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SENSORIMOTOR RESPONSIVENESS
IN RATS WITH UNILATERAL SUPERIOR COLLICULAR
AND AMYGDALOID LESIONS

DISSERTATION

Presented in Partial Fulfillment of the Requirements for
the Degree Doctor of Philosophy in the Graduate
School of The Ohio State University

By

Robert Dan Kirvel, B.A., M.A.

* * * * *

The Ohio State University

1974

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INTRODUCTION

The amygdala and superior colliculus have been traditionally associated with separate anatomical and behavioral systems. However, newer evidence suggests that these two regions of the brain may mediate some strikingly similar functions. Thus, a wide variety of extrinsic stimuli (visual, somatic, auditory and olfactory) are effective in modifying the activity of single units in the amygdaloid complex (Machne and Segundo, 1956; O'Keefe and Bouma, 1969) and very similar multimodal characteristics have been recorded for individual cells in the superior colliculus (Horn and Hill, 1966; Wickelgren, 1971).

Outcomes from ablative studies appear to support these electrophysiological observations. For example, unilateral amygdaloid lesions have been reported to produce a profound deficit in orientation toward stimuli presented to the contralateral visual and somatosensory fields (Turner, 1973), and responsiveness to visual, tactile, auditory and nociceptive stimuli is virtually abolished when these cues are presented to the side of the body contralateral to a unilateral superior colliculus lesion (Sprague and Meikle, 1965).

In view of the dramatic sensory neglects which follow unilateral colliculectomy, Sprague (1966) anticipated that a

hemianopia produced by a large unilateral posterior cortical ablation in cats might be exaggerated by the addition of a colliculectomy on the same side of the brain. He confirmed that expectation, but he also discovered that visual responsiveness to small, moving targets was restored in the previously hemianopic field after a superior colliculus lesion was placed contralateral to a prior posterior cortical ablation. The latter remarkable effect has also been observed by Kirvel, Greenfield and Meyer (1974) in a study of rats prepared with simultaneous unilateral superior collicular and posterior cortical lesions. All of their animals subjected to these lesions on opposite sides of the brain were spared the contralateral visual neglect which invariably accompanied a visual cortical lesion alone.

It remains to be established whether Sprague's effect is peculiar to the systems he explored, or whether other functional recoveries can be induced by combinatorial ablations. The present experiment has been carried out as a first exploration of this question, and deals with the orientative capacities of rats subjected to ablations of the amygdala, the superior colliculus, or both procedures in ipsilateral or contralateral combinations. The inquiry was concerned with the possibility that ipsilateral lesions might enhance, and contralateral lesions suppress sensory neglects and other changes in behaviors which result from either of these operations.

METHOD

Subjects and Surgery

The subjects were 80 male Long-Evans rats, and were 90-120 days old at the beginning of the experiment. The animals were housed in individual cages with food and water available at all times except during testing. Ten subjects were assigned to each of eight groups, and the appropriate surgery was performed stereotaxically while the rats were under anesthetics induced with sodium pentobarbital. Group A received unilateral amygdaloid lesions; group SC received unilateral superior collicular lesions; group I A+SC sustained simultaneous ipsilateral amygdaloid and superior collicular lesions; group C A+SC sustained simultaneous contralateral amygdaloid and superior collicular lesions; group I A→SC sustained successive ipsilateral and unilateral lesions of the amygdala, then superior colliculus; group I SC→A sustained successive ipsilateral and unilateral lesions of the superior colliculus, then amygdala; group C A→SC sustained successive contralateral and unilateral lesions of the amygdala, then superior colliculus; and group C SC→A sustained successive contralateral and unilateral lesions of the superior colliculus, then amygdala.

The lesions were electrolytically produced with a unipolar electrode which was insulated except for 0.5 mm at the tip. An anal cathode completed the electrical circuit. The stereotaxic coordinate values were derived from the atlas of DeGroot (1959). The amygdaloid complex was destroyed with three lesions induced by currents of 2 ma for 20 sec at AP +5.8, L $\pm$ 4.5, DV -3.0; AP +5.0, L $\pm$ 4.5, DV -2.5; and AP +4.2, L $\pm$ 5.0, DV -2.5. Destruction of the superior colliculus was accomplished with two lesions, each of which was induced by a current of 2 ma for 10 sec at AP +1.2, L $\pm$ 1.5, DV +0.2; and AP -0.2, L $\pm$ 1.5, DV +1.0.

In the groups which were prepared with successive ablations, 21 days of postoperative recovery from the first lesion preceded the second and final surgical procedure. This interval was chosen because it has been shown that the transient motor impairments which are seen immediately following colliculectomies (Kirvel et al.) or amygdalectomies (unpublished pilot data) decline and then stabilize over this interval.

Behavioral Procedures

The principal behavioral procedures were versions of the tests employed by Marshall, Turner and Teitelbaum (1971) and by Kirvel et al. Each subject was first handled for five minutes daily for a period of 7 days. Thereafter, tests were conducted on the Preoperative Day immediately prior to surgery and then on

Postoperative Days 2, 4, 10, 20 and 35. Animals with lesions of the superior colliculus alone or of the amygdala alone were also tested on Postoperative Day 56. The additional test day was included so that direct comparisons could be obtained between these preparations and animals subjected to successive lesions; the first operations upon the latter groups occurred 56 days before their final postoperative tests.

The first set of measures were obtained from observations of the animals' spontaneous behaviors when they were placed upon a stable wooden platform. The platform was housed in an alcove and the entire structure was painted flat black. The edges of the platform overhung its base, was 60 by 80 centimeters, and was illuminated by an overhead incandescent lamp that yielded an illumination of 90 ftc on the testing surface.

When the testing began, each rat was first placed in the center of the platform with its nose pointed into the alcove. Then, for one minute, its circling tendencies were assessed by a count of the number of times that the animal turned 360° toward either side of the body. Records were also kept of each subject's abilities to perform spontaneous head turns to the left and to the right and of the animal's grooming behaviors.

Next, the animals were given five tests of lateral orientations to various kinds of extrinsic cues. Their visual orientations were assessed through presentations of a 5 mm white

disc which was affixed to a short length of thin black wire. The disc was moved forward from the rear of the animal's visual field and toward its snout, and was always kept just beyond the tips of the animal's vibrissae. Reactions to the disc in the right and left fields were first determined, and a second test was given if the rat failed to orient and then fix its gaze upon the disc. Records were kept of head turns toward the disc, of head turns away from the disc, and of failures to respond to the disc.

Tests for acoustic orientations were performed by studying the animal's reactions to the sound produced by rubbing together two pieces of No. CE3 emery cloth just behind each ear. Tests for vibrissal orientations involved the passage of a short length of 32-gauge wire through the rat's left- and right-sided perioral whiskers. The same categories of responses were recorded as in tests for visual orientations, that is, of head turns toward and away from the cue and of failures of the subject to respond.

Finally, tests of responsiveness to forepaw pinches and to ear pinches on the left and right sides of the body were performed with a small pair of forceps. The pressures applied were just intense enough for the animal's appendages to be manipulated by the E. A normal rat's reactions to such a stimulus are to turn toward the forceps and, occasionally, to bite it during forepaw

applications. In these tests, the basic measures were the same as in other tests of lateral orientations.

Histological Procedures

Following behavioral testing, the animals were injected with 1.0 cc sodium pentobarbital and were then perfused intracardially with 0.9 percent saline followed by 10.0 percent formalin. Next, the brains were extracted and embedded in celloidin. Sections were prepared in a horizontal plane and at 25 μ in thickness. Finally, every tenth section through the amygdala and the superior colliculus was mounted on slides and stained with cresyl violet.

Lesion Placement

Reconstructions of the largest and smallest lesions in the superior colliculus and amygdala are shown in Figure 1. SC destruction was virtually complete in all subjects in the region of the brachium of the superior colliculus. In most subjects, partial damage was also found in the subjacent tectotegmental region, in the magnocellular division of the medial geniculate body and in the caudal pretectal nucleus. Occasionally, the lesions extended into the dorsolateral border of the central gray matter.

Amygdaloid lesions were large and invariably destroyed nucleus amygdaloideus basalis, pars medialis; nucleus amygdaloideus basalis, pars lateralis; nucleus amygdaloideus centralis;

Figure 1. Extent of amygdaloid lesion in the subject with the smallest lesion (left) and the largest lesion (right) presented in frontal sections (top of figure). Reconstruction of superior colliculus damage in the subject with the smallest lesion (left) and the largest lesion (right; bottom of figure).

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nucleus amygdaloideus corticalis; and nucleus amygdaloideus medialis. Very rarely, some sparing was seen in the anterior-most portions of nucleus amygdaloideus lateralis, pars anterior and posterior; however, these regions were always destroyed at their middle and posterior extents. Damage outside the amygdala frequently occurred to nucleus caudatus, putamen, entorhinal cortex, ventral hippocampus, and internal capsule. Less often, partial damage was found in the optic tract and nucleus reticularis thalami and degeneration was sometimes found in nucleus ventralis thalami.

RESULTS AND DISCUSSION

Circling

One of the most prominent initial consequences of a unilateral superior collicular lesion is forced and ipsiversive circling behavior (Sprague and Meikle, 1965; Schneider, 1969; Kirvel *et al.*, 1974). The rats which sustained colliculectomy in this experiment were no exception to this rule. This is clear from Figure 2, which gives the mean number of such turns as a function of test days. Thus, in the first tests after surgery, subjects in group SC circled nearly eight times per minute; in contrast, the subjects sustaining unilateral amygdaloid lesions circled only once per minute. The effect was transitory, but incompletely so in that, even after 56 days, subjects in group SC continued to circle at a rate that was substantially higher than that observed for subjects in group A. The permanence, albeit with attenuation, of this tendency confirms, trans-specifically, the finding of Sprague, Berlucchi and Di Bernardino (1970) in experiments with cats.

The rate of circling for group A was so low that outcomes for Postoperative Test Day 4 and thereafter could not be distinguished from the very low levels of spontaneous circling observed on the Preoperative Test Day. When the total number

Figure 2. Number of 360° turns toward the side of the body sustaining amygdalectomy (group A) or colliculectomy (all other groups).

of turns accumulated by each subject over all Postoperative Days was used as a measure of circling for statistical analyses, significant differences between group A and all other lesioned subjects ($p < 0.002$) was obtained on the Mann-Whitney (1947) U Test.

Amygdalar ablations in combination with simultaneous superior collicular ablations have neither a potentiating nor an inhibiting effect upon the circling tendency. Thus, within the limits of reliability, the circling measures obtained from groups SC, I SC+A and C SC+A were the same. Similarly, the effects observed in groups which were subjected to serial A and SC ablations are not very different from what would be expected of animals with new or old SC removals at the times that circling tendencies are measured. Thus the two groups of subjects which sustained superior colliculectomies immediately prior to testing (I A→SC and C A→SC) had circling scores that were comparable to those for groups SC, I SC+A and C SC+A.

Both groups I SC→A and C SC→A sustained unilateral colliculectomies 21 days prior to amygdalectomies and 23 days prior to postoperative testing. These groups differed significantly from group A ($p < 0.02$) and from group SC ($p < 0.02$). However, these groups with old SC lesions circled on the first postoperative test day at levels that were not significantly different from the levels observed for the SC group after

20 days' postoperative recovery. That is, circling rates were roughly similar after approximately the same amount of time had elapsed between SC removals and postoperative tests. Accordingly, these findings suggest that the ipsiversive circling produced by collicular removals is simply not manipulable to any great extent by concomitant amygdaloid ablations.

Stimulus Localization

The results for head orientations toward and away from the extrinsic stimuli for animals subjected to one-stage lesions are summarized in Figure 3. As had been expected from the works of Sprague and Meikle and of Kirvel et al., the rats which sustained unilateral colliculectomies all showed initial multimodal sensory neglects when the cues were presented on the contralateral, but not the ipsilateral, side of the body.

The deficits in contralateral visual localizations for group SC were as severe as those observed by Kirvel et al., in animals prepared with unilateral visual cortical-superior collicular ablations. Thus, in that experiment, the visual deficits contralateral to colliculectomy persisted throughout the 20 days of testing, and in this study there was also little evidence of lateral orientations toward moving white discs even after 56 days. Hence it appears to matter very little whether the contralateral or the ipsilateral visual cortex is intact insofar as the visual neglects observed following unilateral

Figure 3. Responses toward (black bars) and away from (interrupted bars) visual (V), auditory (A), whisker touch (W), forepaw pinch (F) and ear pinch (E) stimuli on the side of the body contralateral to the underlined lesion.

SC+A

I SC+A

A

SC

NUMBER OF SUBJECTS RESPONDING

colliculectomy are concerned.

While the neglects of visual, auditory and vibrissal cues were all relatively stable, capacities for lateral orientations toward ear and forepaw pinches recovered after time. Thus, by Day 20, all of the animals in group SC had successfully localized a pinch of the forepaw and the ear on the side of the body contralateral to colliculectomy, and had thereby approached the level of virtually complete responsiveness seen on the ipsilateral side of the body by Day 2.

The orientative abilities of animals in group A contrasted very sharply with those of subjects in group SC. Rats with unilateral amygdalectomies appeared to be essentially normal from Postoperative Day 2 onward and were, in general, quite successful in localizing all cues on either side of the body. Over all the tests, their success rates were 94.8 percent, a value which compares very favorably with the 97.2 percent correct orientations observed for all the subjects when they were tested on the Preoperative Day.

These findings are consistent with those of Bresnahan (1973) who was unable to detect any changes in somatosensory orientations in rats which were prepared with small ablations confined to either the corticomедial or the basolateral regions of the amygdaloid complex. However, they are difficult to reconcile with Turner's conclusion that unilateral amygdalectomies result

in contralateral somatosensory and visual neglects, proprioceptive placing deficits and forelimb disuse. Hence, the present study and that of Bresnahan cast substantial doubt upon Turner's proposition that an amygdaloid "sensorimotor syndrome" results from destruction of the corticomedial division of the amygdalar complex and, also, upon the less specific notion that sensory neglects are produced by destruction of any amygdaloid component.

While negative, these findings with respect to group A subjects help resolve a quandary that was posed by Turner's findings, but that was not discussed by him. Kleiner, Meyer and Meyer (1967), in studies of retention of black-white discrimination habits, had found that bilateral amygdalar ablations have a just detectable effect and only in animals tested very shortly after surgery (two days postoperative; group 2A, p. 461). Inasmuch as Schneider (1969) had shown that orientation deficits which follow a collicular ablation can yield important losses in such situations even though the animal's "discriminative" system is intact, it was difficult to see why profound neglects, if present, would not have been reflected in much larger deficits in the Kleiner et al., preparations. It was possible to think that Turner's observations were specific to the unilateral subject, but that interpretation now seems strained in the light of both Bresnahan's results and the present outcomes.

Turner presumed that his results implied that bilateral amygdalectomies produce bilateral sensorimotor losses, and on this basis he proposed that such losses could well be the sources of the alterations in social behaviors (e.g. Bunnell, Sodetz, and Shalloway, 1970) that follow bilateral amygdaloid ablations. The findings of Jonason and Enloe (1971) and of Jonason, Enloe, Contrucci and Meyer (1973) seemed, when the present study was conceived, to be consistent with Turner's hypothesis because the time courses of the changes he observed and the social disinterests of the preparations studied by the latter workers did not appear to be very different. However, if the striking changes in social reactions of amygdalectomized rats toward other rats are due to recoverable neglects, then such neglects are not detectable in animals prepared with amygdaloid ablations which are identical in extent, but which are unilateral.

Inasmuch as lesions of the amygdala did not produce sensory neglects, it is not surprising that combinations of these lesions with superior collicular ablations failed to yield important interactions with respect to visual and vibrissal responsiveness (Figures 3 and 4). The observed neglects of these stimuli were confined to the side of the body contralateral to the colliculectomy, and were almost unaffected by simultaneous or successive ablations of either the ipsilateral or the contralateral amygdaloid complex. When the same two cues were

Figure 4. Responses toward (black bars) and away from (interrupted bars) visual (V), auditory (A), whisker touch (W), forepaw pinch (F) and ear pinch (E) stimuli presented on the side of the body contralateral to SC lesion.

I A→SC

C A→SC

I SC→A

C SC→A

presented to the subjects on the side ipsilateral to colliculectomy, they immediately oriented toward them during 561 of the 600 presentations.

The principal suggestion of a Sprague-like effect was seen in comparisons between groups I SC+A and C SC+A. In the latter group, the rate of recovery of correct localizations of light ear pinches or light forepaw pinches was somewhat more rapid than in the I SC+A group or the SC group. However, as is clear from the results obtained from tests of localizations for the groups which were subjected to seriatim ablations, there were no other hints that reversals of neglects could be induced by contralateral ablations of the amygdaloid complex.

The visual and vibrissal cue presentations either elicited correct orientations or else the animals performed no responses whatever. There were no exceptions to this rule during 1200 tests. However, in keeping with the results of Sprague and Meikle, auditory cues and ear or forepaw pinches on the animals' neglected side sometimes elicited correct orientations and sometimes elicited reactions to the opposite side of the body (black bars versus interrupted bars, Figures 3 and 4). The latter were more common when the animals were pinched and, indeed the majority of all of the subjects responded to the ear and forepaw pinches as early as Postoperative Day 2. The sums of the correct and incorrect orientations on Day 2 were interesting

because they rather accurately predicted the recoveries of neglects which were seen on Postoperative Day 35.

In the Sprague and Meikle study, pinches of the forepaw of cats with unilateral colliculectomies elicited emotional reactions and escapes which were accomplished by ipsiversive circling. At first glance, the crossed orientations to ear and forepaw pinches observed in this study for group SC and for groups with combinatorial SC and A lesions suggest a similar interpretation. However, the pinches employed were very light and the crossed orientations tended to be of the same magnitude as correctly-directed orientations. There was thus a suggestion that the animals detected the pinches presented to neglected body sides on the contralateral sides, as in the human clinical syndrome that is termed *alloaesthesia* (Critchley, 1955) or *contralateral sensory displacement* (Bender, 1952).

Notably, displacements of reference observed in patients with parietal disease have been associated according to Critchley (1955) in "probably every case" with gross contralateral neglects of one side of the body. The fact that in rats, such neglects are observed in animals which also show the crossed orientations supports what could otherwise be viewed as a presumptuous speculation. And some investigators will probably prefer to attribute the results to a "motor bias" (e.g. Peitchinis and Cooper, 1972), as they also have interpreted the

behaviors which Sprague took as evidence of reinstatements of orientations toward small visual objects in the fields contralateral to visual isocortical ablations in animals prepared with crossed lesions of the superior colliculus. However, the animals examined in this study showed the crossed reactions to contralateral auditory stimuli and pinches on days when they exhibited bilateral grooming and were capable of turning their heads in both directions even when they were not engaged in grooming. Hence any "motor biases" were stimulus-dependent instead of being global in nature, which again suggests, as has been previously argued (Kirvel et al., 1974), that the turning tendencies of SC preparations are secondary to the sensory effects of the lesions.

It is not certain that the hypothesized displacements were explicitly produced by nuclear destructions within the zones of the superior colliculus or amygdala. Thus, A lesions by themselves had no effects, and SC lesions by themselves were productive of only transitory crossed orientations to pinches of the forepaw or ear. However, potentiations were observed which were strongest when the SC and A ablations were ipsilateral and also simultaneously produced.

Such results suggest an interdiction of the anterolateral system that has been described by Mehler (1969), which passes immediately below the SC and whose neospinothalamic component then

progresses to the ventrobasal complex of the dorsal thalamus. A portion of the fibers of this system were unquestionably damaged by the SC ablations, and the amygdalar ablations modestly encroached upon the internal capsule. Together, these injuries, particularly in pathways which may have projections to the rat's parietal cortical homologs, could account for the fact that the crossed orientations were observed to pinch stimuli but not to either visual or vibrissal stimuli. While such an idea is highly speculative, and does not account for some of the results (e.g., the potentiation of crossed orientations in group C A→SC), it is generally consistent with the quasi-parietal effects of ipsilateral SC and A ablation.

Finally, it might be objected that the latter effects, instead of being crossed orientations, were reflections of retained sensitivities to pinches which the rats simply failed to localize. However, every rat in the I SC+A group cross-oriented to forepaw pinches on Postoperative Day 2, and nine out of ten, and eight out of ten of those subjects cross-oriented to forepaw pinches on Postoperative Days 4 and 10, respectively. When the symptom was recovered, an animal that had displayed it, rarely ever showed it again. Indeed, there were only 12 instances in 338 occasions for which a correct orientation to a forepaw pinch was followed by a crossed orientation on a

subsequent test day. Hence, whether due to alloaesthetic displacements or not, the effects themselves were real and worthy of examinations as detailed as are instances of passive neglects.

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