Activity of hindlimb muscles
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Chapter VII

General summary
General Summary.
The present thesis concerns experimental studies of motor activity patterns, as measured using electromyography (EMG), in muscles acting on the ankle joint of freely moving cats. The analysis concerned two main aspects of normal muscle use: (i) how different ankle muscles and muscle portions act together in different "acute" types of motor behavior (i.e. aspects of muscle(-portion) co-ordination in movement and posture; Ch.2-3), (ii) during which total durations of daily time the various muscle(-portions) are active (Ch.4-5) and how this is related to their muscle fiber composition (Ch.6). In a first introductory chapter (Ch.1), an account is given of general background knowledge, including information concerning the techniques employed for the measurements.

Data were collected from a group of five adult, female cats, which were chronically implanted with up to eight electromyographic (EMG) recording electrodes in some of their ankle muscles, i.e. in the tibialis anterior (TA), extensor digitorum longus (EDL), peroneus longus (PL), soleus (SOL), gastrocnemius lateralis (LG) and tibialis posterior (TP). In several cases, recordings were made from anterior and posterior muscle portions (PL, TA, LG). Simultaneous recordings from the various muscles and muscle portions together demonstrated that, in accepted cases, there was no significant amount of "cross-talk" between the electrodes. The implanted electrodes were used for two sets of studies in (relatively) freely moving animals: a/ using long and flexible cable connections, measurements were made of how different muscles and muscle portions were used together in spontaneous movements (i.e. studies of muscle co-ordination); b/ using telemetric techniques, muscles and muscle portions were compared with regard to their accumulated duration of activity per 24 hours (i.e. studies of the degree of muscle use).

The recorded EMG signals reflect the activity of hundreds to thousands of muscle fibres. The central nervous system controls hindlimb muscle activity via specialized nerve cells, the alpha motoneurones, which have cell bodies in the spinal cord and send axons out to the muscle fibres. In the adult, each muscle fibre receives a connection from only one motoneurone while each motoneurone commands many (often hundreds) of muscle fibres. Fibres that are commanded by the same motoneurone thereby belong to the same "motor unit" or "muscle unit". A single muscle may consist of tens to hundreds of motor units. Within a given unit, the various fibres all tend to have similar biochemical and contractile properties. Fibres of different units may, however, differ markedly in their properties. For descriptive purposes, the various units are often classified into different categories or types. Physiologically, the classification is often made on basis of differences in contractile speed and fatigue resistance (slow type S, fast types FR, Fint and FF). Histochemically, the staining reactions of myofibrillar
ATPase are often used for classifying fibres into type I ("slow") and various brands of type II ("fast").

In voluntary contractions, the force of a muscle may be increased using two different mechanisms (usually employed in parallel): a/ a greater number of motoneurones and, thus, motor units may be activated ("recruitment gradation"), b/ active motoneurones may increase their rate of impulse discharge, thereby causing their units to contract at greater forces ("rate gradation"). The recruitment gradation typically occurs in a standardized manner, starting with slow, small and weak units and progressing toward the faster, larger and stronger ones ("size principle"). Besides such recruitment in relation to fibre and unit properties some earlier studies had suggested that, within a given muscle, recruitment might also differ between different motor tasks. Such task-related variations in how single muscles are used are, so far, less well known. New data on this issue are presented in part of the present thesis. This was done by simultaneously recording the activity in different portions of single muscles. Most of these measurements were done for peroneus longus (in some of the experiments also for tibialis anterior and lateral gastrocnemius).

For the cat's peroneus longus, earlier experiments have shown that there is a coarse correspondence between the intraspinal position of motoneurones and the intramuscular position of their muscle fibres: rostral motoneurones tended to command anterior muscle fibres and caudal motoneurones were preferentially connected with posterior muscle fibres. For this reason, we chose to compare the EMG activity of anterior vs. posterior portions in the peroneus longus (PLa vs. PLp), thereby possibly obtaining an indirect impression of the intraspinal cranio-caudal distribution of activity within the pool of peroneus longus motoneurones.

In CHAPTER 2, such comparisons were made for many different kinds of spontaneous movement of the various cats. A consistent relationship was found between the antero-posterior distribution of EMG activity within peroneus longus and particular movement patterns in the cats: activity was predominantly in posterior muscle portions if a cat was simply standing on its hindlegs or preparing to take off for a jump. A predominantly anterior activity was seen in a cat preparing to land from a jump (or simply being held in the air). In many other activities, such as walking around, activity was more evenly distributed within the muscle. The results strongly suggested that the motoneurone pool was often activated in a spatially distinct and heterogeneous manner for different motor acts.

Differences between different kinds of motor behaviour concern the timing as well as the distribution of activity across the various muscles involved. Hence, the findings in Ch.2 suggested that one might find a relationship between the observed task-related aspects of recruitment (the antero-posterior EMG differences within peroneus longus) and the pattern of simultaneously active
muscles within the same limb. Therefore, in CHAPTER 3 we proceeded to explore whether there was indeed a reproducible relationship between the intramuscular distribution of peroneal activity and the combination of other muscles active. For practical reasons, this was done for only a restricted set of muscles per cat (i.e. those provided with implanted electrodes). Two kinds of comparisons were performed: a/ semi-quantitative estimates, using a large number of chart-recordings of EMG-activity. Cases with an anterior or posterior peroneal dominance were compared with regards to whether the other recorded muscles were active or silent ("on/off analysis"). b/ quantitative assessments, using digitized samples from a more limited number of recordings. A wide range of variation was seen in the antero-posterior activity ratio for PL. No evident and consistent relationships were found between such differences in the antero-posterior EMG distribution of peroneus longus and the measured amounts of other muscle activity. However, the "on/off analysis" delivered statistically significant results: a preferential activation of anterior PL portions was seen most often if potential PL agonists were active (ED, TA), or if potential PL antagonists were silent (SO, TP).

Besides such problems concerning the recruitment gradation of muscle activity, we also investigated another quantitative aspect of muscle use: the total duration of muscle activity per day. Data of this kind are essential as a background for analyzing the effects of increased use (e.g. training) and disuse (e.g. after bone fracture) on muscle properties. Still, very little has been previously published on this subject.

In CHAPTER 4, four of the cats were used for long-term (i.e. 24 hr) intermittent recordings of EMG. In this analysis only the simplest and most easily quantified parameter of muscle activity was measured: the total amount of time during which any activity was present (i.e. total "on" duration for each muscle). Marked and significant differences were found in the total accumulated duration of activity per day. The simple ankle and toe dorsiflexors EDL and TA have no marked anti-gravity function in posture and they were found to be used for a relatively short total duration each day (i.e. 1.9 - 4.0 % of the total time). On the other hand, for the ankle extensors LG and SOL much longer daily duty times were found (i.e. from 6.8 % till 13.9 % of total time). The PL, which has an important stabilizing role as an exo-rotator of the ankle joint, also showed a relatively great duration of daily activity (i.e. 5.7 - 9.5 %). For all the three muscles with multiple recording sites (PL, LG, TA), consistent differences were found between the daily duration of activity in anterior and posterior muscle portions (longer posteriorly than anteriorly for PL and TA; opposite way around for LG).

In the CHAPTER 5, data from the 24 h recordings were further analyzed with regard to circadian and individual differences in activity level. The
investigated cats were generally less active during the night than in daytime. In less active periods (e.g. when lying or sitting) the hindlimb-postural needs would be expected to be different from those experienced at times of more intense motor behaviour (e.g. when standing or walking around). This was probably the reason why the differences in activity duration were much smaller in the night than during daytime and also the inter-muscular distribution of duty times were quite different at different circadian periods. Thus, the muscle use was not simple scaled up or down between active or inactive periods.

Similarly, when comparing different individual cats, variations in the general level of activity for one muscle (e.g. soleus) were not consistently present for other muscles. Although a very similar overall ranking between the hindlimb muscles in their daily duty time was found in all the cats, the animals clearly differed in their motor habits, showing to different preferential patterns of hindlimb muscle use.

Finally, after the end of the physiological measurements described in Ch.4-5, the cats were sacrificed and the studied muscles were removed for histochemical analysis (CHAPTER 6). Cross-sections were stained for myofibrillar ATPase and muscle fibres lying close to the various EMG recording sites were classified as types I, IIA or IIB. Thus, in this last stage of the investigation we could directly investigate whether muscles with different daily durations of activity also differed in fibre composition. A positive and significant correlation was demonstrated between the percentage of "slow" type I fibres and the accumulated daily duration of activity. It is important to realize that such a relationship is not self-evident; its existence suggests that, among the muscles of the lower hindlimb, differences in the required amount of postural force is coupled to differences in postural "recruitment threshold", i.e. that muscles with an relatively important role for postural force are relatively easily recruited into postural activity.