Acta Neurobiol. Exp. 1970, 30: 33—42

FRONTAL RATS AND SOME VISUAL TESTS

Irena ŁUKASZEWSKA

Department of Neurophysiology, Nencki Institute of Experimental Biology, Warsaw, Poland

Our previous investigations on the returning behavior of rats (Łukaszewska 1963, 1966ab) suggested that frontal rats are more dependent on visual stimuli than normal subjects. This suggestion was derived from the following findings: (i) frontal Ss performed on a lower level than normal Ss, (ii) the performance of frontal Ss improved considerably after blinding, and (iii) the performance of normal Ss lowered when additional visual cues were introduced into the experimental situation. It could be interpreted that visual stimuli hinder the correct response in our test, and that frontal rats pay more attention to visual stimuli than normal subjects.

There is a relative lack of studies concerning the role of visual cues in frontal rats. In a few early studies no differences were found between frontal and normal subjects in a white-black discrimination and two successive reversals (Bourke 1954) and in a Hebb-Williams maze which has been considered to be a primarily visual task (Landsell 1953 and Gross et al. 1965). Recently however, Jeeves (1967) reported that on an initial pattern discrimination and on each of the eight reversals, frontal Ss required fewer trials to reach criterion than a control group. Further evidence in this line was given by Dąbrowska (1968) who trained rats on a white-black discrimination for 300 trials and then reversed the problem for the next 300 trials. According to the author frontal Ss showed a higher number of correct responses in the whole period of original and reversal learning. Moreover, the inspection of data by Landsell, and Gross and his associates, suggests a somewhat superior performance of frontal than normal Ss, although the differences do not reach the normally accepted level of significance.

Since the problem, besides its theoretical importance, indicated a striking case of superiority of operated animals it seemed reasonable to collect more data on performance of frontal rats in visual tests. In the present study we attempted to investigate the relation between the visual and positional cues in normal and frontal Ss. Two questions were asked: (i) what is the effect of irrelevant visual cues on position discrimination, and (ii) can successive position reversals exert a masking effect on visual discrimination. In addition, frontal and normal animals were subjected to white-black discrimination and ten successive reversals to provide a comparison with earlier papers.

METHOD

Subjects. The Ss were 48 naive male rats of the Wistar strain 100—110 days old at the start of the experiments. 24 Ss were subjected to bilateral removal of the frontal poles under nembutal anaesthesia 2—3 weeks before the experiments. Typical examples of frontal lesion are presented in Fig. 1.

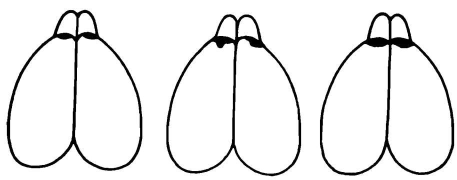

Fig. 1. Typical frontal lesions

Apparatus. All experiments were carried out in an elevated T maze with a stem 30 cm long and 13 cm wide and each arm being 50 cm long and 13 cm wide. At the ends of both arms feeding boxes 22 × 22 × 25 cm were placed. The S could enter into the box by pushing the one way door. The maze stem was painted gray; one arm was white, the other black; the front wall of the boxes and the door were painted as the corresponding arm. In experiment on position discrimination all parts of the maze and feeding boxes were gray.

Pretraining. The pretraining of all Ss was begun after 2 days of familiarization with the wet mash to be used as a reward. On Day 1, Ss were placed at the gray feeding box and permitted to eat, on Day 2 Ss were required to run along straight gray board to the feeding box; the door being kept open. On Day 3 Ss were trained to push the gray door.

Procedure. The Ss were divided into eight groups of six Ss each. Four groups consisted of normal Ss (NP, NVd, NVm and NV); the other four groups consisted of operated Ss (FP, FVd, FVm and FV).

Groups NP and FP were trained on a position discrimination and seven successive reversals on the gray maze. One half of Ss in each group begun the study with left turn correct, one half with right turn correct.

Groups NVd and FVd had to solve a position discrimination and seven successive reversals in the white-black maze. The lateral arrangement of white and black arm varied from trial to trial in accordance with the Gellerman series, thus, the visual cues were uncorrelated with the position of reinforcement. As in the previous groups one half of Ss began the problem with left turn correct, and one half with right turn correct.

Groups NVm and FVm were subjected to white-black visual discrimination. For half of Ss the white colour was positive, for the other half the black colour was positive. However, position of the correct visual cue varied in a different manner than is normally accepted. White (or black) colour was associated with left (or right) maze arm until S met a criterion, then the position of the correct visual cue was switched to the opposite arm until a criterion was achieved and so on throughout the seven successive "reversals".

Groups NV and FV were tested on a white-black discrimination and ten successive reversals. Half of each group started the discrimination with white colour positive, the other half with black colour positive. Position of visual cues varied from trial to trial according to Gellerman orders.

The experimental design for groups NVd, FVd, NVm and FVm was inspired by the paper of Weyant (1968).

In all groups Ss were trained for 12 trials per day until a criterion of 12 successive correct response was achieved in one experimental session. The correct response of the S was rewarded by permission of 10—15 sec eating of wet mash in a feeding box. After an error, defined as touching a door with the nose, the E returned S to the start point (re-run procedure). The Ss were run in rotation. Time between trials was approximately 3 min. A feeding schedule was maintained throughout the experiment on which Ss were given 2 hr of free access to food each day.

Statistics. Analysis of variance two way classification was applied. Student's t test was used to evaluate the differences between means. Original discrete data were transformed using the square root transformation.

RESULTS

Experiment I. The influence of irrelevant visual cues on position discrimination

Group NP and FP which were not supplied with irrelevant visual stimuli did not differ on the original learning of position discrimination either in number of errors or in numbers of trials to criterion. In seven successive reversals normal Ss showed a consistently lower number of errors and needed less trials to achieve criterion than frontal Ss (Table I); however, the differences were not large and did not reach the 0.05 level of significance. No evidence of decrease in errors and trials to criterion over reversals (learning sets) was seen in both groups, probably because the task was extremely easy.

Frontal as well as normal Ss performed slightly worse when visual irrelevant cues were presented. Fig. 2 shows the performance of a) normal Ss and b) frontal Ss on position discrimination and successive reversals with irrelevant visual (group NVd and group FVd) and without irrelevant visual cues (group NP and group FP). In normal Ss two groups

Table I

Mean number of trials (T) and errors (E) to reach criterion on the initial position discrimination (R_0) and on seven reversals ($R_1 - R_7$)

Reversal	R_0		R_1		R_2		R_3		R_4		R_5		R_6		R_7	
	T	E	T	E	T	E	T	E	T	E	T	E	T	E	T	E
Normal Ss	14.0	1.5	12.0	2.0	14.0	2.0	12.0	2.0	10.0	1.2	12.0	2.2	12.0	1.5	12.0	1.5
Frontal Ss	12.0	1.5	18.0	2.8	24.0	3.0	22.0	3.0	18.0	2.1	22.0	2.1	22.0	2.3	20.0	2.1

differ from each other at the 0.05 significance level only on reversal 4; in frontal Ss — on reversals 2 and 3. On reversal 4 the difference barely misses the level of significance. The results presented in Fig. 2ab, although not conclusive, could be interpreted thus: the distractional effect of irre-

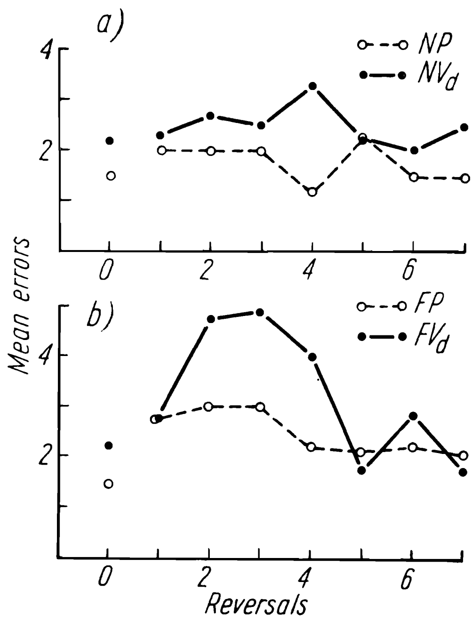

Fig. 2. The performance of normal (a) and frontal (b) rats on position discrimination and reversals with visual irrelevant cues (group NVd and group FVd) and without irrelevant visual cues (group NP and group FP)

levant visual cues is somewhat greater in frontal Ss. Interestingly, in a similar experimental situation Weyant (1968) found no evidence for the disruptive effect of irrelevant visual stimuli in normal rats.

Experiment II. The effect of masking of visual discrimination by successive position reversals

In groups NVm and FVm the correct visual cue was consistently reinforced during the whole period of testing while the reinforcement of positional cue varied from "reversal" to "reversal". Thus, the S could solve the problem in two different ways: (i) as a visual discrimination if he neglected positional cues, or (ii) as a successive reversal of position if he neglected visual cues. In the latter instance the curve of successive "reversals" should not differ from the respective curve obtained in Experiment I on position reversals with no visual cues (NP and FP groups).

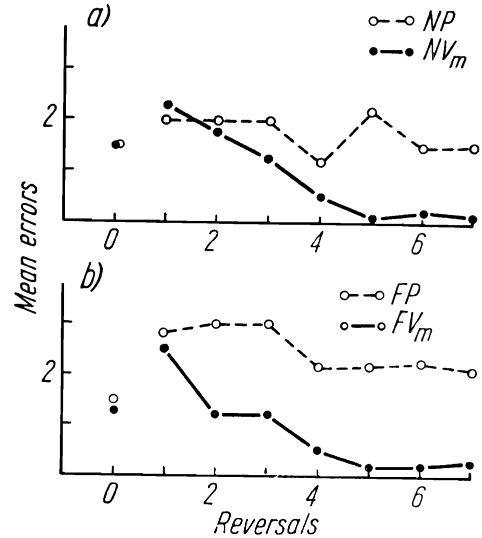

Fig. 3. The performance of normal (a) and frontal (b) rats on position discrimination and reversals (group NP and group FP) and on visual discrimination masked by position reversals (group NVm and group FVm)

As can be seen in Fig. 3b, in frontal Ss both curves are parallel between reversal O and 1. Starting from reversal 2 the curves deviate; the difference between mean number of errors in FP and FVm groups in this and further reversals is statistically significant ($p < 0.05$). It means that already in reversal 2 frontal Ss begin to switch from positional to visual cues. In normal rats the difference between the performance of NP and NVm groups reached statistical significance in reversal 5 (Fig. 3a) indicating that normal Ss switched to visual cues considerably later.

Experiment III. White-black discrimination

In term of error scores no difference between normal and frontal Ss was found throughout the experiment. Table II shows another measure of performance — the mean number of trials required to reach criterion on the original learning and on each of ten successive reversals. Both groups learned the original discrimination after 22 trials. In four reversals (1, 6, 8 and 10) FV group needed more trials than NV group while in six reversals (2—5, 7 and 9) it required less trials. Although the difference is significant only in reversal 3, it should be noted that frontal

Table II

Mean number of trials to reach criterion on the initial white-black discrimination (R_0) and on 10 reversals (R_1-R_{10})

Reversal	R_0	R_1	R_2	R_3*	R_4	R_5	R_6	R_7	R_8	R_9	R_{10}	R_0-R_{10}
Normal Ss	22	42	48	56	36	34	28	34	22	32	20	374
Frontal Ss	22	48	34	36	20	32	34	20	24	24	28	322

* The difference in this reversal is significant at the 5% level.

Ss mastered the whole task after 322 trials whereas normal Ss took 374 trials. The mean difference, 52 trials, means that each frontal S required around four and half days less than a normal S to meet criterion in the last reversal.

DISCUSSION

Our results point to the different relation between visual and positional cues in normal and frontal rats. As was shown in Experiment I frontal Ss were somewhat more distractible by visual stimuli than normal Ss; also they switched attention from positional to visual stimuli considerably earlier (Experiment II) and needed less trials to learn the series of reversals in white-black discrimination (Experiment III). However, the observed differences were not profound, or not in every case confirmed statistically. Thus, the present results could be regarded rather as a further suggestion than a clear evidence of superiority of frontal rats in visual tests. Nevertheless, since there are only few studies on the problem in question, even the inconclusive results seem to be useful to delineate conditions in which superior performance of frontal rats appear.

When one compares the data collected up to now, one finds an apparent lack of agreement. Thus, Bourke (1954) studying the white-black discrimination in a modified Lashley apparatus found that frontal Ss made a slightly larger (though not significantly) amount of errors than normal Ss in original learning and in two successive reversals. On the other hand, Dąbrowska (1968) using a similar apparatus and the same test reported that frontal Ss showed a higher number of correct responses than normal Ss in 300 trials of original testing and 300 trials of reversal; since however the number of errors to criterion was not given in this paper it is not known whether the superiority of frontal Ss refers to learning or to postcriterion performance. Furthermore, inspection of the data presented graphically on "original learning" revealed that in the first three blocks of 50 trials frontal Ss showed less correct responses than normal Ss and only on the next three blocks did they perform beyond the level of normal Ss. In a study of Jeeves frontal Ss needed less trials to learn the pattern discrimination and eight successive reversals in a discrimination box. The differences were significant in reversals R_0—R_5; in the last three reversals the differences seemed to wash out, probably due to the "learning to learn" phenomenon. In the present study the same trend of data was observed; the largest differences in number of trials to criterion between frontal and normal Ss appeared in earlier reversals. However, when number of errors to criterion is taken as a measure of learning the present results confirm rather the finding of Bourke.

This brief summary reveals that the visual superiority of frontal rats is not an easily replicable phenomenon. Attempting to find factors responsible for the observed discrepancies in results one should notice that in both studies showing the effect of the lesion normal Ss needed a considerable amount of trials to learn the original discrimination: in Jeeves' study 93 trials, in Dąbrowska's study the task was also not easy (judging from the curve of performance), while in the present one, only 22 trials were required. Besides, both authors reported that on many occasions normal and frontal animals went to the same side of the apparatus on several successive trials, whereas in the present experiment no repetitive runs in one direction were observed. Since Jeeves as well as Dąbrowska found that frontal rats showed much fewer positional preferences, this appears to be the crucial factor accounting for the better performance of frontal rats in visual tests. It has been demonstrated in several papers that frontal rats are deficient in kinaesthetic problems: in position habit reversal learning (Bourke 1954), in integration of motor chain reflexes (Dąbrowska 1964), in delayed alternation (Loucks 1931), and in delayed responses based on kinaesthetic cues (Łukaszewska 1968). Destruction of the frontal poles probably also results in diminishing the tendency to form the positional hypotheses. Thus frontal Ss spend less time searching through incorrect hypotheses in visual discrimination and in consequence learn more quickly and make fewer errors. Obviously the more difficult the visual discrimination, the more favorable are the conditions for a positional hypothesis, thus, in an easy discrimination where no positional preferences appear, the superiority of frontal rats simply cannot be manifested.

Jeeves (1967) however concluded that the superior performance of frontal Ss is caused by lessening the anxiety which is necessarily produced by successive reversals and thus minimising the interfering factor within the course of learning. If so, frontal Ss should also perform better in position habit reversals, which is not the case; on the other hand, they should not differ on the original learning of visual discrimination in which no anxiety is involved, but this is also not true as has been shown by Jeeves' own data.

Superior performance in visual tests is not exclusively associated with frontal lesions. Liss and Łukaszewska (1966) found that septal rats made considerably fewer error scores in form discrimination than normal Ss. Here again, is much evidence that a septal lesion or septal stimulation produces a deficit in reversal of position habit in the rat (Thompson et al. 1963, Donovich and Schwartzbaum 1966, Gittelson and Donovich 1968). Liss and Łukaszewska demonstrated moreover that septal rats when transferred from pattern to brightness discrimination in which either positive or negative stimulus of previous form discrimination remained the same performed similarly to normal Ss overtrained in form discrimination as opposed to a normal criterion group.

Frontal rats, showing in reversal learning less positional preferences but more consecutive errors to a previously reinforced stimulus (Dąbrowska 1968), are also highly comparable to normal Ss overtrained in visual discrimination. Normal rats overtrained in visual discrimination have a greater tendency to attend to visual cues since the overtraining primarily has the effect of increasing the strength with which the relevant analyzer is switched in (Sutherland 1964, Mackintosh 1965). On the other hand, frontal rats pay more attention to a visual cue since the lesion decreases the strength of kinaesthetic cues. The changed relation between the visual and the kinaesthetic analyzer was clearly shown in Experiment II of present study, where frontal Ss neglected positional cues much earlier than normal Ss and started to solve the task in a "visual" way.

It should be mentioned that in acute experiment on cats with large orbitofrontal ablations Skinner and Lindsley (1967) found enhancement of the primary evoked potentials in the visual cortex.

SUMMARY

The relation between visual and positional cues was studied in normal and frontal rats. In Experiment I one group of normal and frontal Ss was subjected to position discrimination and seven successive reversals on a T-maze, while the other group had to solve the same problem with intra-maze visual cues presented in a pattern not correlated with the

spatial location of reinforcement. The result suggested that visual irrelevant cues disturbed the position reversals somewhat more markedly in frontal than in normal Ss. In Experiment II Ss were given a problem in which the correct visual cue was consistently associated with reinforcement while positional cue was successively reversed. Frontal as well as normal Ss started to solve the problem in a "positional" way, however, frontal Ss switched the attention from positional to visual cues considerably earlier than normal Ss. In Experiment III on white-black discrimination and ten successive reversals both normal and frontal group earned the same error scores. However, frontal Ss needed fewer trials (though not significantly) to reach criterion in several reversals and mastered the whole problem around four and half days earlier than normal Ss.

REFERENCES

BOURKE, W. T. 1954. The effects of frontal lobe damage upon habit reversal in the white rat. J. Comp. Physiol. Psychol. 47: 277—282.

DĄBROWSKA, J. 1964. Reversal learning in frontal rats. Acta Biol. Exp. 24: 19—26.

DĄBROWSKA, J. 1968. Effects of frontal lesions in black-white discrimination test in white rats. Acta Biol. Exp. 28: 197—203.

DONOVICH, P. J. and SCHWARTZBAUM, J. S. 1966. Effects of low-level stimulation of the septal area on two types of discrimination reversal in the rat. Psychon. Sci. 6: 3—4.

GITTELSON, P. L. and DONOVICH, P. J. 1968. The effects of septal lesions on the learning and reversal of a kinaesthetic discrimination. Psychon. Sci. 13: 137—138.

GROSS, C. G., CHOROVER, S. L. and COHEN, S. M. 1965. Caudate, cortical, hippocampal and dorsal thalamic lesions in rats: alternation and Hebb-Williams maze performance. Neuropsychologia 3: 53—68.

JEEVES, M. A. 1967. Some paradoxical effects of bilateral lesions in the frontal cortex in rats. Neurophysiologia 5: 73—84.

LANDSELL, H. C. 1953. Effects of brain damage on intelligence in rats J. Comp. Physiol. Psychol. 46: 461—464.

LISS, P. and ŁUKASZEWSKA, I. 1966. The effect of overtraining and septal lesions on the ability to switch attention between cues. Acta Biol. Exp. 26: 299—307.

LOUCKS, R. B. 1931. Efficacy of the rat's motor cortex in delayed alternation. J. Comp. Neurol. 53: 511—567.

ŁUKASZEWSKA, I. 1963. Inhibition of perseverative tendency in normal and frontal rats (in Polish). Proc. IX Pol. Physiol. As. Meet. (Toruń), p. 189.

ŁUKASZEWSKA, I. 1966a. Return reaction in frontal rats (in Russian). *In* E. Asratian (ed.), Nervnye mekhanismy dvigatelnoj deyatelnosti. Izd. Nauka, Moscow, p. 205—210.

ŁUKASZEWSKA, I. 1966b. The role of visual cues in perseverative behaviour of the rat. Acta Biol. Exp. 26: 39—42.

ŁUKASZEWSKA, I. 1968. Returning behavior in frontal rats. Acta Biol. Exp. 28: 205—212.

MACKINTOSH, N. J. 1965. Selective attention in animal discrimination learning. Psychol. Bull. 64: 124—150.

SKINNER, J. E. and LINDSLEY, D. B. 1967. Electrophysiological and behavioral effects of blockade of the nonspecific thalamo-cortical system. Brain Res. 6: 95—118.

SUTHERLAND, N. S. 1964. The learning of discrimination in animals. Endeavour 23: 148—152.

THOMPSON, R. and LANGER, S. K. 1963. Deficits in position reversal learning following lesions of the limbic system. J. Comp. Physiol. Psychol. 56: 987—995.

WEYANT, R. B. 1968. Relevant and irrelevant cues in spatial learning. J. Psychol. 68: 121—127.

Received 25 March 1969