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The Roles of Various Projection Areas of the Motor Cortex in the Reorganization of the Natural Coordination of Head and Forelimb Movements in Dogs

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A food-related operant reaction was developed in dogs, in which animals had to maintain tonic elevation of the forelimb to hold a bowl while eating with the head tilted towards the feeder. The acquisition of this reaction involved rearrangement of the natural coordination of head and limb movements which appeared at an early stage of training of the dogs. Forelimb elevation was initially accompanied by anticipatory raising of the head, while lowering of the head led to lowering of the elevated limb. Limb elevation could only be maintained in the posture in which the head was raised. The new coordination required for obtaining food, contrary to the innate coordination and consisting of tonic elevation of the limb with the head lowered, could only be achieved as a result of training. Previous studies have established that lesioning of the primary motor cortex (MI) in the hemisphere contralateral to the working limb leads to stable impairment of the learned coordination, with regression to the initial coordination. The present report describes studies of the effects of local lesions of various projection areas of MI on performance of the learned coordination. Dogs which had acquired the learned operant reaction requiring the new head/limb coordination showed impairment only after lesioning of the representation area of the working limb in the MI; lesioning of the representation area of the head had no such effect.

KEY WORDS: motor cortex, head/limb movement coordination, rearrangement of natural coordination, operant learning.

Ioffe established from studies on dogs [2] that the performance of motor skills acquired as a result of rearrangements of natural coordinations to their opposite coordinations depends on the integrity of the motor cortex (MI) and pyramidal tract. An example of such a skill is provided by a food-related operant reaction involving the tonic maintenance of the limb with a lever which the animal uses to hold a food-containing bowl during eating, with the head tilted towards the feeder [5]. At the early stage of training, all dogs showed a stable initial relationship between head movement and forelimb movement. Elevation of the limb occurred with anticipatory upward displacement of the head, while lowering of the head led to lowering of the limb [4, 13]. The simultaneous maintenance of limb elevation with the head lowered required to obtain food, a coordination contrary to the initial coordination, could only be achieved as a result of special training. Ablation of the MI on the side contralateral to the working limb in trained dogs was found [13] to lead to stable impairment of the learned coordination and regression to the initial relationship between head and limb movements. However, when the method of food delivery was altered such that the dogs could eat with the head held high, maintenance of the elevated limb became possible. This led to the conclusion that it was not the local limb movement that depended on the MI, but rather the new coordination of head and limb movements.

The mechanism by which the MI is involved in rearrangement of the initial coordination in dogs has thus far not been studied, and it has not yet been possible to explain the rearrangement on the basis of existing knowledge of the motor functions of the MI [6]. Experiments on other animals have demonstrated that the MI plays an important role

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in controlling the distal parts of the forelimbs – fine wrist movements in cats [11] and finger movements in monkeys [7], which is associated with the ability of MI neurons to perform highly differentiated muscle control [15]. The role of the MI in controlling more ancient axial and proximal muscles, covering large areas of the body which are also represented in the MI, is significantly less well understood. The coordination which we have studied in dogs involves these parts of the musculature.

Ioffe proposed an original hypothesis [2] that "during the acquisition and performance of a new motor coordination, the pyramidal system evidently transmits specialized corticospinal influences inhibiting innate coordinations which hinder performance of the learned reactions" (p. 93). It was suggested that inhibition can affect both some center controlling the innate motor reaction and some of the movements involved in the initial coordination. In dogs trained to the food-related operant reaction, these movements include the raising of the head which accompanies limb elevation, as well as lowering of the limb occurring when the head is lowered. Thus, there are grounds for suggesting that reorganization of the initial coordination may involve both the whole of the MI and its individual projection zones. The aims of the present work were to use local lesioning of different areas of the MI to determine whether only the representation areas of the head and working limb are involved in organizing the learned coordination and to identify the relative importance of each of these areas or whether the integrity of the whole of the MI is needed for the new coordination such that damage to any part would lead to regression to the initial coordination of head/limb movements. Changes in the learned coordination were studied in three groups of dogs after local lesioning of the area corresponding to the working limb, the bilateral projections of the head and neck, and an area with no direct involvement in controlling head and limb movements. The hindlimb representation zone was chosen as the last of these areas.

METHODS

Experiments were performed using eight adult dogs weighing 11–18 kg. All animals were initially trained to a food-related operant reaction by the Popova method [4, 5] (Fig. 1, *A*). During experiments, dogs were placed on an experimental bench in front of a feeder which was a closed cell with a small, round opening at the top, into which the animal could insert only the narrow part of its snout. The upper edge of the feeder was located at the mid-chest level of the dog. Food (50-g portions of sausage meat) were delivered in small bowls around the edge of the rotating disk at the bottom of the feeder. On each rotation, accompanied by a sharp click, the sequential food portion was placed under the opening in the feeder. In order to take the food, the dog had to lower its head to the feeder and flex the forelimb, attached to a lever (a vertical bar) to lift the bowl to the snout and maintain it in this position during eating; lowering of the limb led to lowering of the bowl. Depending on the size and body proportions, the magnitude of the dog's limb elevation during eating ranged from 10 to 15 cm from the level of the support and lowering of the head was from 10 to 20 cm from its lower position, when the dog was looking directly ahead. Animals were trained to perform the operant reaction initially with one and then with the other limb.

After training, animals of group I (D4 and D16) underwent ablation of the medial third of the MI, including the projection zone of the lumbar area and hindlimbs in the hemisphere of the working limb; dogs of group II (D2, D3, and D5) underwent ablation of the medial third of the MI in both hemispheres, including the projection of the head and neck; dogs of group III (D4, D15, and D17) underwent ablation of the lateral third of the MI, which includes the major part of the projection of the working limb. With the aim of improving the differentiation of the results of lesions to the overlapping projection areas, only the main, so-called nuclear zone, was ablated. In dog D4, the medial third of the MI was initially ablated in the left hemisphere, with subsequent ablation of the lateral third in the right hemisphere two months later.

Surgery was guided by dog brain atlases [1, 14] and a map of the motor representation of the dog body in the MI developed by Gorska [10]. Data on the representations of the neck muscles were not identified on this map (because the dog's head was fixed during stimulation of the cortex), and were obtained from other studies [8, 9].

Surgery was performed in sterile conditions under Nembutal anesthesia (35 mg/kg, i.p.). Cortical areas were extirpated by subpial suction. After surgery, animals were given anti-edema agents and long-acting antibiotics i.m. Testing for the learned coordination was started 4–5 days after surgery. In each experiment, dogs performed the operant reaction in 5–10 trials with the right and left limbs. Experiments were performed 1–2 times per week for 1–8 months.

Head and limb raising and lowering were recorded, along with delivery of food. Vertical displacement of the head was measured using a tensometric probe located 50 cm above the animal. The probe was connected to the head via a fine plastic filament attached at the bridge of the nose to an elastic ring around the snout. Limb displacement was measured using a potentiometer connected to the bowl lifting system. Amplified signals from the tensometric probe and potentiometer and food delivery event markers were continuously recorded throughout experiments on a pen recorder and, via an analog-to-digital converter, on a Pentium 2 personal computer with a sampling frequency of 50 Hz for 30 sec from the moment of food delivery.

Data were processed using a program written by Aleksandrov [4]. Each operant reaction was discriminated

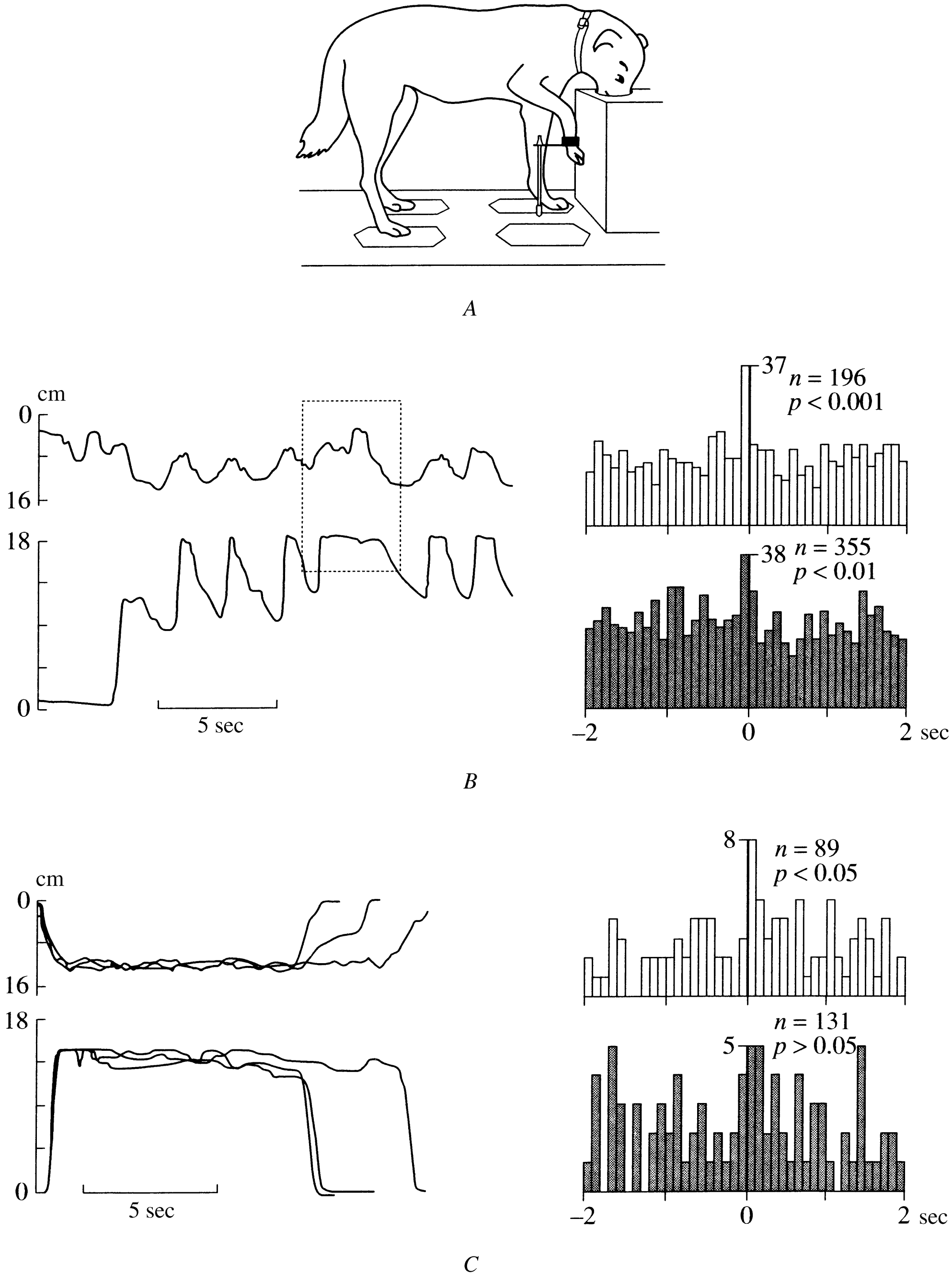

Fig. 1. Rearrangement of the coordination of head and limb movements in dogs on acquisition of a food-related operant reaction. *A*) Posture of the dog during eating; *B*) initial coordination of head and limb movements at the initial stage of training in intact dog D4; *C*) learned coordination at the stage of stabilization of the skill. Plots on the left sides of *B* and *C* show mechanograms of the head (upper) and limb (lower); plots on the right sides show cross-correlation histograms from the experimental data. On head mechanograms, “0” identifies the initial position of the head, when the dog was looking directly ahead; downward deviations of the curve show lowering of the head. On limb mechanograms, “0” identifies the position of the limb on the support; downward deviations of the curve show elevation of the limb. Cross-correlation histograms illustrate the distributions of delays in head movements relative to the onset of limb movements, which are taken as “0” on the horizontal axis; negative and positive numbers show the times of onset of head movements before and after the onset of limb movements, respectively; each bin is 100 msec. The vertical axes show the numbers of head movements in each bin (the size of the largest peak is given numerically); *n* is the number of summations of head movements; *p* is the significance of the histogram peak. Light columns show relationships between elevations; dark columns show relationship between downward movements of the head and limb.

into an initial phase, including the first post-food delivery lowering of the head to the feeder and raising of the working limb, and a maintenance phase. During the maintenance phase, measurements were made of the duration of head and limb fixation and of the amplitude and frequency of rapid up-and-down head and limb movements. We have previously described the criteria for fixation and phasic reactions [4]. The nature of the relationship between phasic elevations and lowerings of the head and limb during the maintenance phase were assessed in each individual experiment by cross-correlation analysis. This was performed using mechanograms to identify the starts of same-direction (up or down) movements of the head and limb, followed by construction of cross-correlation histograms. The start of each limb movement corresponded to the zero point on the time scale. The numbers of head movements during the period from 2 sec before to 2 sec after this point were assessed by summing in 100-msec histogram bins. The significance of the largest peak on the histogram was evaluated by direct calculation of the probability that a peak of the same or greater amplitude would arise by chance in any of 20 bins [6].

The time and amplitude characteristics of movements were averaged for each experiment and the significance of differences was assessed using Student's test.

Histological verification was performed in all experimental animals after natural death several years after surgery. Brains were removed and fixed in 10% formalin. Histological verification of lesion location was performed on serial sections of thickness 30 μm stained by the Nissl method. The margins of the removed tissue were identified, along with the zones of lesions induced by lysis of tissue detritus and the injury zones around the removed tissue, detected from gliosis.

RESULTS

Coordination of Head and Limb Movements During the Food-Related Operant Reaction in Intact Dogs

At the early stage of acquisition of the operant reaction, all animals showed the initial coordination between head and limb movements (Fig. 1, *B*) contrary to that required for obtaining food. When animals responded to the click accompanying food delivery, the dog lowered its snout into the opening and started to elevate the limb with the lever; the head was also displaced upwards, moving it away from the feeder. Lowering of the head led to marked flexion of the limb, such that the bowl fell downwards. Successful seizing of even part of the food from the bowl, i.e., receipt of the reinforcement required for acquisition of the operant reaction needed, at this stage of the experiment, for the experimenter to gently hold the extending limb, slowly lowering the bowl. As soon as the bowl was lowered too much, the dog again lifted it until it had eaten the whole portion. Traces of these reactions, consisting of series of same-direction oscillatory movements of the head and limb, are shown in Fig. 1, *B*. This also shows that maintenance of the limb in the elevated position was only impossible in the posture with the lowered head, though it was performed with the head in the elevated position (emphasized fragment on mechanogram).

The cross-correlation histograms in Fig. 1, *B* show the distribution of the delays between the onset of limb movement, corresponding to "0" on the horizontal axis, and the onset of head movement in the same direction; histograms cover the period from 2 sec before to 2 sec after the "0" point. The largest peaks on both histograms are located on the left-hand side of the vertical axis, indicating that head movements anticipated both elevation and lowering of the working limb; the period of anticipation was 100–200 msec.

After a short period of training (3–5 experiments, 30–70 trials), dogs were trained to maintain the food-containing bowl without the experimenter's help. Independent performance of the operant reaction was achieved rapidly. Oscillation of the head and limb decreased during the maintenance phase and the initial relationship between them disappeared; the duration of stable maintenance of the head and limb simultaneously increased. After a further 5–6 experiments (50–60 trials), the new coordination acquired a stereotypical nature (shown in Fig. 1, *C*). This applied only to the head and the trained limb. The initial interaction persisted between movements of the head and the other limb. Rearrangement of this coordination required repeated training, which occurred over similar or shorter periods as compared with the first training.

Morphological Verification of Lesions

In dogs D4 and D16, the lesioned areas were located in the left hemisphere, in the medial part of the sigmoid gyrus anteriorly and posteriorly to the cruciate sulcus. Lesions in D2, D3, and D5 were in both hemispheres, in the middle part of this gyrus anterior to the cruciate sulcus. In D5, the lesion in the right hemisphere was located more laterally than that in the left hemisphere. The lesioned areas in the left hemisphere in dogs D15 and D17 and the right in D4 were in the lateral part of the sigmoid gyrus. Histological verification showed that lesion areas in all animals affected all layers through the cerebral cortex and, in some cases, the underlying white matter. Gliosis (demyelinization) along fibers was seen only in the zone of cortical extirpation.

Effects of Local MI Lesions

Unilateral extirpation of the medial third of the MI affecting the pelvic and hindlimb projection area (Fig. 2, *A*) was performed in dogs D4 and D16 in the left hemisphere, and impaired the support placing reflex (the so-called placing reaction) of the right hindlimb. As a result, this limb sometimes turned under on the hind side on walking and standing. Both dogs successfully performed the operant

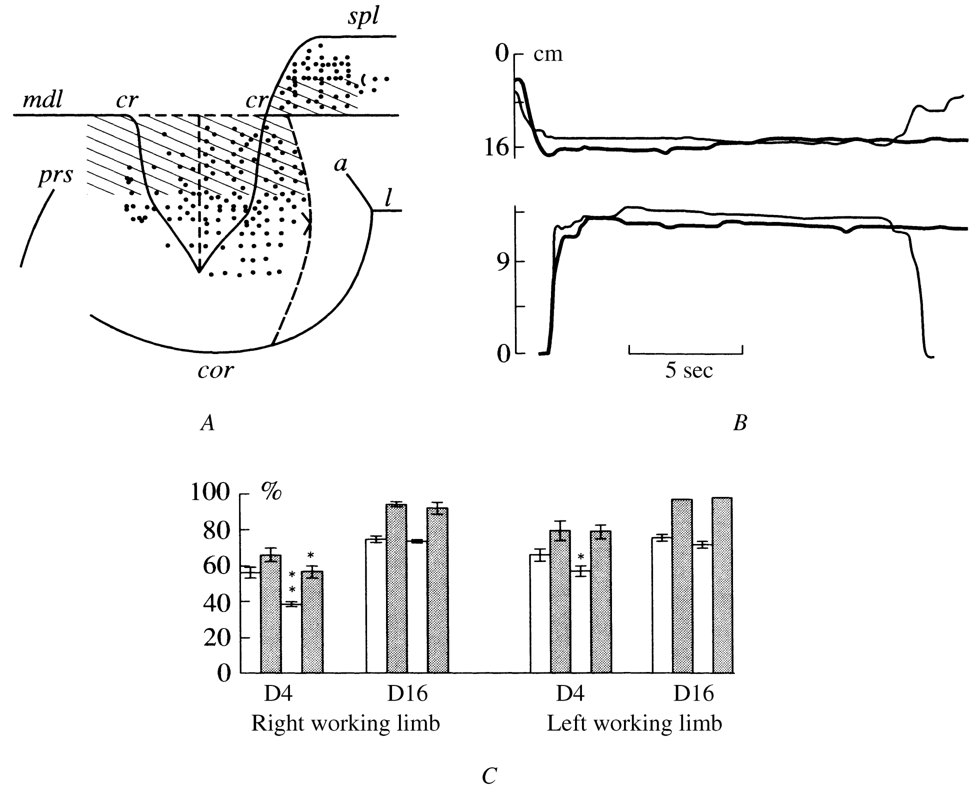

Fig. 2. Coordination of head and limb movements in previously trained dogs after lesioning of the medial third of the MI, which includes the projection of the hindlimbs. *A*) Lesion area (shaded) on a diagram of the motor representation of the hindlimb in the MI (Gorska [10]). Points show locations of contralateral motor responses to electrical stimulation of the brain. *Cor* = coronal; *cr* = cruciate; *proteins* = presylvian; *a* = ansate; *l* = lateral; *spl* = splenial sulci; *mdl* = midline. The doted line passing through the postcruciate sulcus identifies the border between the motor cortex and somatosensory cortex. *B*) Head/limb coordination in trained dog D16 before surgery (thin lines) and after surgery (thick lines). Alignment is in relation to the start of limb elevation. *C*) Comparison of the stability of limb position (light columns) and head position (dark columns) during the maintenance phase before surgery (first pair of columns) and one month after surgery (second pair). The vertical axis shows the mean ($x \pm m$; three experiments) duration of fixation of head and limb position during the maintenance phase in individual tests; the horizontal axis shows experimental animals; *significant differences at $p < 0.05$; **$p < 0.001$. For further details see caption to Fig. 1.

reaction with both the right forelimb, controlled by the lesioned MI, and the left, controlled by the MI of the intact hemisphere, from the first days after surgery (Fig. 2, *B*). Figure 2, *C* shows that at one month after surgery, when scarring of damaged tissue is usually complete, measures of head and limb maintenance (on both the right and left sides) in the learned coordination were as before surgery in dog D16. In dog D4, maintenance of the head also remained unaltered, though maintenance of both limbs was less stable.

Extirpation of the head and neck projection (Fig. 3, *A*) in both hemispheres in dogs D2, D3, and D5 produced no visible movement impairments. The exception was impairment of the placing reaction with the left forelimb in dog D5, which is evidence that the MI limb area in the contralateral hemisphere was also affected. Morphological verification supported this interpretation.

Starting from the first week after surgery, dogs D2 and D3 could perform the operant reaction with both limbs, though D5 could perform it only with the right limb, demonstrating retention of the learned coordination (Fig. 3, *B*).

The operant movement of the left limb in dog D5 appeared during the second week after surgery, though maintenance of the food-containing bowl was impaired. The initial relationship between head and limb movements recovered. However, the dog willingly performed repeated phasic elevations if the experimenter slowed limb lowering, and successfully seized the food. At 1.5 months after surgery (six experiments, 55 trials), the previously learned coordination of head and left limb movements recovered.

The comparison of measures of the learned coordination before and 1–1.5 months after surgery shown in Fig. 3, *C* indicates that maintenance of the lowered head and elevated limb in dog D3 did not change; that in D2 showed a reduction in the stability of maintenance of both the right and the left limbs, and that in D5 showed loss of stability for both the head and the limbs. At six months after surgery,

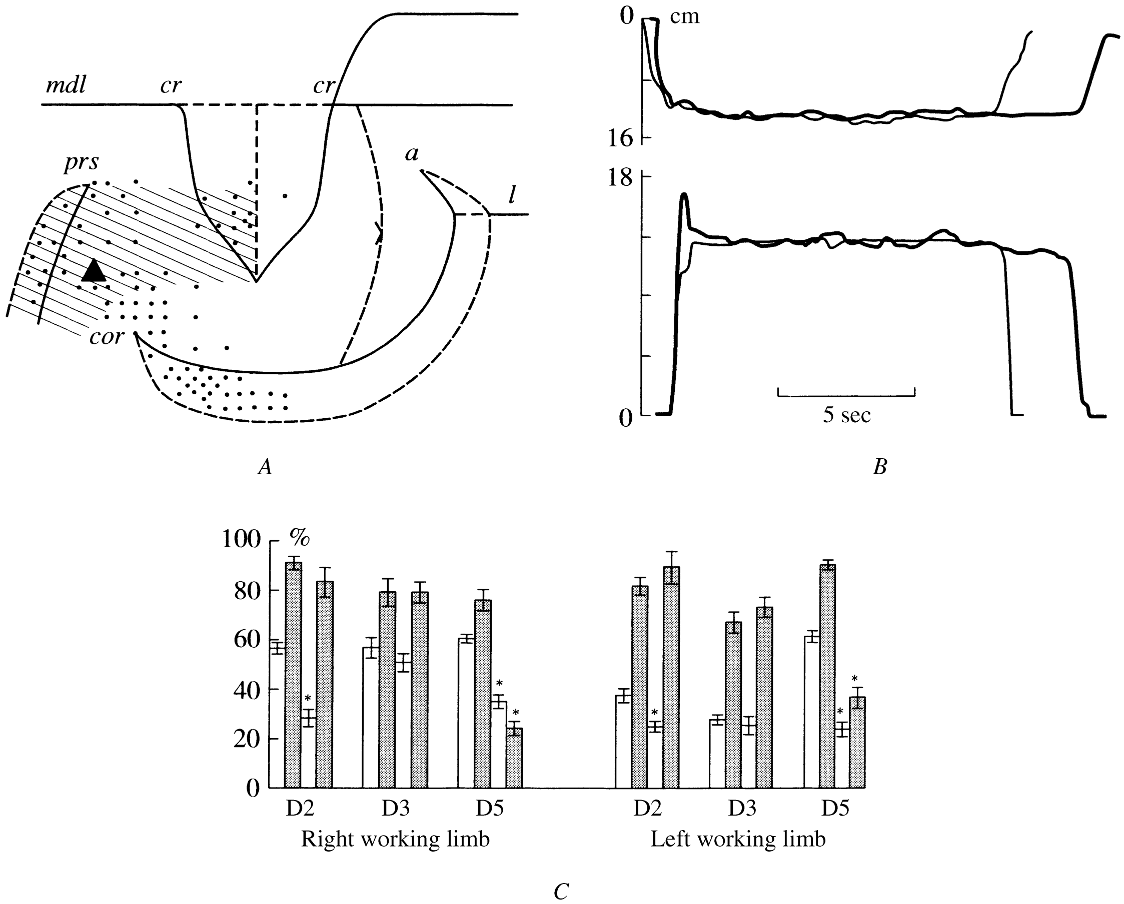

Fig. 3. Learned coordination of head and limb movements after bilateral lesioning of the middle third of the MI, which includes the projection of the neck. *A*) Area of lesion plotted on the motor representation of the chest cage and neck in dogs (Gorska [10]); triangles show the motor representation of the neck in dogs (Fritsch and Hitzig [9]). The depth of the coronal sulcus contains (dots): the projection of the forelimb on the medial slope and the projection of the snout on the lateral slope (Chusid et al. [8]). *B*) Head and limb mechanograms for dog D2 before and after surgery. *C*) comparison of the stability of head and limb position during the maintenance phase before and one month after surgery (1.5 months in D5). *Significant differences at $p < 0.001$. For further details see captions to Figs. 1 and 2.

these measures were completely restored in dog D2, with partial restoration in D5.

Extirpation of the projection of the working limb in the MI (Fig. 4, *A*) performed in dog D4 in the right hemisphere and in dogs D15 and D17 in the left hemisphere led to impairment of the placing reaction of the contralateral forelimb. There were no other clear motor impairments.

Testing of the operant reaction showed that all experimental animals continued to perform the reaction successfully with the limb ipsilateral to the area of the impaired limb. However, they refused to work when the lever was attached to the contralateral limb which had lost its control from the MI. In this case, delivery of food generally failed to evoke an operant movement, while those movements sometimes arising were sharply different from those learned previously. Instead of tonic limb elevation, the animal performed short, single jerks. The dog quite frequently failed to tilt the head to the feeder or even rotated away from it. Repeated presentation of food could provoke freeing movements.

Restoration of the integrity of the food-procuring reactions (glancing into the feeder and lifting the limb with the lever) started in dog D4 at three months, in D15 at five months, and in D17 at six months after surgery. However, the dogs were unable to maintain the elevated limb during eating. Each dog showed return to the initial coordination (Fig. 4, *B*, *C*). During retraining, recovery of the previously learned coordination occurred more slowly than it had formed during the initial training process. Thus, dogs D15 started independent maintenance of holding the food-containing bowl at first training after 36 trials, at repeat training at 11 trials, and after recovery only after 117 trials. During training, operated animals rapidly tired and, unlike healthy animals, performed the operant reaction worse at the end of training than at the beginning.

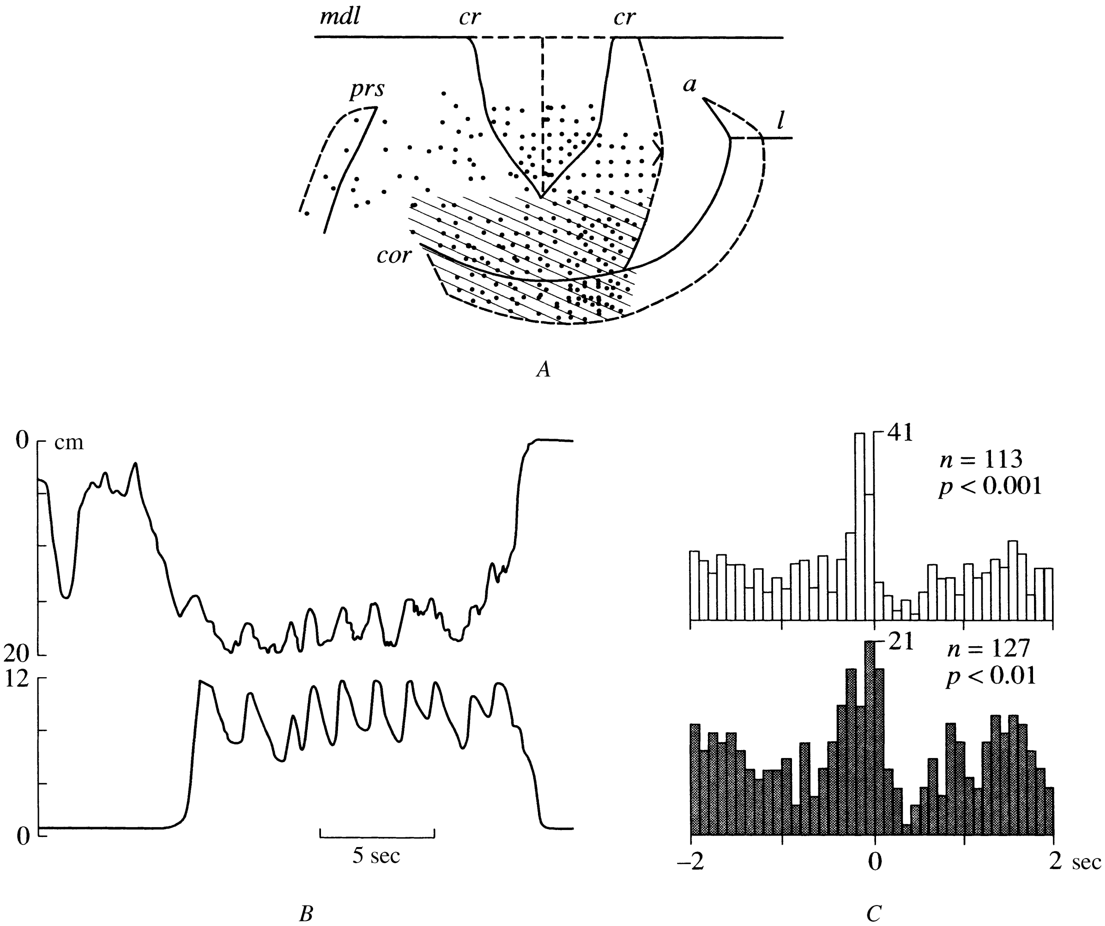

Fig. 4. Return to the initial coordination of head and limb movements in previously trained dogs after lesioning of the lateral third of the MI, which includes the major part of the projection of the working limb. *A*) Lesioned areas plotted on a diagram of the motor representation of the forelimb in the MI (Gorska [10]). *B*) Recording of coordination of head and limb movements in trained dog D15 after surgery. *C*) Cross-correlation histograms showing how elevation and lowering of the limb are accompanied by anticipatory head movements in the same direction. For further details see captions to Figs. 1 and 2.

A characteristic feature of dogs with lesions to the limb areas of the MI was prolonged interference of the old, new, and recovered coordinations. While during the first training before surgery the initial relationship between head and limb movements usually disappeared very quickly, after 30–40 independently performed trials, the relationship was recorded before the end of experiments involving 80–100 performances during recovery after surgery (Fig. 5, *A*, *B*).

As noted above, the operant movement in intact animals on first training, performed independently 50–60 times, acquired a stereotypical nature. The head and limb were stable during most of the maintenance phase (60–90%) and oscillations were of low amplitude (1–2 cm) and were seen in the maintenance phase (duration about 10 sec) no more than 2–3 times (Fig. 5, *C*). After the same number of trials during the recovery period, the duration of stable head and contralateral limb positions was significantly shorter, at 20–40%. The frequency of head and limb oscillations was 2–3 times greater, and small displacements were accompanied by the appearance of larger-scale oscillations (3–8 cm – lower diagram in Fig. 5, *C*). Maintenance of the head and the limb lacking MI control remained unstable to the end of the experimental period. At the same time, maintenance of the ipsilateral limb showed no degradation in any of the dogs, two of which showed decreases in the stability of maintaining the head (Fig. 5, *C*).

DISCUSSION

Previous studies have established that the operant reaction based on a learned coordination of head and limb movements contrary to the initial coordination is stably impaired after extirpation of the MI in the hemisphere contralateral to the working limb [3, 13]. In the present experiments, the results of local lesions to the MI showed that the

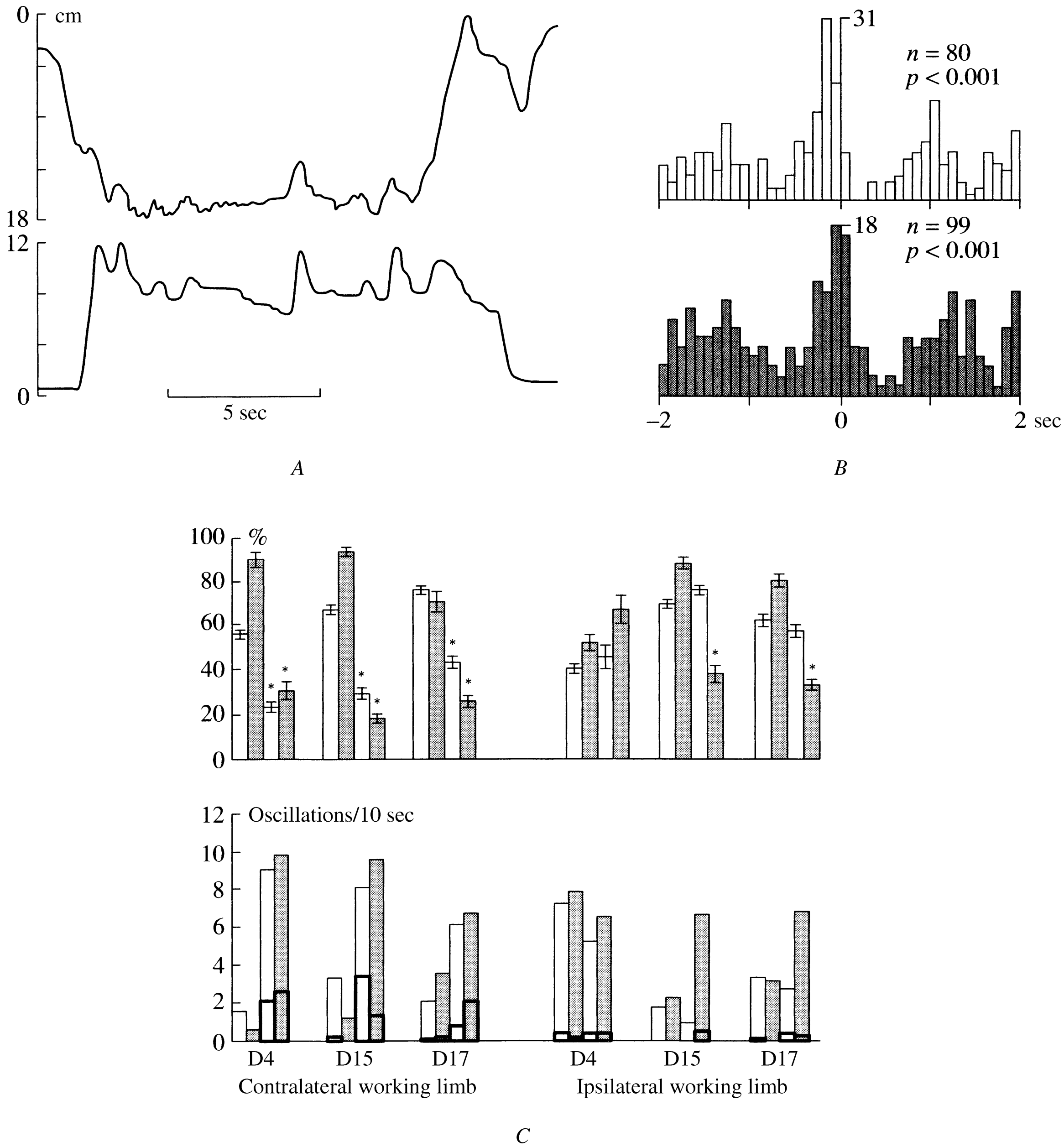

Fig. 5. Prolonged interference of the initial and learned coordinations of the head and limb after recovery of the operant reaction after lesioning of the working limb area in the MI. *A*) Coordination of head and limb movements in dog D15 six months after surgery. *B*) Cross-correlation histograms showing persistence of the initial interaction between oscillations of the head and limb during the maintenance phase. *C*) Comparison of the durations of stable positioning (above) and the frequency of oscillations of the head and limb (below) during the maintenance phase of the operant reaction before and after surgery (four months in dog D4, six months in D15, seven months in D17). *Significant differences at $p < 0.001$; in the lower diagram: columns outlined with thin lines show oscillations of ≤ 3 cm, those outlined with thick lines show oscillations of >3 cm. For further details see captions to Figs. 1 and 2.

motor skill persisted after exclusion of the medial and middle thirds of this structure. It follows from this that integrity of the MI is not a critical factor in its performance.

The only area whose lesioning caused loss of the learned skill in all animals was the lateral third of the MI, covering the major part of the projection of the working limb. The nature of the movement impairment in this situation was similar to that seen after extirpation of the whole of the MI [3, 13]. The only difference was in the timing of impairments. In the present experiments, we lesioned the "nuclear" part of the limb projection and, at 4–6 months, observed recovery of the learned reaction. Recovery was more difficult and was slower than the first training, and evidently occurred because of limb neurons surviving in neighboring parts of the MI – so-called "scattered" elements (Fig. 4, *A*). Exclusion of these cells with retention of the "nuclear" area, judging from the results obtained in dogs of groups I and II, was not followed by the appearance of the learned reaction. However, complete extirpation of the forelimb projection or the entire MI, as demonstrated previously [3], prevented recovery for two and more years. The unplanned partial lesioning of the "nuclear" part of the forelimb projection in dog D5 in the present experiments was followed by relatively mild and rapid recovery of the operant reaction – 1.5 months after surgery. Thus, there appears to be a relationship between the duration of impairment and the level of damage to the limb area in the MI.

The present experiments demonstrated that ablation of the projection of the working limb, like ablation of the whole MI, did not produce general motor impairment (like, for example, paresis or paralysis in humans), but loss of specific movements. Our observations indicate that these movements were the placing reaction and the learned head/limb coordination, i.e., the simultaneous maintenance of an elevated limb and a lowered head. The dogs could maintain the elevated limb in the posture with the head elevated and that with the head lowered to the feeder without limb elevation. These data show impairment of a defined coordination or the *interaction* of head and limb movements. This suggests that the representation area of the head and neck in the MI must have a direct relationship with this interaction. However, ablation of this area was found not to eliminate the learned coordination. We link the temporary decrease in the stability of head and/or limb maintenance seen in most dogs not only after lesioning of the middle, but also the medial third of the MI, with the non-specific traumatic effects of surgery. The fact that exclusion of the head and neck area of the MI had no effect on the learned coordination should indicate that this coordination is independent of the direct influences of the MI on the head and neck muscles and of connections between the projection areas of the head and limb. On the other hand, since only removal of the limb representation produced persistent impairment of coordination, it is possible that fundamental changes occurring during the formation of this coordination are associated with this area. This conclusion in turn suggests that the transition from the initial coordination to the new coordination is achieved because of changes in the organization of the limb movement. This mechanism for rearranging coordination is possible if the initial and learned coordinations are regarded as two different means of performing what is externally one and the same movement – elevation and maintenance of the forelimb.

It can be suggested that in given experimental conditions, the dogs were initially able to elevate and maintain the limb with the lever only by *one available means* – with anticipatory elevation of the head and neck. Gurfinkel et al. [12] found that in humans, elevation of the arm was also anticipated by activation of the dorsal neck muscles and backward deviation of the head. This anticipatory activation was suggested by the authors to overcome the rigidity of the vertebral column, facilitating elevation and maintenance of the arm. It is possible that in our experiments too, head and neck movements in the initial coordination in dogs have facilitatory significance for elevating and maintaining the limb with the lever. The forelimb is known not to have any direct connection with the body skeleton and to be maintained in the trunk by the scapular muscles. Some of these muscles join the scapula to the thoracic and cervical segments of the spine. Tensioning of these muscles on elevation of the head and neck, aiding fixation of the position of the scapula, may facilitate elevation of the limb with flexion at the shoulder joint. This mechanism provides an explanation why head tilting in dogs is associated with lowering of the limb.

The need to maintain the elevated limb in an uncomfortable posture with the head lowered, induced by the conditions of the present experiments, is achieved by acquisition of a *new means* of elevating and maintaining the limb. This must involve a change in the organization, i.e., the muscular pattern of tonic elevation of the forelimb, which may also be formed in the MI controlling the movement of the working limb.

The suggested hypothetical mechanism for the acquisition of a new means of elevating the limb presupposes that the old, initial means persists without change in the trained animal. This is supported by our previous description [4] of the phenomenon of interference between the learned and initial head/limb coordinations. This phenomenon appears not only at the early stage of training, but can also arise after a short period in well-trained animals. We can explain this on the basis that at the beginning of training, interference reflects the gradual replacement of the initial means of elevating the paw with the more effective new means. At the stage of the fixed skill, the initial means of elevating the limb can play an accessory role, when fixation of the position of the elevated limb in the posture with the head lowered for some reason becomes difficult, such that correction of the position of the elevated limb (periodic drawing upward) is mediated by the old means – with anticipatory upward deviation of the head. In our experiments, lesioning of a large area of the working limb representation in the MI evidently produced a significant hindrance to recovery of the new means of elevating the limb. This was apparent as a prolonged unstable maintenance of the elevated limb and lowered head. In these conditions, the initial coordination, i.e., the old means of limb elevation, also showed prolonged persistence.

CONCLUSIONS

1. The rearrangement of the natural coordination of head and limb movements does not involve the whole of the MI. The coordination contrary to the initial coordination persisted after lesioning of the medial third of the MI, which includes the projection area of the posterior part of the trunk.

2. Bilateral ablation of the representation of the head and neck in the MI did not impair the new head/limb movement coordination.

3. Only lesioning of the representation of the working limb in the MI led to profound and long-lasting impairment of the learned coordination and recovery of the initial relationship between head and limb movements, demonstrating the decisive role of this area in the rearrangement of the initial coordination.

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