Activity of hindlimb muscles
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Chapter I

General introduction
General Introduction

The present thesis concerns experimental measurements of activity patterns, as studied 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 the different ankle muscles and muscle portions act together in different "acute" types of motor behavior (i.e. aspects of muscle(-portion) coordination 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).

The sampled muscles included two ankle extensors (i.e. foot plantar-flexors: soleus, SO; lateral gastrocnemius, LG) two ankle flexors (i.e. foot dorsiflexors, tibialis anterior, TA; extensor digitorum longus, ED), one foot endo-rotator (tibialis posterior, TP) and one foot exo-rotator/dorsiflexor (peroneus longus, PL).

In the present chapter, general information concerning muscle composition and usage will be provided as a background for the detailed descriptions and discussions of experimental results in Ch.2-6.

Fiber composition of skeletal muscles.

Skeletal muscles are innervated by specialized nerve cells called motoneurons which, for muscles of the limbs, are localized in the ventral horn of the spinal cord. In adult mammals, each muscle fiber receives innervation from only one motoneuron whereas each motoneuron may command tens to hundreds of muscle fibers. The muscle fibers that all belong to one motoneuron constitute a muscle unit or motor unit (the latter term also includes part or all of the motoneuron itself). Within a single muscle unit, the constituent fibers are generally quite similar to each other with regard to, for instance, their histochemical properties. However, within a single muscle, the various muscle units may have markedly different physiological and histochemical properties. Furthermore, different muscles may display consistent and marked differences with regard to their muscle fiber and unit composition.

With regard to their contractile properties, as studied in isometric contractions, units of the same muscle may differ markedly in speed, maximum force and endurance (i.e. fatigue-resistance). These properties display a characteristic pattern of co-variation such that the weakest units tend to be slow and fatigue-resistant (S units) and the strongest ones are relatively fast but fatigue-sensitive (FF units). In the middle of the range of variation there are also fast units of intermediate force and a relatively high degree of fatigue resistance (FR units, Fint units). It should be noted that such a categorization of the unit population into different "types" is mainly to be regarded as a descriptive convenience; practically all the properties vary in a continuous manner across the unit and fiber
population. In histochemistry, fibers are commonly classified into types I, IIA and IIB on behalf of the properties of their myofibrillar ATPase (Brooke and Kaiser, 1970). Combined physiological and histochemical investigations have shown that there is a general correspondence between the two classification schemes such that, on average, type S ~ I, type FR ~ IIA and type FF ~ IIB. For further general information concerning the properties and recruitment behavior of different units see reviews (Burke, 1981; Henneman and Mendell, 1981; Kernell, 1992).

Gradation of muscle force in motor behavior.

In any part of the body, well co-ordinated movements are produced via the precise control of contractile force in all the relevant muscles. As each muscle consists of a collection of smaller parts, i.e. the muscle units, force modulation can be carried out by activating a greater or smaller number of units (recruitment modulation). In addition, the force of each individual unit can also be graded over a wide range by a change in the spike-frequency of its motoneuron (frequency modulation).

In most known kinds of motor activity generated by the CNS, the recruitment thresholds are, on average and within individual muscles, ranked such that weak units are more easily activated than stronger ones. Thus, the units tend to be recruited in an order of ascending unit-tension, which is advantageous for the smoothness of force gradation; this behavior is often referred to as recruitment according to the "size principle" (see Henneman and Mendell, 1981). In terms of muscle unit "types", such a recruitment hierarchy implies that, in general, the S threshold < the FR threshold < the FF threshold. To an important extent, these differences in recruitment threshold apparently reflect differences in the membrane properties of the respective motoneurons (cf. Kernell, 1992).

Besides these recruitment hierarchies, which are associated with differences in the functional properties of the units ('property-related recruitment behavior'), some published evidence suggests that differences may also exist in the ways in which units are recruited when a target muscle is used in different patterns of co-activation with other muscles, i.e. in different motor 'tasks'. In some cases, units lying in different portions of a given muscle will have different force directions (e.g. deltoid); hence, in such cases, units in different muscle portions will have to be chosen for different directions of desired muscle action (different torque). In a few other cases, however, different 'tasks' have been found to be associated with different recruitment patterns without there being any clear evidence for any associated biomechanical necessity (e.g. Hoffer et al., 1987; ter Haar Romeny et al., 1984; Tax et al., 1990). In some of these latter instances, this 'task-related recruitment behavior' was associated with differences in unit activity within different muscle portions (ter Haar Romeny et al., 1984). Also in anaesthetized
animals, differences in the topographical distribution of activity have been observed as a muscle (PL) was activated via different CNS routes (Kandou and Kernell, 1989). It is, for the interpretation of such findings, of interest that, in many muscles, there is a coarse correspondence between the topographical position of motoneurons in the spinal cord and the site of their fibres within the muscle (e.g. Swett et al., 1970); for further comments, see Kernell (1992; 1998). Furthermore, the observations that the topographical distribution of intramuscular activity may be markedly heterogeneous and task-dependent fit well to findings that also the sensory feedback from intramuscular mechanoreceptors tends to be 'regionalized'. Mechanoreceptors from one portion of a muscle apparently often tend to have their autogenetic reflex effects focussed onto motoneurones innervating the same muscle portion (review of "neuromuscular partitioning": Windhorst et al., 1989).

Plasticity of muscle (unit) properties.
The general contractile properties of each muscle unit type are well adjusted to its general use. Due to the low recruitment threshold of their motoneurons, S units will be involved in most kinds of motor action, including long-lasting postural contractions. Hence, it is functionally relevant that these units have such a good resistance to fatigue. To some extent, the suitable contractile properties of the S units might even be a result of (or, at least, reinforced by) the 'training effects' of prolonged periods of natural activity. It has been demonstrated in several laboratories that if a predominantly fast muscle is subjected to a marked increase of activity (e.g. via chronic stimulation) its properties will gradually change, during the course of several weeks, toward those characteristic for slow units (Eerbeek et al., 1984; review: Gordon, 1995; Gordon et al., 1997; e.g. Salmons and Vrbova, 1969). In the context of such experiments, it would be highly desirable to know which the daily 'training durations' are of muscles and motor units in the course of normal motor behavior. Baseline data on daily activity levels are, however, very scarce in preceding literature; prior to our present investigation, information for the cat was limited to comparisons between lateral gastrocnemius and soleus (Alaimo et al., 1984). One of the central aims of the present thesis was to provide more complete data of this kind for hindlimb muscles of the cat (see Ch.4-6).

Background information concerning the cat's peroneus longus muscle.
Many of the measurements of the present thesis were focussed on the peroneus longus muscle of the cat's hindleg. Therefore, some general background information will here be given for this muscle.

In cats as well as humans, peroneus longus is a major exorotator of the foot. In cats (but not in humans) it also contributes to foot dorsiflexion, i.e. it belongs to
the physiological flexors of the lower leg. It is known to be active during a wide range of movements, including locomotion, scratching, limb shaking, etc. (Abraham and Loeb, 1985; Engberg and Lundberg, 1969; Rasmussen et al., 1978) and also presumably contributes to lateral ankle stabilization when the cat is standing.

The motoneuron pool of peroneus longus is usually mainly located in spinal segments L6-L7 (Vanderhorst and Holstege, 1997). The length-wise distribution of the motoneurons is correlated with the intramuscular site of their peripheral nerve endings (i.e. the site of their muscle units): within the peroneus longus pool, rostral ventral root filaments project preferentially to anterior muscle portions, and vice versa (Donselaar et al., 1985).

In a section through its muscle belly, peroneus longus consists of about 18% type I, 41% type IIA and 41% type IIB fibers (Donselaar et al., 1987). In physiological measurements, the proportions of S, FR, F(int) and FF units were 21, 24, 23 and 33% respectively (corresponding cumulative forces about 5, 18, 25 and 52 %; Kernels et al., 1983). Within the cat's peroneus longus muscle, there is no very marked regionalization of muscle fibre types; units of different kinds seem present across most of the muscle. In preliminary histochemical measurements concerning oxidative enzyme activity, highly oxidative fibres (i.e. fibers of presumably high fatigue-resistance) tended to be somewhat more common in posterior than in anterior muscle portions (Kandou and Kernell, 1989). Similarly, motoneurones with a caudal intraspinal position (whose axons preferentially went to posterior muscle portions) tended to be equipped with slow and fatigue-resistant muscle units somewhat more often than motoneurons with a cranial intraspinal position (correlation significant but very weak; Kernell et al., 1985). In this context it is of importance to note that, for the cat's peroneus longus muscle, the intramuscular site of muscle fibres can not be very important for the direction of muscle force: all units of this relatively slender muscle pull on the same long and rope-like tendon.

Notes on electromyographic techniques.
Most of the measurements of the present thesis were obtained using electromyographic (EMG) techniques in freely moving animals. EMG recordings are essentially extracellular recordings of the compound action potentials of muscle units (see Basmajian and De Luca, 1985). The number of action potentials contributing to the recorded EMG depends on the number of recruited units as well as on their discharge rates. Furthermore, the recorded amplitude of a given action potential depends very markedly on the electrode configuration as well as on the distance from the muscle fibres to the electrode(s). A major problem in this context is to make certain that the recorded activity indeed comes from the intended target muscle. In the present measurements, this was ensured in two ways by the choice of electrodes:
(i) For most muscles, use was made of 'patch' electrodes, fixed to the muscle surface and insulated at their back by a sheet of silicone (see description in Loeb and Gans, 1986). In order to assess the selectivity of these electrodes, two pairs were generally sutured back-to-back onto neighboring muscles and it was ascertained that activity could be recorded from one of these electrodes while the other one was silent (i.e. negligible amounts of 'cross-talk').

(ii) In some recordings (including all those from peroneus longus and tibialis posterior) use was made of embedded fine-wire electrodes which have (thanks to their small size) a restricted recording volume; also in these cases the absence of 'cross-talk' was certified by noting that the presence or absence of activity recorded from the target electrode was independent of that recorded from neighboring muscles with other electrodes.

In many cases, the relative degree of EMG activity was visualized and made more easily measurable by the method of full-wave rectification and smoothing (cf. Loeb and Gans, 1986).

Survey of the experimental measurements of this thesis.
The first two experimental chapters (Ch.2-3) concern the first sub-theme of the present thesis: measurements of how the different ankle muscles and muscle portions acted together in different "acute" types of motor behavior. Firstly, in Ch.2, attention is focussed on the question of whether the distribution of EMG activity within peroneus longus was related to the motor behavior of the cat, i.e. whether the topography of intramuscular PL activity was related to motor 'task'. This was indeed found to be the case. Inspired by these results, a preliminary analysis followed, as detailed in Ch.3, of the manner in which changes in the intramuscular distribution of peroneus longus activity was related to intermuscular patterns of co-activation between peroneus longus and other sampled ankle muscles. In spite of the great complexity and variety of observed activation patterns, some promising consistencies were found which may be used as a starting point for further work along these lines.

The following three experimental chapters (Ch.4-6) concern the second subtheme of the thesis: during which total durations of daily time the various sampled muscle(-portions) were active and how this was related to their muscle fiber composition. In all these cases, the EMG monitoring concerned the most active units of each muscle, i.e. presumably the (most active) S units.

Firstly, in Ch.4 the sampled muscles and muscle portions were compared with regard to their average 24 hr behavior. Very marked differences in the mean cumulative duration of activity per day was found, extending from about 2% of total time for extensor digitorum longus up to about 10% for peroneus longus and 14% for soleus. Furthermore, in all the three muscles that were investigated with regard to regional variations (peroneus longus, tibialis anterior, gastrocnemius
lateralis), consistent differences were found between the activity durations for anterior and posterior muscle portions.

In Ch.5 the variability of long-term activity levels for the various muscles was analyzed in relation to (i) the time of day, and (ii) individual preferences of different cats. The results underlined that, in both instances, levels of activity do not necessarily co-vary in a 'linked' manner between individual muscles around the same joint. Many of the daily or inter-animal variations were evidently markedly related to differences in prevalent co-ordination patterns, which took place in addition to the expected variations caused by differences in overall 'levels' of motor activity.

Finally, in Ch.6, results of Ch.4 were analyzed in relation to the unit and fibre composition of the sampled muscles, demonstrating the presence of a significant relation between long-term activity durations and the relative percentage of S-units/type-II fibres.

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