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Co-activation of ipsi- and contralateral muscle groups during contraction of ankle dorsiflexors

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Summary

Seventeen adult, healthy subjects, age 38.4 ± 0.24 years (mean \pm SEM) 7 of which were females, were studied. Each subject was seated on a specially designed chair with trunk and legs fixed and the foot strapped to a rigid plate that was attached to a load cell. The position of the strap was adjusted so as to lie across the foot at the level of the metatarsal bones. The knee and ankle joints were adjusted to 90 degrees. To record EMG activity, pairs of surface electrodes were placed over the belly of both the right and left tibialis anterior, quadriceps, hamstring and contralateral triceps surae muscles. Two experimental paradigms were used, A and B. In A the subject was asked to sustain maximum voluntary contraction (MVC) of the ankle dorsiflexors until the force decreased to 50% of the initial value; in B the subject was asked to carry out contractions of the ankle dorsiflexors for 6 seconds followed by 4 sec relaxation periods. The initial contraction was 20% of MVC followed by 40, 60, 80 and 100% of MVC which represented one cycle. The subject was asked to repeat this cycle 10 times. Voluntary contraction of ankle dorsiflexors was regularly accompanied by activation of other muscles, usually first in the same leg, later in the contralateral leg during MVC of ankle dorsiflexors. When intermittent contractions with step wise increments of force developed by the ankle dorsiflexors were carried out, co-activation of ipsilateral and contralateral muscle groups occurred before the force of the contracting muscles decreased. Our study shows a relatively regular pattern of co-activation of the muscle groups and this may be an indication that the source of the increased excitatory drive is a motor pattern generator. Under the conditions used here motor pattern generators might reveal features which are not apparent when excitability is not increased by voluntary contraction. The study of co-activation of other muscle groups during an isolated movement might be relevant for understanding the changes of motor control in patients with motor dysfunction.

Introduction

An important aspect of human performance is the ability to carry out well organized sequences of synchronized activation and suppression of defined motoneuron pools. The ability of the central nervous system (CNS) to achieve activation of discrete pools of mononeurons during a particular isolated, single-joint

movement has a component of coordination, which involves muscles in addition to those that are exercised. Failure to modify the activity of distant motoneuron pools may interfere with the performance of a single joint movement and could occur even before the exercised muscle group is no longer able to sustain the required force. Such a disturbance of the motor program may then lead to decreased performance which is often perceived as fatigue. Although fatigue is usually described as the inability of a muscle group to maintain a required or expected force (Edwards 1981), in colloquial language fatigue describes a generalized condition when an individual is no longer able to carry out a sequence of movements. This "fatigue", though diffi-

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cult to assess, may be more important for human performance than the decrease of voluntary force during movement of single joints that has been extensively studied and taken as a measure of human fatigue (Edwards et al. 1977).

Indications that the performance of individual muscle groups is influenced by changes of excitability within the CNS was already noticed by Welch (1898) at the end of the XIXth Century. The observation that the performance of the exercised muscle groups improves when the contralateral limb is exercised was further documented by Hellebrandt et al. (1956). Later the development of the technique that enabled simultaneous recordings of electrical activity from different muscle groups revealed the so-called "associated movements", where co-activation of synergistic proximal muscle groups occurred during sustained movement of the wrist (Fog and Fog 1963). This co-activation was a precisely patterned movement and was shown to be related to the motor task (Gellhorn 1947).

In addition to such patterned associated movements, Davis (1942) described that with increasing effort to maintain force in a particular muscle group, a large number of other muscles becomes active. An example of this is the finding that during maximal voluntary contraction (MVC) of the right hand, muscles of the left hand gradually became activated as well (Podivinsky 1964). In this case, the recruitment of the muscles of the left hand was related to the level of force developed by the muscles of the right hand. Thus, the unique ability of the CNS to selectively control individual muscles, or even motor units decreases during an effort to sustain force. It is, however, not clear whether this inability to isolate the activation of a discrete group of motor units in the working muscle is associated with the gradually developing decrease of tension of the exercised muscle or with the increasing effort that is required by the subject to maintain the required force.

In this study we attempted to assess the relationship between the decrease of force in the exercised muscle and the level of co-activation of other muscle groups in the lower limbs during voluntary movement. In order to test this, the subject was asked to maintain maximal voluntary force of a defined group of muscles (paradigm A) while simultaneous EMG recordings of other muscles were carried out. To avoid interference with possible local changes in the contracting muscle, in paradigm B, the exercise consisted of repeated contractions at increasing levels of force interspersed with periods of rest. These experiments are designed to test the hypothesis that when voluntary effort is increased in order to maintain a given force or to repeat stereotyped movement, the functional relationship between the excitatory and inhibitory influences of spinal motoneurons can be altered and this is reflected in the

co-activation of muscle groups that are not involved in the generation of force during the voluntary movement.

Material and methods

The present study was designed to examine the effects of sustained or intermittent exercise of the ankle dorsiflexors on the activity of other leg muscles on the ipsilateral and contralateral side.

Seventeen healthy adult subjects, age 38.4 ± 0.24 years (mean \pm SEM), 7 of which were females, were included in this study. Each subject was seated on a specially designed chair with the foot strapped to a rigid plate. The strap was attached to a load cell whose signal was amplified by a bridge amplifier. The position of the strap was adjusted so as to lie across the foot at the level of the metatarsal bones. The knee and ankle joints were at 90 degrees with straps to fix this position and a strap around the upper body to restrain trunk movements. The subjects were asked to place their hands in their laps. EMG activity was recorded using pairs of recessed cup surface electrodes placed with a 3 cm center to center spacing oriented on the long axis and centered over the muscle belly. The skin was prepared so that intraelectrode impedances were less than $5 \text{ k}\Omega$. The leads were connected to EMG amplifiers and recorded with sensitivity of 0.5–1.0 mV/cm for the exercised TA muscle and 0.2 mV/cm for all the other non exercised muscles with a frequency bandpass of 30 Hz to 1 kHz. All EMG channels were simultaneously displayed with load cell amplifier output (force) on a pen recorder and stored on a FM tape recorder (Fig. 1). To assess the force that could be developed by the dorsiflexors, each subject was asked to perform 2–3 brief MVCs and the equipment was adjusted accordingly.

Paradigm A

The 17 subjects for this study were divided into 2 groups. In group 1 (9 subjects), EMG was recorded from the exercised tibialis anterior (ExTA), ipsilateral quadriceps (IQ), hamstring (IH) along with contralateral quadriceps (CQ), and contralateral tibialis anterior (CTA). In group 2 (8 subjects), two separate recording sessions were carried out. In one recording session the left, and in another session the right leg was exercised. EMG was recorded from the ExTA, IQ, IH, along with CQ, CH and CTA. Three separate recordings were carried out during each session. The interval between these was 3 min. Subjects in group 1 had no visual feedback to monitor MVC, in subjects from group 2

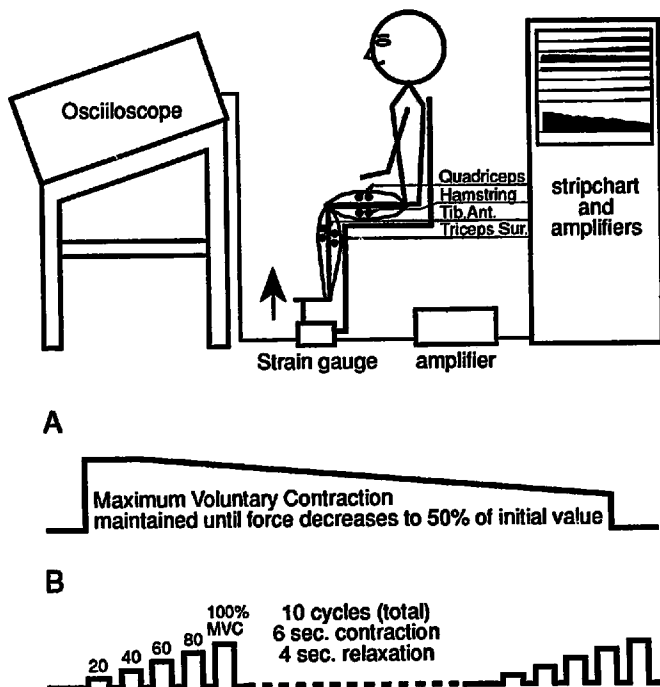


Fig. 1. Schematic representation of the method used for recording muscle force and EMG. The subject is seated in a specially designed chair, with one foot strapped to a rigid plate. Force developed during voluntary ankle dorsiflexion is measured by a load cell, amplified and displayed on the oscilloscope screen in front of the subject as well as on the strip chart recorder. Surface EMG is simultaneously recorded from ipsi- and contralateral muscle groups. The task to maintain MVC until force declines to 50% of the initial is shown in A, and the task of repetitive step-wise increase of voluntary contraction in B.

visual feedback was used. This consisted of a display of the level of force generated on an oscilloscope screen.

Paradigm B

Paradigm B was applied in subjects from groups 1 and 2 in separate sessions. The experiment consists of 3 short attempts to generate MVC from which readings of maximal force were obtained. The screen of the oscilloscope was then set up so that the subject could monitor the generation of 20%, 40%, 60%, 80% and 100% MVC during 6 sec of contraction followed by 4 sec of rest. The subject began the first cycle of exercise by increasing the contraction after each rest period of 4 sec from 20 to 100% in 20% increments. This cycle was repeated ten times. This paradigm was similar to that used by Bigland-Ritchey et al. (1986).

Data were analyzed manually for onset of co-activation using an amplitude of 20 μ V as the amplitude at which a muscle was considered to be active. The time from the beginning of the exercise to the first co-activation of any non exercised muscle group was used for the calculation of average onset time (delay) of co-activation. In addition the 20 μ V minimum was also used to establish the sequence in which muscles were co-activated.

Results

Sustained maximum voluntary contraction of ankle dorsiflexors

In this series of experiments (group 1), the subjects were asked to develop MVC of their right ankle dorsiflexors without any visual feedback. During the trial, the force was initially maintained and the time needed for the force to decrease to 50% of its initial value was 65.9 ± 8.29 sec. At this point the recording was ended. In addition to force recordings from the ankle dorsiflexors, EMG was simultaneously recorded from the exercised as well as several other ipsi- and contralateral muscle groups. Figure 2A shows an example from such a recording session. Simultaneously recorded EMG activity from the exercised muscles showed a gradual decrease of amplitude and frequency. Sustained MVC of the dorsiflexors in one leg was always accompanied by EMG activity in other muscle groups (Fig. 2A). Co-activation usually occurred first in mus-

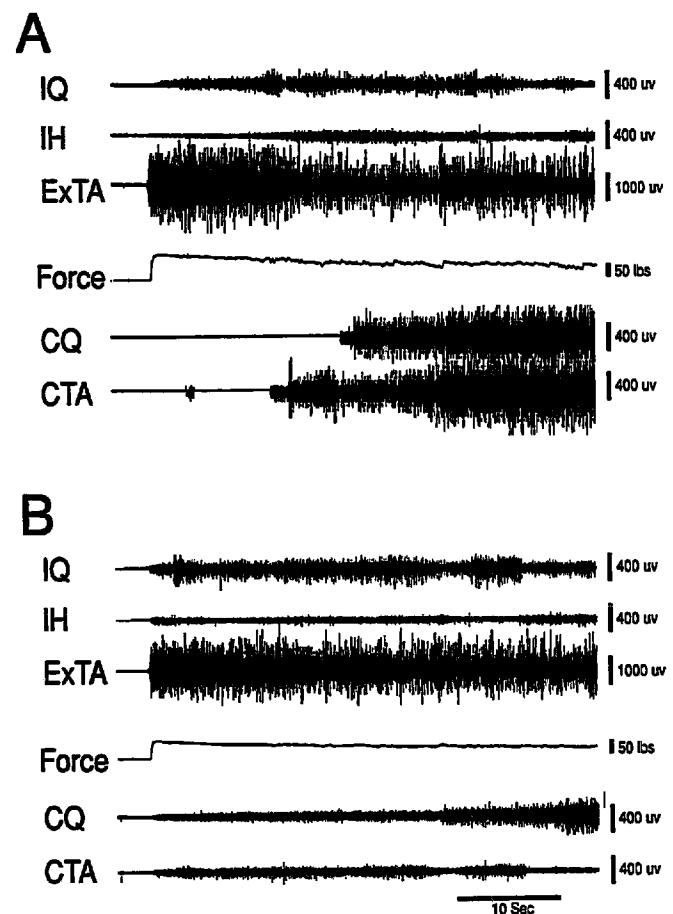


Fig. 2. Records of surface EMG from ipsilateral quadriceps (IQ), hamstrings (IH), voluntarily contracted tibialis anterior (ExTA), contralateral quadriceps (CQ) and tibialis anterior (CTA) are shown along with a record of force during sustained MVC. In A the recordings were carried out without visual feedback, in B with visual feedback. The recordings in A and B were carried out in 2 different subjects.

cles on the ipsilateral side, followed by activity on the contralateral side (TA, Q). While the muscles on the ipsilateral side were active the force of the dorsiflexors was still maintained; contralateral muscle groups were more often activated when the force of the exercised TA muscle decreased. Results obtained from such recordings are summarized in Fig. 3. It shows that ipsilateral co-activation occurred before there is any reduction in force developed by the exercised muscle. The contralateral muscle groups were activated when MVC force dropped to $79.1 \pm 3.7\%$ (Fig. 3A). Figure 3B illustrates the delay in the onset of activation of ipsilateral and contralateral muscle groups. This was 4.2 ± 3.6 sec for the ipsi, and 21.9 ± 5.1 sec for the contralateral muscle groups. Thus the time to co-activate the ipsilateral muscles was less than that for the contralateral muscles.

In group 2, the same test was carried out with the addition of visual feedback of force developed by the dorsiflexors. An example of such an experiment is shown in Fig. 2B. In this group, co-activation of ipsilateral muscles occurred before the force declined and contralateral muscles were co-activated when the force declined to $89.8 \pm 1.7\%$ (Fig. 3A) of its initial value. There was no delay in the onset of activation of ipsilateral muscle groups (IQ, IH) and the delay of onset of activation of contralateral muscles was 7.5 ± 4.7 seconds (Fig. 3B). The availability of visual feedback sig-

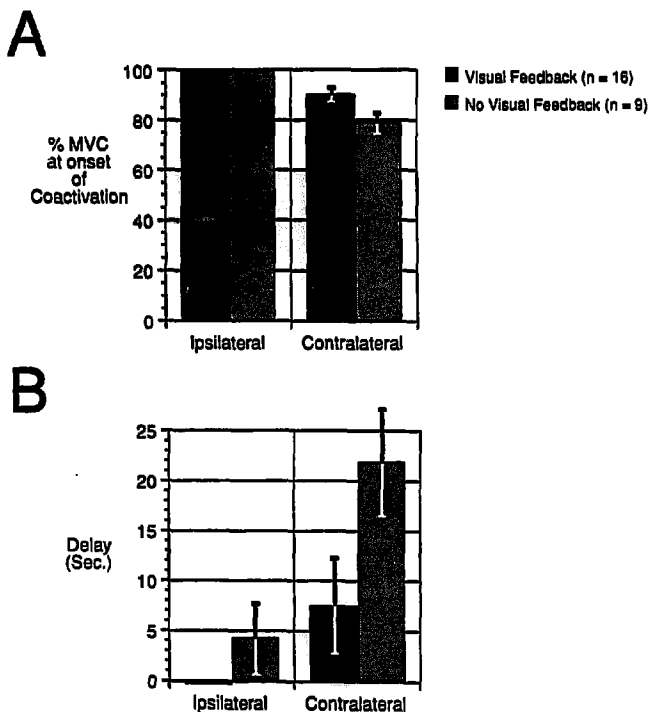


Fig. 3. (A) Summary of the force expressed in % of MVC developed by ankle dorsiflexors at which ipsilateral and contralateral muscles are co-activated with and without visual feedback. (B) Delay in co-activation of ipsilateral and contralateral muscles. Vertical bars indicate \pm SE.

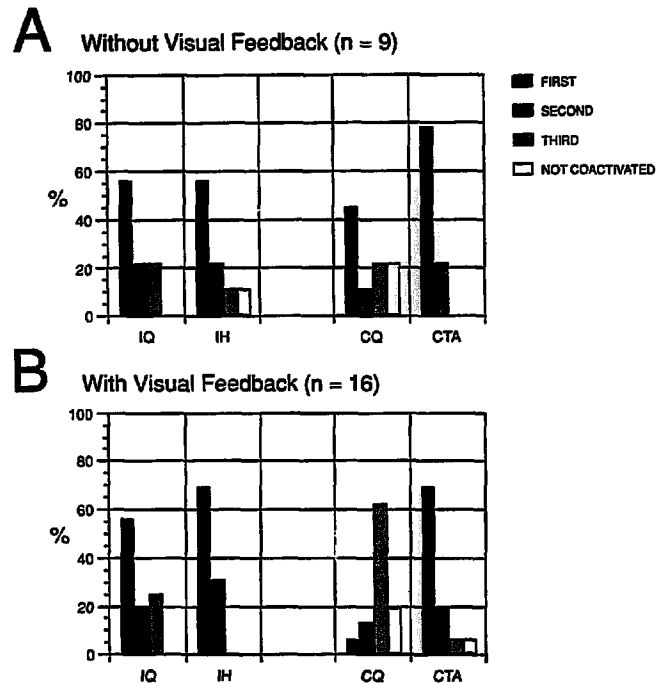


Fig. 4. Sequence of co-activation of different muscle groups is shown. The percentage of subjects that co-activated particular muscle groups first, second, third or not at all was calculated. A shows results without, and B with visual feedback provided.

nificantly shortened the delay at which co-activation of both ipsi- and contralateral muscles occurred ($P < 0.05$).

The recruitment order of the various muscle groups on the ipsi- and contralateral sides was also examined. All recorded ipsilateral and contralateral muscles were usually co-activated, but the order of co-activation was different in individual subjects. A summary obtained from both group 1 and group 2 is shown in Fig. 4. The results were calculated so that the number of subjects in whom a particular muscle group was co-activated first, second, third or not at all is expressed as a percentage of the total number of subjects (100%). It can be seen in Fig. 4A that in group 1 (without visual feedback), the IQ responded first in 56%, second in 22% and third in 22% of subjects. The IH was the first responding muscle in 56%, sometimes simultaneous with IQ, the second in 22% and third in 11% and did not respond at all in 11% of all subjects tested. Of the contralateral muscle groups, CTA responded first in 78% of the total number of subjects and as the second in 22%. The CQ responded as a first muscle in 45%, second in 11%, third in 22% and not at all in 22%. Figure 4B illustrates the sequential order of co-activation of unexercised muscles in subjects from group 2 that had visual feedback. The IQ co-activated first in 56%, second in 19% and third in 25% of the recording sessions. IH co-activation occurred first in 69% and second in the remaining 31% of the recording sessions.

CQ was first to co-activate in only 6%, second in 13%, third in 62% and failed to co-contract in 19% of the recording sessions. The CTA was co-activated first in 69%, second in 19%, third in 6% and did not co-activate in 6% of the recording sessions. When comparing Fig. 4B to Fig. 4A, it can be seen that the effect of visual feedback is minimal on the IQ, IH, and CTA. However, CQ is more readily co-activated without visual feedback.

Intermittent contractions of increasing strength of the ankle dorsiflexors

All subjects were asked to perform an exercise consisting of 6 sec contractions at 20, 40, 60, 80 and 100% of their MVC interrupted by 4 second rest periods, as previously described (paradigm B, see Fig. 1). With repeated contractions of dorsiflexors, the amplitude of EMG activity of the exercised and non-exercised muscles increases. An example of a recording from one subject during the first and tenth exercise cycle is shown in Fig. 5A and B. Fig. 5A also shows that ipsilateral muscles can be coactivated even in the first cycle at 20% of MVC and contralateral muscles at 40%

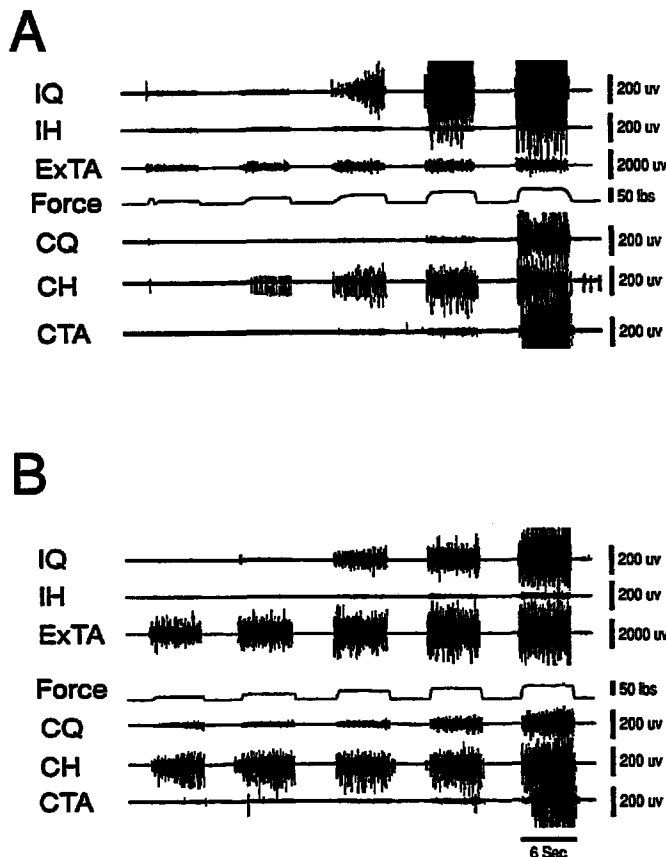


Fig. 5. Records of surface EMG from IQ, IH, ExTA, CQ, CH, CTA are shown along with a record of force during intermittent dorsiflexion at 20, 40, 60, 80 and 100% of MVC. This cycle was repeated 10 times. The first cycle is shown in A and the 10th cycle in B from a single recording session.

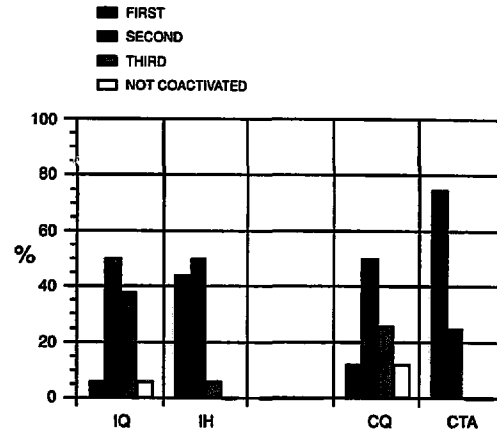


Fig. 6. The sequence of co-activation of different muscle groups during intermittent contractions is shown. The percentage of subjects that co-activated particular muscle groups first, second, third or not at all was calculated as described for Fig. 4.

of MVC. More co-activation was seen when the force reached 60, 80 and 100%. With repetition of the contractions, the magnitude of the responses increased and, finally, EMG activity increased in nearly all muscle groups when exercised muscles developed 60% of MVC.

The cycle in which co-activation began to occur ranged from the first to the tenth within the group of subjects. Figure 6 is the summary of data recorded with experimental paradigm 2, i.e. intermittent contractions of increasing strength of the ankle dorsiflexors, collected in the group of 8 subjects from group 2. The calculations were carried out as in Fig. 4 to show the percentage of subjects in which particular muscle groups were co-activated first, second, third or not at all. It can be seen that IQ was the first ipsilateral muscle co-activated in only 6%, second in 50%, third in 38% and not at all in 6%. IH was co-activated first in 44%, second in 50% and third in 6%. CQ co-activation occurred first in 12%, second in 50% third in 26% and not at all in 12%. CTA co-activation was seen first in 75% and second in 25% of the recording sessions. When taken together, the following observations can be made: (1) IH precedes IQ in co-activating; (2) CTA is the earliest contralateral muscle to be activated. If we compare this finding during intermittent contractions with findings of co-activation during sustained ankle dorsiflexion in group 2 (Fig. 4B), there is little difference in the sequential order of co-activation.

Discussion

In this study surface EMG recording electrodes were used to assess motor activity of individual muscle groups. While this method gives information on the

overall activity of the muscles studied it has the drawback that occasionally, due to spacial spread of the EMG signal from the exercised muscle, some electrical activity can be recorded from other, neighboring or antagonistic muscle groups which are in fact silent. This spread is usually referred to as cross-talk. In the present study, where the ankle dorsiflexors were exercised, such cross-talk is most likely to be recorded by electrodes placed over the triceps surae. We have found by recording simultaneously from the dorsiflexors and the triceps surae that about 6% of the signal during a brief MVC of the ankle dorsiflexors may indeed be picked up by the triceps surae electrodes. This value is similar to the average value of 5.0% reported by Merletti and De Luca (1988). In addition, the triceps surae may be co-activated during dorsiflexion of the ankle joint in an involuntary attempt to stabilize the ankle. In view of these circumstances, which could complicate the interpretation of our results, we have omitted in this study data obtained from the plantar flexors.

The results of this study show that co-activation of several muscle groups of the lower limbs during isometric, unilateral ankle dorsiflexion is regularly seen. It occurs first in muscles that are ipsilateral to the exercised muscle. Among contralateral muscles, the TA is preferentially co-activated in most subjects. This was the case no matter whether a continuous or intermittent contraction was used. Visual feedback increases the extent of co-activation and reduces the delay. These typical features of co-activation indicate that it is a centrally organized phenomenon.

To perform an isolated movement of a joint requires, in addition to excitation of the motoneurons to the working muscle, specific inhibition of motoneuron pools to other muscles as part of the motor program developed by the CNS. Co-activation of motoneuron pools to muscles not involved in the required movement may occur when the central inhibitory drive fails, or when the central excitatory drive is high enough to overcome the inhibitory components of the motor program.

The mechanisms that leads to the observed co-activation of other muscle groups are not clear. Local changes in the exercised muscle might be involved in triggering this process. However, this is unlikely in view of the present finding that intermittent exercise induces similar co-activation as sustained contractions. Intermittent exercise used in this study does not cause metabolic changes associated with muscle fatigue. This was verified using NMR spectroscopy by Moussavi et al. (1989). The perception of imminent failure to produce the required force may, even in the absence of peripheral muscle fatigue, nevertheless initiate changes in the CNS that lead co-activation of other muscle groups.

Goal oriented associated movements were described by Gellhorn (1947). He found by using multichannel EMG recordings from the forearm and arm muscles that when the hand is moved toward the body, regardless of the orientation of the palm, co-activation of the biceps was seen, while moving the hand away from the body, the triceps muscle was co-activated. These results show that the associated movements follow a regular pattern. The co-activation of ipsilateral muscles during an attempt to activate ankle dorsiflexors seen in this study could be part of a goal-oriented response suggested by Gellhorn (1947). However, the co-activation of homologous muscles in the contralateral leg seen here can not be part of a planned movement. Such activity could impair motor performance and, therefore, contribute to fatigue. Movements of contralateral muscles during efforts to maintain force of the exercised muscle group have been described for the upper limb where, as in the present recordings, homologous muscles of the other hand were co-activated (Green 1967).

Co-activation of muscles in the upper limbs was discussed as associated movements (Fog and Fog 1963, Abercrombie et al., 1964, Zulch and Muller 1969), motor overflow (Yensen 1965, Stern et al. 1976) or synkinetic movement (Cambier and Dehen 1977). Though using different terminology all these reports described unintended movements that accompanied a planned task. The primary manifestation of these unintended movements is usually found in the contralateral, symmetrical muscle groups (Hellebrandt and Waterland 1962, Fog and Fog 1963, Missiuro 1963, Todor and Lazarus 1986). This is consistent with our results that, in most individuals tested, the activation of the contralateral homologous muscle groups preceded that of the heterologous muscles which often displayed motor unit activity only with a greatly increased effort. It appears, that with increasing effort to sustain an isolated movement, the mechanisms that usually accomplish this no longer function.

At present, we can only hypothesize at the events in the CNS that bring about these changes. During increasing effort to maintain an isolated movement there may be a general increase in excitability which could spread to other pools of motoneurons, so that previously subthreshold input may become effective. Such non-specific spread of excitation could then produce a relatively uncoordinated co-activation of other muscles. Our experiments show a relatively consistent pattern of co-activation of the muscle groups and this may indicate that the source of the increased excitatory drive is a motor pattern generator. Alternately it could be that there is a constant level of excitatory drive from supraspinal structures, and that the effort needed to sustain the contraction at a particular force prevents precise control mechanisms from operating adequately.

Our results favor the first possibility, for an increase in "attention" through visual feedback led to a more instantaneous co-activation of other muscle groups. There is also evidence from studies of cerebral evoked potentials, movement related potentials (MRP), that when associated movements are successfully inhibited, the negativity of MRP or the readiness potential is confounded by an overlapping slow activity (Chisholm and Karrer 1988). According to Chisholm and Karrer this alteration in MRP may be related to the effort needed to inhibit associated movements in order to perform a sharper and more discrete response. However, when the goal is to maintain constant force then feedback most probably works against the organization of such "sharper and more discrete response" of the premotor, frontal lobe of the brain involved in the planning and initiating of voluntary movement. Independently, Freude and Ullsperger (1987) in their study on MRP during fatiguing and non-fatiguing hand movements reported more profound changes in the negativity of readiness potentials when the subject performed repetitive movements sustaining 20% of MVC as opposed to much smaller changes in MRP when repetitive hand contractions were 50% of MVC. Therefore, when we attempt to perform repetitive motor tasks, there are changes not only within the executive system of motor control but also in a series of corresponding brain events involved in initiating and planning movements before their neurocontrol is set and executed.

Further studies will be necessary to elucidate which of the underlying mechanisms of motor control are primarily responsible for the reduction of the ability to perform specialized motor tasks during increased effort to sustain force.

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