Muscle Activity during Forelimb Stepping in Decerebrate Cats

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Abstract In decerebrate cats with the lower thoracic cord transected, electromyographic activities were analyzed in up to 41 forelimb muscles, almost all muscles involved in forelimb stepping (intrinsic hand muscles were not included). From the active period in the step cycle, muscles were classified into three groups: extensors, of which activity is like that of elbow extensors; flexors, activity like that of elbow flexors; others, including dorsiflexors of the wrist, pronators, and supinator. The results were well consistent with those from conscious animals as well as efferent pattern of fictive locomotion in elbow and distal muscles. Nevertheless, in some proximal muscles discrepancies were noted, suggesting their changeability depending on environmental conditions. Recording from almost all muscles allowed to estimate rhythmic change of the overall output of the forelimb central pattern generator.

Key words: cervical enlargement, locomotion, electromyography, Schiff-Sherrington cat, mesencephalic locomotor region.

In decerebrate cats, forelimb stepping is well elicited after the lower thoracic cord is transected [1, 2]. The same preparation can also display fictive locomotion, rhythmic motoneuronal discharges of stepping in the immobilized animal [2–4], and has been used for studying the forelimb central pattern generator [5]. We [6–8] found that interneuronal groups within the cervical spinal cord rhythmically fired at various periods in the step cycle of fictive locomotion. The active phases may be specific for the interneuronal groups. For understanding roles of each group in the central pattern generator, such specificities may be compared not only with each other but also with the overall activity of the forelimb central pattern generator. To assess the overall activity, we examined forelimb muscle activity during stepping movement (in this paper) and unit activity of cervical interneurons during fictive locomotion (in the subsequent paper [9]).

Stepping movements in decerebrate cats with the lower thoracic cord transected vary from animal to animal [1], whereas a flexion-extension pattern of each limb is basically preserved. The inter-specimen variation seems larger than that of conscious animals (e.g. [10]). Even though the large variation is presumably due

to stepping in animals with the central nervous system being in an anomalous condition, decerebration, it can be related to utilization of the forelimb central pattern generator in limb movements other than locomotion. Therefore, both the basic pattern of muscle activity and its variability are needed for analysis. Electromyographic pattern of forelimb muscle activity has been analyzed in conscious cats [10–13] but not in decerebrate cats (cf. [14–16]). In this paper, forelimb electromyographic activity during stepping is investigated with notice of its variability in decerebrate cats.

METHODS

Preparation. Under halothane anesthesia cats ($n=9$) were decerebrated and spinalized. A tracheotomy was performed, a cannula inserted for securing the respiratory tract, a catheter inserted into the right common carotid artery for monitoring blood pressure, the left common carotid artery ligated. The animals were rigidly mounted in the stereotaxic frame with the head and the thoracic spine fixed. After a large bilateral craniotomy, decerebration was performed surgically at the precollicular-postmamillary level, the brain rostral to the transection removed, and the lower thoracic cord was transected. The forelimbs were placed on the belt of a treadmill installed under the stereotaxic frame and the hindquarters were suspended with the limbs pulled caudally. Blood pressure was continuously monitored and any drop below 70 mmHg was counteracted by intravenous infusion of dextran and noradrenalin. The rectal temperature was kept near 38°C by heat irradiation.

Production of stepping movements. After anesthesia was terminated and the animals recovered from narcosis, forelimb stepping occasionally occurred by moving the treadmill belt (belt speed fixed at 0.8 m/s). If it did not, stepping was evoked by electrical stimulation of the mesencephalic locomotor region (MLR; the point around P2.5, L4.5, H0.0 in Horsely-Clarke coordinates) [2, 17]. Current pulses (pulse train, interval 30 ms, duration 0.5 ms, strength less than 30 μ A) were delivered from a tungsten-in-capillary microelectrode (insulated with a glass pipette, the exposed tip diameter, ca. 30 μ m and length, 50–90 μ m) with an anodal Ag-AgCl electrode attached to the temporal muscle.

Recording. During stepping, electromyographic (EMG) activities were recorded from various muscles (see RESULTS) mainly on the left side (in some cases, both sides). Bipolar electrodes (enamelled copper wire, diameter 100 μ m, bared about 1 mm at the tips) were surgically placed in the bellies of the muscles by means of a hypodermic needle under visual control. Electrode placement was confirmed after each experiment by dissecting the animal. EMG activities were differentially amplified (1,000 times), filtered (band-pass with -3 dB points at 80 Hz and 5 kHz), and stored on 14-channel FM magnetic tape, which were displayed on an ink-writing oscillograph.

Analysis. The phase relations of EMG activities between different muscles

Fig. 1. Electromyographic activity of forelimb stepping. A sample recording; from top to bottom, EMG activities arranged in order from proximal to distal muscles. Stepping was elicited on a moving belt (belt speed 0.8 m/s) by mid-brain stimulation in a decerebrate cat with the lower thoracic cord transected.

were analyzed from paper records (Fig. 1), which displayed 14 muscle activities in parallel. From a paper record containing more than 50 steps, a sequence of 30 consecutive steps with fairly constant cycle durations was selected for analysis. For the selected steps, phases of the onset and termination of EMG discharges were measured with respect to the beginning of the cycle, the burst onset of triceps brachii, medial or lateral head. The means were calculated and were normalized with the mean cycle duration, and the active periods of the respective muscles in the step cycle were determined. The mean cycle duration was 770 ± 100 ms.

RESULTS

As shown in Fig. 1, during stepping, forelimb muscles were rhythmically active with the step cycle, the active phases being slightly different from each other. Some discharged twice per cycle. The active phase was analyzed for 41 forelimb muscles, which include almost all muscles except intrinsic hand muscles (Figs. 2-4).

Shoulder and elbow muscles

Elbow and shoulder muscles were clearly classified into extensor and flexor

Fig. 2. Active periods of shoulder and elbow muscles. Left: Schema of muscle arrangements. Middle: For each muscle, active periods obtained from different animals are represented by different bars. Active periods were shown for two step cycles in the normalized scale. Right: Cumulative plots of active periods shown on the middle panel.

from their discharge periods in the step cycle as shown in Fig. 2. Extensor group includes supraspinatus (SSp), infraspinatus (ISp), subscapularis (SSc), and three heads of triceps brachii (long (TLo), medial (TMe), and lateral (TLa) heads). Flexor group includes acromiodeltoideus (AD), spinodeltoideus (SD), teres major (TMa), cleidobrachialis (CB), cleidocervicalis (CC), biceps brachii (Bi), brachialis (Br), and brachioradialis (BRD) (here, CC may belong to the extrinsic muscle group mentioned below, but it acts on the elbow joint with CB, hence, it is included).

TLo, TMe, and TLa, elbow extensors, became active in the late swing phase, and maintained their activity during the subsequent stance phase. The onsets of these muscle activities were synchronized with each other, while in some cats, TLo activity preceded those of TMe and TLa. It was noted that duration of activity in TLo was shorter than in the other triceps muscles. SSc, ISp, and SSp, which act on the shoulder joint, were active nearly in phase with the elbow extensors, whereas their onset times in relation to that of TMe showed rather large inter-animal variation, and their duration tended to be longer than elbow extensors.

Activity of Br and BRD were alternated with that of the elbow extensors; they were typical elbow flexors. Inter-animal variations of both onset and termination

were less than those of shoulder extensors. Bi, which may also belong to the elbow flexor, showed additional bursts, prior to the typical flexor bursts. CC and CB were almost like Br and BRD but they became active earlier. Similar tendency was observed in shoulder flexors, TMa, SD, and AD. AD showed bursts not only in the swing phase but also in the stance phase.

With the normalized representation, elbow extensors were active from 0 to 60% (means of TLa and TMe), while elbow flexors were active from 73 to 95% (means of Br and BRD). The former was denoted by the extensor phase, the latter denoted by the flexor phase. EMG activities were usually described in connection with the movement-related phases, such as stance and swing phases. However, in the present study, EMG activities were of interest in relation to interneuronal activities during fictive locomotion (the following paper), in which the stance and swing phases make no sense. Therefore, active periods of any muscles described below will be referred to the extensor and flexor phases. From potentiometer recording of the elbow angle (two cats), the stance and swing phases were estimated as 12–80 and 80–112%, respectively (see Figs. 5 and 6).

Extrinsic forelimb muscles

In scapulae muscles, acromiotrapizeus (AT), spinotrapizeus (ST), and omo-transversarius (Om, levator scapularis ventralis) were active during the flexor phase, although weak extensor-like activity was observed in some cats (dotted lines in Fig. 3). Rhomboideus capitis (RCa), rhomboideus minor (RMi), serratus

Fig. 3. Active periods of extrinsic muscles. The same format as Fig. 2, except that the active period of elbow extensor (TMe) is shown at the bottom.

ventralis (SV), and levator scapulae (LV) were active during the extensor phase but the durations were longer than those of the elbow extensors. RCa was one of the muscles showing large inter-animal variation. It showed two active phases, one at the transition from the flexor to extensor phase, the other at the inverse transition, while main active period was extensor-like.

In the pectoralis group, the deep component of pectoralis major, PMa(d) was flexor- and/or extensor-like, while superficial component, PMa(s) rather flexor-like. Pectoantebrachialis (PAB) was clearly flexor-like. Latissimus dorsi (LD), extrinsic muscle inserting the humerus, was briefly activated just prior to bursts of the elbow flexor in 5 cats (one of them showed additional, weak discharges at the early extensor phase), or showed the extensor-like activities in 2 cats.

Distal muscles

Palmar flexors, including flexor carpi radialis (FCR), flexor carpi ulnaris (FCU), palmaris longus (Pal), and flexor digitorum profundus (FDP), were similar to each other. They had extensor-like activity, while the onsets delayed to that of the elbow extensors, except for FDP (u, the ulnar head).

In dorsiflexors, extensor carpi radialis (ECR), extensor carpi ulnaris (ECU), extensor digitorum communis (EDC), and extensor digitorum lateralis (EDL) made a subgroup; they started discharges in the middle of the flexor phase and maximal activity appeared just prior to the beginning of the extensor phase. They showed another distribution peak at the end of the extensor phase. Correspond-

Fig. 4. Active periods of distal muscles. The same format as Fig. 3.

Fig. 5. Summarizing diagram of electromyographic activity during forelimb stepping. Onset times of swing (upward arrow) and stance (downward arrow) are shown at the bottom; they were estimated from two experiments with potentiometer recording of elbow joint angle.

ingly, such muscles showed double discharges in many preparations. Abductor pollicis longus (APL) and extensor indicis proprius (EIP) were activated like EDC, EDL, and ECU, but double discharges were not clear. Inter-preparation variations were larger in dorsiflexor muscles than in palmar-flexor muscles.

Pronator teres (PrT) and pronator quadratus (PrQ) tended to discharge like flexor and extensor, respectively. Supinator (Sup) was often activated at two switching phases, from the flexor to extensor and from the extensor to flexor phase. Such three muscles were nevertheless characterized by large inter-animal variation.

Figure 5 summarizes the present results. Muscles were classified into 3 groups: extensors, flexors and others; the extensors were active with the elbow extensors and the flexors active with the elbow flexors. PrT, PrQ, Sup, and dorsiflexors of the wrist are classified as a separate group. Extensor and flexor groups were activated alternately. Nevertheless, the alternation was not strict; there was an extensive overlap among muscles positioned on the different joints. It was noted that in both extensor and flexor groups, the more proximal joint the muscle inserted, the earlier onset of active period it had.

Figure 6 illustrates overall activities of forelimb muscles. Cycle histogram of number of simultaneously active muscles (A) showed a single peak; a minimum appeared just before the flexor phase; then, active muscles gradually increased in number during the flexor phase, reached a maximum early in the extensor phase, which corresponded to the beginning of the stance phase, and then returned to the minimum. The cycle histogram of onsets of muscle activities (B) showed clear

A TOTAL ACTIVITY **B ONSET** **C TERMINATION**

NORMALIZED CYCLE PERIOD

Fig. 6. Overall forelimb muscle activity during stepping. Cycle histograms of number of active muscles (A), onset times of muscle activities (B), and their terminations (C). Up- and down-ward arrows, onset of swing and stance phase, respectively.

double peaks per cycle, corresponding to those of extensor and flexor groups, while the cycle histogram of terminations (C) showed triple or more peaks, among which two peaks at the ends of the extensor and flexor phases were for extensor and flexor groups, respectively. The other peaks occurred during the extensor phase, suggesting several components of muscle activities supporting the extensor phase.

DISCUSSION

The results are well consistent with those obtained from conscious, unrestrained cat for elbow and further distal muscles [10–13]. There are, however, discrepancies in some muscles; e.g., LD, TMa, and AT are reciprocal to those

observed in conscious animal [10]. In comparison with locomotion of conscious dog [18–20], LD, AT, ST, PMa, SD, and AD showed discrepancies. Such muscles act on the shoulder joint or the scapula. The most critical condition in the present study was usage of the stereotaxic frame. The animals were rigidly fixed in a prone position to the frame with the head and the thoracic spines. The treadmill installed under the frame was adjusted and fixed in height, so that the forelimbs (which extended downwards) just touched on the belt surface with the forepaw. Thus, during stepping, the head and vertebrae were not able to change in height from the belt surface as well as in the lateral position. This situation may provide an anomalous constraint on scapular and shoulder movements, which could result in the discrepancies of activity pattern.

Changeability of activity in proximal muscles can be also indicated by the finding that some shoulder flexors changed their activity pattern in different movements in the same decerebrate cats with the lower thoracic cord transected; they exhibited extensor-like activity in stepping while they did flexor-like in the one-step act, which may be one kind of proprioceptive placing reaction evoked in response to forcible caudad displacement of the corresponding limb [21].

As the present results are compared with the efferent pattern during fictive locomotion [22–24], it is noted that both have quite similar spatio-temporal pattern for distal muscles; e.g., double discharges in some dorsiflexor muscles during stepping movements were well consistent with double depolarization of membrane potential in those motoneurons [24]. Thus, it may be supposed that muscle activity pattern obtained from the present study reflects the output of the central pattern generator. The present study examined activities of almost all muscles involved in stepping. Neglecting differences in numbers of motoneurons innervating each muscle, one may suppose that the cycle histogram of number of simultaneously active muscles (Fig. 6A) reflects rhythmic change of overall motoneuronal discharges in the cervical enlargement. Motoneuronal discharges result from excitation of the central pattern generator as well as reflex pathways. Even so, the cycle histogram seems to express total output of the central pattern generator, because the central pattern generator primarily determines the spatio-temporal pattern of muscle activity during stepping. Further discussion on the central pattern generator will be made in the subsequent paper [9].

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