Transient Changes in Operant Behavior of Pigeons During Bilateral Electrical Forebrain Stimulation

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Zeier, H. and K. Akert. Transient changes in operant behavior of pigeons during bilateral electrical forebrain stimulation. Physiol. Behav. 3 (2) 293-296, 1968.—Low intensity levels of bilateral electrical stimulation (0.1 mA) in the archistriatum elicited attention reactions in pigeons and decreased their instrumental response rate on a 1-min variable interval (VI) schedule of food reward. Stimulation in the palaeostriatum caused a mild increase, while stimulation in neostriatum and septal area had no effect. Stimulation of the archistriatum at higher intensities (0.8 mA) caused electrolytic tissue damage in the area of the electrode tip and was followed by a marked increase of the response rate. Nevertheless, these effects were confined within the stimulation periods, and no evidence for irreversible changes in operant behavior was obtained. The results demonstrate the relatively high sensitivity of archistriatum as compared with other telencephalic structures in the avian brain.

Archistriatum Forebrain stimulation Palaeostriatum Pigeon Operant behavior

Variable interval schedule

In a previous study [10] the effects of archistriatal, palaeostriatal and septal lesions were compared with respect to instrumental responses in a variable interval (VI) schedule as well as to general behavior. Archistriatal animals gave signs of reduced fear and aggression and their response rate of operant behavior was strikingly increased. This effect was evident with even relatively small bilateral lesions. In contrast, the symptoms in palaeostriatal and septal animals were less obvious.

The present investigation is concerned with the effects of electrical stimulation of the same structures and again using a VI schedule for the measurement of changes in operant behavior.

METHOD

Animals

Twenty-six wild pigeons (Columba livia) from city parks with no previous test history were used. They had an age of 6-12 months and were housed individually in cages. Throughout the experiment they were maintained at about 85 per cent of their free feeding weight.

Surgery

Monopolar stainless steel electrodes were implanted bilaterally and symmetrically in each animal. Electrodes were put into the archistriatum, palaeostriatum, neostriatum and septum. The surgery was done under aseptic conditions with Equi-Thesin® anesthesia (0.25 cc per 100 g). The electrodes had a dia. of 0.3 mm and an uninsulated tip of 0.5 mm. They were inserted stereotactically according to the atlas of Karten and Hodos [4]. The indifferent electrode was a small stainless steel ball fixed with dental cement within the skull of the forehead. Two needle electrodes with female plugs were held in place by a cap of dental cement. The stimulation experiments were started 2 weeks after the implantation. On completion of the experiment, the animals were perfused through the heart with a 0.9 per cent NaCl solution, followed by a buffered 10 per cent formalin solution (pH 7.2). Serial sections were prepared at 50μ with the freezing microtome and stained with cresyl violet.

Apparatus

The animals were tested in a chamber 40 x 40 x 40 cm. A pecking key was mounted on the front wall, 18 cm above the floor. The key was lighted with a red light and the test chamber with a 220 V a.c. 35 W lamp during the whole session. In the food magazine below the key, free access to hemp seed for 3 sec was delivered as reinforcement. A white noise introduced to the chamber helped to mask external noise. The apparatus was operated with automatic programming and recording equipment [8, 9]. The animals were observed through a one-way glass.

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Procedure

The animals were adapted to a 23 hr food deprivation schedule. Then they learned to peck at a key for food reinforcement. The animals were trained on a continuous reinforcement schedule until they reached 100 responses within 10 min during 5 successive days. One week after electrode implantation the animals were put on standard daily 20 min sessions with a 1 min variable interval (VI) schedule of reinforcement. During 5 days they were adapted to the cable connection or to the stimulation receiver. On the sixth day the stimulation sessions were started.

Stimulation

Electrical stimulation was supplied from a Grass S4 stimulator via a stimulus isolation unit. The stimulus was monitored across a resistor of 100 ohms in series with the preparation. Symmetrical points of both hemispheres were stimulated simultaneously. The stimulation parameters were biphasic rectangular pulses of 1 msec duration and 100 cps. Four trains of 30 sec duration were delivered during the 20 min period of the VI session. At least one min of pecking was allowed before delivering the first stimulation train. Subsequent trains were spaced irregularly within the remaining quarters of a session. Care was taken to allow at least 2 min interval between pre- and post-stimulatory recording periods of each train. The animals received 10 stimulation sessions, one daily on 10 consecutive days (not including Sundays). The control group had implanted electrodes and a wire connection, but no stimulation was applied.

Responses were recorded before (pre-stimulation rate) during (stimulation rate) and after (post-stimulation rate) the stimulation trains. The stimulation and post-stimulation rates were expressed in percent of pre-stimulation rate. The data were tested with the Mann-Whitney U test by comparing each of the experimental groups to the control group.

RESULTS

The points of stimulation were verified histologically and are plotted in Fig. 1. Two levels of stimulation intensity were used: low intensities being applied to all structures, high levels to archistriatum and neostriatum only.

1. Effects of Low Intensity Stimulation (0.1 mA)

The average changes of the response rate in the ten stimulation sessions of four experimental and one control group are given in Table 1.

Obvious changes were produced consistently by archistriatal stimulation. The response rate decreased approximately 30 per cent below the pre-stimulation level. The difference with respect to the control group is significant ($p < 0.001$). These animals showed attention reactions during the stimulation and brief arrests in the pecking activity.

Stimulation of the palaeostriatum caused a mild increase in response rate, which was obtained consistently during all 10 stimulation sessions (Fig. 2). The difference between this result and that of the control group is significant at the 0.05 level. No changes in overt behavior were noted during stimulation sessions.

Septal and neostriatal response curves fail to show any significant changes as compared with the control group.

<table>
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<th>Location of Electrodes</th>
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<td><strong>Fig. 1.</strong> Frontal sections through pigeon brain. Levels according to the atlas of Karten and Hodos [4]. AS: Archistriatum; CH: optic chiasma; HS: hyperstriatum; LF: lateral forebrain bundle; NS: Neostriatum; PSa: palaeostriatum augmentatum; PSp: palaeostriatum primitivum; SA: septal area.</td>
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The analysis of post-stimulatory behavior shows that no group differs significantly from the control. Nevertheless, the curves in Fig. 2 show a tendency for feeble decrease of response rate in archistriatal animals and for a slight increase
FIG. 3. Localization of electrodes in the palaeostriatum. Note minimal damage in the immediate vicinity of the needle track after low stimulation intensity. (Abbreviations see Fig. 1)

FIG. 4. Localization of electrodes in the archistriatum. Electrolytic injury in the area of the electrode tip caused by stimulation with high intensity. (Abbreviations see Fig. 1)
FIG. 2. Procentual changes of the VI response rates in 10 stimulation and post-stimulation periods for 4 experimental groups and the control.

in palaeostriatal subjects. No microscopic changes were present in these animals except for the usual gliosis in the immediate vicinity of the needle track (Fig. 3).

2. Effects of High Intensity Stimulation (0.8 mA)

Four animals of the archistriatum group were subsequently stimulated with 0.8 mA during 10 sessions. This lead to injury in the area of the electrode tip (Fig. 4) and to a marked increase of the response rate (Fig. 2) which is highly significant ($p < 0.001$). This increase was, however, confined to the stimulation period. In the post-stimulation period there was no significant effect.

Control stimulation in the neostriatum with 0.8 mA did not change the response rate.

DISCUSSION

Bilateral electrical stimulation with low intensity in the archistriatum elicited a clear cut decrease of the response rate, whereas stimulation in the palaeostriatum effected a mild increase. Stimulation in the septum and neostriatum had no effect. Stimulation of the archistriatum with strong intensity effected a striking increase of the response rate and electrolytic lesions in the area of the electrode tip. Admittedly, the testing procedure was designed primarily for the evaluation of reversible stimulation effects. The presence of irreversible changes, e.g. caused by electrolytic lesions could be expected to show up in post-stimulatory and pre-stimulatory values. Yet, the post-stimulatory effects were feeble and pre-stimulatory values gave no evidence of any permanent changes. It is interesting that larger lesions in the same areas also produce an increase of response rate [10].

The results of stimulation demonstrate the relatively high sensitivity of archistriatum as compared with other telencephalic structures in the avian brain. This corresponds with experimental data from the mammalian amygdala which were reviewed by Gloor [2]. In the present study, stimulation with an intensity which was ineffective in other areas evoked attention reactions and lowered the response rate on the VI schedule. The effect of low intensity electrical stimulation is opposite to the consequences of circumscribed lesions in the same area [10]. In the light of this observation the striking increase of the response rate elicited with high intensity stimulation would at first appear to be related to archistriatal injury. As already mentioned, however, this effect was confined within the stimulation periods and no signs of a post-stimulatory change could be detected. Therefore, the first assumption seems untenable. More likely is the hypothesis of current spread. This would suggest that more distant
structures were stimulated at higher intensities, while the circumpolar areas had been made unresponsive by electrolysis. Phillips [7] elicited feeding responses with low intensity stimulation and with increased current strength obtained fear and flight reactions from the medial archistriatum of Mallard ducks. Similar differences between low and high intensities of electrical stimulation were noted in mammalian amygdaloid experiments [1, 6].

The increase of the response rate seen with stimulation of palaeostriatum is consistent with data derived from self stimulation experiments in the pigeon. Macphail [5] has made the claim that this area is characterized by positive reinforcement. Likewise the fact that self stimulation of the septal area is aversive [5] leads one to expect a decrease in the response rate. The failure to obtain this result might be due to the position of the electrodes which were located in the anterior part of the septum. Our own experiments with septal lesions [10] have shown that the response rate could be influenced only, if the lesions were placed more caudally at the level of the anterior commissure.

The negative results of neostriatal stimulation corresponds with findings of Harwood & Vowles [3] who evoked increased preening and feeding behavior, but no increase in the instrumental response rate on intermittent reinforcement schedules.

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REFERENCES