THE CONDITIONED REFLEX ACTIVITY OF DOGS BEFORE AND AFTER BILATERAL EXTIRPATION OF THE PARIETAL CORTEX

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(Presented by Academician V. N. Chernigovskii)
Translated from Byulleten' Éksperimental'noi Biologii i Meditsiny, Vol. 51, No. 2, pp. 9-13, February, 1961
Original article submitted January 26, 1960

There are few reports in the literature of research into the conditioned reflex activity of dogs after extirpation of the parietal region on one side. From the little information available [5, 6, 8], according to which the parietal region of the dog takes part in the analysis and integration of simple sound and light stimuli and mechanical stimuli of the skin, it is difficult to judge the character of the localization of these functions, for in all these cases the parietal region was removed together with other regions of the cortex (occipital, temporal, postcoronary). Removal of the parietal lobes [7] led to the temporary (5-7 days) disappearance of the conditioned motor reflexes to a sound stimulus. A study which we made of the efferent pathways of the parietal region of the dog [3] showed that from this point of view this region is complex – it has projection connections with those subcortical structures with which other regions of the cortex are connected, especially the precoronary, occipital and postcoronary regions.

As a consequence of the foregoing considerations, we studied certain functional properties of the parietal region of the dog.

EXPERIMENTAL METHOD

We studied the conditioned reflex activity in the experimental animals before and after the bilateral extirpation of this particular region (Area 5 and Area 7).*

The investigation was carried out on two dogs (Kashtanka and Belyak). In the course of the work we studied the motor reactions of the dogs when allowed to move about freely in a chamber [1]. We used simple sound and visual stimuli and mechanical stimuli of the skin as conditioned stimuli. The parietal cortex was removed in two stages – the parietal region of one hemisphere was first removed, followed 2-3 weeks later by that from the other hemisphere. The dog was sacrificed four months after the second operation.

EXPERIMENTAL RESULTS

The dog Kashtanka. The conditioned motor reaction to a positive sound stimulus – bell 1 – appeared after eight reinforcements. Differentiation to bell 2 was consolidated after the 52nd application. The conditioned motor reaction to a positive light stimulus – white light 1 from a 100 w lamp – appeared and became constant after seven reinforcements. Differentiation of the light stimuli – light 9 – was consolidated after six applications

* We have studied the cytoarchitectonics of these areas and compiled a cytoarchitectonic map of this region [2].

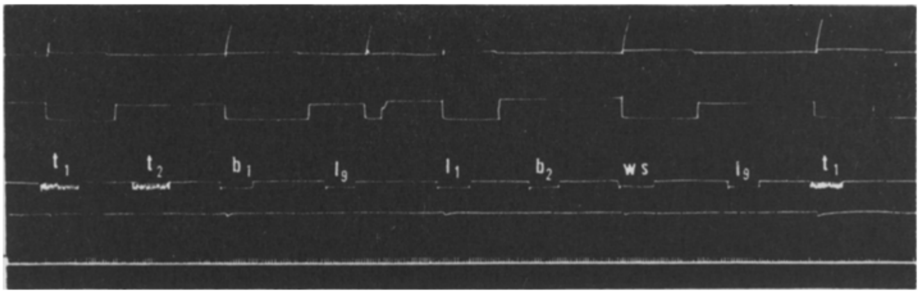

Fig. 1. Character of the conditioned reflex activity of the dog Kashtanka before the first operation. Significance of the curves (from above down): marker of the dog's visit to the feeding bowl; marker of the dog's visit to the sleeping corner; marker of application and duration of action of the conditioned stimulus; marker of presentation of the feeding bowl for reinforcement of the conditioned stimulus by an unconditioned; automatic time marker (1 second). b_1) Bell 1; b_2) bell 2; l_1) light 1; l_9) light 9; t_1) touch 1 (right thigh); t_2)touch 2 (right shoulder); ws) white square (+); wt) white triangle (−).

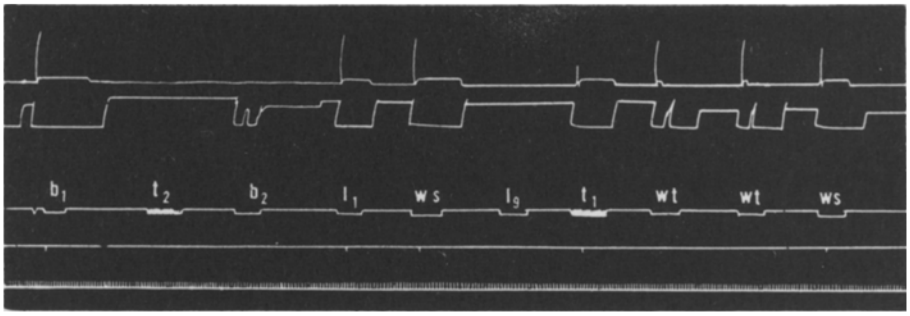

Fig. 2. Character of the conditioned reflex activity of the dog Kashtanka before the second operation. Legend as in Fig. 1.

of the stimulus (the brightness of the light stimulus was determined by the degree of blackening of an x-ray film placed in the path of the beam of light in the form of a filter). The positive conditioned reflex to mechanical stimulation of the skin – touch stimulus 1 in the region of the right thigh – appeared at the 26th combination and was consolidated after 51 applications. Differentiation in the form of touch stimulus 2 in the region of the right shoulder appeared after four applications of the stimulus. In addition an attempt was made to produce reflexes to objective stimuli: positive – a white square, and negative – a white triangle. The kymograph tracing shown above gives an idea of Kashtanka's conditioned reflexes before the first operation (Fig. 1).

The parietal cortex from Kashtanka's left cerebral hemisphere was then ablated. After the operation the dog reacted in a lively manner to surrounding stimuli, pricking the skin of the limbs was accompanied by their withdrawal, and no abnormality of the gait was observed. On the third day after operation Kashtanka took part in the experiment. It was found that the animal's conditioned reflex activity was essentially unchanged: the dog reacted to all the positive stimuli that were applied by a movement towards the feeding bowl; when the differential stimuli were applied the dog remained in its initial place. After the first operation the production of differentiation to the white triangle was continued. The animal no longer walked to the feeding bowl after the third application of the triangle. Differentiation to the triangle, however, was unstable, sometimes disappearing and then subsequently reappearing.

In Fig. 2 we show a tracing of the conditioned reflex activity of the same dog before the second operation. On the day after the second operation (extirpation of the parietal cortex of the right hemisphere) the dog was lethargic, moved about very slowly, placed its hind limbs wide apart, and performed a series of sliding movements with them on the floor. There was a slight predominance of the tone of the extensor muscles of the limbs. Vision was disturbed, and the dog often collided with objects on its left side. No disturbances of pain sensation were observed. On the third day after operation Kashtanka took part in the experiment. The conditioned reflexes and differentiation to all the stimuli applied were preserved. Motor disturbances, however, were present — the dog slowly raised itself up to the feeding bowl and its hind limbs slipped about the floor; disturbances of vision were also observed. From the sixth day after operation the above-mentioned motor disturbances and the disturbances of vision began to disappear gradually. In later experiments no changes in the conditioned reflex activity were likewise found.

In order to test the strength of the process of inhibition in the dog after extirpation of the parietal cortex, the application of the differential sound stimuli (bell 2) was specially prolonged to two minutes (instead of the usual 20 seconds). This procedure caused no appreciable disturbance of the conditioned reflex activity. The positive sound stimulus (bell 1) was then extinguished. The conditioned motor reaction to this stimulus did not appear after 25 failures to reinforce the bell 1. During this period no significant disturbances of the conditioned reflex activity were observed in the dog. Kashtanka was sacrificed four months after the second operation. During this period no changes were found either in the conditioned reflexes which we studied or in the dog's behavior.

In the second dog (Belyak), as in the first (Kashtanka), conditioned reflexes were produced to sound (bell 1 and bell 2) and light stimuli (light 1 and light 9) and to mechanical stimulation of the skin (touch stimuli 1 and 2). The conditioned motor reflex to bell 1 appeared after 13 combinations with food reinforcement; differentiation to bell 2 became stable after 45 applications. The motor conditioned reaction to light 1 appeared after six combinations, and the negative reaction to light 9 after two applications. The conditioned reflex to touch stimulus 1 appeared after three combinations, and differentiation to touch stimulus 2 at the third application.

The parietal cortex on both inner and outer surfaces of the right hemisphere of the dog Belyak was then ablated, and the procedure was repeated on the left side 20 days later.

Neither the first nor the second operation caused changes in the previously produced conditioned reflexes (Fig. 3). As in Kashtanka, however, motor disturbances were observed in Belyak (the dog moved about slowly, widely separated its hind limbs and performed sliding movements) together with disturbances of vision (the dog collided with objects situated on the side opposite the site of operation). Cutaneous sensation could not be tested because of the dog's marked aggressiveness. The above-mentioned disturbances were very clearly noticeable for 5-6 days after the operation after which they gradually began to disappear.

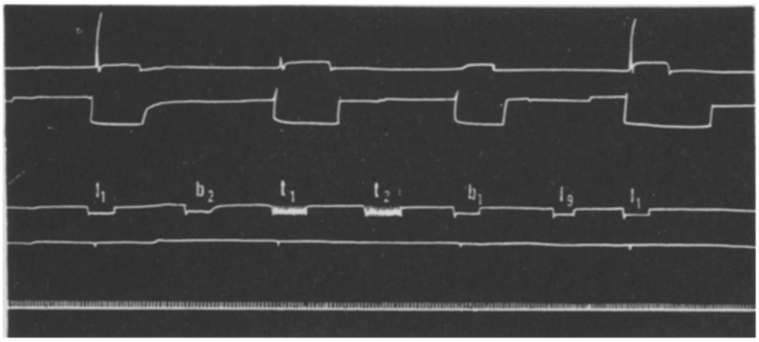

Fig. 3. Character of the conditioned reflex activity of the dog Belyak on the fourth day after the second operation. Legend as in Fig. 1.

In the dog Belyak, as in Kashtanka, the action of the differential sound stimulus (bell 2) was deliberately prolonged, and this was followed by extinction of the positive sound stimulus (bell 1). These procedures caused no change whatever in the conditioned reflex activity of the dog Belyak.

When our findings are compared with the results of investigations by other workers, it must noted that similar phenomena were described by Bekhterev [4] and Peele [9] in association with lesions of the parietal region in the dog and the monkey. The disturbances of pain and tactile sensation observed by Bekhterev may be attributed to the fact that he removed not only the parietal cortex but also the postcoronary region. So far as the other disturbances (movement, vision) are concerned, as our investigations showed these are evidently associated with the destruction of the parietal region (although the effect of postoperative trauma cannot be excluded).

After extirpation of the parietal region in the dog we thus were unable to detect changes affecting the conditioned reflexes, investigated during free movement of the animal, to simple sound and light stimuli and to mechanical stimulation of the skin. At the same time the motor and visual disturbances which we observed after bilateral ablation of the parietal region may indicate that the parietal cortex participates in the functions of both the motor and the optic analyzers. This view is in agreement with our previous findings [3] that various areas of the parietal region are interconnected, namely: Area 7 is connected by efferent fibers with the posterior part of the lateral nucleus of the thalamus, with the superior colliculus and with the nuclei of the pons; Area 5 sends efferent fibers into the medial lamina of the globus pallidus, into the middle part of the lateral nucleus of the thalamus, into the lateral part of the substantia nigra, into the nuclei of the pons and into the spinal cord.

On the basis of our findings relating to the functional characteristics and the connections of the parietal region in the dog it may be postulated that scattered elements of the optic and motor analyzers are situated in the parietal cortex.

SUMMARY

Conditioned reflexes were examined in two dogs allowed to move freely in response to sound, light, and skin-mechanical stimuli. Both the unilateral and bilateral removal of parietal area provoked no significant disturbances in the conditioned reflex activity of dogs. However, in bilateral extirpation of this area motor and visual disturbances were observed. These data as well as evidence obtained earlier and relating to the connections in this area lead to a suggestion that the parietal area participates in the function of the motor, as well as of the visual, analyzer.

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