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CONDITIONED AUDIO-VISUAL TARGETING REFLEXES IN SPLIT BRAIN CATS

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Abstract. A conditioned audio-visual targeting reflex was elaborated in 12 freely moving cats. The cats had to localize the loudspeaker emiting by a tone of 1,600 Hz, of 500 ms duration and 80 dB intensity. Each time one of the eight loudspeakers placed in front and behind the cat was activated and the targeting reaction rewarded by food. Normal cats attained the 80% criterion for the front and rear loudspeakers in 20 and 30 sessions, respectively. The influence of the transection of the corpus callosum on acquisition and retention of the targeting reaction was investigated. The split brain animals with pre-operative experience in the situation did not show any retention, but relearned the targeting of the frontal sources in 20 sessions. No relearning of the posterior sound sources was observed. The animals that had only post-operative training did not reach 80% of correct responses in 50 sessions. Corpus callosum transection influences the integration of the targeting reaction in different ways, depending on the position of the sound source and on pre-operative training.

INTRODUCTION

In Pavlov's laboratory Bykov and Speransky (1) showed in 1924 that tactile symmetrical differentiation was a matter of considerable difficulty, but after sectioning of the corpus callosum the differentiation was easily established. Sperry (16) described an analogous occurrence in patients with a surgical transection of the corpus callosum. If a stylus was used to stimulate "a point on a particular joint of a particular finger was held palm up and was screened from the visual field", the patient could find the stimulated point on the same hand, but unlike a normal person he was quite unable to find a corresponding mirror point on the opposite hand, and was also unable to verbally determine the stimulated point if it was on subordinate hand. Gazzaniga et al. (7) showed that performances, in which visual inflow was restricted to one hemisphere and the response involved the hand whose primary cortical representation was on the same hemisphere, were little affected, whereas those performances requiring interaction or direct cooperation of both hemispheres showed marked disruption.

Dobrzecka (3) demonstrated that the transection of the corpus callosum induced a facilitation of symmetrical tactile stimuli differentation in dogs. The facilitation was observed if the right and left side of the animals trunk were stimulated, but not if the distal parts of the fore or hind legs were stimulated. Myers and Sperry (10) trained chiasm-sectioned cats in a visual pattern discrimination task with one eye, and afterwords they bilaterally extirpated the primary visual cortex. They observed that the recall was immediate, or nearly so, for the simpler discrimination. Recall failed however in the case of more complicated discriminations. Dobrzecka et al. (4, 5) showed that the effect of the interaction between the corpus callosum transection and the extirpation of the somatosensory cortex was a consequence of the cortical representation of the receptive field of the stimulated system.

Corballis and Beale (2) reviewed the factual evidence and stated that left-right discrimination tests are specially difficult for animals and humans to solve. They suggested that an interhemispheric fiber system, such as the corpus callosum "symmetrices" memory traces, and thus preserves structural symmetry. Based on the literature, Gazzaniga (6) stated that the interhemispheric exchange of visual, tactile, olfactory, proprioceptive and auditory information is totally disrupted after commissurotomy and that a learned task integrated in both hemispheres is also disrupted.

There is not much information about the role played by the commisural pathway in sound localization. Naumann (11) did not find significant influences after sectioning the corpus callosum. The present study analizes the ability of cats, with a section of the corpus callosum, to target a source of a sound with their eyes.

METHODS

Subjects were 16 adult male cats divided into three groups: a control group (CG, $n = 8$), a group with pre- and post-operative training (PpG, $n = 4$) and a group with post-operative training only (PoG, $n = 4$).

Training procedure. Cats on 24 h food deprivation were trained in a cage 100 cm long × 100 cm wide × 80 cm high. Eight loudspeakers oriented toward the center of the cage were placed in the corners. Thus four loudspeakers were in front of the cat (L1, L2, L3 and L4) and four behind it (L5, L6, L7 and L8). The animal was observed through a one-way vision screen. At the beginning of training one or two loudspeakers were used to teach the subject that it would receive food in the feeder every time it looked at the loudspeaker from which a sound was delivered. Usually 16 or 32 trials sufficed for the cat to learn this task. Only then was it submitted to the experimental procedures requiring subjects to visually localize the loudspeaker from which the sound was delivered.

The auditory stimulus was a 1,600 Hz tone of 500 ms duration and 80 dB intensity delivered at random from the eight different loudspeakers. The auditory stimulus was emitted when the subject was looking in the direction of the feeder and especially when its body was oriented perpendicular to the screen. Each loudspeaker was activated twice in a session. The animal received pieces of meat delivered through a rotatory feeder as a reward, and it received up to maximum of 100 g of food during and immediately after the training session.

Each cat was trained during 50 sessions with 16 trials in each session. The intertrial intervals lasted 1–3 min, depending on the time the animal needed to orient its body perpendicular to the screen. A trial was considered correct when the cat was able to localize the activated loudspeaker with its eyes at the first attempt. If the trial had no correct response it was repeated up to a maximum of three times at the same interval as the normal trials. A trial was incorrect when the cat did not look at the activated loudspeaker and reacted in general with a targeting reflex but not always focusing on the activated loudspeaker.

Surgery and histology. The transection of the corpus callosum was performed in a stereotaxic instrument. Chloralose anesthesia (70 mg/kg) was injected intraperitoneally. After trepanation, the rura was opened along the interhemispheric fissure to expose the corpus callosum. Two electrode holders were used to make the transection, but instead of an electrode, a needle was placed into each holder. The sharp end of the needle was inserted into the holder and a loose thread was introduced through the eye of the needle. The needles were sterotaxically oriented in such a way that the eyes remained under the corpus callosum level: one at the occipital extreme and the other at the frontal pole. The loose thread was pulled and the corpus callosum sectioned. In order to avoid bending the needles while pulling the thread, a piece of wood was placed between the needles. Its length was exactly that of the required interneedle distance. Antibiotics were subsequently administered. At the end of the experiment the cats were anestethized with Nembutal. The brain was perfused with 10% formaline and subsequently tissue surrounding transection examined. Of the 14 cats operated, only eight received the transection of the corpus callosum without injury to other structures, and these eight subjects are considered in the results. In these cats the anterior commisure was intact. The results were statistically analysed by the t-test.

RESULTS

Control group (CG) performance. In the first five sessions the scores for both sets of loudspeakers were different: 65% of correct responses for the front ones and 57% for the rear set. The animals reached the criterion of 80% correct responses to the speakers placed in front of them (L1–L4) after 20 sessions, while 35 sessions were required to meet the criterion of correct responses to the speakers placed at their rear (L5–L8). At the end of the 50 sessions of training the animals showed 90% positive responses for the front group of loudspeakers while the level of correct responses for the rear speakers remained at 80%. The statistical comparison of the performance seen in Fig. 1 indicated that the differences between responses to each set of speakers were significant ($t = 2{,}9$; $P < 0.05$).

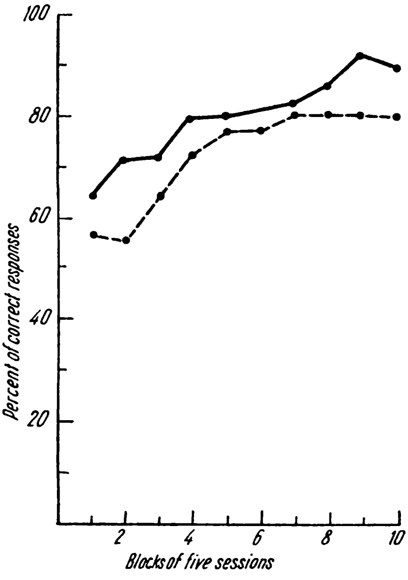

Fig. 1. Course of the learning process in the control group (CG). Solid line, front speakers (L_1–L_4); dashed line, rear speakers (L_5–L_8).

Comparison of learning and post-surgical learning (*PpG*). The transection of the corpus callosum produced a decrease in the retention scores for both sets of speakers the scores for the front set fell to 66% while those for the rear set to 36%. Post-operative retraining produced an increase of the scores to 79% for the front speakers until the fourth session, but no further increase was observed until 50th session. Conversely, responses given to the rear speakers did not show any increase during the entire retraining period (Fig. 2). t-tests showed no statistical differences between the pre- and post-operative performance for the front speakers, but significant differences emerged for the rear set (Table I).

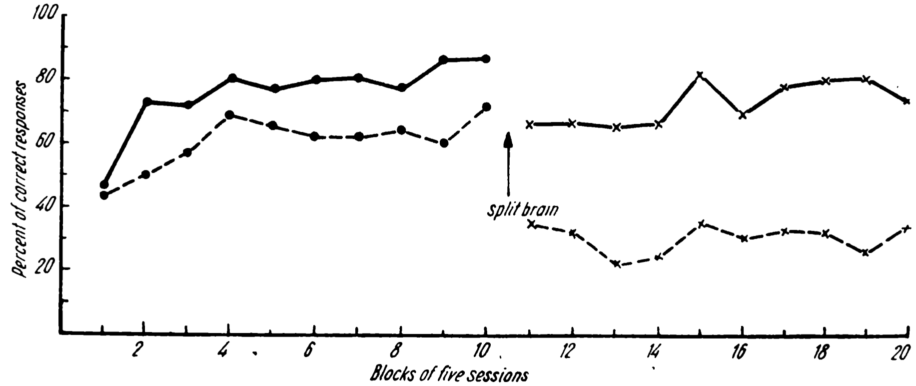

Fig. 2. The course of pre-operative learning and post-operative retention in PpG group. Denotations as in Fig. 1.

TABLE I

t test of comparison of performance in respect to speaker position

Speaker position	Before-after operation (PpG)	Control-post-operative training (CG-PoG)
L1	0.814	2.300*
L2	0.079	5.370**
L3	0.653	5.324**
L4	2.170	2.307*
L5	2.39*	3.109*
L6	3.06*	3.093*
L7	3.17*	2.908*
L8	5.57**	2.730*

Comparison between learning of control group (CG) and operated group (*PoG*). During the first ten sessions an increase of correct responses was observed; the curve then tended to stabilize (Fig. 3). Up to the 50th session a slight improvement in the amount of correct responses to the front speakers was seen, whereas a decrease occurred to the rear set. In no case did correct performance reach the levels required by the learning criterion. The comparison between the operated and the normal animals was made for each loudspeaker separately. This analysis indicated that both groups differed significantly for all the speakers (Table I).

Comparison between control and both surgical groups. The differences between the CG and both operated groups indicates that the surgical effects were different, depending on the pre-operative experience and on the position of the speakers (Fig. 4). The comparison of the differences CG-PoG-control and without pre-operatory experience groups — between the performance related to the anteriorly (L1–L4) and to the posteriorly placed loudspeakers (L5–L8) are statistically significant ($t = 5.00$, $P < 0.01$) and greater than the differences CG-PpG-control and post-operative trained groups — for the same comparison ($t = 3.04$,

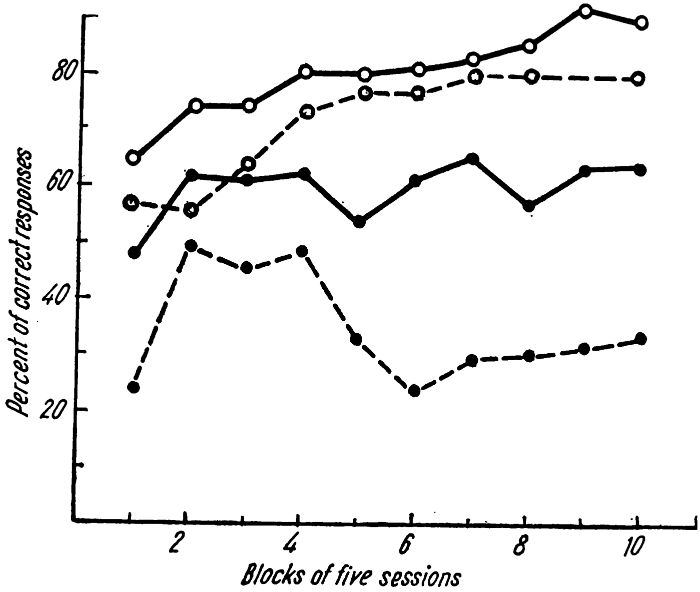

Fig. 3. The course of the learning of control group (CG) and the group which received only post-operative training (PoG). Open circles, CG; filled circles, PoG. Other denotations as in Fig. 1.

$P < 0.01$). However there are not significant differences between CG-PoG and CG-PpG for the loudspeaker placed behind the animals and only a tendency for those placed before them.

Fig. 4. Differences in percentages of correct responses between the control group (CG) and the group with pre- and post-operative training (PpG) and between the normal group and the group with post-operative training (PoG). Denotations as in Fig. 1.

DISCUSSION

The time taken by the wavefront to reach both ears (Δt) is, in the opinion of some investigators, the main clue for the localization of sound. If this hypothesis is correct, no differences should exist in the localization of sounds coming from sources placed in front or behind the animals. In general, Δt is a very ambiguous clue for localization, since all points lying on a hyperbola of revolution about an axis through both ears will have the same Δt (20).

Even if intensity and phase cues contribute to the localization of the sources of a sound the present findings are still puzzling. It is then necessary to try to understand our data by searching for other explanatory hypotheses. It is known that cats do not target the source of a sound directly with their eyes on the basis of direct auditory information impinging upon the neural system, but rather through a complementary feedback coming from the muscles of the pinna activated by the sound (13, 15). The movement of the pinna is controlled by the seventh nerve nucleus. This nucleus receives information from the ipsilateral superior olivary complex, the trapezoid body (9), the inferior colliculus (18), trigeminal nucleus (19) and the telencephalon, more specifically from the sensory motor cortex (14) and perhaps from other structures also. These data suggest that the neurons of the facial nucleus integrate different reflexes activated by a sound, from some very rapid ones, such as contraction of the stapedius muscles, to the movements of the pinna and complex movements of the face which appear with a longer latency. However the activation of coordinated movements of the eyes and head as part of the audio-visual targeting reflex shows that directly or indirectly the auditory information can set motor nuclei other than the facial nucleus into action.

In normal cats, the neural integration processes utilized to target a source of a sound in the frontal plane seem to be different from those involved in the targeting of a source placed in the rear. The pinna movements that serve to localize frontal sources are short and quick, in general performed by the pinna ipsilateral to the sound. To localize sources placed in the rear, the pinna executes long testing tracking and scanning movements and often both auricles are involved. To target a frontal source, small eye or head movements are required, while to target a rear source large head and body movements are needed. The whole posture of the body is involved, including labyrinthic and neck reflexes. These observations suggest that the localization of a rear source is much more difficult. Nevertheless a serious unsolved problem that remains is how the auditory information can activate such a complex pattern of movements.

The animals operated after training did not show retention, but were able to relearn only to target the front set of speakers, whereas animals without pre-operative training did not learn at all. Observations in our laboratory (15) have shown that the unilateral denervation of the auricular muscles produces learning deficits in the localization of tonal sources placed both ipsilateraly and contralateraly to the operated ear. These behavioral deficits are more important on the denervated side, but affect the localization of the set of speakers placed behind the animals more than those placed before them. These findings suggest that symmetrical functions of the hemispheres are required in order to learn an audio-visual instrumental targeting reaction and to relearn to target a source placed behind the animals. The integrative process underlying the targeting reaction directed to a source placed behind the animals is certainly more complicated than that required to localize a source placed in front of them. In the opinion of Myers et al. (10) the interhemispheric connections are more important as the tasks to be solved are more complicated. The differences of our results with those of Naumann (11) could be explained by the differences in training procedures, especially in the position of the speaker. The large deficit of our operated group is mainly related to the localization of the source placed in the rear field, while the localization an the front field is not so deeply disturbed.

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