5 Hz) is acceptable. Importantly, high-frequency resolution is not affected by segmentation and remains measurable out to the Nyquist frequency of 1,000 Hz.

The general lack of synchrony and coherence observed between recordings from distant muscles strongly suggests that cross-talk did not influence these recordings. However, cross talk could potentially exist between EMG recordings made by nearby pairs of EMG electrodes. In this and a previous study (Hansen et al. 2001), careful consideration was given to EMG electrode placement to minimize the likelihood that pick-up from one pair of bipolar electrodes would be influenced by current spread from within the pick-up area of a second pair of bipolar electrodes (Roeleveld et al. 1997). This matter is further discussed in relation to interelectrode distance and muscle anatomy by Hansen et al. (2001). Nevertheless, as stated in METHODS, there was evidence of cross-talk in 7 of the 21 subjects tested. In these seven subjects, cross-talk between EMG records was identified by two features: a large and very narrow central peak (<2–3 ms) in the cumulant and significant broadband coherence throughout the EMG spectrum. Correlation methods are an extremely sensitive measure for the identification of cross-talk, and the exclusion of data displaying it is an essential step in the assessment of the contribution of common drive to populations of motor units. Crucially, the data analyzed in this study displays only weak synchrony and coherence estimates were only significant in specific parts of the EMG spectrum <50 Hz. It therefore is highly unlikely that cross-talk contributed to the recordings used in the analysis of EMG records from the same or nearby muscles. Furthermore, spike trains obtained from the TA muscle via bipolar wire electrodes during pilot experiments produced results equivalent to those seen with surface EMG recordings (Halliday et al. 2000). We are therefore confident that the results of the analysis performed is not contaminated by cross-talk and accurately reflects the manifestation of modulated physiological processes, which weakly couples the activities of restricted populations of motor units.

In the time domain, cumulant estimates representing early, mid, and late swing show clear evidence of modulation in the magnitude of the central peak associated with short-term synchronization. Similarly, the secondary features associated with oscillatory features of motor unit coupling also vary. Part of this modulation reflects the changing level of EMG activity associated with the different phases of swing and a more

**FIG. 3.** Coupling of EMG signals recorded from different leg muscles during walking at 4 km/h in a single subject A shows the EMG recorded from surface electrodes placed on (from top to bottom): the distal part of the TA muscle, the proximal part of TA, the soleus muscle (Sol), the lateral gastroc muscle (LG), and the quadriceps muscle (Q). The coherence and cumulant were calculated for muscle combinations in which overlapping EMG activity was seen. B and C: coherence and cumulant for the 2 TA recordings (duration of overlapping segment used for the analysis: 600 ms). D and E: paired Sol:MG recording (duration of analyzed segment: 300 ms). F and G: for paired Sol:Q recording (duration of analyzed segment: 200 ms). H and I: for paired TA:Q recording (duration of analyzed segment: 200 ms). Due to the long record length represented in this figure, the upper 95% confidence limit for the coherence estimate (based on the assumption of independence) is <0.01, the line indicating this value has merged with the abscissa in the coherence plots.
accurate estimate of the extent that modulation occurs in motor unit synchronization during gait can only be judged from a joint consideration of the cumulant and coherence.

Coherence $<8$ Hz was commonly observed between muscles acting across different joints and between close synergists. However, it is likely that this low-frequency coupling is related to the periodicity of the gait cycle and to the burst envelope of the recorded EMGs rather than to any feature of a shared synaptic drive because no central peak was observed in the cumulant from muscles acting across different joints. When coherence was detected at frequencies $>8$ Hz, a central peak in the corresponding cumulant was detectable, suggesting that the higher frequency features seen out to 50 Hz are associated with a synchronizing synaptic drive. The coherence observed in the 8- to 15-Hz and 15- to 20-Hz frequency bands deserves special comment as it was clearly modulated in the swing phase in parallel with the modulation observed in the magnitude of the central peak and the appearance of secondary features in the cumulant. Although the magnitude of TA EMG activity differs in early, mid, and late swing, the changes seen in the position of the coherence peaks occurring in the 8- to 15-Hz and 15- to 20-Hz ranges support the view that the frequency content of the shared synaptic drive that contributes to components of short-term synchronization is modulated during swing. In contrast, processes contributing to generation of the low level coherence seen near 30 Hz do not appear to be modulated.

In studies performed on motor-unit synchronization during tonic isometric contractions, coherence between 12 and 32 Hz is commonly seen and has been demonstrated to represent a rhythmic modulation of motor unit activity brought about by 12- to 32-Hz activity in a common presynaptic drive (Farmer et al. 1993). The current findings can be interpreted in a similar way and strongly indicate that part of the synchronizing presynaptic drive observed during stepping has rhythmic components and that those components occurring between 8–15 and 15–20 Hz are modulated during swing. It is conceivable that the differences in synchronization evident in early and late swing could result from changes in the firing activity of a
single presynaptic source activity, but it is equally plausible that different populations of common last-order interneurons with distinct spectral signatures may be involved. Therefore we cannot be certain if the coherence seen at 8–15, 15–20, and 30 Hz represents activity in a single source of common presynaptic drive or reflects different synchronization influences on motor-unit firing. Nevertheless, our findings reveal that synchronization between motor units from a single muscle is relatively weak during walking and that the distribution of a common synchronizing input to different motor pools is highly restricted.

Human walking needs to be driven by adaptable patterns of muscle activation to accommodate the variety of locomotor tasks that can be accomplished during over ground walking. It is therefore appealing to consider that the lack of a powerful shared presynaptic drive to motor pools during human walking reflects features of a control system that enables the generation of flexible patterns of muscle activation during gait.

Our results demonstrating limited correlation between EMG recordings are consistent with the recent findings of Buchanan and Kasicki (1999) and Sigvardt and Miller (1998) that the interneurons generating motoneuron synchronization during fictive swimming have a relatively limited divergence. They are, however, in stark contrast to the results of coherence analysis performed on neurograms obtained for episodes of fictive locomotion generated by mesencephalic locomotor region (MLR) stimulation in the cat. In these studies, Hamm et al. (Hamm et al.1995, 1999, 2001; Trank et al. 1998) provide evidence for the distribution of a powerful and widely divergent synchronizing locomotor drive that is consistent with Graham Brown’s (1911) half-center concept of locomotion generation. The differences in the degree and extent of the synchronization observed in human, cat, and lamprey studies are therefore perplexing and, we suggest, are unlikely to be due to simple species differences. One possibility may be a non-linear effect resulting from MLR stimulation on the synchronization patterns observed in the cat experiments reported by Hamm and co-workers (Hamm 1995, 1999, 2001; Trank et al. 1998). Further studies are needed to address this.

In conclusion, our results strongly suggest that human locomotor drive occurs through premotoneuronal pathways that display limited divergence. The synchronization that we report here cannot represent the major synaptic influence that drives motor output during walking but rather may be a feature associated with the fine control of stepping. The synchronization we observe may arise from the rhythmic activation of local spinal interneurons, the phase-dependent reflex effects of movement-related afferent feedback or a consequence of descending supraspinal influences. In man and other primates, it is generally accepted that walking has a greater reliance on supraspinal control than seen in other vertebrates (Eidelberg et al. 1981; Fedirchuk et al. 1998) and that the corticospinal tract contributes to the basic locomotor EMG activity (Petersen et al. 1998, 2001). Furthermore, the presence of significant transcortical reflexes during human treadmill walking highlights the importance of cortical control in human locomotion (Christensen et al. 2000). Given this and the knowledge that corticospinal pathways generate short-term synchronization in motor units during tonic contractions (Conway et al. 1995; Farmer et al. 1993), it is important to establish what role corticospinal pathways may have in generating the patterns of synchronization reported here and in Hansen et al. (2001) as this may have significance for locomotor recovery after spinal cord injury or cerebral stroke.

This work was supported by grants from the Danish Health Research Council, The Danish Sports Research Council, The Novo Nordisk Foundation, The Danish Society of Multiple Sclerosis, and The Royal Society of London. Present address of L.O.D. Christensen: University Laboratory of Physiology, Parks Road, Oxford, OX1 3PT, UK.

REFERENCES


