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PROREAL SYNDROME IN DOGS

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Abstract. Proreal lesions were made in dogs trained on different forms of delayed alternation (involving either a single or two tones), spatial reversal, and go left–go right task. Proreal animals were impaired on a variety of delayed alternation tasks. On the basis of two additional spatial tests (with and without delay) involving double choice to auditory stimuli presented in spatial contiguity or discontiguity with responses, it is concluded that CS-R spatial contiguity test is solved by localization of foodwells whereas the discontiguity test is learnt on the basis of kinesthetic cues involved in head turnings. Proreal lesions impair only the tests based on localization, whereas learning based on discrimination of kinesthetic cues is, on the contrary, improved. The results suggest that impairment of delayed response tests is due to the overwhelming role of responses based on kinesthetic cues which interfere with correct performance based on localization of foodwells.

In the paper delivered at the previous Pennsylvania Symposium related to the analysis of delayed response impairment in prefrontal dogs (Konorski and Ławicka 1964), several hypotheses were discussed. One of them suggested that prefrontal deficit on delayed response test may be interpreted as an effect of an increased reflexogenic strength of the actual stimuli.

The present paper explores this problem further by analysing the data obtained on prefrontal dogs trained on a delayed alternation task and its variation.

General experimental procedure

The general experimental procedure will refer not only to the delayed alternation task but also to other tests described in this report. In all

experiments the dogs were trained in a room, 8 × 4 m, with two food dispensers, F_1 and F_2, situated at the side walls, and a starting platform (S) situated between (Fig. 1). The experimenter (E) was seated at the

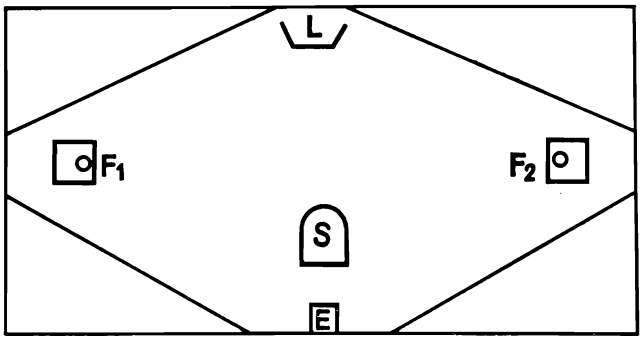

Fig. 1. Experimental situation. F_1, F_2, food dispensers; L, loudspeaker; S, starting platform; E, place of experimenter.

table placed against one wall of the room next to the starting platform and could move by remote control the foodcups in the food dispensers, which became thus accessible for the animals. The auditory stimuli presented by the experimenter were delivered from a single loudspeaker (L) situated in the middle of the room. In all tests the animal responses consisted in approaching the foodwells; if the animal chose the correct foodwell, the response was reinforced by food delivery. If the dog made an error, food was not presented and the stimulus was repeated with the usual intertrial interval; the extra stimulus presentations after an initial error were scored as repetitive errors.

All animals were unrestrained during the intertrial intervals; after approaching the foodwell they were trained to return to the starting platform again. Unless indicated, training on a problem was continued until the animals reached criterion of 90% correct responses in five successive daily sessions: the same criterion was used for pre-operative learning, pre- and post-operative retention.

Each group of dogs participated on a single test.

Delayed alternation task: 1-tone procedure

Two groups of normal dogs were trained on a delayed alternation which required an alternated approach to F_1 and F_2. Each response was evoked by a single tone, 900 cycle/sec (T_3), presented at 1 min intertrial intervals from trial to trial. The daily session consisted of 18 trials, 9 to the left and 9 to the right foodwell, presented in alternated order, as

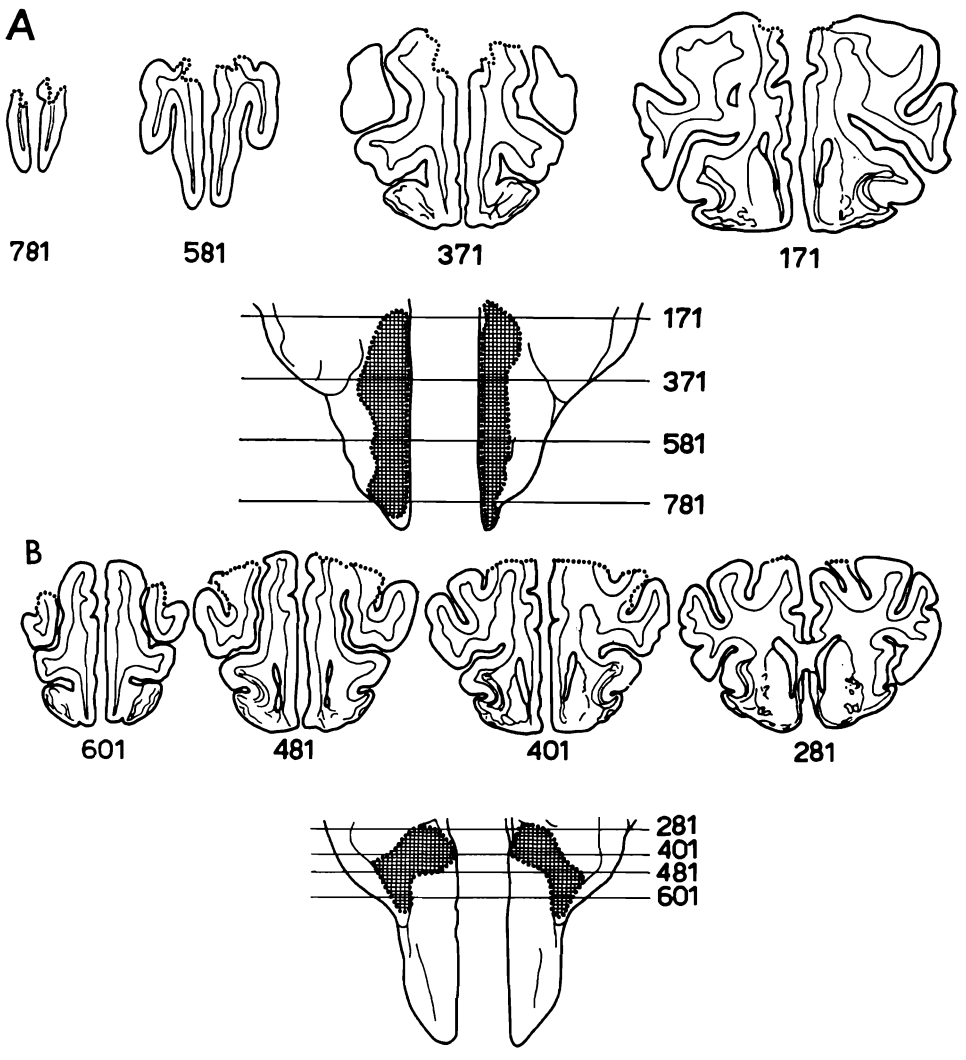

Fig. 2. Reconstructions of representative proreal (*A*) and precruciate (*B*) lesions.

illustrated in Table I. After achieving criterion one group received the proreal, and the other precruciate lesion; representative reconstruction of each may be seen in Fig. 2. Following surgery only the proreal dogs were severely affected on the delayed alternation task: as shown in Fig. 3 the proreal group succeeded in returning to the pre-operative criterion level only after many more errors than during the pre-operative learning. Particularly in the first post-operative block of five experimental sessions many repetitive errors were observed (Fig. 4), which never occurred in such high number pre-operatively, even in the early

TABLE I

Experimental procedure on delayed alternation in 1-tone group[a]

1.	1 min	$T_3 \longrightarrow R_1$ +
2.	2 „	$T_3 \longrightarrow R_2$ +
3.	3 „	$T_3 \longrightarrow R_1$ +
4.	4 „	$T_3 \longrightarrow R_2$ +
5.	5 „	$T_3 \longrightarrow R_1$ +

a Five first trials are shown; + indicates presentation of food.

stage of the acquisition learning. As presented in Fig. 4, during the following five days the number of repetitive errors decreased considerably. Since such a high number of repetitive errors might suggest an increased difficulty in spatial reversal — a deficit reported in experiments with prefrontal monkeys (Mishkin 1964, Butter 1969, Iversen and Mishkin 1970), other groups of dogs were trained on spatial reversal.

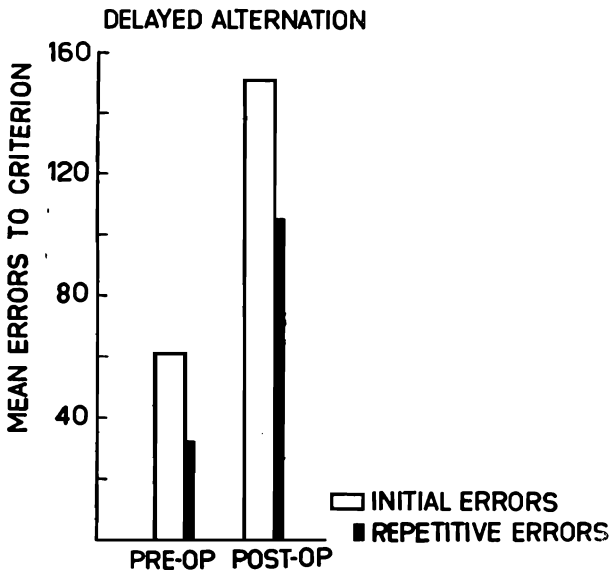

Fig. 3. Mean errors preceding criterion on delayed alternation before and after proreal lesion. The group consisted of four animals.

Spatial reversal

As in the preceding experiment, normal dogs were trained in the same experimental room with two food dispensers, but in this task the animals were required to approach consistently a single foodwell in

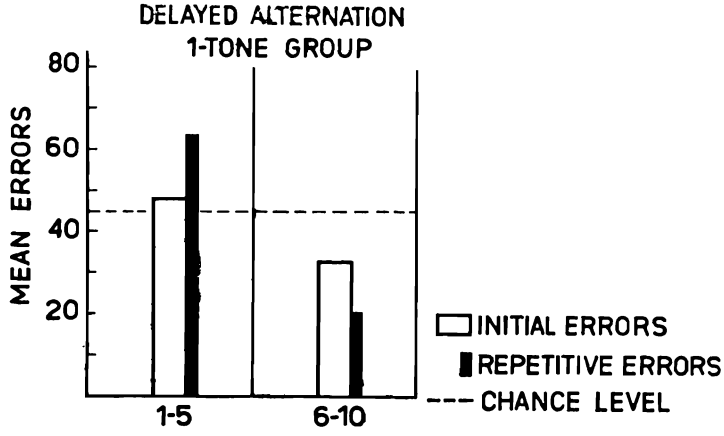

Fig. 4. Mean errors on first and second block on delayed alternation. Each block represents post-operative performance on 5 successive experimental days, i.e., 90 trials.

response to the presentation of a tone delivered on the average at intertrial intervals of 1 min (50, 60 or 70 sec). As in delayed alternation, the daily session consisted of 18 trials; the animals were trained until they reached a criterion of no more than 5 errors in 5 successive experimental sessions. After attaining criterion all dogs were tested on first reversal during which the opposite foodwell was baited throughout successive daily sessions, until the dogs attained the same criterion as during the initial learning. At this stage of training one group of animals was given the proreal lesion, whereas the other served as unoperated control.

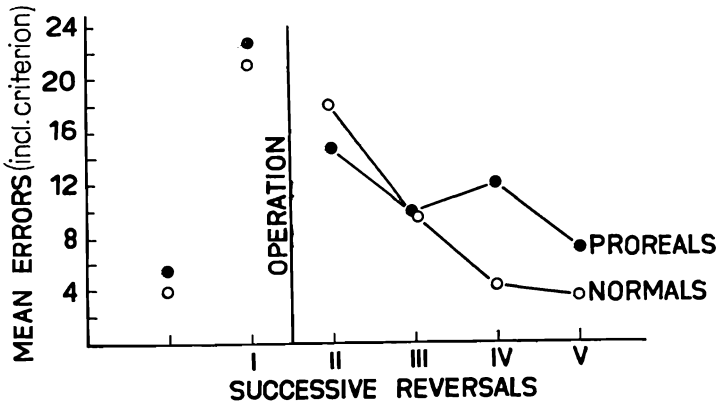

Fig. 5. Mean errors on spatial reversal. Pre-operative scores represent initial learning and first reversal of two unoperated groups. Each group consisted of four animals. (From W. Ławicka and J. Szczechura, unpublished data.)

One week later both groups were trained on successive reversals. As may be seen in Fig. 5, the proreal group had no deficit in spatial reversal in the early post-operative stage in which the proreal alternation group exhibited a most severe impairment. Performance of the operated group was significantly impaired at the forth reversal.

Since the first sign of deficit appeared at a later stage of post-operative testing, it seemed rather unlikely that it might be responsible for the delayed alternation impairment. However, even if the animals were relatively unimpaired on the reversal task requiring many trials in a single reversal problem (Gross and Weiskrantz 1964), they might have deficit on a spatial task involving reversal on a single trial. To examine this possibility two groups of normal dogs were trained on variation of delayed alternation.

Variation of delayed alternation

In this test each trial consisted of two runs separated by a 1 min interval (Table II). In the first, pre-delay run, the animals approached the foodwell from which a click, associated with the delivery of food reward, was heard. One minute later, a tone was presented from a loudspeaker situated in the middle of the room, signalling the second, post-delay run on each trial. To the presentation of the tone one group of animals was trained to approach the foodwell opposite to that, from which they obtained food in the pre-delay run (AB group), whereas the other group was required to repeat the pre-delay run (AA group). Thus, as may be compared in Table II, each trial in the AB group consisted of two alternated runs, while in the AA group, of two repeated runs; the post-delay runs in both groups were performed with 1 min delay. The daily procedure involved eight double run trials separated by 1 min intertrial intervals in a single session. The two foodwells, F_1 and F_2, on the pre-delay runs were presented randomly on successive trials. On the

TABLE II

Experimental procedure in variation of delayed alternation[a]

AB group			AA group		
1.	1 min	$F_1 \longrightarrow R_1$ +	1.	1 min	$F_1 \longrightarrow R_1$ +
	2 ,,	$T \longrightarrow R_2$ +		2 ,,	$T \longrightarrow R_1$ +
2.	3 ,,	$F_2 \longrightarrow R_2$ +	2.	3 ,,	$F_2 \longrightarrow R_2$ +
	4 ,,	$T \longrightarrow R_1$ +		4 ,,	$T \longrightarrow R_2$ +
3.	5 ,,	$F_2 \longrightarrow R_2$ +	3.	5 ,,	$F_2 \longrightarrow R_2$
	6 ,,	$T \longrightarrow R_1$ +		6 ,,	$T \longrightarrow R_2$

a Three double run trials are shown; + indicates presentation of food.

pre-delay runs no errors were observed; if an animal made an error on the post-delay run, the tone was repeated with the usual 1 min interval. Subjects in both groups were trained until they reached the usual criterion and then were submitted to the proreal lesion. As shown in Fig. 6, in effect of proreal removal not only AB group but also AA group

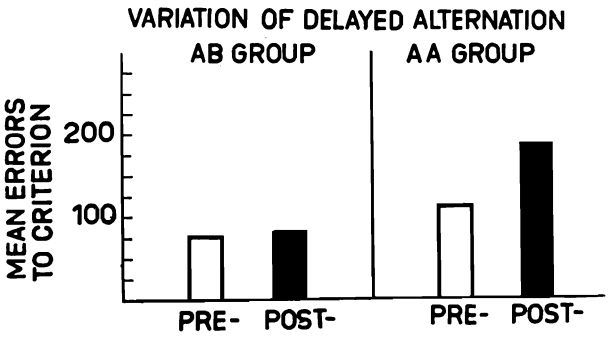

Fig. 6. Mean errors preceding criterion on variation of delayed alternation before and after proreal lesion. Each group consisted of three animals.

was impaired: since it is rather unlikely that the impairment of the AA group depends on a different mechanism, than that of the AB group, it may be concluded that the deficit in both groups cannot be due to the spatial reversal impairment. Thus, these results indicated that poor performance of the proreal alternation group cannot be interpreted as spatial reversal deficit, even in the limited case requiring a single trial per reversal problem.

In discussion of the other possible mechanism underlying the deficit on delayed alternation and its variation, it should be added that although these tests involve the factor of delay, it seemed unlikely that the impairment may be related to the problem of immediate memory (Jacobsen 1936). In fact, in our previous experiments it has been found that both prefrontal cats and dogs (Ławicka and Konorski 1959, Ławicka 1969) in the delayed response situation with triple choice, often attempted after making an error to correct themselves by immediately approaching the correct foodwell. Moreover, it appeared that the prefrontal dogs tested on delayed response under the conditions of sham-trials procedure (Konorski and Ławicka 1964, Ławicka 1969) were able to solve this task, the evidence opposing, once again, the interpretation of the proreal symptom in terms of short-term memory deficit.

The high number of repetitive errors on the post-operative retraining of the alternation group might be due to perseverative interference, or inability to shift from one form of response to another. Although no per-

severative tendency was observed in proreal dogs on Pavlovian differentiation (Szwejkowska et al. 1963, Brutkowski and Dąbrowska 1966, Ławicka 1969) which requires responding to the positive stimulus and refraining from responding to the negative stimuli not followed by food reinforcement, it might be assumed that perseverative interference is selectively related to the learning situation involving two positional instrumental responses both reinforced by food.

However, this assumption is inconsistent with the results obtained on another spatial test without delay and involving two positional responses each trained to a different auditory stimulus presented in spatial discontiguity with the foodwells. In dogs two pairs of auditory stimuli were presented, each pair differing either in quality or location (Konorski and Ławicka 1964, Ławicka 1969), while in monkeys the location cues were used (Goldman and Rosvold 1970); in neither case did damage to the proreal or principalis areas affect the subjects' choice response.

These results, inconsistent with the notion that prefrontal disorder may be specifically related to spatial tests, suggested a difference in solving a delayed response type test and the go left–go right test, since the former one was impaired after proreal lesion, while the latter was unaffected by the same cortical damage. As indicated earlier, this difference cannot be referred to as the short-term memory deficit.

It seemed probable, however, that comparison of the animals trained in these two learning situations might reveal the strategy for solving each of these two tests. Thus observation of two normal groups of animals was undertaken in the following experiment.

CS-R spatial contiguity vs. CS-R spatial discontiguity in the double choice situation (go left–go right task)

Two groups of normal dogs were trained in the double choice situation with two foodwells; one group had the two auditory stimuli situated each on its respective foodwell (i.e., under the conditions of spatial contiguity between the stimuli and responses), whereas the other group had the two auditory stimuli located in the vertical plane at the starting platform (i.e., under the conditions of CS-R spatial discontiguity). The auditory stimuli in each group did not differ in quality but only in location. There were 18 trials in a daily session during which the stimuli were presented in random order. In the first stage the animals in both groups were trained to respond to the actual presentation of stimuli until they reached the usual criterion of 90% correct responses in five successive daily sessions. Thereafter, the subjects were trained on delayed responses with the same pairs of stimuli; this stage involved leashing of the subject at the starting platform at the end of 1 min intertrial in-

terval, presentation of the CS for 3 sec, and unleashing of the dog at the end of the delay. Training with delay consisted of a series of trials with 0 sec delay, following by another series with 15 sec delay, each trained to the same criterion, as indicated above.

As may be seen in Fig. 7 the animals in the CS-R spatial contiguity group attained criterion immediately, both to the actual stimuli and in

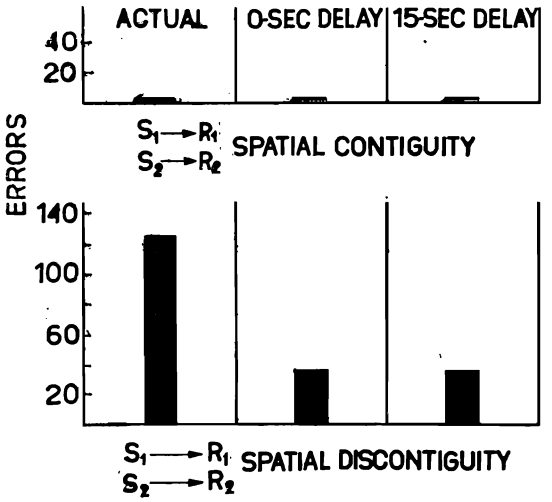

Fig. 7. Mean errors preceding criterion in two normal groups. Each group consisted of three animals.

the series with delay. The animals' responses were correct irrespective of the subject's position on the starting platform during the stimulus onset, and, in the delay trials, of the bodily orientation during or after the delay period. Thus, the animals' behavior clearly indicated that approaching the correct foodwell occurred on the basis of its localization in the experimental situation.

By contrast, all animals in the spatial CS-R discontiguity group learnt the go left–go right task to the actual stimuli with a considerable number of errors (Fig. 7) which reappeared at the beginning of each series with the delay trials. It was observed that the animals were responding correctly only when they adopted a steady position at the starting platform and learnt to perform a definite turning of the head in response to each stimulus. If the animal remained in the proper position, turning of the head led to the correct approach response. On the contrary, when the initial position was different, the same head turning might lead to approaching the wrong foodwell. During the delayed response series the situation was similar: at the onset of the stimulus the animal made the

proper head movement, followed by turning of the whole body towards the direction of the correct foodwell and maintained this position through the delay period: this allowed him to approach the correct foodwell after having been unleashed.

Thus, on the basis of these results it might be concluded that the dogs solve the go left–go right task in two different ways, depending on whether the signalling stimuli are in spatial contiguity or discontiguity, with responses. When confronted with the go left–go right task under the conditions of CS-R spatial contiguity, the animal localizes the signalled foodwell in the surrounding space and is then able to approach it, irrespective of bodily orientation before the onset of the stimulus and throughout the delay period.

On the contrary, when the stimuli and responses are spatially discontiguous, learning is mediated by two different head movements, each established to a different stimulus. In consequence, in the latter case the posture of the body before the stimulus onset and during the delay period, is critical for the correct response.

Accordingly, whereas the solution of the former task is based on discrimination of the foodwells' location in space, the solution of the latter task is based on kinesthetic discrimination between two opposite head turnings, each performed to the appropriate stimulus.

Since, as indicated earlier, the go left–go right task under the condition of CS-R spatial discontiguity is unaffected by the proreal removal, it may be inferred, that the kinesthetic discrimination established to the auditory stimuli is unimpaired after this lesion. Moreover, a high number of repetitive errors on delayed alternation might suggest that they appear as a result of an association formed between the single auditory stimulus evoking the approach response and the kinesthetic cues involved during the preceding trial.

To support this hypothesis, we should be able to find such a learning situation which reveals clearly, that after proreal damage the animals start to react on the basis of associations formed between the actual exteroceptive stimuli and kinesthetic cues, although pre-operatively they were reacting on a different basis.

It may be noted, that experiments of this kind are provided by the classical delayed response situation, on which the signalling stimuli are contiguous with responses. It has been found (Ławicka 1959) that whereas normal dogs respond to this test without any tendency to preserve their bodily orientation towards the correct foodwell, prefrontal animals completely change their behavior by learning to fixate persistently the signalled foodwell throughout the delay period (Ławicka and Konorski 1959). Thus, prefrontal dogs solve the classical delayed response test in

exactly the same way, as normal dogs solve the problem involving CS-R spatial discontiguity where the kinesthetic discrimination mechanism is involved.

More direct evidence confirming the hypothesis of a double mechanism involved on spatial tests was provided by the following delayed alternation task involving two different auditory stimuli.

Delayed alternation task: 2-tone procedure

Normal dogs were trained on delayed alternation on which instead of a single tone, two different tones, T_1 (300 cycle/sec) and T_2 (1500

TABLE III

Experimental procedure on delayed alternation in 2-tone group[a]

1.	1 min	$T_1 \longrightarrow R_1$ +
2.	2 ,,	$T_2 \longrightarrow R_2$ +
3.	3 ,,	$T_1 \longrightarrow R_1$ +
4.	4 ,,	$T_2 \longrightarrow R_2$ +
5.	5 ,,	$T_1 \longrightarrow R_1$ +

a Five first trials are shown; + indicates presentation of food.

cycle/sec) were presented from trial to trial, as illustrated in Table III. The animals attained criterion after the same number of errors, as the other group trained with a single tone, T_3 (900 cycle/sec) (Fig. 8). Since

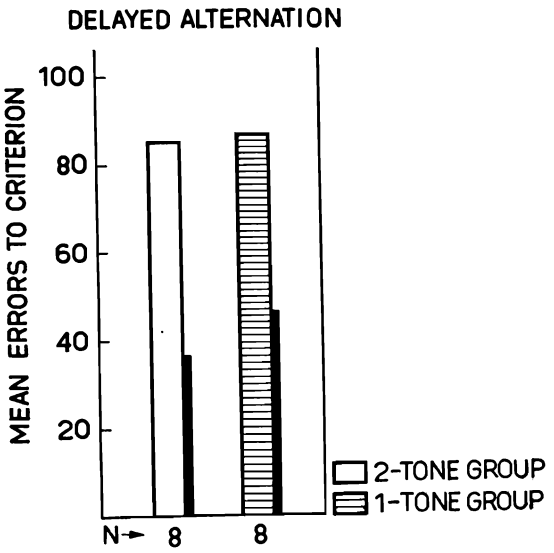

Fig. 8. Mean errors preceding criterion in two normal groups.

the 1-tone group could solve the task only on the basis of the alternation principle, i.e., by determining each actual response by the preceding trial, the data suggested that the 2-tone group was responding on the same basis. To examine this, the 2-tone group was submitted to the additional test trials. They consisted of three succeeding exprimental sessions on which T_1 and T_2 were substituted by a single tone frequency, T_3. As presented in Fig. 9, during the test trials the performance of the

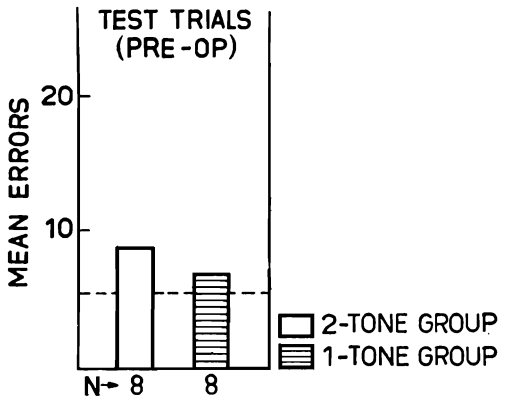

Fig. 9. Performance on delayed alternation during 3 day test trials. Broken line — performance level on the last 3 days preceding test trials. In 2-tone group T_1 and T_2 are substituted by T_3, while in 1-tone group T_3 is substituted by T_1 and T_2.

animals dropped only slightly from the usual, pre-test level: thus, the data from the test trials supported the assumption that the 2-tone group did not use the auditory stimuli as determining cues, but solved the test on the basis of an alternation principle.

Thereafter, the animals were operated and received either proreal or control lesion: in the effect of proreal damage the 2-tone group was impaired, but in comparison to the 1-tone group the animals demonstrated relatively low degree of impairment (Fig. 10). This raised the question of the factor which might be responsible for the striking difference in the post-operative relearning of these two groups: was it possible that operated animals in the 2-tone group shifted their strategy post-operatively and were responding on the basis of an association, formed between each stimulus and respective response? To examine this possibility the proreal animals were submitted to the same 1-tone test procedure, as before the operation.

The post-operative test trials (Fig. 11) revealed that the proreal 2-tone group was unable to alternate, when confronted with a single tone procedure. This result indicated that the animals post-operatively began

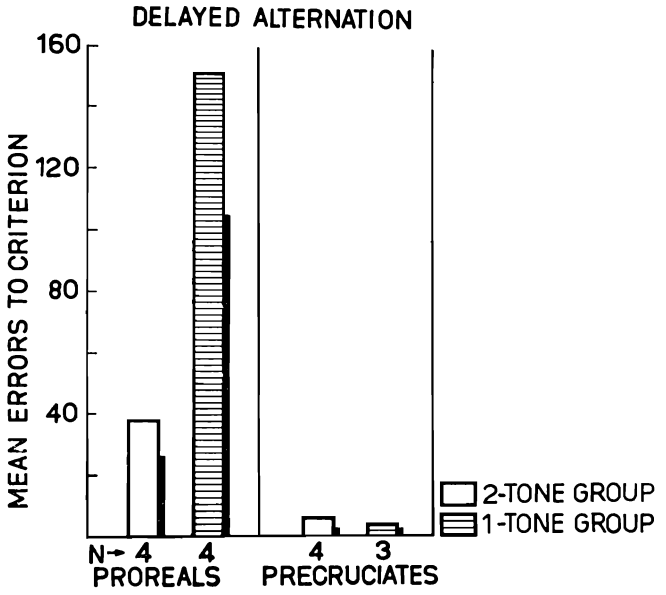

Fig. 10. Mean errors preceding post-operative criterion in two proreal and two control operated groups.

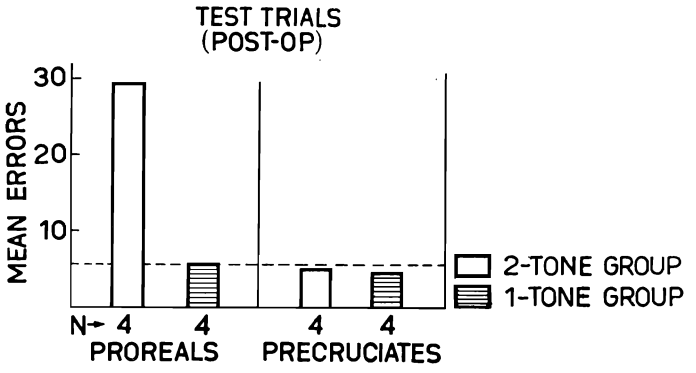

Fig. 11. Performance on delayed alternation during 3 day test trials. Broken line, performance level on the last 3 days preceding test trials. In 2-tone group T_1 and T_2 are substituted by T_3, while in 1-tone group T_3 is substituted by T_1 and T_2.

to utilize tones for determining their responses, a strategy which might be responsible for their fast post-operative retraining. In order to obtain more direct evidence that an association between each tone frequency and respective response has been formed, another kind of test trials was introduced, in which T_1 and T_2 were presented in random order. As shown in Fig. 12, the proreal animals solved this "go left–go right" task correctly, whereas the control operated failed. This paradoxical result may be understood if we assume that only proreal dogs established the

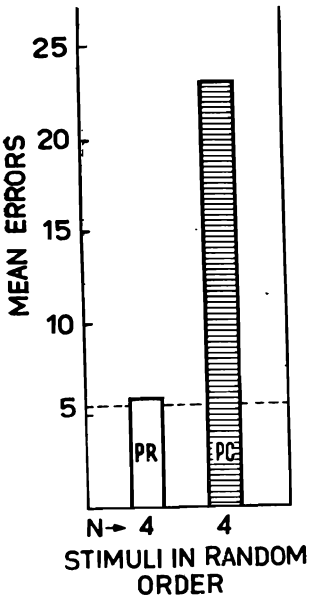

Fig. 12. Performance of the proreal (PR) and precruciate (PC) 2-tone groups during 3 day test trials. Broken line, performance level on the last 3 days preceding test trials.

association between each stimulus and the following response, while the operated controls were responding, as they did pre-operatively, according to the alternation principle.

Thus, these data raised the question why the proreal dogs shifted their strategy of responding. As an answer, two possibilities seemed possible: according to one, it might be assumed that as a result of the proreal lesion the animals lost the ability to alternate their responses. According to the other, it might be suggested that the proreal damage resulted in an increased tendency to form associations between actual exteroceptive and kinesthetic cues to such a degree, that it interfered with responding based on localization of foodwells.

Assuming that the last hypothesis is correct, it might be then expected that the proreal dogs should be better, in comparison to the normal, in the initial learning of a problem involving discrimination of kinesthetic cues, established to the actual, exteroceptive stimuli.

The experiment below confirmed this suggestion.

Go left–go right task

Before surgery all animals were habituated to the experimental room and divided into two groups: one received proreal lesion, whereas the other served as unoperated control group. The operated and control groups were trained on the go left–go right task with two tones, T_1 and T_2, each signalling respective response and spatially discontiguous with responses. As in previous tests there were 18 trials per day, given at

1 min intertrial intervals. As may be seen in Fig. 13, illustrating the results, the proreal animals were, indeed, better to normals in the acquisition learning of the go left–go right task.

On the basis of these results, we may assume that the proreal animals have an increased tendency, in comparison to normal ones to form as-

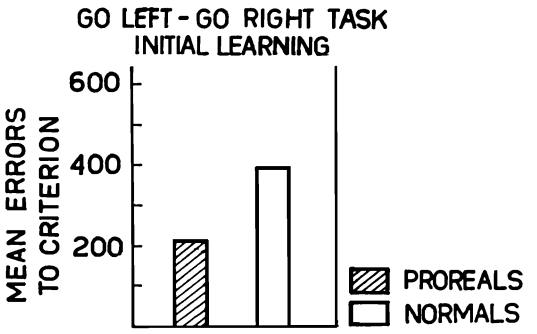

Fig. 13. Mean errors preceding criterion in proreal and normal group. Each group consisted of four animals.

sociations between the exteroceptive and kinesthetic cues. This tendency is advantageous on go left–go right task under conditions of CS-R spatial discontiguity, because the solution of this task is based precisely on this mechanism. On the other hand, it is strongly disadvantageous on those tests, in which the responses are determined by localization of foodwells, because in this case all external-kinesthetic cue associations interfere with solving the problem.

It should be added that there are tests, like 2-tone alternation task, where the normals and the proreals clearly utilize different ways of solving this problem. As indicated earlier, the same is true with respect to the classical delayed responses which in normal dogs are solved by localization of foodwells, while in prefrontal animals by pseudo-delayed technique, consisting of fixation of the proper foodwell and utilizing kinesthetic cues.

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