

LOCOMOTOR ACTIVITY FOLLOWING LATERAL FRONTAL LESIONS IN RHESUS MONKEYS¹

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Effects of bilateral frontal lesions on locomotor activity were studied under various stimulus conditions. 8 monkeys were tested after, and 13 monkeys before and after, partial ablation of lateral frontal granular cortex or as unoperated controls. Ss with lesions that included sulcus principalis were hyperreactive to light. Their locomotor activity in light as well as darkness was more enhanced by relatively familiar auditory stimuli, and more depressed by relatively novel stimuli than that of unoperated Ss, or of Ss with lateral frontal lesions which spared sulcus principalis.

Rhesus monkeys, after lateral frontal lesions, show increased locomotor activity. It is not clear whether these operatees are hyperactive because they are "spontaneously" more active or because they are more "reactive" to certain or all external stimuli. Furthermore, the minimum lateral frontal lesion which will produce this syndrome has not been defined. The present study was concerned with these two problems.

EXPERIMENT 1

Locomotor activity of unoperated monkeys and monkeys with lateral frontal lesions either confined to sulcus principalis or sparing sulcus principalis was measured under each of the following four conditions: darkness, light, sound in darkness, and "tactile" stimulation (produced by a strong draft) in darkness.

Method

Subjects. Eight immature rhesus monkeys served as Ss. Three Ss (No. 12, 16, and 26) had

previously received bilateral lesions of the banks and depths of sulcus principalis (P group); 3 Ss (No. 13, 14, and 17) had received bilateral ablations of lateral frontal cortical tissue which spared the banks and depths of sulcus principalis (NP group); 2 Ss (No. 21 and 24) served as unoperated controls (U group). Reconstructions of the lesions have been presented in a previous report (Gross & Weiskrantz, 1962). Before the start of the present experiments the P and NP groups had received identical experience on a number of delayed response, auditory discrimination, and visual discrimination tasks in a Wisconsin General Test Apparatus (WGTA). The U group had received similar but not identical WGTA test experience.

Apparatus. All activity measures were obtained in the soundproof room of the laboratory. The Ss were taken from their living quarters in a cage, 22 × 17 × 24 in., which was bolted to the floor of the soundproof room. An infrared beam parallel to the top, and at right angles to one side of the cage passed through the center of the cage and fell on a photocell. The frequency of interruption of the beam was the raw activity measure. The beam was produced by a 4 v. bulb and was focused by a series of lenses through an infrared filter onto a Mullard OCP 71 phototransistor. The *Light* condition was produced by a 100 w. Mazda frosted bulb 5 ft. from the center of the top surface of the cage. The *Sound* condition was produced by a bell; its intensity at the center of the testing cage was 80 db. The *Fan Down* condition was produced by an electric fan with blades 16 in. across, mounted 12 in. above the top of the testing cage; the fan produced a considerable downward draft in all parts of the cage. The *Fan Up* condition was a control for the auditory stimulation produced by the Fan Down condition; in the Fan Up condition the direction of rotation of the fan was reversed, producing an upward draft which could not be detected (by *E*) in the cage. The sound intensity produced by the fan in both conditions was 61 db. at the center of the cage. Beam crossing was recorded and stimulus conditions programed automatically from outside the chamber.

Design. Before the start of the experiment, each S was placed in the activity situation for 1 hr., in the dark. Each experimental session was divided

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TABLE 1
ORDER OF STIMULUS CONDITIONS

Sessions	Successive periods of 20 min.										
	1	2	3	4	5	6	7	8	9	10	11
Experiment 1											
1, 5, 9	D ₁	D ₂	D ₃								
2, 6, 10	D ₁	L	D _L								
3, 7, 11	FU ₁	FD	FU ₂								
4, 8, 12	D ₁	S	D _S								
Experiment 2											
1	D ₁	D ₂	D ₃	L	D _L	S	D _S	L+S	D _{L+S}		
2	D ₁	D ₂	D ₃	S	D _S	L+S	D _{L+S}	L	D _L		
3	D ₁	D ₂	D ₃	L+S	D _{L+S}	L	D _L	S	D _S		
Experiment 3											
1	D ₁	D ₂	D ₃	L	D _L	S	D _S	L'	D _{L'}	S'	D _{S'}
2	D ₁	D ₂	D ₃	L'	D _{L'}	S'	D _{S'}	L	D _L	S	D _S

Note.—L = light; S = sound in darkness; L+S = sound in light; L' = lower intensity light; S' = lower intensity sound in darkness; FU₁ = initial fan condition producing sound in darkness; FD = fan condition producing draft and sound in darkness; FU₂ = final fan condition producing sound in darkness; D₁ = initial dark; D₂ = second consecutive dark; D₃ = third consecutive dark; D_L, D_S, D_{L+S}, D_{L'}, and D_{S'} = dark condition immediately following, respectively, conditions L, S, L+S, L', and S'.

into three 20-min. periods. There were 12 such sessions. The order of testing under different stimulus conditions and the symbol for each condition are shown in Table 1. Recording began 30 sec. after the door to the soundproof room had been closed. All activity sessions began between 4 and 5 P.M.

Results

Results of statistical comparisons² among activity measures for the three groups under different stimulus conditions are summarized in Table 2. The groups did not differ significantly in the first two dark conditions (D₁ and D₂), but the activity of the U group declined more rapidly so that by the third dark period (D₃) it was significantly less active than either of the operated groups. This was the only condition in which the activity of the NP group differed from that of the U group. The P group was more active in the light (L) and in the presence of sound (S) than the other Ss. The activity of the P group in the FU₁ condition (sound

but no draft) was significantly greater than that of the other groups. But when the draft was added (FD), the activity of the P group decreased, and that of the other groups increased, making the differences among the groups no longer significant. In FU₂, when the draft was removed, the activity of the U and NP groups became again less than that of the P group. The activity of the groups did not differ at the end of the dark condition following the light condition (D_L) or following the sound condition (D_S). (The greater activity of the P group in Conditions L and S did tend to carry-over into the beginning of the subsequent dark periods D_L and D_S, hence the significant difference between the groups in Condition D_S.)

EXPERIMENT 2

The results of Experiment 1 suggest that sulcus principalis lesions produce increased activity in the presence of light or sound, but not, at least initially, in the dark. However, since both the light and the sound conditions were familiar and the "draft" condition was highly novel, it is not clear whether

²All *p* values were obtained by two-tailed *t* tests using the Animal x Treatments mean square from analysis of variance as the error term (except in two cases where the requirements for this analysis were not met and instead the sign test, as indicated, was employed).

TABLE 2
RESULTS OF STATISTICAL COMPARISONS BETWEEN GROUPS

Comparison	More Active Group											
	D ₁	D ₂	D ₃	L	D _L	S	D _S	FU ₁	FD	FU ₂	L+S	D _{L+S}
Experiment 1												
U & NP	—	—	NP*	—	—	—	—	—	—	—	—	—
U & P	—	—	P*	P*	—	P**	P**	P*	—	—	P**	—
P & NP	—	—	—	P*	—	P**	P*	P*	—	—	P**	—
Experiment 2												
U & NP	—	—	—	—	—	—	—	—	—	—	—	—
P & T	—	—	—	—	—	—	—	—	—	—	—	—
U+NP & P+T	—	—	U+NP*	P+T***	—	U+NP**	—	—	—	—	—	—

Note.—In each comparison in Experiment 1, the group showing significantly greater activity is designated. In each comparison in Experiment 2, the group showing the significantly greater increase in activity over its preoperative level is designated. (See also note to Table 1).

— = no significant difference.

* $p < .05$.

** $p < .01$.

*** $p < .001$.

modality or novelty or both were the aspects of the stimuli relevant to the increased activity. The results also suggest a possible effect on activity of lateral frontal lesions which spare sulcus principalis, namely, less "response decrement" (French & Harlow, 1955) in the absence of increased activity.

In the present experiment, Ss were tested both before and after operation. In addition to Ss with lesions similar to those in Experiment 1, a third group of operated monkeys was tested. This group received lesions that constituted approximately a combination of the P and NP lesions. All Ss were tested under each of the following conditions: darkness, light, sound in darkness, and a new condition, sound in light. These Ss, unlike those in Experiment 1, had not received extensive laboratory experience with auditory stimuli.

Method

Subjects. The Ss were 14 immature rhesus monkeys. Twelve of them formed a group matched in experience throughout the period in which the present experiment was conducted. They were experimentally naive and had been in the laboratory 3-6 weeks when the experiment began. The preoperative phase of this experiment coincided with training on an object discrimination in a WGTA; the postoperative phase coincided with training on a delayed alternation task in a WGTA (Gross,

1963). Of these 12 Ss, 3 (No. 10, 30, and 38) received bilateral ablations of the banks and depths of sulcus principalis (P group), 3 (No. 1, 7, and 32) received bilateral ablations of the depths and anterior bank of the arcuate sulcus and of rostral cortex on the lateral surface of the frontal lobe except for the banks and depths of sulcus principalis (NP group), 3 (No. 34, 36, and 37) received bilateral lesions of the entire lateral frontal granular cortex (T group), and 3 (No. 6, 8, and 31) served as unoperated controls (U group). Reconstruction of the lesions have been presented elsewhere (Gross, 1963). The two remaining Ss (No. 26 and 5) received lesions similar to those of the P group. No. 26 had been in the colony longer than any other S and had participated in Experiment 1. Thus no preoperative data in the present situation were available for this S. Like the other Ss in Experiment 1, No. 26 had received extensive test experience which included a number of auditory discrimination tasks. The sojourn of No. 5 in the laboratory was intermediate between that of No. 26 and the four groups; No. 5 had not had any WGTA experience but had been trained on a delayed response task in an automatic apparatus. It had also participated in a pilot study in which it had been exposed to the apparatus and stimuli used in Experiment 1.

Apparatus. All activity measures were obtained in a dark room during the evening when the wing of the building containing the test room was closed and where sounds from other parts of the building were not detectable by E. The test cage, photocell device, and recording and programing equipment were the same as in Experiment 1. The Light condition was produced by the same bulb as in Experiment 1 mounted in a 10 in. aluminum

photoflood reflector 20 in. above the top of the cage; the Sound condition was produced by the same bell as before but its intensity in the center of the cage was now about 75 db.; in the Light and Sound condition, the above two stimuli were presented concurrently.

Design. Before the beginning of this experiment, each *S* was placed in the activity situation for 3 hr. in the dark. Each *S* participated in three experimental sessions before operation, and three sessions after operation, or in the case of the *U* group, after an equivalent period of time (except for No. 26, which, as noted above, was not tested preoperatively). Each experimental session was divided into nine 20-min. periods. The order of testing under different stimulus conditions and the symbol for each condition are given in Table 1. Recording began 30 sec. after the door to the testing room was closed. All activity sessions began between 7:30 and 8:30 P.M.

Results

Under no condition were there any significant differences between the changes in locomotor activity of the *P* and *T* groups, the two groups with lesions including sulcus principalis. Nor were there ever any significant differences between the *NP* and *U* groups. As in Experiment 1, there were no differences among the four groups in the first two dark conditions (D_1 and D_2). In the third dark condition (D_3) the groups also did not differ, unlike Experiment 1. However, when the animals with principalis lesions (*P* and *T* groups) were compared with the animals without such lesions (*U* and *NP* groups), the former showed a slight decrease in activity in this period. In the light, the *P* and *T* groups were much more active following operation than the *NP* and *U* groups. When the bell was on in the dark (Condition *S*), the activity of the *T* and *P* groups after operation was reduced to a much greater extent than that of the other *Ss*. When the light and sound stimuli were presented together (Condition *L + S*), there was very little difference among the groups. There were no significant differences among the four groups in the dark periods following other conditions (Conditions D_L , D_S , and D_{L+S}). See Table 2.

The change in No. 5's activity after operation was similar to that of the *P* and *T* groups under all conditions except *S* and *L + S*. Unlike the *P* and *T* groups, activity of No. 5 in Conditions *S* and *L + S* in-

creased after operation. The activity of No. 26 was similar to the postoperative activity of No. 5 except that it was slightly more active in Conditions *S* and *L + S*.

EXPERIMENT 3

Would activity of the *Ss* be the same 6 mo. after operation as it was in the first month after operation? Would a loud sound still suppress activity of the *P* and *T* groups? Is degree of activity in the light related to the intensity of the light stimulus, and more important, is there an interaction of this effect with locus of lesion?

Method

Subjects. The *Ss* were the 12 matched monkeys used in Experiment 2, the *P*, *NP*, *T*, and *U* groups. In the approximately 6-mo. period between the end of Experiment 2 and the start of this experiment, all *Ss* had received similar training on auditory discriminations, visual discriminations, delayed response tests, and a series of visual discrimination reversals.

Apparatus. The apparatus and procedure were the same as in Experiment 2, except that two additional stimulus conditions were employed. The first was produced by halving the wattage of the bulb used in the Light condition (*L*); it is designated as *L'*. Another new condition was produced by a Grason-Stadler white noise generator; it is designated as *S'*. The intensity of the white noise in the testing cage was 40 db. The *Ss* had previously received considerable exposure to this sound.

Design. Each *S's* locomotor activity was measured in two sessions of 11 20-min. periods each. The order of the conditions is summarized in Table 1.

Results

There were no significant differences in the activity of the groups during the first three dark conditions (D_1 , D_2 , and D_3) of this experiment and the first three dark conditions of the postoperative phase of Experiment 2 (sign test). The only other conditions of this experiment which were comparable to conditions of the postoperative phase of Experiment 2 were the *L*, D_L , *S*, and D_S conditions of the first session. Here, the only consistent difference between the two sets of data was that the activity of *Ss* with principalis lesions (Groups *P* and *T*) was no longer decreased by the loud bell.

All groups were more active in the more

intense light (L) than in the less intense light (L') ($p < .01$), but there was no interaction of Groups \times Treatments. Similarly, all Ss were more active in the presence of the loud fire bell sound (S) than in that of the low intensity white noise (S') (sign test, $p = .006$). Although it was impossible in this case to test formally for interaction of Groups \times Treatment, inspection of the data did not suggest any such interaction.

DISCUSSION

The only significant difference in activity of the NP group and the U group was in the third initial dark period (D₃) of Experiment 1. Since this effect was not replicated in Experiment 2, it may be concluded that no effect on activity of lateral frontal lesions sparing sulcus principalis was established.

The Ss with lesions including sulcus principalis may be termed "hyper-reactive to light." In Experiment 1, the P group was more active than the other groups in the light, but not in the dark. Similarly, in Experiments 2 and 3, after operation the P and T Ss showed an increase of activity in the light, but not in the dark.

In Experiment 1, where Ss had received previous experience with intense auditory stimuli, the P group was more active than the other Ss in the three sound conditions (S, FU₁, and FU₂). But in the novel sound and draft condition (FD), this difference disappeared. In Experiment 2, where the four groups had little laboratory experience with auditory stimuli, the activity of the P and T groups was markedly suppressed by the loud bell. This was not the case for the two Ss with extensive experience with auditory stimuli, No. 5 and 26. Fur-

thermore, in Experiment 3, after 6 mo. in the laboratory and considerable exposure to auditory stimuli, the bell no longer suppressed activity of the P and T groups to a significantly greater extent than of the NP and U groups. Thus, novel stimuli *depressed* and relatively familiar stimuli *enhanced* the activity of the monkeys with lesions that included sulcus principalis (P and T groups). These results confirm the importance of novelty as a determinant of locomotor activity (French, 1959; French & Harlow, 1955) and may explain the conflicting reports of the effect of auditory stimuli on activity of frontal operatees (e.g. Issac & DeVito, 1958; Kennard, Spencer, & Fountain, 1941).

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