VARIED INFLUENCE OF DAMAGE TO THE MOTOR CORTEX ON PRECISION AVOIDANCE AND ESCAPE REACTIONS IN DOGS*

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The influence of local extirpation of the representation of the forelimb in the motor area of the cortex on the performance of precision elevations of this limb was investigated. Even imprecise avoidance reactions to an acoustic signal did not recover spontaneously. Irregular motoric reactions which were insufficient in amplitude could easily be restored in the course of retraining, but precise movements (both rapid fused, as well as relatively slow stepwise movements) did not recover for at least a half year after the operation. By contrast with this, precise rapid reactions in response to electrical stimulation of a "working" limb (inducing unconditioned reflex flexion) remained essentially preserved, i.e., the capacity to stop the movement in the correct (previously learned) position of the limb was preserved. The capacity to fix the position of the raised limb was not lost, but was persistently impaired. The capacity to overcome the unconditioned reflex flexion during the performance of extensor "slow" escape reaction was reduced sharply and persistently. Limb presentation reactions regulated by vision were essentially spontaneously and nearly completely restored within a month.

In many studies, in accordance with the atlas of Adrianov and Mering [1], the entire posterior sigmoid gyrus of the dog brain has been regarded as the motor cortex. However, the results of electrical stimulation of this region, supplemented also by some morphological investigations, have led Konorski et al. [11, 19, 20] to the conclusion that it includes both the motor (MI) as well as the somatosensory (SI) cortex (their boundary passes approximately in the middle of the posterior sigmoid gyrus (through the dimple), i.e., somewhat more caudally than in the cat [15]). The authors of [11, 19, 20] have carried out an investigation of the differences in the functional role of these regions in the control of instrumental reactions. However, the reflex that they have used, of placement of the forelimb on the food dispenser, was preserved after unilateral ablations of both the SI and the MI, while with bilateral extirpations of SI or MI, the disturbances were expressed mainly in the absence of the reflex for two to three weeks in the case of each of the lesions. Thus, differences were not identified directly in the functional specificity of these cortical regions.

It was demonstrated in our previous study [7] that spontaneous (without retraining) restoration of previously developed precision avoidance reactions takes place over the course of two weeks after the operation following the extirpation of the representation of the forelimb in SI. By contrast with this, prolonged coarse disturbances in the precision of the reactions were observed with local lesions of the MI [2]. However, whether it is necessary to speak of a specific disturbance of precision in particular in this case, or whether this was more likely a matter of a reduction of a capacity to initiate flexor reactions, remained unclear. The elucidation of this question was initially the basic objective of the present study.
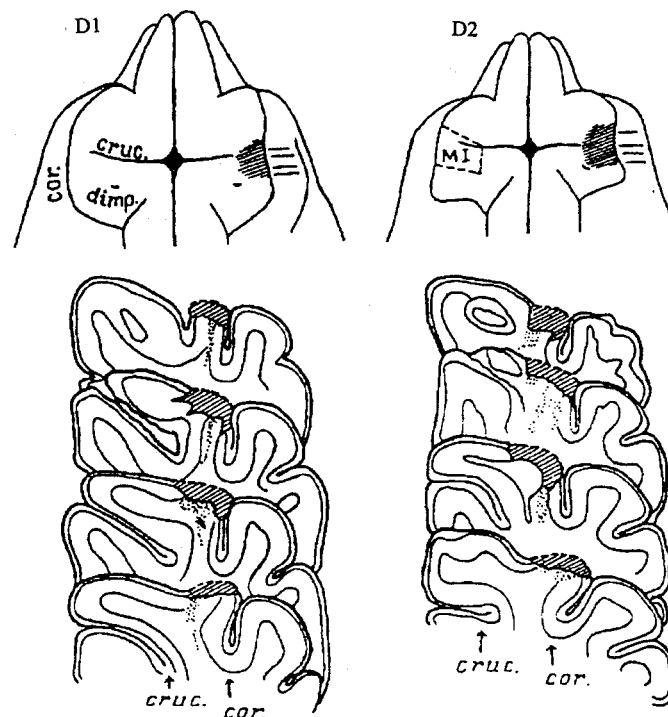
Fig. 1. Localization of the region of ablation (hatched) in the motor cortex in D1 and D2. The regions of fiber degeneration are denoted by dots in the sections. The region of the representation of the forelimb in accordance with [11, 14] is outlined in the left intact hemisphere of D2. A deformation (compression) at the site of the ablated cortical area can be seen from the comparison of the right and left hemispheres.

METHODS

The experiments were carried in adult mongrel dogs (D1, D2). Throughout the experiment the animal was kept on a bench in a soundproof box. Each of the limbs was tied to four rods which could shift freely 17 cm along the vertical. The elevation of the rod of the left forelimb was recorded on an automatic writer. The bearing force of each of the limbs was also recorded by means of four strain gauges. An acoustic tone of 200 Hz, lasting 15 sec, served as the conditional signal (CS). The dog was required to raise and maintain the limb during the isolated action of the CS (5 sec) for the following 10 sec at a height from 7 to 11 cm, in the "safety zone" (SZ). In case of an imprecise reaction or when the limb left the SZ as a result of its being imperfectly sustained in that zone, electrodermal stimulation was applied to it (EDS), which the dog could escape by shifting the limb into the SZ. The EDS was applied in the region above the radiocarpal joint (an ÉSu-1 stimulator; 1 msec, 30 Hz, 3–8 mA).

The correct choice of the strength of the EDS has great significance for the development of the precision reflex and the testing of its state following the operation. The jerk (T1) or elevation (T2) thresholds of the limb (usually 0.6–1.2 mA) cannot serve as adequately defined indicators. We considered the value of the TV [unexpanded acronym (PZ in Russian), here speculatively interpreted as "threshold value" — Translator], which can provisionally be termed the threshold of pain sensitivity (usually 2.8–4.4 mA) as the principal indicator. In order to determine the TV, elevation of the limb into the SZ was induced at first by turning on a weak, gradually increased EDS. The dog then periodically tried to lower the limb below the SZ and again escaped the EDS (as in Fig. 4A). If these escape reactions were performed in a stable manner for no longer than 0.1 sec (as a result of rapid unconditioned reflex flexion with a latency of about 40 msec), we considered the strength of the EDS to have reached the magnitude of the TV (the EDS was not turned on during these measurements in the case of elevations of the limb above the SZ). EDS up to 1.5–2.0 TV in strength was required for the development of the avoidance reactions; this approximately corresponded to the threshold of the vocal reaction. In order to stabilize a reflex, 1.2 TV was sufficient.
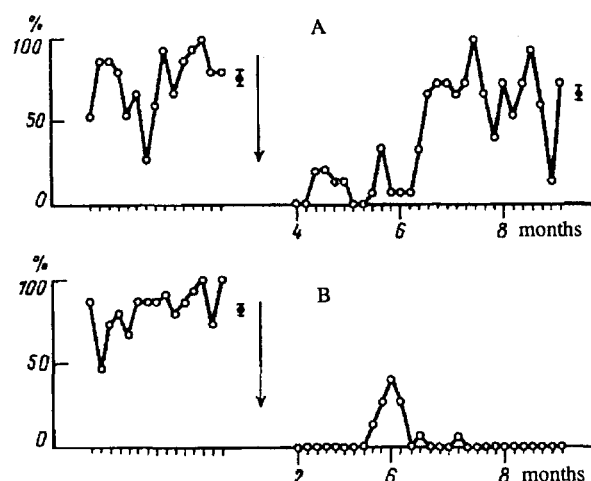
Fig. 2. Per cent of precision avoidance reactions before and after injury of the MI in two animals: D1 (A) and D2 (B). Each point corresponds to one experiment. The figures along the abscissa: number of months passed following the operation, which is designated by the vertical arrow. The means and the standard errors (for the baseline and for the period following the recovery in D1) are given to the right of the curves.

The formation and stabilization of all the components of the precision reflex required up to two to three thousand combinations [see 6, 8, 12] (15 combinations during each trial). By the end of training the dogs performed 75-82% precision reactions. All of the learned reactions were completely retained following a four-week break in the experiments (we had previously demonstrated [8] that the precision reactions developed in this manner can be maintained fully after a year's break). The reaction was considered a precision reaction if by the end of 5 sec of the isolated action of the CS the limb was raised into the SZ and then maintained in the SZ no less than 1 sec.

The operation was carried out under nembutal anesthesia (40 mg/kg intraperitoneally) under sterile conditions. After dissection of the skull and the dura mater above the sigmoid gyrus of the right hemisphere, extirpation of the MI was carried out in the region of the representation of the "working" limb (Fig. 1) by means of subpial suction, in accordance with data on the localization of this region [11, 14]. The denuded section of the brain was then closed by a fibrin film, and the muscles and skin sutured in layers.

The animals were administered a lethal dose of nembutal after the experiments were concluded. The brain was fixed in a 10% solution of formalin. The histological control of the localization of the lesions, carried out by serial frontal sections of the brain (50 μ), Nissl stained, showed that the major portion of representation of the left forelimb in the MI was destroyed in both animals, with the exception of areas lying in the depth of the coronal and cruciate sulci. An area of cortex close to the dimple was also preserved in D1, while in D2 the ablation partially impinged on the premotor region.

INVESTIGATION RESULTS

The experiments were resumed six days after the operation. The left forelimb placement on support reactions were absent throughout the entire period of observations. In the first few weeks, the reflex returning the supinated limb to the normal position was completely absent; substantial recovery took place within a month, but full normalization did not occur even after a year.

Motoric Reactions in Response to Acoustic Signal. The number of positive reactions (even a minimal raising of the limb) in response to the CS was 98-99% prior to the lesion of the MI. After the operation positive reactions were completely absent. In order to clarify whether spontaneous recovery of the reactions takes place, retraining was excluded for two to four months. Only occasional Cs [sic] (one to two times a week) were presented, and were never accompanied by EDS. Dog 1 (D1)
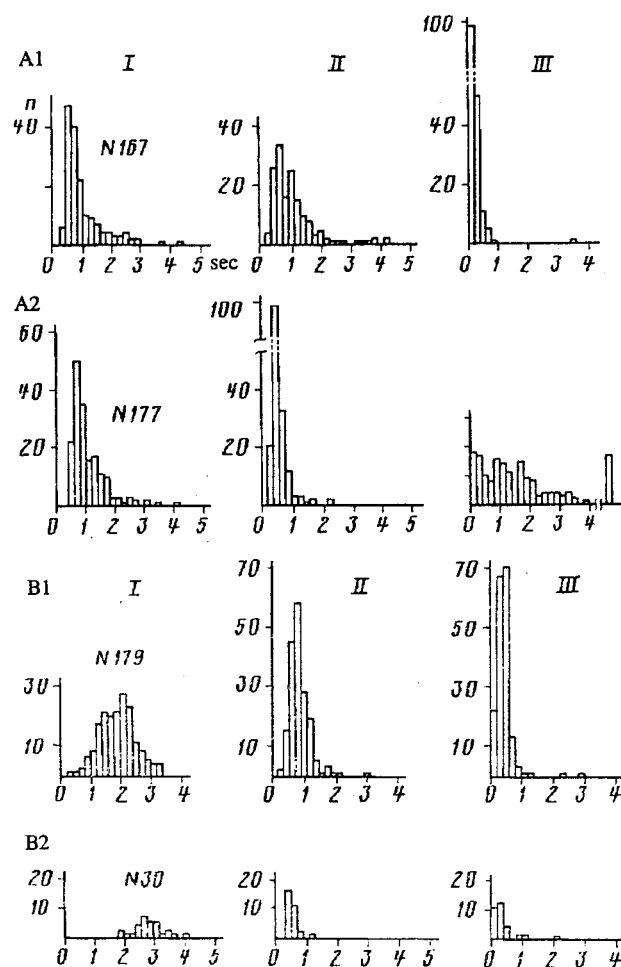
Fig. 3. Distribution of the temporal parameters of the precision elevations of the limb in D1 (A) and D2 (B), before (A1, B1) and after (A2, B2) the injury to the MI. I) Distributions of latencies of reactions; II) of time from the beginning of elevation to the reaching of the SZ; III) times from the first entrance of the limb into the SZ to fixation. Along the abscissa: time intervals; along the ordinate: number of reactions with a given value of these parameters. N) Sample size. In A column denoting the number (17) of instances in which the limb was not fixed in position after the elevation into the SZ is separated on the right below.

reacted only with partial and irregular weakening of support on the "working" limb, while even postural reactions of this kind were not observed in D2. Positive reactions were completely lacking.

Retraining (combinations of CS and EDs [sic] following the typical protocol) was begun in D1 four months after the operation. The reactions appeared as early as in the first experiment in three combinations out of 15, but the height of the elevations of the limb was inadequate. In succeeding experiments positive reactions appeared in approximately half of the trials, and they became regular only by the seventh month (after 400 combinations): the number of these increased sharply to 96%. The number of precision reactions increased sharply at the same time, practically reaching the preoperative level (Fig. 2A). However, all of the principal parameters characterizing the pattern of the reactions changed significantly (p < 0.01 according to the chi square test) (Fig. 3A). The number of shortest-latency (0.3–0.6 sec) reactions decreased. The number of instances increased sharply in which, after raising its limb, the dog did not fix it for several seconds in the SZ. The dog moved the limb up and down in the region of the SZ before holding it in place in 44% of the precision reactions, whereas such searching movements were practically not observed prior to the operation. The dog at first raised the limb higher than the SZ in 57% of the cases (as against 1.5% before the operation), but then relatively slowly lowered it into the SZ. After the recovery of the precision reactions, the number of slow (duration greater than 0.5 sec) stepwise elevations of the limb into the SZ was 18%,
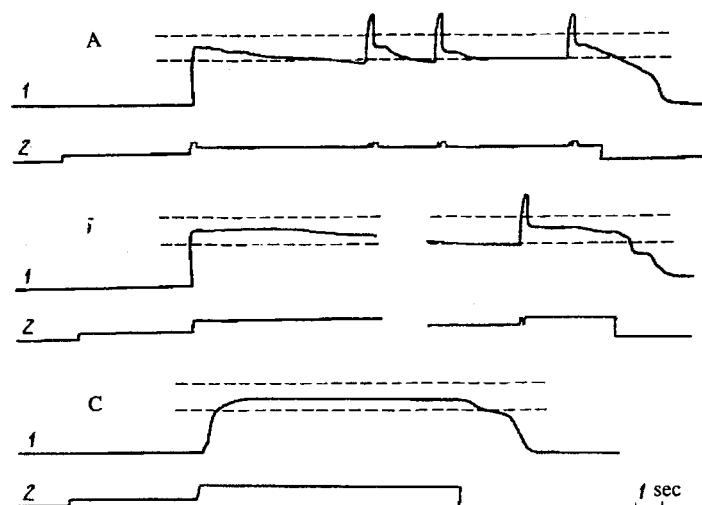
Fig. 4. Precision escape reactions after the extirpation of MI with the complete absence of avoidance reactions. A) Flexor and flexor-extensor rapid reactions (the combination of stimuli was prolonged to demonstrate the stability of the reactions). B) Maintenance of the character of the reactions in which, while placing the limb in the SZ, the dog does not avoid the electrical stimulation (the recording is presented fragmentarily, since the combination was prolonged in connection with the presentation of stimuli according to a nonstandard protocol). C) Slower but precise flexor reaction with continuing EDS. 1) Mechanogram of the movements of the left forelimb. The "safety zone" is delimited by broken lines. 2) Markers of the presentation of the stimuli: first step up, acoustic signal; second, EDS (the highest level of the marker, the time of the real action of the EDS; the middle level, the EDS turned off by a correct reaction).
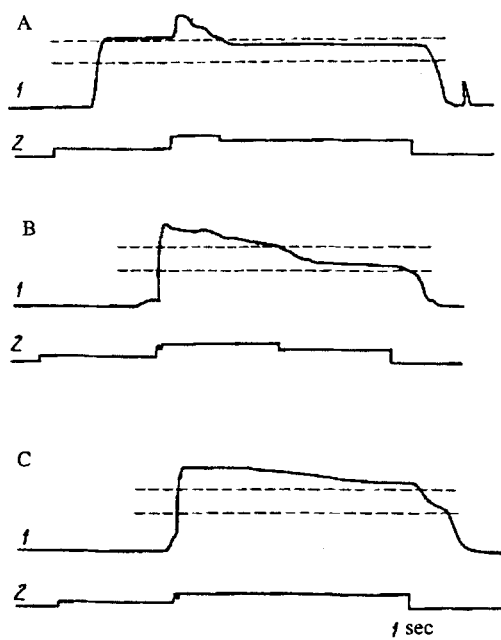

Fig. 5. Slow extensor escape reactions. A) Before; B, C) after extirpation of MI. Designations as in Fig. 3.

while before the operation it was 71%. That is, rapid elevations of the limb were restored primarily, probably because such reactions in particular were more often successful.

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In D2 retraining was begun two months after the operation, and positive reactions appeared only after 1.5 months of retraining, and postural reactions became relatively regular and complete. The positive reactions remained unstable for a long time; their number ranged from 14 to 86% during an experiment. Even a year after the operation, in the course of intensified retraining, positive reactions were absent in response to more than 20% of the combinations, i.e., 20 times more often than before the operation. Elevations of the limb were, as a rule, inadequate in amplitude.

Precision reactions began to appear in the course of retraining only in the sixth month following the operation, reaching 40% in one of the experiments, but they practically completely disappeared before the end of the observation period (11 months), as early as in the seventh month, despite the fact that trials were attempted regularly (Fig. 2B). Since the number of precision reactions was very low (only 30), it was impossible to fully assess the change in their pattern. However, it is fairly clear that as in D1, the frequency of the short-latency reactions decreased, while the frequency of the relatively rapid elevations among the precision reactions increased (Fig. 3B).

Changes in Holding the Position of the Limb. It could be seen in the first few experiments following the lesion of the MI that the animals retained the capacity to hold the elevated limb in the specified position to a significant degree. In particular combinations, the maximal time of continual, practically immobile maintenance of the position (with a displacement of not more than 2 mm) could reach 9 sec. But on average, the time of such fixations significantly (p < 0.01 by the Student t test) decreased by more than a factor of 2.5 in both dogs. In the course of retraining, no substantial improvement of maintenance of position took place even after the recovery of the precision reactions in D1.

Maintenance of Precision Escape Reactions. At first we assumed that the animal's capacity to perform a precision learned movement could be judged most correctly on the basis of the avoidance reactions (in response to the CS), when there were no special signals indicating entry into the SZ. In performing the escape reaction, on the other hand, the animal does have such a signal, the turning off of the EDS when the limb enters the SZ. However, the presence of this feedback is not essential if the escape reaction exhibits the character of a rapid fused movement of the preprogrammed type, i.e., is performed without adjustments involving the use of external feedbacks (proprioceptive, visual, etc.), and, thus, has predetermined parameters (see [5]). It was found unexpectedly that such rapid precision (RP) reactions may be essentially completely preserved following extirpation of the MI.

Flexor rapid precision escape reactions were performed during 0.15-0.3 sec (from the beginning of elevation to fixation in the SZ). The rapid portion of the movement (comprising 80-90% of the amplitude) occupied 0.1-0.2 sec. Before the operation such reactions were manifested mainly in those rare instances in which the dog did not raise the limb in response to the CS. Then the application of the EDS was able to induce both the RP reaction and a reaction which was excessive in amplitude as well (given more intense EDS, exceeding the TV 1.3 times). Sometimes relatively slow elevations of a limb were also observed in the presence of relatively low EDS strengths. The dogs were able to persistently perform the RP reactions, but we intentionally gave such strong EDS that the limb, as a result of intense unconditioned reflex flexion, ended up above the SZ in the majority of instances, and the dogs were compelled to perform extensor escape reactions which were of special interest to us.

After the extirpation of the MI, responses to the CS were lacking, but RP reactions were regularly observed from the very beginning of retraining in response to the EDS. The principal results in these terms were obtained in D2. The P2 threshold increased sharply, equaling the TV. A gradual decrease in P2 took place over the course of a half year to a level close to the preoperative level. When EDS which were close in strength to the usual working values were applied (one and two times TV), the dog immediately began to react stably with RP movements (Fig. 4A). Reactions which were insufficient or which were excessive in amplitude were observed as a rule only in the case of the weakest or the most intense EDS, respectively. The allowable variations in the magnitudes of the EDS at which the reactions remained precise were very broad (by a factor of 1.6).

In order to convince ourselves of the preprogrammed character of these reactions, we carried out a number of trials (in the second and third experiments following the beginning of retraining), in which the current was not switched off when the limb was raised into the SZ, and thus the dog did not have the corresponding external feedback regarding the precision of the movement. The reactions to the EDS were precision reactions in 19 trials out of 22. The dog raised the limb, and despite the continuous stimulation, held it in the SZ more than 0.5 sec. Of these 19 precision reactions, 11 were rapid (Fig. 4B) and eight were less rapid, but precise, with prolonged fixation in the SZ (with relatively weak EDS, Fig. 4C). The prolonged fixation of the limb in the SZ during continuing stimulation (of moderate strength) may apparently be explained by the high degree of stereotypy of the behavior of the dog.

In D1, less than half of the flexor escape reactions were rapid both before the operation and afterwards. Special trials for the analysis of these reactions were not carried out.

Extensor RP Reactions. The capacity to perform precision reactions was manifested even more obviously in D2 in the situation in which the EDS was applied to the elevated limb, thus inducing sharp unconditioned reflex flexion, the elevation of the limb above the SZ, after which RP extension and fixation of the limb in the SZ followed immediately (Fig. 4A). The entire flexor-extensor reaction was performed in 200–250 msec. These reactions were highly stereotypic and clearly preprogrammed in character. They were observed in 30 instances out of 57 in 15 experiments before the operation. Their manifestation depended mainly on the intensity of the EDS: high-strength stimulations could block the extensor reaction.

The extensor RP reaction was absent after the operation at the beginning of retraining when there was initial excessive flexion in response to the EDS, but it then began to appear persistently (Fig. 4A). The current was not turned off in the SZ in 11 trials; nevertheless all of the reactions were precision (Fig. 4B). The level of fixation of the limb following rapid extension depended little on its initial position during the first shock.

Thus, it was demonstrated that during the time when the avoidance reactions following the lesion of the MI are markedly and persistently disrupted, the precision escape reactions may be essentially completely preserved.

The extensor RP reactions in D1 were not manifested before the operation, since we had not developed them specially.

Slow Extensor Escape Reactions. If in the first 0.25 sec the dog has not been able to escape EDS applied above the SZ by means of the RP reaction, then it required additionally more than 0.5 sec in order to escape the EDS by overcoming the unconditioned reflex flexion induced by it (Fig. 5A). Such reactions have been regarded as a model of the conditioned reflex reworking of an inborn reaction [2, 6, 12]. These were substantially disrupted following extirpation of the MI, but were not lost entirely. It can be stated that the "idea" of this movement was preserved; the dogs always attempted to perform the escape reaction, but these attempts were successful only at low EDS strengths (Fig. 5B). When the magnitudes of the stimulation were substantial, the animals were not able to overcome the unconditioned reflex flexion in order to lower the limb into the SZ (Fig. 5C). The maximal strength of stimulation at which this reaction was possible decreased significantly ($p < 0.01$ by the Student t test) by a factor of 1.9–2.1 as compared with the preoperative period, when the dogs escaped EDS right up to 2 times TV. In addition, if preoperatively the escape reactions exhibited the character of a typical active movement (extensions carried out relatively rapidly and with visible strain), postoperatively the reaction usually looked like a passive slipping of the limb at a rate of about 0.5–1 cm/sec. The recovery in the course of a year of retraining was insignificant.

Characteristics of Reactions Controlled by Vision. Preoperatively the D2 exhibited a consolidated reflex of offering the paw to the experimenter. After the damage to the MI this reflex was completely absent for two weeks. It recovered after a month, but was not completely regularly manifested. Regularity, on the other hand, was restored after 5.5 months. We also observed a similar pattern of practically spontaneous recovery of the paw presentation reactions in another dog, with a local lesion of the MI, which had been used in other experiments. It is worth noting, however, that the natural visual placing-reactions were persistently disrupted.

We have also demonstrated that exclusion of visual control by the placement of a baffle between the head and the limb does not essentially affect the performance of the precision reactions, either before or after lesions to the MI and SI [8].

DISCUSSION OF RESULTS

The trained intact animals performed the precision avoidance reactions either in the form of a rapid fused movement of the preprogrammed type, or after an initial imprecise movement, adjustments of the position of the limb followed, probably with the use of proprioceptive feedback. The extirpation of the representation of the "working" limb in the MI disrupted the animal's capacity to bring the limb to the required position by either the first or second means. Apparently, the dogs either entirely lost the sensation of the position of the limb, or the sensation was altered in such a way that a low elevation of the limb was regarded by them as sufficient. Probably the animals lost the capacity for this reason to bring the limb into the correct position by making corrections using proprioceptive feedback.

The loss of the preprogrammed avoidance reactions, on the other hand, may be explained not by the destruction of the program itself, but by the loss of the principal pathways of its realization, the corticospinal and corticorubrospinal [4]. A sharp decrease in the magnitude of the descending message to the flexor motoneurons may evidently explain the prolonged absence and further persistent decrease in the amplitude of the elevations of the limb in response to the CS.

The conditioned reflex flexor component of the escape reactions evidently suffer as significantly as the avoidance reactions, but EDS provides for the initiation of the movement by means of unconditioned reflex flexion, and the animal's task consists in the limitation of its amplitude or in the rapid return of the limb so that it ends up in the SZ; this is evidently

achieved through a specific magnitude of activation of the extensors. Since the strength of the EDS could vary significantly in the course of the experiment, the animal apparently learned (prior to the operation) to react with tension of the extensors which corresponds to the intensity of the flexion. After the extirpation of the MI, the situation is aggravated by the fact that the activating inflow of the motoneurons decreases sharply. Nevertheless, the dogs maintained the capacity to perform precision escape reactions. Such highly invariant rapid reactions are probably possible through the participation of the internal feedback pointed out by A. Lundberg [17]: all of the descending and segmental excitatory and inhibitory influences reaching the motoneurons are initially integrated in the propriospinal neurons which send information through the lateral reticular nucleus to the cerebellum. When it receives anticipatory information regarding the intensity of flexion in this manner, the cerebellum probably forms a corresponding extensor message which predetermines the final position of the limb.*

It can be seen from this that, while extirpation of the MI indeed leads to persistent disruption of the precision of the avoidance reactions, this still does not prove that the MI specifically participates in the control of the precision of preprogrammed movements of this type. But, on the other hand, the possibility of such participation in a unitary system with the cerebellum or independently of it cannot, of course be denied. The possibility of the recovery of the precision avoidance reactions in D1 a half year after the operation was probably associated with a somewhat smaller volume of the lesion as compared with D2 (see Fig. 1).

In the case of the SI lesion, the initial pattern of motor disturbances was the same as after the MI lesion, but recovery took place spontaneously and the pattern of the restored reactions did not differ from the initial pattern [7]; therefore, it may most likely be the case that the changes observed were the result of a temporary disturbance of the functional state of the MI. We have demonstrated that recovery does not correlate with compensation of the somatosensory input to the MI (according to the criterion of EP) [9]; this also argues in favor of the hypothesis of the nonessential character of the participation of the SI (possibly, with the exception of field 3a, the localization of which in dogs is not known exactly) in the control of precision reactions.

Analysis of our and published data (see [8]) definitely points to the fact that visual control of movement may be accomplished without the participation of the MI (and all the more so, the SI); therefore, movements controlled by vision (placement of the paw on the dispenser, offering the paw, etc.) may, after the injury to MI, be relatively rapidly and completely compensated through visual feedback, while movements performed "in an internal system of coordinates" (not projecting to an external object), as, for example, the avoidance reactions, turn out to be acutely and persistently disrupted. T. Górska [3] was the first to direct attention to facts of this kind. The above, however, does not at all exclude the fact that the MI may in the norm take some part in the control of movements monitored by vision, especially if we are talking not of visual-motor coordination of the natural type, as discussed above, but of artificially developed coordinations [10].

Data showing that the capacity to overcome unconditioned reflex flexion of the limb during the performance of the extensor escape reaction is sharply disrupted following the lesion to the MI (by contrast with the SI) are in good agreement with the point of view that the function of the MI is specifically important for the performance of learned reactions associated with overcoming inborn coordinations [4, 8]. However, it must be said that it would be enough to adduce the thesis that extirpation of the MI sharply reduces the possible magnitude of "voluntary" effort to explain the result in question [13, 16].

CONCLUSIONS

Local extirpation of the representation of the forelimb in the motor region of the cortex in dogs leads to the following changes in learned precision reactions of that limb.

1. The avoidance reactions are acutely disrupted (elevation of the limb in response to the acoustic signal) both of the preprogrammed type (rapid, adroit, precise) as well as of the nonprogrammed type:

a) even imprecise reactions do not recover spontaneously over the course of at least two to four months;

b) only reactions which are insufficient in amplitude and are irregular recover relatively rapidly in the course of retraining;

c) if the recovery of precision reactions (in the course of retraining) is in fact possible, it is so only a half year after the operation; the pattern of the recovered reactions differs sharply from the preoperative pattern.

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*The idea of such an explanation of our data was suggested by V. I. Maiorov (M. V. Lomonosov Moscow State University).

The enumerated motor disturbances point to a significant decrease in the capacity to initiate "voluntary" flexion, and to a disruption of the mechanism of adjustment of the position of the limb using proprioceptive feedback.

2. Precision (mainly of the preprogrammed type) escape reactions (in response to electrostimulation of the "working" limb which induces its unconditioned reflex flexion) may remain essentially completely preserved. This points to the preservation of at least that part of the program of the motoric reaction which supports the cessation of the movement of the limb in the required position.

3. The capacity to fix the position of the raised limb is not lost, but is persistently impaired.

4. The capacity to overcome unconditioned reflex flexion of the limb to which EDS has been applied is decreased acutely and persistently during the performance of the learned extensor escape reaction.

5. Movements monitored by vision (offering of the paw) suffer to a substantially lesser degree than the avoidance reactions. Their practically complete spontaneous recovery takes place within a month.

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