

# The Role of the Motor Cortex in the Control of Axial and Proximal Muscles in Learning

O. G. Pavlova, V. N. Mats, and V. N. Ponomarev

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The involvement of the motor cortex in controlling the muscles of the shoulder and scapula during formation of a new motor coordination of the head and forelimb was studied in dogs. Dogs were trained to flex the forelimb to operate a lever to raise a bowl containing food and hold it up during feeding with the head tilted towards the feeder. At the early stage of training, raising of the limb occurred with anticipatory upwards displacement of the head and, on lowering the head to the feeder, lowering of the elevated limb; this is the natural coordination of head and limb movements. The new coordination needed to obtain food – maintaining the elevated limb in a posture with the head lowered – could be achieved only as a result of learning and was critically dependent on the integrity of the motor cortex. In the natural coordination, limb elevation consistently involved the main shoulder flexors, i.e., the deltoid and teres major muscles, and inconsistently involved teres minor, infraspinatus, supraspinatus, and trapezius. In this latter group, muscles often operated in antiphase to the main shoulder flexors, i.e., were active on standing and stopped being active before limb elevation. Learned limb elevation in the posture with the lowered head involved all the muscles listed, some rearranging their initial activity to the opposite. Lesioning of the greater part of the forelimb representation in the motor cortex in trained dogs led to recovery of the natural coordination of head and limb movements and the initial muscular pattern during limb elevation. Thus, it was only with involvement of the motor cortex that the initial pattern of the activity of the phylogenetically ancient axial and proximal musculature underwent rearrangement and started to operate in a new way.

**Keywords:** motor cortex, learning, rearrangement of innate coordination, electromyogram, shoulder and scapula muscles.

The role of the motor cortex (MI) and pyramidal tract in motor activity is predominantly associated with fine, precise movements of the hand. This is evidenced by results obtained from numerous studies not only in primates [7, 15, 17, 22], but also carnivores (cats and dogs) [11, 12]. The involvement of the MI in controlling the phylogenetically more ancient and less differentiated proximal and axial muscles has received little study. Most studies to date have addressed the activity of MI neurons during stretching of the hand towards an object (reaching) and on walking, i.e., motor coordinations which have already been developed during ontogeny. In monkeys, MI cells have been shown to

respond to changes in the angular rates of the elbow and shoulder joints [21]; the responses of MI neurons sensitive to changes in hand position in space depend on hand position [23, 24]. Belozerova et al. [8] observed modulation of the activity of neurons controlling forelimb movements in cats on walking across a smooth floor; walking across the rungs of a horizontal ladder, which requires accuracy of movement, was associated with a sharp increase in the activity of these cells. Monkey experiments reported by Graziano et al. [13] showed that on use of prolonged (500 msec) electrical stimulation corresponding to the natural movement development time, the MI can induce hand movements with complex coordination, involving large groups of muscles. These movements are directed toward defined points in space or the monkey's body. The reproducibility of movement responses to stimulation of the MI

Institute of Higher Nervous Activity and Neurophysiology,  
Russian Academy of Sciences, Moscow;  
e-mail: pavlovaog@mail.ru.

in different animals points to their genetic determination. It remains unknown whether the MI is involved in constructing new patterns of proximal and axial muscle activity during learning.

Studies at the behavioral level have previously demonstrated [2, 3] the obligatory involvement of the motor cortex and its associated pyramidal fibers in mediating movements not seen in the innate set of movement activities. Examples of such movements are provided by learning-rearranged natural motor coordinations. In the present study, experiments on dogs addressed changes in shoulder and scapula muscle activity on rearrangement of a natural coordinated movement of the head and limb to an opposite coordination controlled by MI.

### Methods

Experiments were performed on six adult dogs (S2, S4, S15, S17–S19) in compliance with the requirements of the Institute of Higher Nervous Activity and Neurophysiology, Russian Academy of Sciences in relation to animal experiments and humanitarian principles as stated in the directives of the European Community (86/609/EC) and approved by the medical ethics committee. The involvement of the muscles of the elbow and shoulder joints and the scapula, i.e., biceps brachii, the deltoid, teres major, teres minor, infraspinatus, supraspinatus, trapezius, and the rhomboid [18] (Fig. 1) was studied in intact animals during raising of the forelimb at the early stage of acquisition of the operant reaction, at the late stage of learning, and in previously trained dogs after local lesioning of the MI.

**Behavioral reactions.** Animals were trained to a food-related operant reaction by the Popova method [6] (Fig. 1). During the experiment, dogs were placed on a bench in front of a closed feeder with a narrow window facing upwards. On the base of the feeder, food-containing bowls were placed around the circumference of a disk fitted with a repeater device. On each rotation of the disk, the next bowl appeared beneath the feeder window. Food was raised by pulling on a rod attached to the forelimb with a tight-fitting cuff. In order to receive food, the animal had to lower the head towards the feeder and flex the working limb at the shoulder and elbow joints to move the food-containing bowl to a location from which the food could be eaten and keep it in this position; the bowl went down when the limb was extended. The amplitude of tonic limb elevation varied from 10 to 15 cm in different animals. The amplitude of lowering the head towards the feeder was 10–20 cm from its initial position, i.e., when the dog could see directly ahead. The learning criterion was successful performance of the food-procuring skill with head and limb movements with stable time and amplitude characteristics. Experiments generally consisted of 15–20 trials with intervals of 30–90 sec.

**Surgery.** Surgery was performed in sterile conditions under ketamine anesthesia: premedication with i.m. 0.5% Relanium, 0.5 mg/kg; induction of anesthesia with i.m. 5%

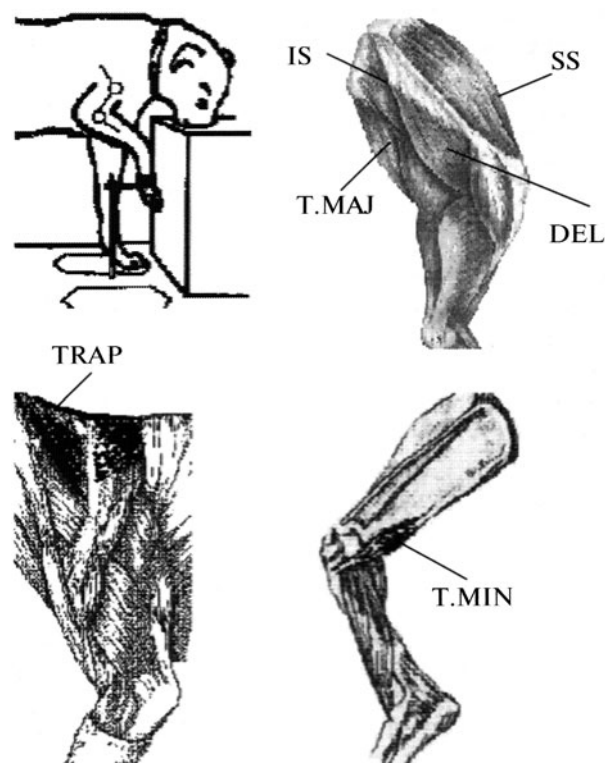


Fig. 1. Operant elevation of the forelimb and the muscles whose activity was studied during its acquisition. IS – infraspinatus; SS – supraspinatus; T. MAJ – teres major; DEL – deltoid; TRAP – trapezius; T. MIN – teres minor.

Callypsol, 5 mg/kg and 2% Rometar, 0.1–0.2 mg/kg; maintenance with a mixture of 5% Callypsol (1 ml), 2% Rometar (1 ml), and 0.9% saline (3 ml), 0.5–1.0 ml given i.v. during surgery when waking occurred. During surgery, animals were warmed with an electric heater; respiratory rate and heart rate were monitored periodically. After surgery, animals were given antiedema agents and long-acting antibiotics i.m.

All animals underwent chronic implantation of intramuscular recording electrodes, which consisted of pairs of steel multicore wires in Teflon insulation, deinsulated at the tip, with an external diameter of 0.3 mm (Cooner Wire, AS632, USA). The free ends of the wire were brought under the skin to the site of attachment of the socket to the dorsal surface of the neck. The socket, consisting of a cable and contacts [5] was attached to the skin with silk sutures. A protective double adhesive cloth tape, closely collaring the neck, was placed over this. The duration of recording through a given electrode was 2–8 weeks. Failed electrodes were replaced with new ones, placed in the same socket.

In dogs S4, S15, and S17, acquisition of the operant response was followed by removal of most of the representation of the “working” limb in the MI by subpial suction,

as defined by the muscle motor MI representation map for dogs [10].

**Recording.** Raising of the “working” limb was recorded using a potentiometer connected to part of the feeder elevation mechanism; vertical displacement of the head was recorded using a tensometric probe located 0.5 m above. The tensometric probe was connected to the head with a fine plastic filament attached at the level of the bridge of the nose to an elastic ring placed over the snout. Mechanograms were recorded on a personal computer with a step of 10 or 20 msec; mechanograms started at the moment the disk rotator was switched on for delivery of food.

Four electromyogram (EMG) leads were recorded simultaneously using an analog-to-digital converter, providing amplification of the input signal in the band 50–5000 Hz, with rectification and integration over time intervals of 10 msec. Integration results for each interval were digitized using a 12-channel analog-to-digital converter. Amplitudes were calibrated by delivering a sine-wave signal of amplitude 400  $\mu$ V and frequency 500 Hz to the input of the instrument. EMG traces were processed using a program to smooth myograms and mechanograms with a sliding mean of five points, along with averaging by alignment of curves relative to the beginning of limb elevation and to the moment of placing the paw on the support and calculation of the standard deviation (SD).

EMG recordings were made at the initial stage of acquisition of the operant response (dogs S17–S19), when limb elevation was performed with anticipatory deviation of the head upwards, at the stage of the acquired skill on raising of the limb in the posture with the head lowered (dogs S2, S4, S15, S17–S19), and in trained dogs after lesioning of the MI, which led to recovery of the natural head and limb movement coordination (dogs S4, S15, and S17).

**Histological verification.** After experiments, animals were euthanased by Nembutal overdose. Brains were extracted and fixed in 10% formalin solution, followed by histological processing and embedding in celloidin. Serial celloidin sections of thickness 40  $\mu$ m (every 5th section) were stained by the Nissl method and used to reconstruct the lesion.

## Results

**Muscular organization of limb elevation performed with simultaneous elevation of the head, i.e., the natural coordination.** At the early stage of training, attempts to obtain food from the feeder resulted in the dogs displaying a characteristic stereotypical coordination of head and working limb movements. When the animal lowered its head to the feeder and tried to bring the food-containing bowl to the snout by lifting the paw and lever, limb elevation was always preceded (usually by 100–300 msec) by an upward movement of the lowered head (mechanograms in Fig. 2, A and B). As a result, the head moved away from the feeder. Subsequent tilting of the head towards the food

induced extension of the limb and lowering of the bowl. The kinetics of the natural coordination have been described in more detail elsewhere [4].

The muscle pattern of limb elevation in trained dogs S17–S19 had both common and individual features. Limb elevation always activated the two major shoulder flexors, i.e., the deltoid (DEL) muscle and teres major (T. MAJ) (Fig. 2, A and B). Lifting of the lever with the paw involved simultaneous flexion of the shoulder and elbow joints, though activation of the elbow flexor biceps brachii (BIC) did not occur. This means that the decisive role in the limb elevation movement was played by flexion at the shoulder joint. Flexion at the elbow occurred passively, due to posterior displacement of the lower end of the humerus.

Apart from the two shoulder flexors identified above, some of the other muscles joining the scapula to the shoulder – teres minor (T. MIN), infraspinatus (IS), and supraspinatus (SS) – and the spine – the rhomboid (RH) – and neck – the trapezius (TRAP) – can take part in limb elevation. However, the pattern of the activities of these muscles were inconsistent from dog to dog and in individual dogs. Thus, instead of DEL and T. MAJ, dogs S18 and S19 showed activation of TRAP, dog S18 showed activation of T. MIN and dog S17 showed alternate activation of IS and SS. It was characteristic that at the early stage of training, these muscles often operated in antiphase with the two major shoulder flexor muscles. For example, in S17, T. MIN and TRAP (Fig. 2, A) and in S18 IS and SS (Fig. 2, B) were active during support on the working limb and showed cessation of activation prior to elevation of the working limb. RH behaved in this way in all three dogs. Thus, limb elevation with simultaneous head elevation consistently involved the two major shoulder flexors DEL and T. MAJ, while the activity patterns of most of the muscles studied were inconsistent.

**Muscular organization of learned operant limb elevation performed with simultaneous lowering of the head.** During training, the initial coordination of head and limb movements in dogs underwent a gradual rearrangement to its opposite, i.e., limb elevation came to be performed in a posture with the head lowered. Acquisition of this skill was accompanied by significant changes in the initial organization of the operant limb movement. In trained dogs S2, S4, S15, S17–S19, limb elevation was characterized by a new and more complex muscle pattern. Activation of the two major shoulder flexors was supplemented by activation of T. MIN, IS, SS, and TRAP. These muscles were synchronously recruited before limb elevation and simultaneously terminated their activity when the limb was placed on the support. Only RH continued to function as previously: it was active when the “working” limb was placed on the support and its activity ceased on elevation. In dogs S4, S18, and S19, BIC was often activated on limb elevation. The averaged traces in Fig. 3, A illustrate the stereotypical nature of both movement and muscle reactions. Figure 3, B

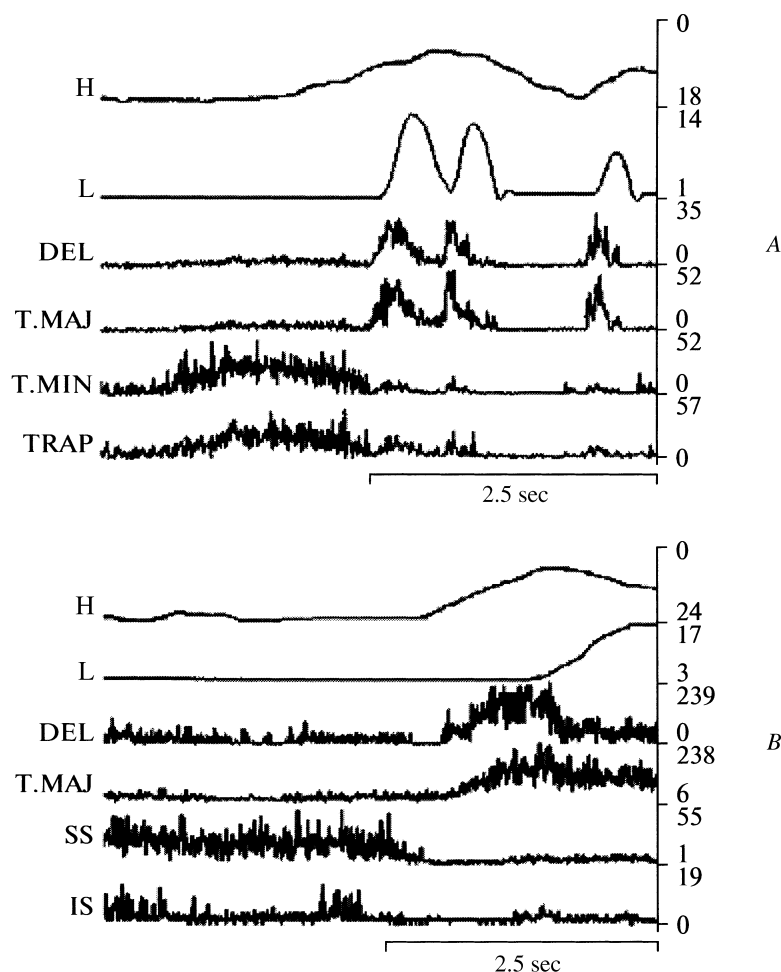


Fig. 2. Patterns of activity of shoulder and scapular muscles in dogs at the early stage of acquisition of the operant reaction, when limb elevation was performed with anticipatory upward displacement of head, i.e., as in the natural coordination. The vertical axes show the amplitudes of head (H) and limb (L) movements in the vertical plane, cm ("0" on the mechanogram corresponds to its position when the dog was standing looking directly ahead; downward deviations of the curve show lowering of the head; the initial position on the limb mechanogram was the position on the support; upward deviation corresponded to limb elevation), EMG amplitude, units (100 units corresponds to the sine wave calibration signal at 330  $\mu$ V). Muscles are identified in Fig. 1. See text for more detail.

shows the new activity pattern, common to different dogs, for T. MIN, IS, SS, and TRAP, which on limb elevation in the natural coordination operated differently. Thus, during training, a number of muscles not only acquired consistent activity, but also changed their initial activity to its opposite.

*Muscular organization of operant limb elevation in trained animals after lesioning of the MI.* Partial lesioning of the representation of the working limb in the MI in trained dogs S4, S15, and S17 led to loss of the learned skill and disintegration of the new muscle pattern for limb elevation. The initial means of elevating the limb, with concomitant elevation of the head, was restored.

As the limb area in the MI was partially lesioned, slow recovery of the operant reaction occurred 3–5 months after

surgery. (In complete ablation of the MI, as described previously [3], this motor skill was not restored.)

During recovery, interference between the initial and new coordinations of head and limb movements was seen over a prolonged period. Having lifted the food-containing bowl, the dog stopped letting the limb drop when lowering the head to the feeder, though the limb dropped with every tilt of the head and the subsequent elevation of the limb involved an anticipatory upward movement of the head. As a result, traces of head and limb movements during eating had a characteristic tooth-like appearance, which is clearly apparent in Fig. 4, A. The gradual return to elevation and maintenance of the limb in the position needed to receive food, with the head lowered, was accompanied by restora-

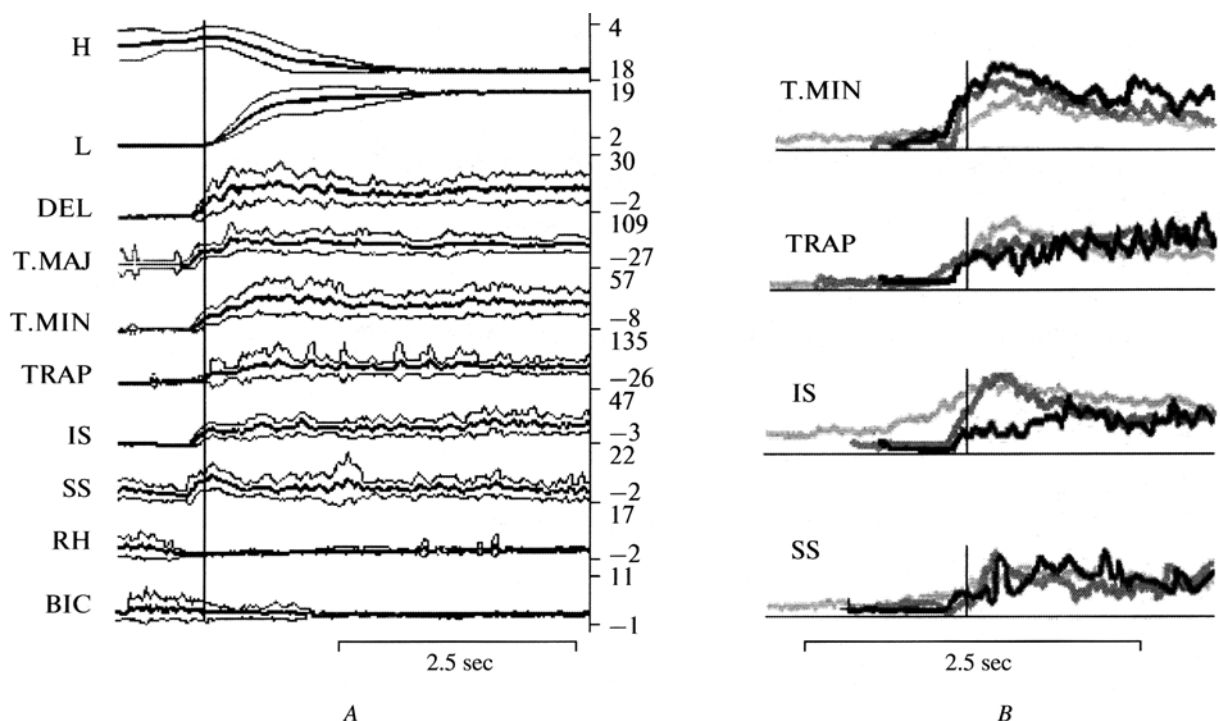


Fig. 3. New pattern of activity of shoulder and scapular muscles in dogs trained to elevate the limb in the posture with the head lowered. *A*) Averaged ( $n = 5$ ) mechano- and myograms of dog S17. Thick lines show mean values and thin lines show mean square deviations; vertical lines crossing the curves show the onset of limb elevation, which was used to align averaged mechano- and myograms. RH – rhomboid; BIC – biceps brachii; see Fig. 2 for further designations. *B*) Averaged myograms from dogs S4, S2, and S18 (dark, gray, and light lines respectively); calibration mark for teres minor: 282  $\mu$ V for S2, 411  $\mu$ V for S4, 157  $\mu$ V for S18; for the trapezius: 311  $\mu$ V for S2, 347  $\mu$ V for S4, 37  $\mu$ V for S18; for infraspinatus: 270  $\mu$ V for S2, 291  $\mu$ V for S4, 26  $\mu$ V for S18; frequency supraspinatus: 190  $\mu$ V for S2, 223  $\mu$ V for S4, 50  $\mu$ V for S18.

tion of the previously acquired limb elevation muscle pattern. Figure 4, *A*, and *B* shows that as in the learning process in intact dogs, partial lesioning of the representation of the “working” limb in the MI was followed by complete rearrangement of T. MIN activity.

## Discussion

Acquisition by dogs of a new coordination of head and forelimb movements, different from the initial, involved significant rearrangement of shoulder and scapular muscle activity. The new pattern of the activity of these muscles was critically dependent on the integrity of the MI. The data obtained here lead to the view that the previously described ability of the MI to control the activity of individual muscles is important not only for the acquisition of fine, precise hand movements involving phylogenetically younger distal muscles, but also for the construction of new motor coordinations involving the phylogenetically ancient axial and proximal musculature.

*The initial and learned coordinations – two different levels of organization of forelimb elevation.* The transfer from the initial motor coordination (limb elevation with anticipatory upward displacement of the head) to the new

learned coordination (limb elevation in the posture with the head lowered) reflects substitution of the means of elevating the forelimb. Externally similar limb elevation patterns in the natural and learned coordinations differ: a) in terms of their organization, i.e., they have different muscle patterns; b) in terms of their structural bases, i.e., limb elevation in the learned coordination is linked with the MI, but is independent of this structure in the natural coordination; c) in terms of origin: one means of limb elevation is common to all dogs, the other is achieved only as a result of learning. These two means of elevating the limb should, according to Bernstein [1], be assigned to different levels of movement construction. In the natural coordination, limb elevation is continuously linked with head elevation. At the beginning of training, despite the fact that head elevation moves the dog closer to the food, it repeats from trial to trial, stereotypically and stamp-like, with every limb elevation. These cooperative movements of the head and limb can be regarded as a synergy, while the new learned means of elevating the limb in the posture with the head lowered is assigned to the pyramidal level (field 4, i.e., the MI) [1].

There are grounds for the view that limb elevation in the natural and learned coordinations has biomechanical dif-

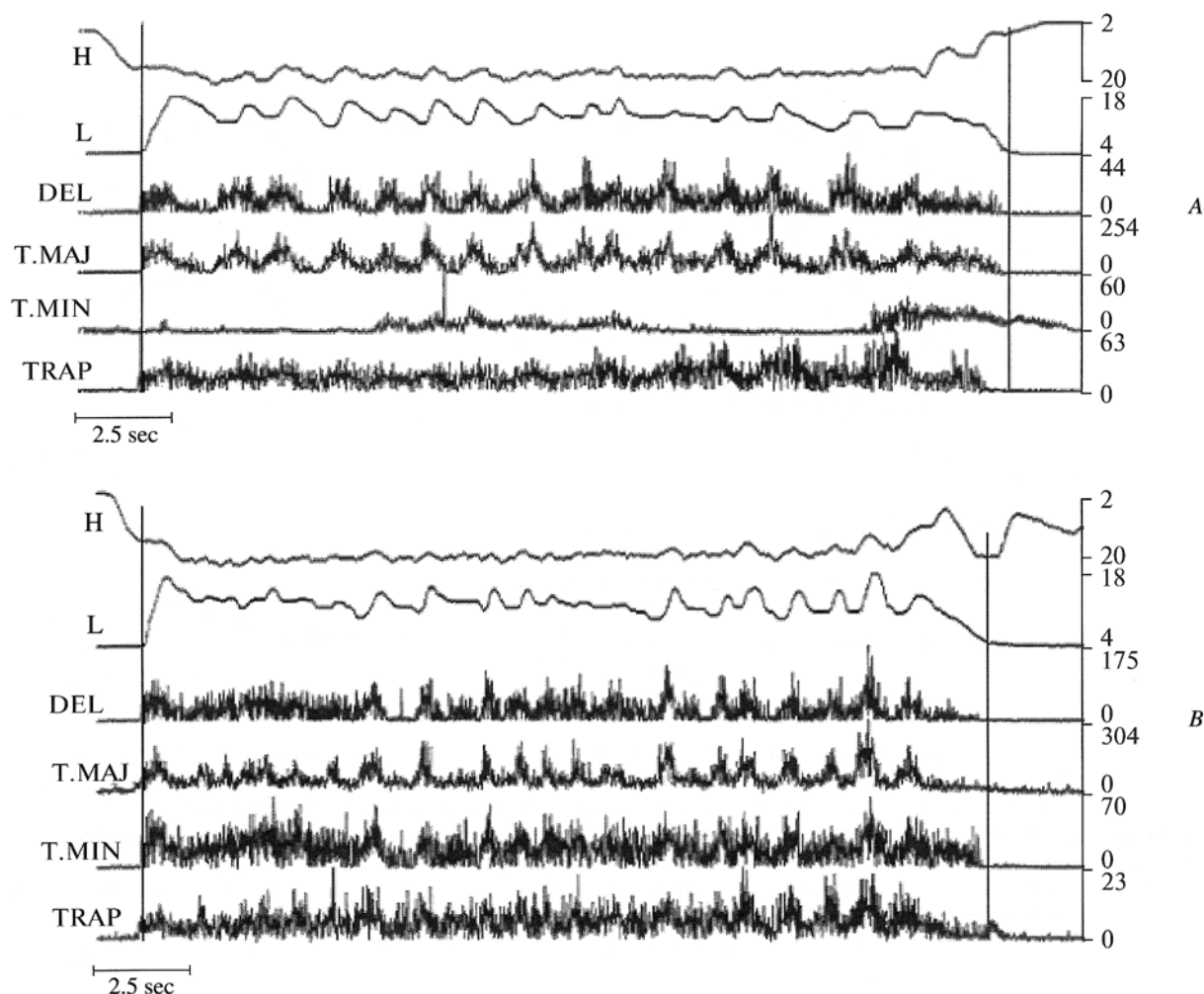


Fig. 4. Rearrangement of the activity of teres minor during restoration of the innate coordination after partial lesioning of the MI. A) At the beginning; B) at the end of restoration. Vertical lines show the beginning of limb elevation and placing the paw on the support. See caption to Fig. 2 for further details.

ferences. The actual movement of each component of the kinematic circuit is determined by the geometric sum of three components: 1) muscle strength; 2) external forces (gravity, environmental resistance, etc.); 3) reactive forces (muscle strength associated with the body's other, distal joint systems) [1]. We will consider the kinematic circuit including head and limb movements in dogs at the early stages of training. The forelimb of quadruped mammals does not have a strict articulation with the skeleton; the limb is connected to the scapula, which is held onto the body by muscles. Muscles running from the upper part of the scapula attach it to the head and neck. Thus, the scapula is an intermediate component between the head and the limb. Visual observations of the acromion on elevating and lowering the head show that the scapula rotates backwards on lowering the head and forwards on elevation of the head. The biomechanics of this natural coordination can be represent-

ed as follows. On elevation of the head anticipating elevation of the limb, the scapula is displaced forwards, which must lead to stretching of the major shoulder flexors DEL and T. MAJ, which run from the posterior border of the scapula to the shoulder (Fig. 1). Preliminary stretching of these muscles (on elevation of the head) allows them to develop greater contraction force on limb elevation. In the learned coordination, elevation of the limb was performed in different conditions, without accompanying elevation of the head. This was associated with changes in the organization of limb elevation, i.e., its muscular pattern. As Bernstein [1] emphasized, the greater the involvement of reactive and external forces in the movement, the more economically it is constructed in relation to the expenditure of active muscle exertion. The difference in the organization of limb elevation seen here in the natural and learned coordinations supports this view. In the natural coordination, head movement cre-

ates a reactive force on movement of the limb. And in this case, activation of a small number of muscles is sufficient for limb elevation. Of the muscles studied here, this applied to the DEL and T. MAJ. In the new means of elevating the limb without anticipatory elevation of the head, the muscle pattern showed a marked increase in complexity, DEL and T. MAJ being supplemented by T. MIN, IS, SS, and TRAP.

*Characteristics of muscle activation on limb elevation in the natural and learned coordinations.* The functions of a muscle are determined by the details of its attachments. The two shoulder flexors, DEL and T. MAJ, are always involved in any limb elevation, both with accompanying head elevation and in the posture with the head lowered. The T. MAJ muscle runs from the posterior border of the scapula to the posterior surface of the middle part of the humerus. Contraction of this muscle can only produce flexion of the shoulder, which decreases the angle between the posterior border of the scapula and the humerus. The major part of DEL starts at the surface of the scapula behind the acromion and, like T. MAJ, is attached to the middle part of the humerus, but to its anterior rather than its posterior part. As a result, it can take part not only in flexion of the shoulder, but also in maintaining its extension when the working limb provides support during standing. This double function is more clearly apparent for T. MIN and IS. T. MIN runs from the inferior part of the posterior margin of the scapula, the IS from the surface of the scapula behind the acromion; these two muscles clamp the head of the humerus and attach to its anterior surface. Contraction of these muscles can fix the position of the shoulder both in flexion and in extension. Cessation of the activity of these muscles before elevation of the limb in animals with the new head and limb movement coordination is explained by the fact that during training, the dog learned to unweight the working limb before the elevation. In trained dogs, T. MIN and IS are linked with the operation of the main flexors of the shoulder, increasing their actions on limb elevation apparently to a greater extent while holding the elevated limb during eating with the head lowered. Along with the flexors, operant limb elevation in trained dogs involves the extensors of the shoulder joint: the SS and TRAP. This coactivation of shoulder joint flexors and extensors evidently accounts for the accuracy with which movement tasks are performed [14], i.e., reliable fixation of the position of the shoulder joint in the holding phase. The single muscle whose activation persisted in trained dogs when resting on the working limb and ceased before limb elevation was the RH. This runs upwards from the base of the scapula and attaches to the spine with its partner on the opposite side. Contraction of the RH pulls the scapula towards the spine and fixes its position on resting on the other limb, and its inactivation releases the scapula for its displacement during limb elevation. The nature of BIC activity shows that the activity of this muscle is insignificant during limb elevation in the natural coordination, though its activation could play

an accessory role in some dogs maintaining the elevated limb in the posture with the head lowered.

*Contribution of the MI to controlling the axial and proximal musculature.* Rearrangement of the natural head and limb movement coordination during training is accompanied by the formation of completely new patterns in the activity of the phylogenetically ancient axial and proximal muscles of the shoulder and scapula. The MI plays the decisive role in organizing these patterns. Lesioning of the MI led to loss of the learned movement, and the muscle pattern concomitant to this movement undergoes disintegration and the initial pattern was restored. Especially indicative of the role of the MI in learning was the observation that on substitution of the initial means of elevating the limb by the new means, a number of muscles (T. MIN, IS, SS, TRAP) acquired the opposite actions. This rearrangement may be a manifestation of the ability of the MI to control individual muscles. Cabel et al. [9], having recorded a link between neuron activity and overcoming an isolated load on each of the main joints of the upper limb, showed that the MI is involved in the voluntary control of the proximal limb muscles. A clear example of the precise control of the axial musculature by the motor cortex may be provided by the exact prehensile movements of the tail in short-tailed opossums based on monosynaptic connections of the MI with the sacral segment of the spinal cord [19].

The hypothesis that the motor cortex may be very important for the voluntary control of not only the distal, but also the phylogenetically ancient muscles, was first demonstrated in the studies reported by Kuypers [16], who found monosynaptic terminals of pyramidal fibers on motoneurons in the thoracic segment of the spinal cord in humans, these cells innervating the intercostal respiratory muscles. Phillips and Porter [20] suggested that these connections of the cortex with the spinal cord may allow control of the respiratory musculature during speech and singing, creating new patterns of activity for old (axial) muscles. Our dynamic experiments showed that during learning a new means of elevating the limb, the MI produced different changes to the activity of individual muscles in different animals, creating a completely new muscle pattern, albeit common to all the animals.

## Conclusions

1. Different involvements of the muscles of the shoulder and scapula were demonstrated in two means of elevating the limb with flexion at the shoulder joint: a) in the natural coordination with anticipatory upward movement of the head and b) in the learned limb elevation performed in a posture with the head lowered.

2. In the natural coordination, not involving the MI, limb elevation was accompanied by regular activation of the two large shoulder flexors, the deltoid and teres major. Teres minor, infraspinatus, supraspinatus, and trapezius had different roles in limb elevation. These muscles often oper-

ated in antiphase with deltoid and teres major, i.e., they were active during support on the working limb and terminated their activity on limb elevation.

3. The learned limb elevation in the posture with the head lowered, controlled by the motor cortex, was achieved via significant changes in the muscle pattern. Along with the deltoid and teres major muscles, teres minor, infraspinatus, supraspinatus, and trapezius were activated, the latter often replacing their initial activity with the opposite.

4. The role of the MI in controlling phylogenetically ancient axial and proximal muscles is to organize, during the process of learning, new muscle patterns distinct from the innate patterns, allowing movements in accordance with changing environmental conditions. Exclusion of the MI led to loss of the learned and recovery of the ancient patterns of muscle activity.

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