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ON THE LOCUS OF EXTINCTIVE INHIBITION

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Asratian (1961) has argued persuasively that the Pavlovian assertion that extinctive inhibition develops originally in the center of the conditioned stimulus (CS) and that the competing allegation that inhibition begins in the center of the unconditioned stimulus (UCS) are both demonstrably inaccurate. His experiments on trans-switching and dual or binary conditioning have provided strong, albeit indirect, evidence to support his conclusion that the primary site of extinctive inhibition must be in the conditioned connection itself. Earlier work on this topic was summarized by Konorski (1948).

When one of two simultaneously conditioned responses (conditioned by means of his binary procedure in which two UCSs are repeatedly paired) is extinguished, the reverse CR shows no attenuatoin. More specifically, when food and foot-shock are given to the subject together, the food becomes an effective CS in producing leg flexion while the shock becomes effective as a CS in producing an alimentary CR. Both stimuli, of course, retain their original ability to elicit their own unconditioned reactions. Solitary presentation of, say, the food without the foot-shock results in eventual extinction of the conditioned leg flexion. The unconditioned alimentary response to the food persists. When, now, the subject is tested with foot-shock presented alone, this stimulus is seen to have retained its ability to elicit a conditioned alimentary response as well as an unconditioned leg flexion.

Asratian, logically, argues that results of this type cannot be explained by assuming that the extinction procedure generates inhibition

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in *either* the CS center or the UCS center, since the learned relationship is preserved in its opposite direction. To be sure, he overlooks the cogent possibility that, when the food is presented repeatedly alone until the conditioned leg flexion extinguishes, inhibition may develop in the primary projection area for the food stimulus. When foot-shock is delivered, if conditioning reflects a connection between the primary projection area for the shock stimulus and the alimentary response system, the inhibition hypothetically present in the primary projection food center should have no inhibitory effect in the reverse testing.

The purpose of the present experiment was to compare transfer of extinctive inhibition from one CS to another under two basic conditions: (i) when each of the two CSs is associated with a different UCS and (ii) when both of the CSs are associated with the same UCS. If extinction of the CR to one of the CSs results in extinction of the CR to the other CS when they have both been associated with the same UCS, but not when each has been associated with a different UCS, this would be difficult to interpret except by assuming that extinctive inhibition is generated principally in the center of the UCS.

METHODS

Subjects. Forty-eight male, volunteer human *S*s, ranging in age from 17 to 22 were assigned randomly to four groups of 12 *S*s each. The *S*s were paid $1.00 (U. S.) each for serving in the experiment.

Apparatus. Two pure tone CSs, 800 and 1200 Hz in frequency, were used. Both tones had an intensity of 40 db (physical reference) and a duration of 5.0 sec. They were produced by General Radio Company audio equipment and delivered by Trimm ANB-7 earphones. Intensity was rated at the earphones.

A 5 ma d-c shock of 0.1 sec duration was the UCS. It was produced by an Argonaut constant current stimulator and delivered to the right or left ankle of the *S* through $^3/_4$ inch zinc electrodes coated lightly with saline electrode paste.

Zinc-zinc sulfate $^3/_4$ inch electrodes in lucite cups filled with NaCl electrode paste were used to pick up the exodermal GSR as a d-c resistance change from the palm and back of the *S*'s right hand. The response was amplified by a Biophysical Instruments Company amplifier and recorded on a Texas Instruments Company Rectiriter with a paper speed of 3 inches/min. All response were transformed to units of change in log conductance.

Procedure. Data were collected in a dark, sound-proof IAC series 1200 audiometric chamber. The *E* and the equipment were in an adjoining room. After the shock electrodes, GSR electrodes, and earphones were properly placed, instructions were read to the *S* by *E*. All *S*s were given the same instructions; to remain still and attend to the stimuli.

The experiment consisted of four phases:

1. Habituation — all 48 *S*s were given 16 CS-only trials, 8 trials with each of the tones presented in a counterbalanced order.

2. Conditioning — all *S*s received 24 tones (twelve 800 cycle/sec and twelve 1200 cycle/sec) and 24 shocks during this phase of the experiment. *S*s in Group 1 received the 800 cycle/sec tone paired with shock to the right ankle in a delayed conditioning paradigm on one-half of the trials, unsystematically ordered, and the 1200 cycle/sec tone paired with shock to the left ankle in the same paradigm on the other one-half of the trials. For one-half of the *S*s the tone-shock relationship was reversed (i.e., the 800 cycle/sec tone was paired with shock to the left ankle and the 1200 cycle/sec tone was paired with shock to the right ankle). Both the 800 and 1200 cycle/sec tones were paired only with shock to the left ankle in a delayed conditioning paradigm for one-half of the *S*s in Group 2. The other half of the *S*s in Group 2 received both tones, paired in the same way, with shock only to the right ankle. *S*s in Group 3 received the 24 tones *randomly* paired with shock to either the left or right ankle in a delayed conditioning paradigm. For Groups 1, 2, and 3 trials were presented with an ITI ranging from 20 to 60 sec and averaging 40 sec. *S*s in Group 4 received the 24 tones and the 24 shocks unpaired in a random order with an average ITI of 30 sec, ranging from 20 to 40 sec.

3. Extinction — one-half of the *S*s received extinction trials with the 800 cycle/sec tone (the other one-half with the 1200 cycle/sec tone) to a criterion of two non-responses.

4. Transfer of extinction — one-half of the *S*s received additional extinction trials with the 1200 cycle/sec tone (the other one-half with the 800 cycle/sec tone) to a criterion of two non-responses.

The four phases of the experiment followed immediately after one another. The galvanic skin response (GSR) was measured on all trials. A response was counted if it was reliably readable on the chart and if it followed the onset of the stimulus by not less than 1.0 sec and not more than 7.0 sec.

RESULTS

Figure 1 shows the mean magnitude of the GSR to the CSs for the four groups for the first two pairs of habituation trials and across 12 pairs of conditioning trials. Although the groups did not differ significantly in habituation ($F = 2.19$, $p < 0.20$), these data are included in the figure as reference points for examining the conditioning data. As can be seen in Fig. 1, the three conditioning groups (Groups 1, 2, and 3) showed an increase in GSR magnitude to the CS over the first four acquisition trials. Starting with Trial Block 3, response diminution appears to have begun.

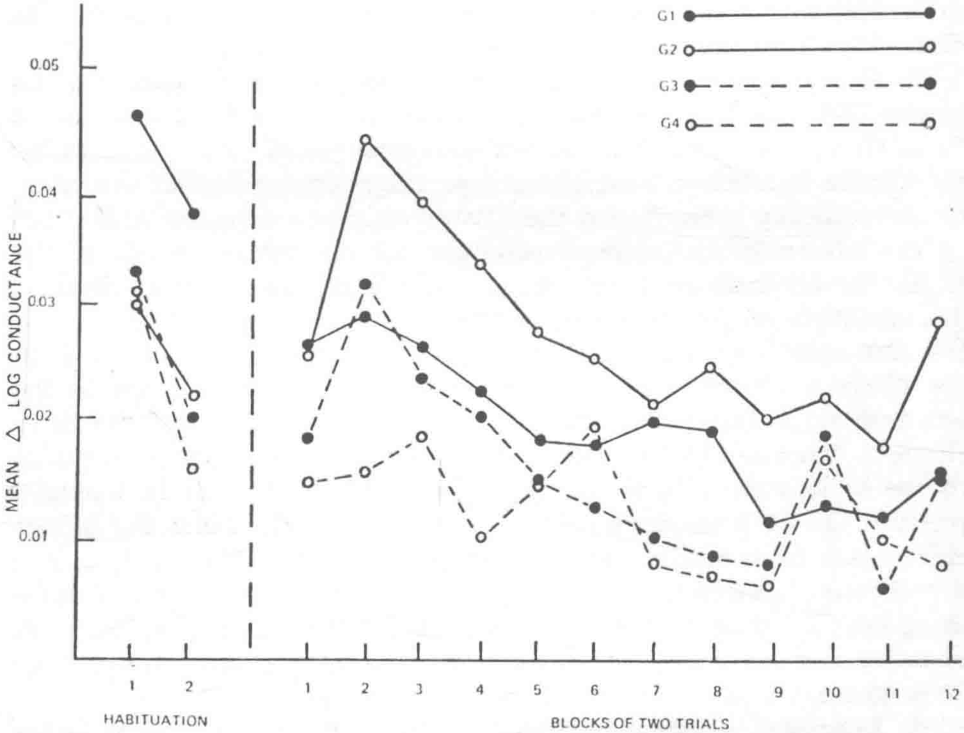

Fig. 1. Mean magnitude of GSR to the two CSs during habituation and conditioning.

Analysis of variance of CR magnitude for the twelve conditioning Trial Blocks showed that the effect of Trials was significant ($F = 5.92$, $p < 0.001$). The Groups effect was also significant ($F = 4.04$, $p < 0.025$), due primarily to the difference between Groups 2 and 4. Duncan's Multiple Range Test showed Group 2 to be significantly higher than Group 4 ($p < 0.05$). The Trials × Groups interaction failed to achieve significance, indicating that the conditioning groups did not differ significantly from the controls in the overall trend of their performance across conditioning trials. Analysis of variance conducted on the data of only the first four trials of conditioning showed significant Groups and Trials effects

($F = 3.17$, $p < 0.05$ and $F = 3.62$, $p < 0.025$, respectively) indicating differences between the groups and across trials in the early stage of conditioning prior to the influence of response diminution.

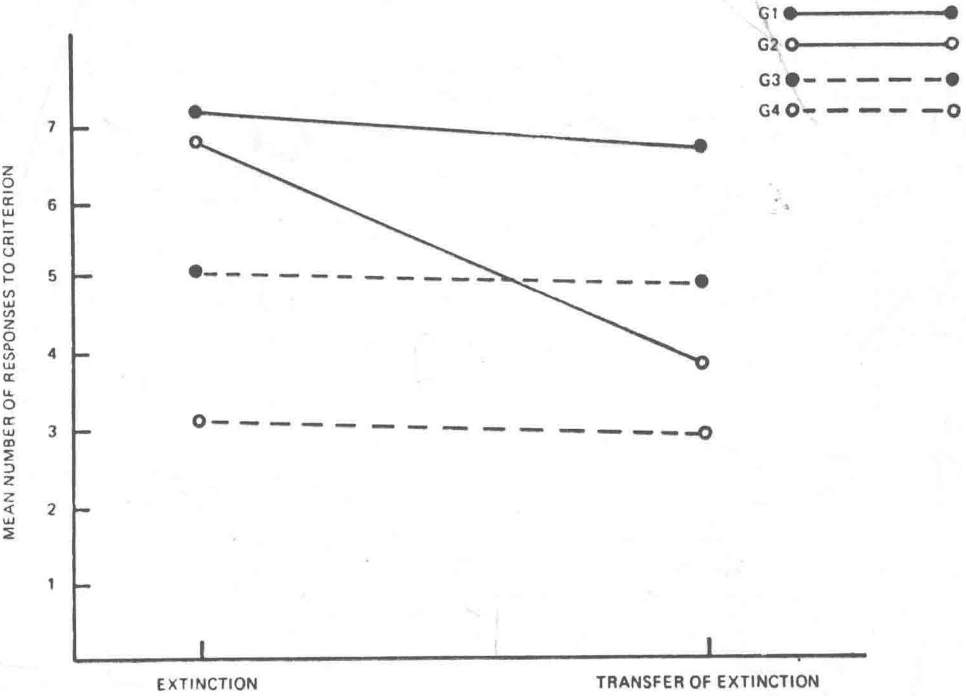

Fig. 2. Mean number of responses to criterion during extinction and transfer of extinction.

Figure 2 shows the mean number of CRs to the extinction and transfer of extinction criterion of two non-responses, in the four groups.

Analysis of variance showed that the groups differed significantly in mean number of responses made to reach the extinction criterion ($F = 3.10$, $p < 0.05$). Group 1 ($\bar{X} = 7.2$) was very similar to Group 2 ($\bar{X} = 6.8$), and both were superior to Group 3 ($\bar{X} = 5.1$) which was, in turn, superior to Group 4 ($\bar{X} = 3.1$). The inferiority of Group 4 adds further support to the assumption that conditioning occurred in Groups 1, 2, and 3. A Chi Square analysis of the number of *S*s responding during the first six extinction trials showed that the groups differed significantly in number of *S*s responding ($\chi^2 = 44.65$, $df = 18$, $p < 0.001$). This effect was due primarily to the fact that Group 4 was consistently below the other three groups on the extinction trials. These data provide additional evidence for the assumption that conditioning occurred in the other three groups.

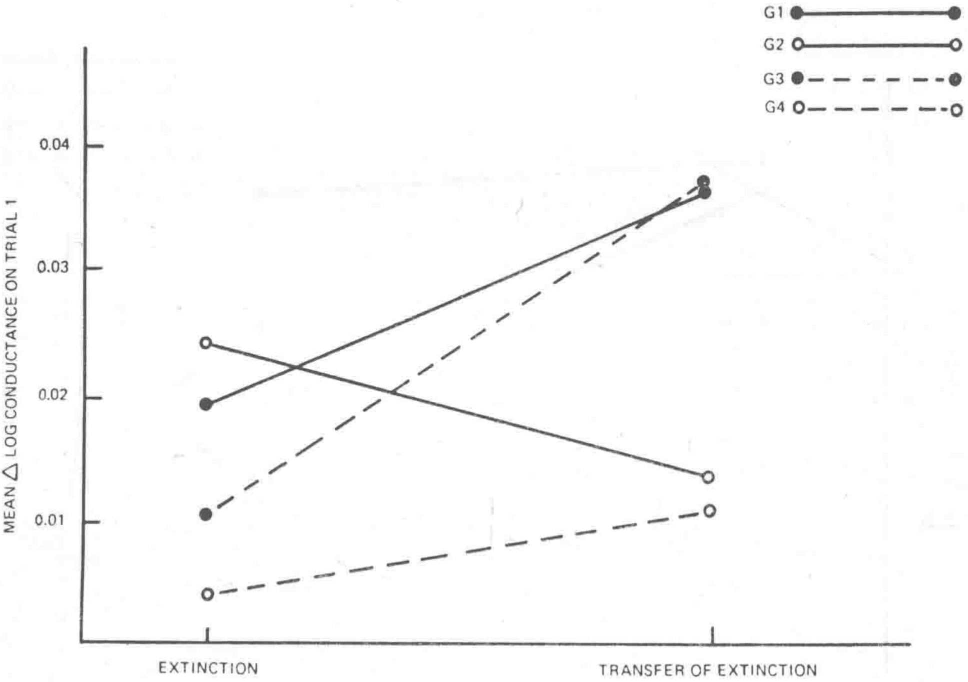

Fig. 3. Mean magnitude of GSR to the tone on Trial 1 of extinction and on Trial 1 of transfer of extinction.

Figure 3 shows the mean magnitude of GSR to the tone on Trial 1 of extinction and on Trial 1 of transfer of extinction for the four groups. Analysis of variance of response magnitude on Trial 1 of extinction shows that the differences among the four groups failed to achieve significance ($F = 2.822$, $p < 0.10$). Duncan's Multiple Range Test showed that Group 2 and Group 4 were significantly different ($p < 0.05$), and that the differences between Groups 1 and 4, and Groups 2 and 3 approached significance (both $p < 0.10$). Groups 1 and 3, and, to a lesser extent, Group 4, showed an increase in magnitude of response on the first transfer of extinction trial as compared to the first extinction trial. Group 2 showed a decrease in response magnitude from Trial 1 of extinction to Trial 1 of transfer of extinction. Analysis of variance showed no significant difference between groups and the extinction-transfer of extinction contrast fell short of significance ($F = 3.619$, $p < 0.10$). The Groups × Phase interaction was significant ($F = 2.902$, $p < 0.05$), due to the disparate performance of Group 2.

DISCUSSION

The assumption that conditioning took place in the three groups receiving paired presentations of the tone and shock (Groups 1, 2, and 3) was supported by the data collected in the conditioning phase of the experiment, which showed a significant overall Trials effect across all 12 Trial Blocks, and, of more importance, a significant Trials effect on the first four trials. Further support for the assumption of the occurrence of conditioning was sought in the extinction data. The significant differences found among the groups in number of responses made to reach extinction criterion supports the assumption that conditioning occurred. Also the Chi Square analysis of number of *S*s responding on the first six extinction trials showed a significant difference among the groups. In both instances, Group 4 was clearly inferior to the three conditioning groups. In addition, the superiority of Group 2 over Group 4 is readily interpretable in terms of the conditioning assumed to have taken place in Group 2 (but not in Group 4). However, conditioning should also have occurred significantly in Groups 1 and 3, since they also received paired presentations of the tone and shock. Apparently the conditioning that occurred in Groups 1 and 3 was somehow attenuated. The only important difference in procedure between Groups 1 and 3, on one hand, and Group 2, on the other, and, therefore, the most likely cause of this attenuation, was the number of different UCSs presented. While Group 2 had only one UCS, both Group 1 and Group 3 had two different UCSs present. It may be, therefore, that multiplicity of USC had a suppressing effect on the acquisition of the conditioned response in this experiment. The explanation of this finding is not immediately apparent.

The extinction data did not reflect conditioning differences identical to those seen in acquisition. These data implied a near equality of strength of conditioning for Groups 1 and 2, with Group 3 inferior. Groups 1 and 3 were shown to suffer somewhat in conditioning, supposedly because of their multiple UCSs. Group 3 appeared also to suffer in extinction. The only procedural difference between Group 3 and Groups 1 and 2 was in the variable pattern of the CS-UCS pairings received by Group 3 during conditioning. Again, however, no immediate explanation of this finding is apparent.

The similarity of Groups 1 and 2 in extinction did not carry over to transfer of extinction (Fig. 2). While Group 1 displayed substantial response strength in the second extinction phase of the experiment, Group 2 did not. This difference may be understood in relation to the procedural differences that were present during the conditioning and extinction phases of the experiment. The *S*s in Group 1 had apparently established two distinct CS-UCS associations during conditioning. One of these associations was extinguished during the extinction phase of the experiment. The other was extinguished in a similar number of trials during the transfer of extinction phase of the experiment. The lack of any apparent transfer of extinction is readily understandable under the assumption that extinctive inhibition was generated only in the center of the appropriate UCS and did not influence the conditioned response of the other UCS. In this connection, it must be noted that the two UCS primary projection areas in question (shock to right ankle and shock to left ankle) are found in different hemispheres of the brain, even though the center of the unconditioned response is identical for both.

It may be that the present experiment falls outside of the purview of Asratian's theory because it involved only a single session while Asratian's studies were of longer duration. On the premise that short-term and long-term memory may involve different nervous processes, of course, this disagreement with Asratian's theory may be less than critical.

Group 2, which showed reduced response persistence in the second extinction phase, had an opportunity to establish associations between two different CSs and a single UCS during the conditioning procedure. During extinction the association between one of the CSs and the UCS was weakened; and, as is apparent in the transfer of extinction data, the other association was weakened at the same time. This would be expected on the assumption that extinctive inhibition developed in the common primary projection area for shock.

Group 3 ranked between Groups 1 and 2 in response persistence in the second extinction phase of the experiment. This group, like Group 1, had more than one UCS, but the variability of the pairings of the two CSs with the two UCSs may have produced somewhat similar associations to the two different CSs (although not as similar as those produced in Group 2). Therefore, Group 3's response persistence in the second extinction phase was reduced somewhat by the first extinction phase, but not nearly to the extent shown by Group 2.

The increase in response magnitude from the first to the second extinction phases in Groups 1 and 3, and the decrease apparent in Group 2 (Fig. 3) also are in accord with the notion that extinctive inhibition develops in the primary projection orea of the unconditioned stimulus, with the additional assumption that a paradoxical contralateral induction occurs. The magnitude data, of course, also may be interpreted in terms of orienting response (OR) theory (Sokolov 1960), assuming that the presentation of a novel stimulus evokes an OR. The more novel the stimulus, the greater the magnitude of the evoked OR. The GSR is, of course, an important component of the OR. The novelty of the incoming stimulus is defined in relation to previous stimuli received by the organism. Trial 1 of the final phase of the experiment may be viewed as a test occasion for an OR. The magnitude of the OR occurring on Trial 1 of transfer of extinction should depend upon the novelty of the tone presented (as contrasted with the tone experienced during the extinction phase of the experiment). Since the physical difference in the tones presented is the same for all groups (i.e., 400 cycle/sec), the differences in magnitude of OR occurring may be attributed to differences in the novelty of the tones arising from their different histories. Groups 1 and 3 were conditioned by a procedure that magnified, or at the very least maintained, the existing difference between the two tones, by associating them with two different UCSs (i. e., giving them *different* "meanings"). These groups therefore displayed large ORs when presented with the other tone during transfer of extinction, after having received one tone during extinction. Group 2 was conditioned with a procedure that may have reduced the significance of the existing physical differences between the two tones by associating both of them with the same UCS (i.e., giving them the *same new* "meaning"). It is, therefore, not surprising that Group 2, unlike Groups 1 and 3, showed no appreciable OR to the tone in the second extinction phase after having experienced the other tone in the first extinction phase of the experiment.

SUMMARY

An experiment investigating the locus of extinctive inhibition was run in four phases: habituation, conditioning, extinction, and test for transfer of extinction. Tone CSs and electric shock UCSs were used. The GSR was the response measured. The conditioning data suggested that multiplicity of UCS has a suppressing effect on the acquisition of a CR. It was further suggested, on the basis of both the conditioning and extinction data, that weaker conditioning (in terms of resistance to extinction) results from variable CS-UCS pairing during conditioning. The transfer of extinction data appeared to support the assumption that extinctive inhibition first develops in the primary projection area of the unconditioned stimulus, contradicting Asratian's theory. It was noted, however, that the work on which Asratian based his conclusions involved long-term experiments, while the present study employed only a single training and testing sequence in one session.

This research was based upon the second author's M. S. thesis done at Ohio University under the supervision of the first author. The research was supported in part by USPHS grant MH12262-04.

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THE EFFECTS OF LESIONS OF AUDITORY CORTEX ON DISCRIMINATION OF SOUND LOCALIZATION IN DOG

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The studies by Neff on cats (Neff et al. 1950, 1956) have demostrated that bilateral ablations of the temporal cortex produce dramatic impairments of auditory cue localization. It was considered useful to test his results by a completely different method, namely by utilizing go–no-go differentiation to two auditory stimuli, sounding from different places in standard conditioned reflex experiments.

MATERIAL AND EXPERIMENTAL PROCEDURE

The experiments were performed on 19 mongrel dogs 1.5–4 years old, weighing 11–16 kg. The animals were trained on the stand in a soundproof CR chamber. The feeder with ten bowls was situated in front of the animal. The bowls were successively put into position by remote control. Cubes of bread mixed with minced meat and moisted with broth were used for reinforcement.

After the animals had been habituated to the chamber and experimental procedure, they were trained in instrumental responding. The auditory stimulus, the source of which was in front of the dog, was presented, whereupon the technician raised the dog's right foreleg and placed it on the feeder. Then immediately the bowl with the food was presented and the stimulus was discontinued. When the leg was not raised, the food was not given.

After a few days the dog learned to place his foreleg on the feeder

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actively, in response to the CS, and the movement was immediately reinforced by food. The intertrial movements, not being reinforced, were extinguished.

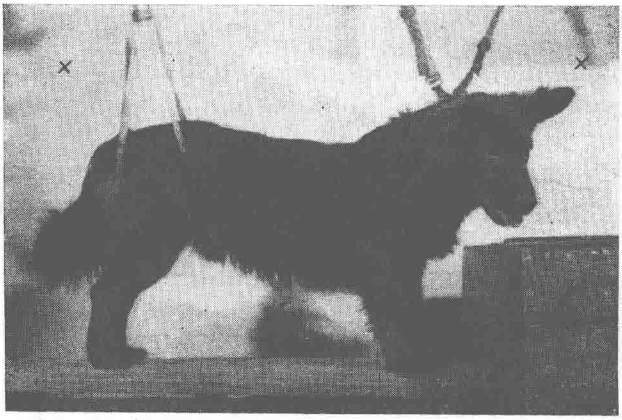

Fig. 1. The dog on the stand. × denotes the sources of the auditory stimuli.

When the dogs began to react regularly to the CS, differentiation training began. In some trials the auditory stimulus, the source of which was behind the dog (Fig. 1), was given and then the presentation of food did not follow. Five positive and five negative trials were given in each session in random order with 1–2 min intervals. The non-reinforced CS lasted always 5 sec.

Thirteen dogs were used in these experiments. In case of eight dogs two metronomes beating with the frequency of 120 per second were used as the CSs, the metronome sounding from the front being positive, and that from behind being negative. In the remaining five dogs the tones 900 cycle/sec emitted from two loudspeakers were used as the CSs, that in front being positive, that behind, negative.

The criterion of the differentiation training was 90% correct responses in a block of ten sessions (100 trials). After the dogs had reached this criterion, control experiments were performed in which the location of the devices producing the auditory stimuli were exchanged. This was done in order to see whether the animals were guided actually by directional cues, or by slight difference in the quality of both sounds (metronomes or tones). It turned out that this procedure produced, in the metronome group, a slight disorder in animals' responding, not exceeding however 10% of all responses. As far as the tone group is concerned, all the dogs were undisturbed, except one animal in which, for unknown reason, a considerable disinhibition of the negative CR occurred. This shows that the directional cues were in fact decisive in the animals' performance both for metronomes and tones, although the dogs did discriminate between the sounds of the metronomes produced by each of the two apparatuses used in these experiments.

After the preoperative training had been completed, the animals were subjected to surgery. In Nembutal narcosis and in aseptic conditions the temporal areas of the cortex were removed on the right and on the left side in two stages. The interval between the two operations was 3–4 weeks. The gray matter was removed by subpial suction and care was taken to spare the white matter and claustrum. About 10 days after the surgery the experiments were resumed.

In the metronome group four dogs sustained ablations including the whole ectosylvian gyri (anterior, medial and posterior) and sylvian gyri (anterior and posterior); two dogs sustained only ectosylvian ablations and two dogs sustained only sylvian ablations. All five dogs in the tone group sustained the combined ectosylvian and sylvian ablations (Fig. 2).

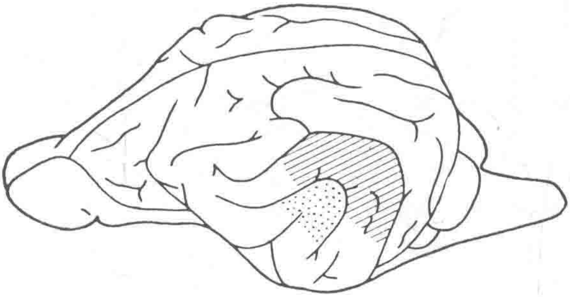

Fig. 2. Extent of lesions. Hatched area, ectosylvian lesion; dotted area, sylvian lesion.

Six other dogs were used as controls and were trained in non-directional cues. In three dogs the same two metrononomes were used, but they were placed side by side in front of the animals. One of the metronomes was positive, the other one negative. In the remaining three dogs two tones were given from a loudspeaker situated in front of the animals; tone 900 cycle/sec was positive, tone 400 cycle/sec was negative. All six dogs were subjected to combined ectosylvian-sylvian ablations.

To sum up the following six groups of animals were used in our experiments: M-D-ES group, M-D-E group, M-D-S group, T-D-ES group, M-noD-ES group and T-noD-S group. M-D, means metronome directional cues, T-D, tone directional cues; M-noD, metronome non-directional cues; T-noD, tone non-directional cues. ES, means combined ectosylvian-sylvian lesion; E, ectosylvian lesion; S, sylvian lesion.

RESULTS

Directional cues. After unilateral temporal lesions the general behavior of the dogs as well as their CR activity, was completely normal, except in a few cases in which the inhibitory responses to the negative CSs were disinhibited. After the second operation, however, the behavioral disturbances in some dogs were manifest: the animals were disquiet and failed to accept food. These symptoms were transient and disappeared after a few days. Only in one dog (M-D-ES 1), a clear visual deficit was observed after operation, and the CRs to the positive CSs were absent for a number of days.

TABLE I

Training in discrimination of directional cues before and after operation

Dog	Number of trials		Number of errors			
			Before operation		After operation	
	Before operation	After operation	Positive trials	Negative trials	Positive trials	Negative trials
M-D-ES 1	400	800	16	28	45	95
M-D-ES 2	300	700	6	35	3	152
M-D-ES 3	300	800	12	6	0	107
M-D-ES 4	400	500	15	40	0	81
M-D-E 1	300	800	21	16	3	202
M-D-E 2	300	600	9	12	2	80
M-D-S 1	300	100	11	59	0	7
M-D-S 2	200	100	5	8	0	2
T-D-ES 1	600	1500[a]	12	58	45	219
T-D-ES 2	500	1300	8	58	3	215
T-D-ES 3	900	1500[a]	15	180	31	465
T-D-ES 4	700	1500[a]	26	111	127	334
T-D-ES 5	700	1500[a]	17	104	7	234

[a] The dog failed to reach criterion.

The effects of bilateral lesions on the CR performance are presented in Table I and in Fig. 3 and 4. It can be immediately noticed that after joint ablations of ectosylvian and sylvian gyri there is a dramatic impairment of the differentiation of the directional CSs. This impairment was clearly visible on simple observation of the experimental dogs. Before operation both CSs, the positive and negative one, produced clear directional responses, consisting in the dog's looking intensely towards the source of the stimulus. After operation this response was gone: the animal reacted to the CS by increased alertness and an instrumental response, but failed to turn to its source; this was particularly manifest in respect to the negative (that is, posterior) stimulus.

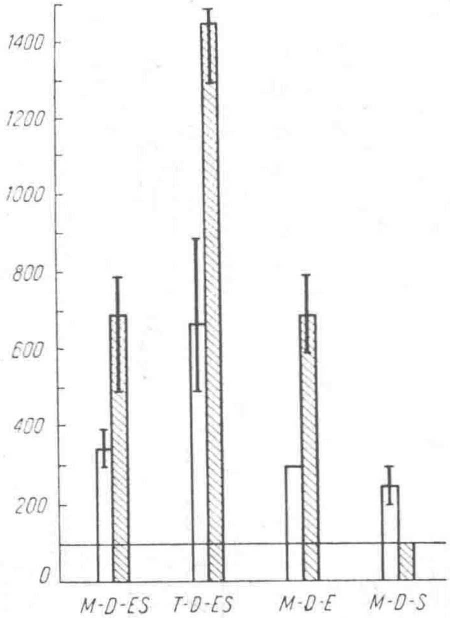

Fig. 3. The effect of temporal lesions in dogs trained in directional auditory discrimination. Each column denotes mean number of errors. White columns, before operation, hatched columns, after operation. The vertical lines show the range of number of trials. M-DE-S, M-D-E, M-D-S, metronome discrimination before and after ectosylvian-sylvian, ectosylvian and sylvian lesions respectively. T-DE-S, tone discrimination before and after ectosylvian-sylvian lesions. The line on the 100 trials level means training criterion.

It can be seen both in Table I and in Fig. 3 and 4 that the original training was much easier in case of the metronome differentiation than in the tone differentiation. The postoperative retraining took also a different course in both groups of animals. Whereas in the metronome group subjected to the joint ectosylvian-sylvian ablations, the animals reached criterion after twice as much trials as in original training, in the tone group only one animal (T-D-ES 2) reached criterion, while the rest failed to do so even after 1500 trials. As seen in Fig. 4, their performance did not improve after this lengthy retraining.

In order to see which part of the temporal cortex is essential for this test, the following partial lesions were made in four animals: in two of them the whole ectosylvian cortex was removed, in the two others the