

BEHAVIOR ELICITED BY ELECTRICAL STIMULATION OF THE BRAIN OF THE STELLER'S JAY

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Many descriptive studies on communicative behavior in birds have been interpreted in terms of drives or tendencies. These concepts are rather vague and simplistic (see criticism by Hinde 1959, 1969; Brown and Hunsperger 1963; Brown 1964b), but to many workers they carried the explicit connotation of corresponding internal states (e.g., Thorpe 1951, 1954; Tinbergen 1952; van Iersel and Bol 1958). Prominent among the internal determinants of behavior is the activity pattern of the brain, yet little was accomplished in the way of correlating observations on bird behavior with the activity of histologically identified brain regions until the work of Akerman (1966) on the Rock Dove or "Pigeon" (*Columba livia*) and Phillips (1964) on the Mallard (*Anas platyrhynchos*). Since then, considerable progress has been made at identifying parts of the brain from which particular displays and vocalizations can be evoked by localized electrical or chemical stimulation, and a variety of species has been studied [Domestic Chickens (*Gallus gallus*), Putkonen 1967; Phillips and Youngren 1972; Phillips et al. 1972; Peek and Phillips 1972; Mallard, Maley 1969; Quail (*Coturnix coturnix*), Potash 1970a, b; Rock Dove, Delius 1971; Goodman and Brown 1966; Ringed Turtle Dove (*Streptopelia risoria*), Harwood and Vowles 1967; Hutchison 1967; Komisaruk 1967; Vowles and Tarala 1973; Red-winged Blackbird (*Agelaius phoeniceus*), Brown 1965, 1971, 1972; Newman 1970; Herring and Lesser Black-backed Gulls (*Larus argentatus*, *L. fuscus*), Delius 1971].

These data enable more realistic concepts about the internal states that mediate communicative behavior in birds than can be obtained from studies of behavior alone. The present work was stimulated by a field study of the displays, vocalizations, and social organization of the Steller's Jay (*Cyanocitta stelleri*) (Brown 1963, 1964a). That work will be used as a basis of comparison for the behavior observed in the present study. In the 1964 paper, hypothetical neural states were discussed as correlates of the observed behavior, yet no direct information about the neural cor-

relates of behavior was available to test any of the hypotheses. With the use of electrical stimulation of the brain (ESB) by means of fine electrodes implanted beneath the surface of the brain, it has been possible to re-examine some of these hypotheses and to start to learn something about the neural states that might be associated with certain vocalizations and displays in Steller's Jays. The present work employs ESB to investigate some functional relationships between vocalization and crest erection and to aid in establishing the neuro-anatomical basis for certain types of communicative behavior in Steller's Jays.

MATERIAL AND METHODS

SUBJECTS

Nine Steller's Jays (5 males, 4 females; 3 adults, 6 yearlings) weighing 99–121 g at operation were trapped from a wild population at Flagstaff, Arizona, in the winter of 1969–70. They were housed in aviaries at the University of Arizona, Tucson, and at the Southwestern Research Station, Portal, Arizona. A few days before its operation each individual was placed in the stimulation box, which became its new home; it remained there until sacrifice.

Experiments were performed from January through July 1970 at the above locations. Jays were fed mynah pellets as a staple, supplemented with sunflower seeds, moths, and table scraps.

OPERATION AND ELECTRODES

At operation each jay was weighed and aged by the plumage criteria of Pitelka (1945). From 0.32 to 0.35 ml of the anesthetic Equi-Thesin (Jensen-Salsbury; chloral hydrate and pentobarbital) was injected in the pectoral muscles. After the jay had lost consciousness, it was wrapped in a roll of paper, sealed with masking tape, and placed in the stereotaxic apparatus (Brain Research Instruments, Philadelphia, Pa.). A midline incision in the scalp exposed the skull. The method of orienting the head in the stereotaxic apparatus was the same as that described by Brown (1971) for the Red-winged Blackbird. Briefly, the head was oriented with the midsagittal sinus in the midline and the center of the confluence of this vessel with its lateral branches around the cerebellum in the vertical plane of the earbars. The clamping of the upper mandible fixed the cranium in the stereotaxic apparatus and left the lower mandible free for vocalization. A small hole was drilled in the skull with a dental drill to admit each electrode; the dura was pierced with a needle before the electrode was inserted.

Monopolar electrodes were made by stretching 12-cm lengths of Driver-Harris enameled Nichrome wire, dipping each piece in Insl-X (E33), and sharpening the tips to conical points by rotating them by hand against a rotating grindstone in a dental drill. None of the insulation was removed from the tip except that removed in sharpening the point. Final diameter of the electrodes was 0.20 mm. In two jays (SJ2,4) two double-shafted electrodes (two monopolar electrodes cemented together with 1.0–1.5 mm tip separation) were used. Two monopolar electrodes were implanted in the other jays, with an attempt to place one in the torus semicircularis of one side and one in the hypothalamic or septal area of the other side. All electrodes were inspected visually under a binocular dissecting scope for breaks in the insulation; in addition, each was tested for electrical leaks by watching for bubbles along the shaft while passing current through the electrode while it was immersed in saline. Only electrodes passing both of these tests were used. A stainless steel screw inserted into a hole drilled in the posterior part of the skull served as the indifferent electrode. Stimulation (100 μ a, 30 Hz, biphasic, 1.0 msec pulses) was continuous while each electrode was being lowered. When the bird called, stimulation was stopped and the electrode was secured in place with dental cement (Fastcure, Acralite Co., Inc., Brooklyn, N.Y.); if the bird did not call, the electrode was either removed to explore another track, or it was implanted in a "silent" area. Electrodes and a lead from the skull screw were soldered to a female miniature connector (ITT Cannon, Los Angeles; Type MTA1-100PL 1; 5 mm long \times 1.5 mm wide) using a heat sink; the entire assembly except for the external part of the connector was covered with dental cement. The skin was then sutured around the base of this electrode assembly.

STIMULATION BOX

The jays were housed singly in a stimulation box designed for photography so that the jay would have some room for locomotion but still always be within the field and depth of focus of the wide-angle lens of a 35-mm, single-lens reflex camera, which was used as a one-way viewing device. The box was constructed of plywood except for the glass front, which was covered externally by a black cloth, through which the camera lens protruded. The internal floor area was trapezoidal (20 inches across in front, 26 inches across in back, and 8 inches front to back); the interior was 20 inches high. Illumination of the box by fluorescent and incandescent bulbs was controlled by a timer to approximate the current day length. Food, water, and a perch were continuously available at all times. During stimulation, the jay was attached to the stimulator through a matching male miniature connector, a short length of Flexible wire (Caltron Industries, Berkeley, Calif.), a mercury commutator, and hookup wire.

ANALYSIS OF CALLS

A Uher dynamic microphone resting on foam rubber above a wire screen in the roof of the stimulation box led to a Uher 8000 4-track tape recorder. During recording, one track was used for commentary by the experimenter while the other track was used to record the bird's vocalizations at 3 $\frac{3}{4}$ ips. Sound spectrograms were made with a Kay Co. Sona-graph set at "high shape." These were photographed with high-contrast copy film.

STIMULATION PARAMETERS AND PROCEDURES

Stimulation experiments on conscious jays in the stimulation box were begun 2 or more days post-operatively. A Nuclear-Chicago stimulator was used to deliver symmetrically biphasic rectangular pulse pairs to the last seven jays and monophasic cathodal rectangular pulses to the first two jays. Although frequency, pulse duration, train length, intertrain interval, and current were all varied in particular experiments, the *standard stimulus* for purposes of comparison among jays and electrodes was symmetrically biphasic with no delay between positive and negative pulses, had a frequency of 30 Hz, a cathodal pulse duration of 1.0 msec, train length of 30 sec, intertrain interval of 90 sec (or more when necessary), and current to 200 μ a. (At 30 Hz and biphasic pulses of 1.0 msec, a current of 300 μ a, but not 200 μ a, caused bubbling at the electrode tips when in saline, due to electrolysis.) The stimulator automatically maintained a constant current by varying the voltage output. The current and voltage were simultaneously monitored at the output of the stimulator on a Hewlett-Packard 1200A dual trace oscilloscope set on differential; current was calculated from the voltage drop across a 1% 1000 ohm resistor in series with the brain. In all stimulations reported here, the stimulus was turned on at the stated current and maintained constantly at that current; all threshold measurements were determined in this way. In no case was a threshold determined by slowly raising the current during a stimulation.

MICROTECHNIQUE

While they were unconscious from an overdose of 0.40–0.45 ml of Equi-Thesin, birds were sacrificed by perfusion through the left ventricle first with 40–45 ml of 0.9% NaCl and then 40–45 ml of 15% formalin and 0.8% potassium ferrocyanide. The skull was immediately cleaned and refrigerated for at least a day in 60 ml of the second perfusate before removing the brain. Measurements of the left testis or ovary were made after sacrifice. Brains were embedded in celloidin and sectioned at 35 μ . Alternate sections were stained for cells (cresyl violet) and myelinated fibers (a modification of the Pal-Weigert method). Nomenclature of the brain structures follows Brown (1971).

RESULTS

The behavioral responses evoked by ESB with each electrode (E) are summarized in table 1. The anatomical positions of most of the electrode tips are plotted in figure 15 by electrode number on sections taken from the atlas of the brain of the Red-winged Blackbird in Brown (1971).

EVOKED VOCALIZATIONS

Of the 9 jays tested, 6 responded to stimulation up to 200 μ a by vocalizing; 9 of the 22 electrode sites tested yielded vocalization. At all nine sites, the predominant vocalization evoked by stimulation was the Wah. Some examples of Wahs evoked by ESB and of Wahs produced naturally are shown in figures 1, 2, and 13.

TABLE 1. Summary of behavior evoked by ESB in Steller's Jays.

Electrode	Jay & sex	Call thr.	Crest effect	Crest thr.	Evoked behavior
1	1M	S	NE	—	No effect at 180 μ a
2	1M	S	NE	—	Becomes excited, jumps around at 80 μ a
3	2M	S	U	100	100 μ a slight arousal; 160 μ a fluff, maintenance behavior
4	2M	S	U	100	100 μ a manipulates and stores items, crest to 20°
5	2M	S	U	140	100 μ a activity; 200 μ a more active
6	2M	150	D	100	100 μ a tense, sleek, crouch
7	3F	S	U	65	65 μ a fluff, forage, maintenance
8	3F	S	NE	—	150, 200 μ a sleek, crouch
9	4M	200	U	180	No effect till 180 μ a; at 200 μ a alert
10	4M	S	NE	—	No effect until arousal followed by seizure at 100 μ a
11	4M	S	U	100	180–200 μ a stay on perch, look around
12	4M	S	NE	—	60 μ a turn and lean head to left repeatedly
13	5F	S	NE	—	100 μ a slight wing movement; 200 μ a left wing held 3–4 cm from body
14	5F	S	D,U	30,50	10 μ a swallow; 30 μ a headshake; 40 μ a eject tongue; 50 μ a back and turn
15	6M	50	U	50	60 μ a spread tail
16	6M	S	NE	—	40 μ a open bill; 80 μ a briefly lower bill; 200 μ a same
17	7F	63	U	50	60 μ a locomotion; 65 μ a spread tail
18	7F	60	D,U	60	60 μ a aggressive pecking, Wah, Rattle, Guttural
19	8F	55	U	45	70 μ a spread tail, stay on perch, flick wings
20	8F	90	D,U	100	60 μ a peck; 100 μ a crest down; 110 μ a crest up; 120 μ a Wah, Shook
21	9M	29	U	29	44 μ a spread tail
22	9M	45	U	40	45 μ a peck; 55 μ a attack companion

Note: M = Male. F = Female. S = Silent. U = Up. D = Down. NE = No effect.

The consistency of the vocal response to ESB is exemplified by the observation that in each of 179 cases of evoked calling with electrode E19 (15–300 Hz, 0.03–3.0 msec pulses) only Wahs were given. Similarly, in each of 40 cases with electrode E22 only Wahs were given. This call and the Shook are the two most common calls of the Steller's Jay and are given in a wide variety of natural circumstances (Brown 1964a). In nature, the Wah is more characteristic of aroused perched jays and the Shook of jays that are flying or have just landed.

The Shook was evoked by ESB at only one electrode (E20) in one bird (SJ8). During one 30-sec stimulation at 30 Hz, 120 μ a, 1.0 msec this jay gave 5 Shooks (Fig. 1E) after about 27 Wahs. The Shooks could not be consistently elicited; this was the only stimulation in which Shooks were evoked, even though Wahs were evoked on 87 other stimulations with this electrode at various currents from 70–200 μ a at 30 Hz and at other frequencies from 15–300 Hz and other pulse durations from 0.03–3.0 msec. Although the Shooks ob-

tained by ESB are not identical to those obtained naturally and shown in figures 1C and D; all those illustrated are within the range of natural variation.

The Rattle, a call of the Steller's Jay given in nature exclusively by females (Brown 1964a), was evoked by ESB with one electrode (E18) in one (SJ7) of the four females tested (evoked Rattle shown in fig. 1B). In nature the Rattle is used in a variety of agonistic situations, usually in connection with supplanting attacks and as a threat. Electrodes were tested in eight females; four gave ESB-evoked vocalizations. Occurrence of the Rattle was unpredictable and sometimes required long latencies (25–59 sec); it could not be evoked more easily at higher currents. It occurred at threshold currents (60 μ a) as well as at higher ones (130 μ a). Rattles were obtained in only 5 of the 13 stimulations which elicited vocalization at E18. The other vocalizations evoked with this electrode were mainly Wahs, but also included some Gutturals (fig. 1B), which typically immediately preceded the Rattle.

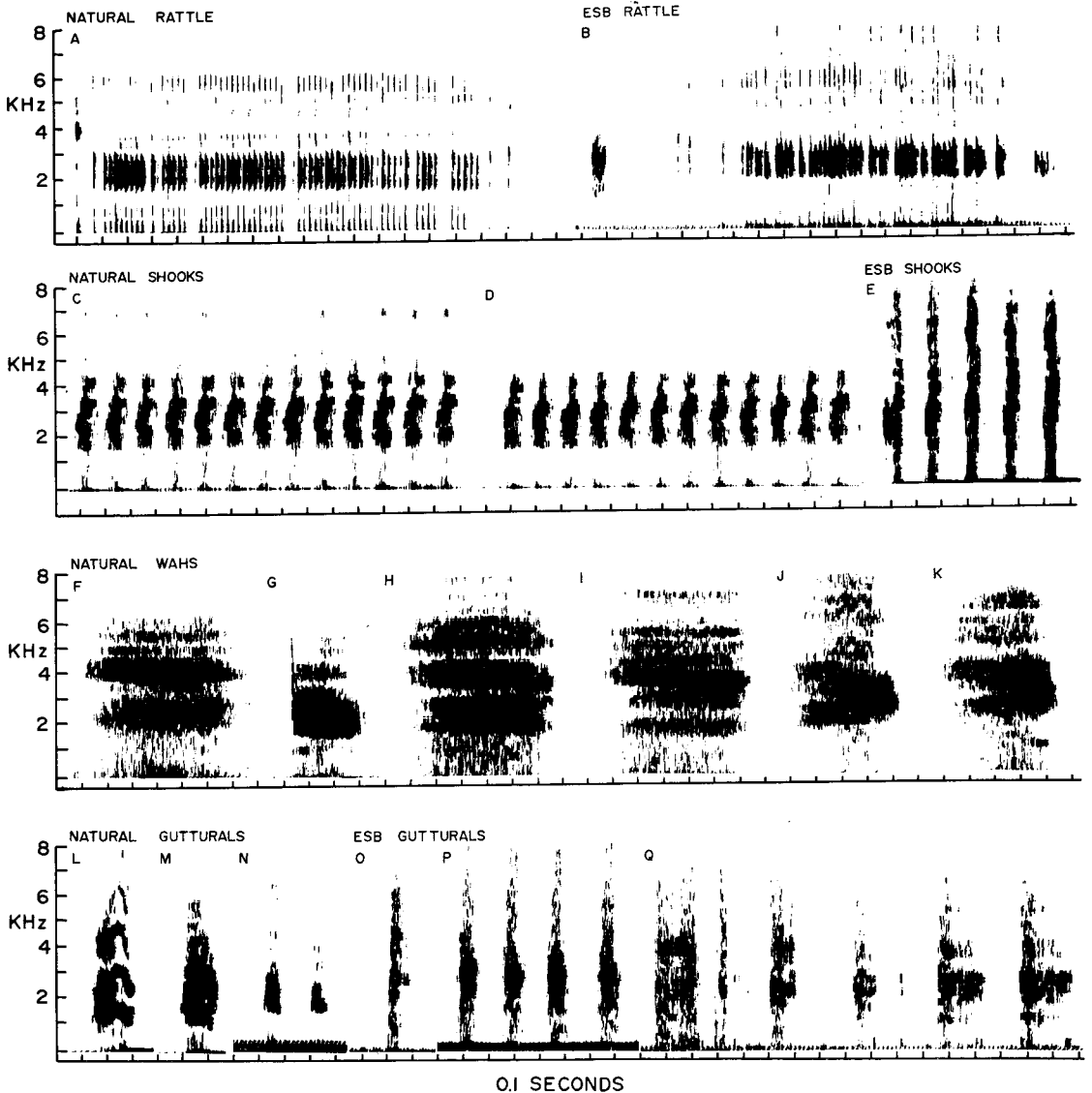


FIGURE 1. Natural and ESB-evoked calls of Steller's Jays. A: Natural Rattle; SJ8. B: Rattle preceded by Guttural evoked by ESB in anterior brain stem; E18, SJ7. C: Natural Shooks given by SJ9 in cage. D: Natural Shooks given by SJ8 in cage. E: Shooks evoked by stimulation of the anterior brain stem at E20 in SJ8. F & G: Natural Wahs given by SJ9 in cage. H-K: Natural Wahs given by SJ8 in cage. L: Natural Guttural resembling a squeal, given by SJ8. M & N: Natural Guttural calls given by SJ9. O: Guttural call evoked by stimulation in midbrain (E17) in SJ7. P: Guttural evoked by stimulation of the anterior brain stem (E18) in SJ7. Q: Sequence of Guttural calls given in one stimulation in the midbrain (E17) of SJ7.

Guttural calls were evoked by ESB in association with Rattles at one electrode (E18, SJ7) and in association with Wahs (perhaps actually weak and abbreviated Wahs in this case) in one other (E17, SJ7). Guttural calls in nature comprise a heterogeneous assemblage and occur in a wide variety of contexts that are characterized chiefly by mild agitation and frustration (Brown 1964a).

Only 4 (Wah, Shook, Rattle, Guttural) of the 11 main types of vocalization described by Brown (1964) were evoked by ESB in this study. Perhaps the stimulation box did not

provide the proper environment for some of the missing vocalizations; but this seems unlikely since Song, Growls, and Too-leet-like calls not evoked by ESB were given by the same jays pre- and postoperatively while alone in the stimulation box and unstimulated.

Evoked vocalizations were impressively regular in latency (time from stimulus onset to first call). Latency was typically a function of the current applied. A typical example of this relationship is shown in figure 3. As current was increased above threshold for calling, the latencies became reduced and their range

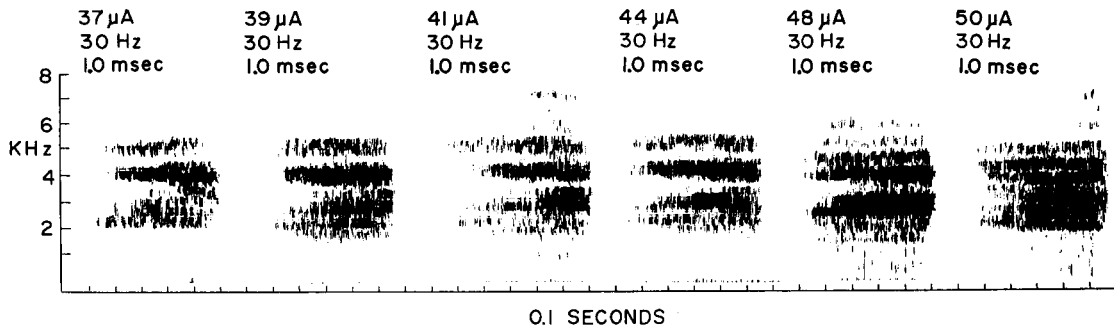


FIGURE 2. Variation in Wahs evoked by stimulation of the midbrain vocalization area (E21) in SJ9 at different current levels. Compare the relatively small amount of variation due to current with variation due to frequency shown in figure 13. For concurrent effects on crest angle and relationships to threshold for Wahs see figure 6b.

of variation decreased from many seconds near threshold to a few tenths of a second at high currents.

The rate of calling also typically varied as a function of the applied current. This relationship for an electrode in the hypothalamus (E20) is shown in figure 4. As current was increased, the rate of calling increased from about one per 5 sec to one per 0.5 sec. Latency declined as call rate increased.

CREST ELEVATION

The crest of the Steller's Jay may be raised from its lowest level, flat on the head, to a fully erect position in which its leading edge makes an angle with the long axis of the bill of 90° or more. This angle can usually be esti-

ated to within 10° and provides a convenient method for expressing the position of the crest (fig. 5). Crest position is an integral part of all displays of the Steller's Jay and is continuously expressive of the behavioral state of the bird even when not "displaying." It probably plays an important role in communication in the species.

A variety of effects of ESB on crest position was found. At currents up to 200 μa, elevation of the crest with ESB was found with 14 electrodes (E3, 4, 5, 7, 9, 11, 14, 15, 17-22); depression of the crest with 4 electrodes (E6, 14, 18, 20); and little or no effect on crest position in 7 electrodes (E1, 2, 8, 10, 12, 13, 16).

When stimulation had a positive effect on crest erection, increasing the stimulus current within a restricted range caused a higher crest

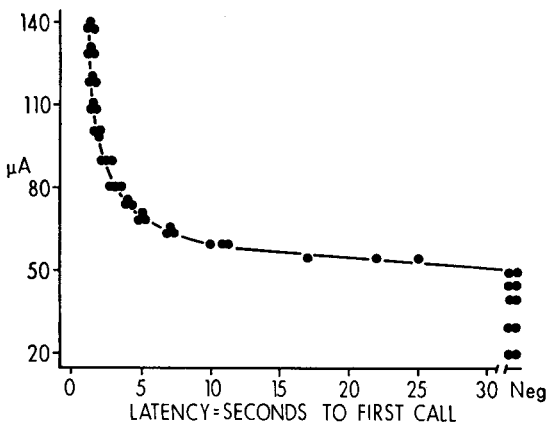


FIGURE 3. Latency for calling evoked by ESB as a function of stimulus current for an electrode (E19) in the midbrain vocalization region of a Steller's Jay. Each point represents one stimulation. Current levels were tested in ascending order with one stimulation every 3 min or longer. Stimulation was continued for 30 sec if no calling occurred but was terminated immediately after the first call to minimize fluctuations in excitability. Frequency 30 Hz. Pulse duration 1.0 msec.

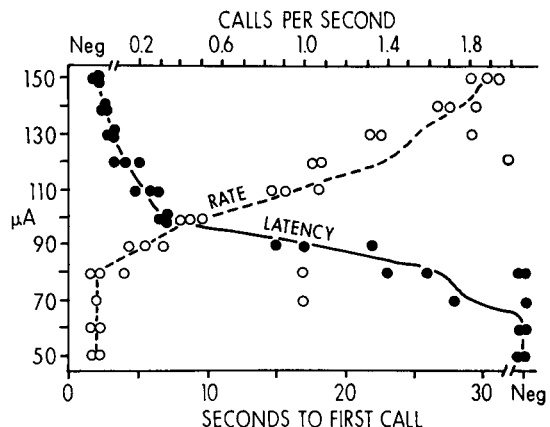


FIGURE 4. Rate of calling evoked by ESB as a function of stimulus current and in relation to latency of calling for an electrode (E20) in the hypothalamic vocalization region of a Steller's Jay. Each point represents one stimulation. Current levels were tested in ascending order with one stimulation every 3 min or longer. All stimulations lasted 30 sec. Rates based on responses with long latencies are less reliable than those with short latencies.

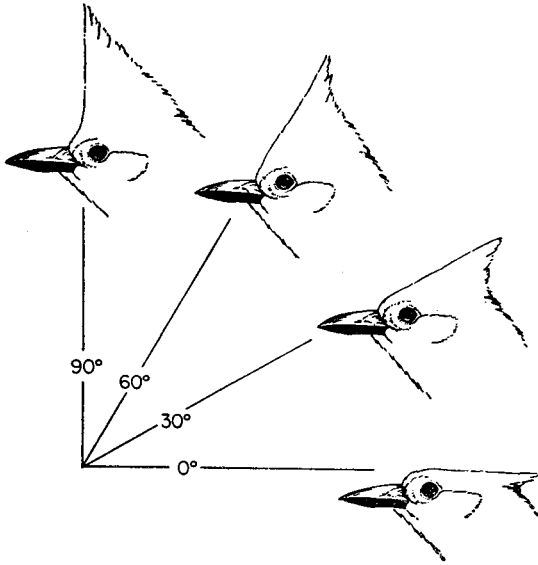


FIGURE 5. Method of estimating degree of elevation of the crest in the Steller's Jay. The angle made by the leading edge of the crest and the long axis of the bill is estimated to the nearest 10°.

elevation. Four examples of this relationship are shown in figure 6. Crest elevation did not necessarily rise to the maximum with increased current. Figure 6b shows a case in which crest elevation increased from zero to 60° with increasing current but then declined with higher currents.

Since the crest was normally not elevated in jays at rest, opportunities for observing a negative influence (depression) of ESB on crest elevation were fewer than for a positive influence. Electrodes were not routinely tested for depressive effects. To test for a depressive effect with E20 (hypothalamus) the stimulation box was kept warmer than usual so that general erection of the contour feathers of the head and body prevailed as the stimulus began. Crest elevation under these conditions varied from 30 to 50°. With ESB at 100 μ a, the crest was lowered in 12 of 12 successive trials to a minimum of 0–30°. At the end of stimulation, the crest returned to the 30–50° range. The jay was silent at this current intensity but pecked aggressively toward objects in the stimulation box in all 12 stimulations.

Paradoxically, this electrode (E20) also had a positive effect on crest elevation at slightly higher current levels, as shown in figure 6a, perhaps due to stimulus spread. The same electrode caused both depression and elevation of the crest, depending on circumstances and current level. A similar case probably occurred with E18 (anterior commissure). Although not systematically tested, this elec-

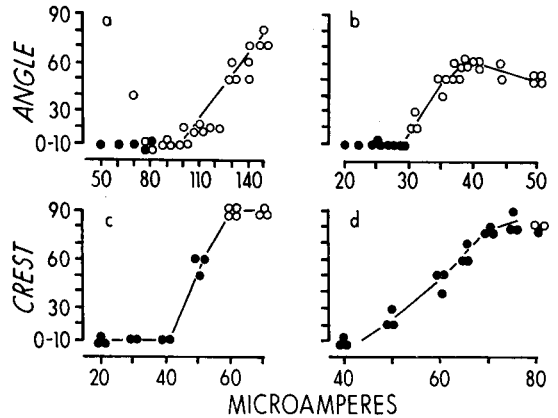


FIGURE 6. Maximum crest angle evoked by ESB as a function of stimulus current and in relation to vocalization. Closed circles: Silent. Open circles: Calling. Each point represents one stimulation. Current levels were tested in ascending order at intervals of 2 min or longer. Stimulations lasted 10 or 30 sec. All stimulations were at a frequency of 30 Hz and used a pulse duration of 1.0 msec. a: Calling beginning at low crest angles; E20, hypothalamus. b: Maximum crest angle lower at high current levels; E21, midbrain. c: Calling begins when maximum possible crest angle reached; E19, midbrain. d: Calling begins at higher threshold than that for maximum possible crest angle; E17, midbrain.

trode produced sleeking of body and crest plumage at low stimulus intensities and elevation of the crest at the same and higher intensities.

With ESB at E14 while the crest was elevated because of ambient temperature the crest was depressed during stimulation in 14 successive trials by from 20–70°, from a mean of 51° to a mean of 14° (30 μ a, 30 Hz, 1.0 msec). Crest depression in this case might have been related to activation of the trigeminal sensory system, thus causing hallucinated sensation in the bill, rather than to "emotional" state. This interpretation is suggested by the following parallel between field and laboratory observations. At 10 μ a, mild swallowing movements occurred; at 20 μ a, slight crouching was added; at 30 μ a, head-shaking from side to side appeared, as if to throw off matter from the bill, and the bill tip was sometimes touched to the floor; at 40 μ a, there appeared tongue ejection movements such as those used to push matter from the mouth; at 50 μ a, postural components appeared, including backing and turning, and the crest was elevated to 10–20°; at higher currents the postural elements dominated and became highly exaggerated and the crest was raised to 50°. It is interesting to compare this syndrome to field observations.

In nature, the crest was actively depressed

in many activities involving the bill, such as drinking, feeding, foraging with the bill, and bill-wiping (a cleaning movement) (Brown 1964a). This suggested that stimuli arising from touching the bill tended to cause crest depression reflexly. Since stimulation with E14 evoked behavior which was consistent with the interpretation of an unpleasant, hallucinated, oral or facial sensation, it is tempting to suggest that the associated crest depression was a part of this pattern of response. The electrode tip of E14 was not precisely located due to an error in microtechnique, but it appeared to be near or in the main sensory nucleus of the trigeminal nerve, which innervates the bill; this would be consistent with the above interpretation.

Crest erection was commonly associated with vocalization in nature in the Steller's Jay (Brown 1964a); it was also commonly associated with vocalization when induced by ESB. At all seven electrodes with which calling was evoked at thresholds below 100 μa , crest erection also occurred. Crest erection occurred as a response to ESB with 6 of the other 15 electrodes tested ($P < 0.025$; Fisher exact probability test).

Crest erection resulting from ESB occurred in the absence of vocalization when the response pattern was characterized by general fluffing of the contour feathers on the body and head, accompanied by maintenance behavior (E3, 4, 7). The combination of moderate crest elevation and various kinds of maintenance behavior (e.g., sun-bathing, preening, foraging, opening nuts) was commonly observed in nature (Brown 1964a).

The thresholds for calling and crest erection typically bore a consistent relationship to each other for any one electrode but not for all seven electrodes as a class. In some cases, calling began before or at about the same current level as crest erection (fig. 6a, b), while in others crest erection appeared first and calling came only at higher current levels (fig. 6c, d).

BEHAVIOR EVOKED BY STIMULATION OF THE MIDBRAIN

At three midbrain tegmental sites, the evoked behavior lacked calling altogether or had it at a high threshold (120 μa at E6). Crest erection failed to occur with any of these electrodes (E6, 8, 12) even at currents through 200 μa . The responses evoked with these three midbrain electrodes were weak in terms of vigor of movement. Locomotion was missing in all three at 100 μa ; the jays remained on their

perch and looked around (E6, 8), or shuffled feet and wings (E8), or turned and leaned to the side contralateral to the electrode (E12). At currents through 200 μa , little more was added; one jay (E6) sleeked its plumage, jumped off the perch, called, and looked around; one (E8) sleeked and crouched; and one (E12) sleeked, opened its bill, and almost fell from its perch because of excessive leaning to the contralateral side. It is perhaps significant that in all three of these cases the plumage was sleeked and that the electrodes were in the torus externus.

A fourth midbrain electrode (E5) which failed to evoke calling was located in the optic tectum. ESB with E5 induced only slight increases in activity at currents up to 200 μa . A little hopping around the stimulation box occurred at currents from 140–200 μa .

In contrast to the above three midbrain electrodes, the behavior evoked with the four midbrain electrodes with thresholds for calling under 100 μa (E15, 17, 19, 21) invariably included crest erection at low thresholds. Typically, at threshold currents, calling was evoked with no other postural changes except crest erection; the jay would simply remain perched and begin calling at a fairly steady rate. With E17, steady calling occurred at threshold (63 μa) with no crest erection in earlier stimulations; when retested later, calling was consistently preceded by crest erection. With E21 and some other electrodes in this group, the crest was erected a little with each call and relaxed a little between calls. At high currents for crest erection, the crest was erected to maximum early in the 30-sec stimulation and held a little lower in the latter part of the stimulation period (E21). The calls with all four electrodes were exclusively Wahs. In all four cases, spreading of the tail occurred at thresholds somewhat higher than for calling (fig. 7c); with E21, tail-spreading occurred rhythmically with each call, as sometimes occurs in nature. If the current was raised even more, the calling rate increased (fig. 4); the wings were spread partially; and the jay jumped around rapidly inside the stimulation box (E17, 21), or the jay crouched on the floor (E19, 15) and spread its wings (E19). Some examples of Steller's Jays stimulated in the midbrain vocalization region are shown in figure 7. When stimulated at E20 and 21 in the presence of a companion, the stimulated jay did not direct its attentions toward or away from the companion and appeared to be oblivious of its presence (although this cannot be discerned from the photograph in fig. 7d).

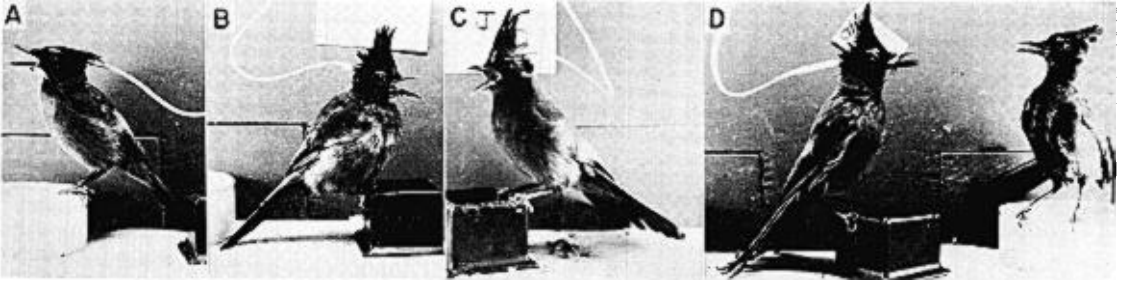


FIGURE 7. Stimulation in the lateral-midbrain vocalization area of Steller's Jays. A: Calling with crest down; E21, SJ9. B: Calling with crest up; E15, SJ6. C: Calling with tail-spreading; E15, SJ6. D: Calling by SJ9 (stimulated at E21) in presence of SJ8 (unstimulated). Compare with hypothalamic stimulation in Fig. 8D.

BEHAVIOR EVOKED BY STIMULATION OF ANTERIOR BRAIN STEM

Responses to ESB with a hypothalamic or anterior brainstem electrode (E1, 3, 4, 7, 18, 20, 22) were more varied than those with a mid-brain electrode. A response pattern that was characterized by calling, vigorous pecking, and crest erection at low thresholds (100 μ a or less) was obtained with three electrodes in this group (E18, 20, 22). The calls were mostly Wahs but rarely included Rattles (E18), Shooks (E20), and assorted Guttural calls (E18). Typically, pecking, crest elevation, and calling tended to appear together at about the same threshold (E18) as the first response to the stimulus, but pecking clearly had a lower threshold than did calling with E20 and 22 (fig. 10).

The pecking gave the impression of being aggressive rather than food-related. It was typically directed at the rubber perch, the glass front of the cage, or the food or water dish. The pecking evoked by ESB was equivalent to bill-rapping which was commonly observed in wild jays in aggressive contexts as a displacement activity (Brown 1964a:247); in both bill-rapping and ESB-evoked pecking the blow is delivered with the lower mandible

only (fig. 8) as in normal pecking at acorns, branches, and other objects in jays (Brown 1964a:247) (but not titmice; Ludescher 1968). One jay grabbed the electrode leads and held on. When stimulated in the presence of another jay, the responses of the stimulated jay were variable. SJ9 directed his pecks at the other jay on most trials except at threshold for pecking, at which level he pecked only at inanimate objects. SJ8 ignored a second jay in the stimulation box and pecked at inanimate objects at all current levels tested. Although considerable pecking was done to the food and water dishes, it was directed at the dish rather than its contents; and food and water were not ingested during or just after stimulations with these electrodes. On some occasions the bird dipped its bill into the water during stimulation (E20) but did not raise the bill afterward as it would have in normal drinking. Swallowing was seen at the start of stimulation in 10 of 10 stimulations with E20 but always before the reaction of pecking, calling, and crest elevation developed. At higher current levels pecking, calling, and crest elevation became more intense and were sometimes accompanied by spreading of the tail and jumping up with spread wings as if to fly (E22), or by awkward abnormal postural effects (E18).

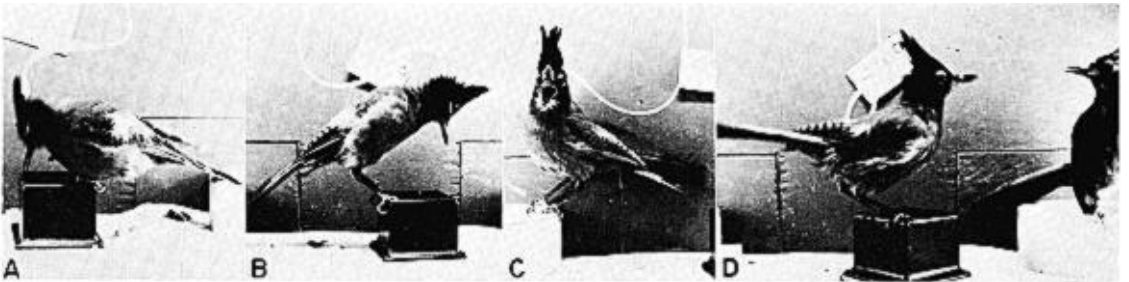


FIGURE 8. Stimulation in anterior brainstem vocalization area in Steller's Jays. A: Pecking at perch (bill-rapping); note opened bill; E20, SJ8. B: Pecking at perch; bill is not yet opened; E22, SJ9. C: Calling with crest erect; note frontal streaks; E22, SJ9. D: Pecking by SJ9 (stimulated) at SJ8 (not stimulated); E22. Compare with midbrain stimulation in figure 7D.

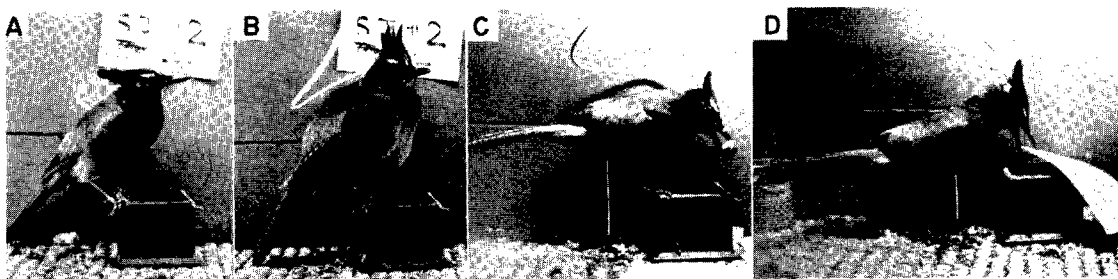


FIGURE 9. Stimulation in or near the medial forebrain bundle in a Steller's Jay. A: Before the stimulation shown in B. B: Fluffing of the contour feathers, including the crest; E3. C: Storage of a peanut inside the square perching block by SJ2; E4. D: Covering of stored peanut with 3×5 card by SJ2; E4.

The reaction sometimes outlasted the stimulus up to 1 min (E18, 22).

One electrode (E1) placed in virtually the same location (anterior commissure) as another (E18) in the above group failed to give the same response pattern. When stimulated with E1, this jay gave no response at all at $160 \mu\text{a}$, and nothing more than lifting and turning its head at $200 \mu\text{a}$. Only at $250 \mu\text{a}$ did it give a few calls, and these were inconsistent. The high resistance with this electrode suggests that a poor electrical connection might have been at least part of the cause. (Resistance of the brain-electrode assembly combination for this electrode was 65,000 ohms, as opposed to the range of 8,000–19,500 ohms for 16 other electrodes. The other electrode in the anterior commissure, E18, had a resistance of 18,000 ohms.)

A second response pattern was shared by three other anterior brainstem electrodes to varying degrees (E3, 4, 7). This was a basically nonagonistic response and was characterized by mild arousal followed by fluffing of the feathers and maintenance activities (fig. 9). The various maintenance behaviors did not seem specific to the particular electrode and were not very repeatable; rather, stimulation seemed to induce a mood of constructive activity which was repeatable but was expressed in various ways depending on the external stimuli and the individual bird.

For example, ESB with E4 (medial to the medial forebrain bundle just below the area septalis) at $200 \mu\text{a}$ consistently and reliably produced immediate fluffing of the feathers of the body with raising of the crest to 70° (see fig. 9a, b). This was not accompanied by signs of fear, discomfort, or uneasiness as in the midbrain stimulations in which crest erection occurred. On the contrary, maintenance acts such as drinking, picking up, storing and retrieval of food, bill-wiping, and shaking of the body were typical.

With ESB at E3 at $100 \mu\text{a}$ in the medial

forebrain bundle as it leaves the area septalis, the jay manipulated peanut shells, pieces of a white card, wire and food pellets in its bill, stored shells and food, ate and drank; the crest rose moderately (to 30 or 40°).

The "pleasant" effects of ESB with this type of response were suggested especially by the response with E7. At the start of the session this particular jay was tense, crouched, and sleek; stimulation at $65 \mu\text{a}$ induced mild looking around, fluffing of plumage, and putting the bill in the food and water containers. Afterward the jay preened, bill-wiped, and looked relaxed and "comfortable." Bill-wiping, eating, defecation, and preening also occurred in various stimulations at or under $100 \mu\text{a}$; higher currents evoked seizure behavior or an abnormal posture, perhaps due to stimulus spread.

BEHAVIOR EVOKED BY STIMULATION OF THE FOREBRAIN HEMISPHERES

Although aimed at brainstem structures, three electrodes (E2, 9, 16) were placed in the forebrain hemispheres. ESB with these electrodes failed to yield evoked vocalizations and had little or no effect on the crest.

ESB with E2 in the tractus occipito-mesencephalicus evoked no response until at $80 \mu\text{a}$, the jay began jumping and turning sideways to the contralateral side; at higher current levels through $200 \mu\text{a}$, the turning became more rapid but neither calling nor crest elevation occurred.

ESB with E9 (medial neostriatum) was without effect through $160 \mu\text{a}$. At $180 \mu\text{a}$, the crest rose to 30 – 40° , but the jay's ongoing activities of pecking and eating were uninterrupted. At $200 \mu\text{a}$, the crest rose to 50 or 60° and calling occurred in 9 of 18 stimulations while the jay continued its pecking, manipulation, and eating of food pellets. It is noteworthy that the calling was not accompanied by signs of fear or aggression.

ESB with E16 (border of palaeostriatum

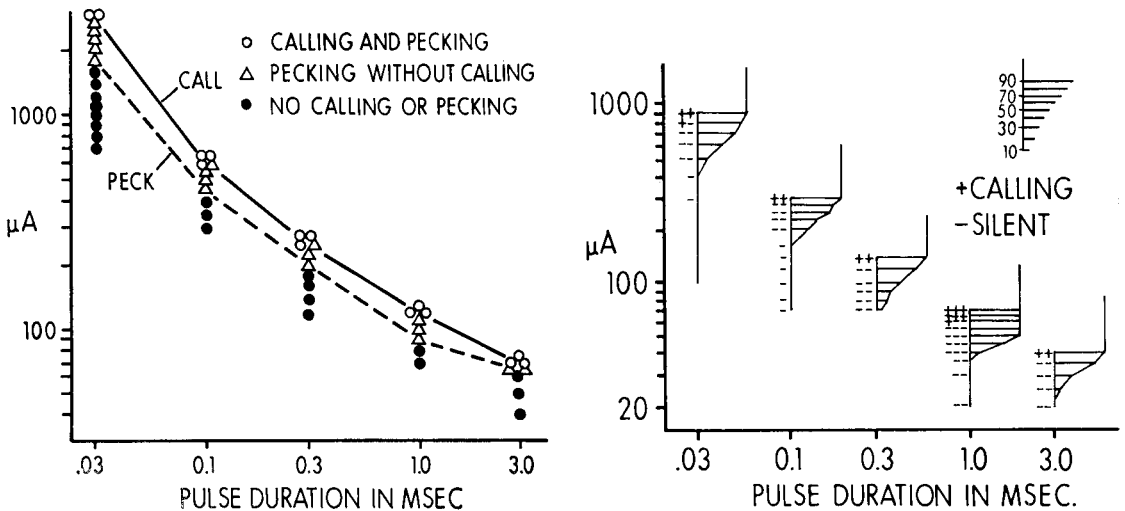


FIGURE 10. Effects of various pulse durations on threshold for behavior evoked by ESB in the Steller's Jay. Frequency 30 Hz; stimulation period 10 sec. Left: Thresholds for pecking and calling for an electrode in the hypothalamus (E20). Right: Maximum crest elevation in a 10-sec stimulation period and calling as functions of pulse duration and current; E19, midbrain.

and optic chiasma) through 200 μa yielded no vocalization and no change in crest position. The jay remained on its perch and responded only by opening its bill a little and shuffling its feet once or twice with each stimulation.

EFFECTS OF VARIOUS PULSE DURATIONS

One of the parameters of the electrical stimulus that directly affects the behavioral response is the duration of the pulses that are applied to the brain. The effects on evoked behavior of systematically varying pulse lengths were studied with four electrodes (E15, 19, 20, 21). Representative findings are shown in figure 10. The principal effect of lengthening the stimulus pulse duration was to reduce the threshold for the response, as shown for calling, pecking, and crest elevation in figure 10. However, pulse duration was not completely interchangeable with pulse height (expressed as μa); longer pulses were generally less efficient in terms of coulombs needed at threshold for calling, pecking, and crest elevation. The threshold relationships between calling and pecking (fig. 10a) and between calling and crest elevation (fig. 10b) did not seem to be affected by changes in pulse duration. At all pulse durations tested, pecking appeared at slightly lower currents than calling with the hypothalamic electrode (E20). Similarly, crest elevation appeared at slightly lower current strengths than calling at all pulse durations tested with the mid-brain electrode (E19) in the same jay.

EFFECTS OF VARIOUS PULSE FREQUENCIES

The primary effect of varying the frequency of the stimulus pulses was to alter thresholds. Since a higher frequency provides more coulombs to the brain in a fixed time interval, thresholds tended to be inversely proportional to frequency, but with notable exceptions. The variation in threshold for calling due to variation in pulse frequency was studied at three electrodes (E15, 19, 20) using a constant pulse duration. The results for E19 and 20 are shown in figure 11. There was a decline in threshold with increasing frequency for the midbrain electrode (E19), but the decline was not proportional to the increase in frequency. At the hypothalamic electrode (E20), the decline occurred from 15–120 Hz but not from 120–300 Hz.

With the above method of comparing responses to different frequencies, it is impossible to compare the effects of two frequencies directly at a given current because the total coulombs at different frequencies must differ. To enable frequency comparisons at equal coulombs the pulse duration was shortened to compensate for the increase in frequency. This was done in such a way that the product of pulse frequency and width remained constant at 30. This was done with five electrodes. The results are shown in figure 12. In these graphs, lines of equal coulombs are horizontal and straight. The lowest point on the curve is the combination of frequency and pulse length that is most economical in terms of coulombs

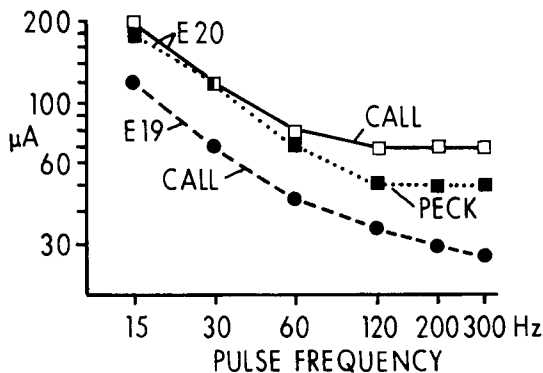


FIGURE 11. Thresholds for calling and pecking evoked by ESB as a function of stimulus pulse frequency for a hypothalamic (E20) and a mesencephalic (E19) electrode in the same Steller's Jay (SJ8). Thresholds were determined to within 10% of the indicated value with 10-sec stimulations at a minimum interval of 2 (E19) or 3 (E20) min. Pulse duration was 1.0 msec in all stimulations.

required to produce calling. The most economical frequency in all cases included 30 Hz and also in some cases 15 or 60 Hz. Frequencies above and below these optima were increasingly inefficient. The inefficiency of higher frequencies was especially apparent for the two hypothalamic electrodes (E20 and 22), where the threshold for calling at 300 Hz was over five times that at 30 Hz for E20 and four times for E22.

The quality of the calls given at various pulse frequencies was sometimes noticeably different. At high frequencies, Wahs evoked by stimulation of the midbrain with E21 became longer, higher-pitched, and changed in their harmonic structure, as shown in figure 13. With other electrodes the differences between high and low frequencies were similar but less extreme. The change in call structure from low to high pulse frequency is not the same as the change in call structure from low to high pulse height; this can be ap-

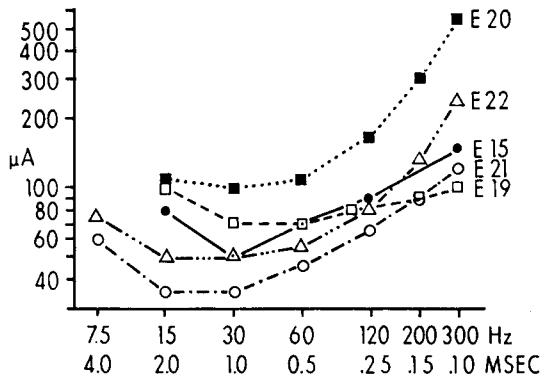


FIGURE 12. Thresholds for calling evoked by ESB as a function of stimulus pulse frequency and duration with hypothalamic (E20, 22) and mesencephalic (E15, 19, 21) electrodes in Steller's Jays. Pulse duration was adjusted to frequency so that all stimulations at a given current level are equivalent in terms of coulombs at all frequencies tested. Thresholds were determined to within 10% of the indicated value using 10-sec trains of pulses at intervals of at least 2 min.

preciated by comparing the series of calls shown in figure 13 with the series in figure 2. The two series are directly comparable because both were done with the same electrode in the same individual. The transition from call structures typical of low pulse frequencies to those at high frequencies was gradual. It seems better in this case to regard the various calls produced at different frequencies as variations of one basic call type rather than as different calls characteristic of different frequencies. The calls evoked at 15–30 Hz resembled those heard in nature most closely; calls evoked at 200 and 300 Hz sounded abnormally strident and high-pitched, and those at 60 and 120 Hz were intermediate in call structure.

An *abbreviation* effect on calling and certain associated behaviors was noted at high frequencies (200–300 Hz) at most electrodes for

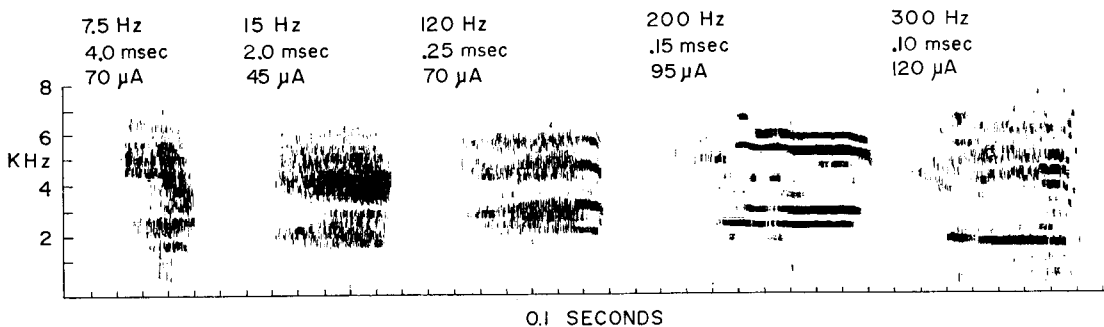


FIGURE 13. Variation in Wahs evoked by stimulation of the midbrain vocalization area (E21) in SJ9 at different frequencies. Compare with figure 2. Thresholds for calling at the different frequencies are shown in figure 12. The quality of the calls at 200 Hz was described as "whining"; at 300 Hz as "loud squawks."

which high frequencies were tested (E15, 19, 20, 22) but was not seen at E21. At these frequencies the period of calling was abruptly terminated just after the response had started. In contrast, at lower frequencies (15–60 Hz) calling and associated behavior tended to persist as long as the stimulus was kept on. For example, with E19 in six stimulations of 10 or 30 sec at 300 Hz, calls were given immediately in all but ceased after 2 or 3 sec for the remainder of the stimulus. The other components of the response with E19 were similar; the jay crouched with spread wings and its crest rose from 0 to 90° in the first second, but she rapidly resumed her prestimulus appearance and appeared to be unaffected by the last 20–23 sec of stimulation. These effects occurred with pulse durations of 0.1 and 1.0 msec.

Pecking seemed to be less subject to the abbreviation effect than calling. With E19, pecking was inconsistent and weak at 15 Hz but strong and regular at higher frequencies. Calling continued during stimulation at low frequencies but was quickly terminated at high frequencies; but pecking continued while the stimulus was on at all frequencies up through 300 Hz (pulse durations 1.0 and 0.1 msec) (see also fig. 11).

A *telescoping* effect of high frequencies was also typical. In the response described for E19, the most conspicuous components (calling, crouching, wing spreading, and crest erection) appeared with short and nearly identical latencies. At 30 Hz, the response evolved gradually; crest elevation first, then calling, followed at higher currents by tail-spreading and at the highest currents by crouching and spreading, all at quite different latencies. Increasing the current at 30 Hz also had a telescoping effect on the latencies of the separate components. But at 300 Hz the range in which the components could be separated as to latency by manipulation of current level was diminished nearly to zero.

The effects of high frequencies on crest erection were similar to those on calling. Thresholds were high at low frequencies and low at high frequencies if there was no compensation for the increased coulombs at high frequencies. When the increased coulombs at high frequencies were compensated for by decreased pulse duration so that the product of frequency and pulse duration was constant at 30, thresholds rose at frequencies above and below 30 Hz for E21, as shown in figure 14. This was also the most efficient frequency for

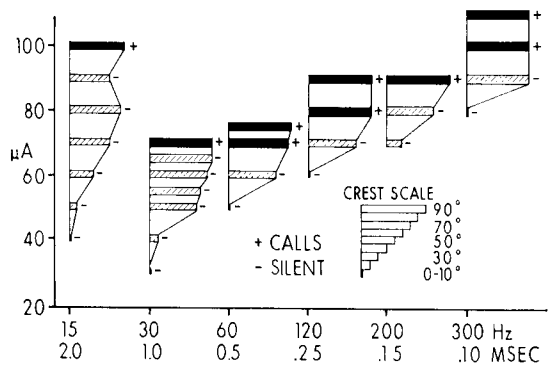


FIGURE 14. Maximum crest angle evoked by ESB in 10-sec stimulations with an electrode (E19) in the midbrain calling area. Stimulations were at a minimum interval of 2 min. Each bar represents the mean of a variable number of stimulations. A black bar indicates the presence of vocalization. A hatched bar indicates absence of vocalization.

crest erection with E19. The abbreviation effect was present for crest erection, as described in the previous paragraph. The telescoping effect of high frequencies is illustrated in figure 14. The range of current values from the highest current at which no elevation occurred to the lowest value at which full elevation occurred was relatively wide at low frequencies and became progressively narrower with higher frequencies; it spanned 60 μA at 15 Hz and 10 μA at 300 Hz. When the absolute current values are converted to percentages of threshold, the telescoping effect is just as evident. Figure 10 shows that the telescoping effect on crest elevation does not occur with short pulse durations at 30 Hz; so the effect shown in figure 14 cannot be attributed to the simultaneous variation of pulse duration.

NEUROANATOMY

Most of the stimulation sites tested in this study are shown in figure 15. It is interesting to compare the calling sites with those for the only other passerine species for which data exist, the Red-winged Blackbird (Brown 1971), and with the data for the most thoroughly studied species of bird, the Domestic Chicken (Putkonen 1966; Peek and Phillips 1972; Phillips et al. 1972; Phillips and Youngren, 1972).

The stimulation sites for Steller's Jays have been plotted on the brain atlas sheets used for the Red-winged Blackbird since the differences in brain anatomy are relatively minor. Consequently, figure 15 can be compared directly with the data for the blackbird in Brown (1971). The AP numbers on the figure belong to the blackbird, not the jay. The data

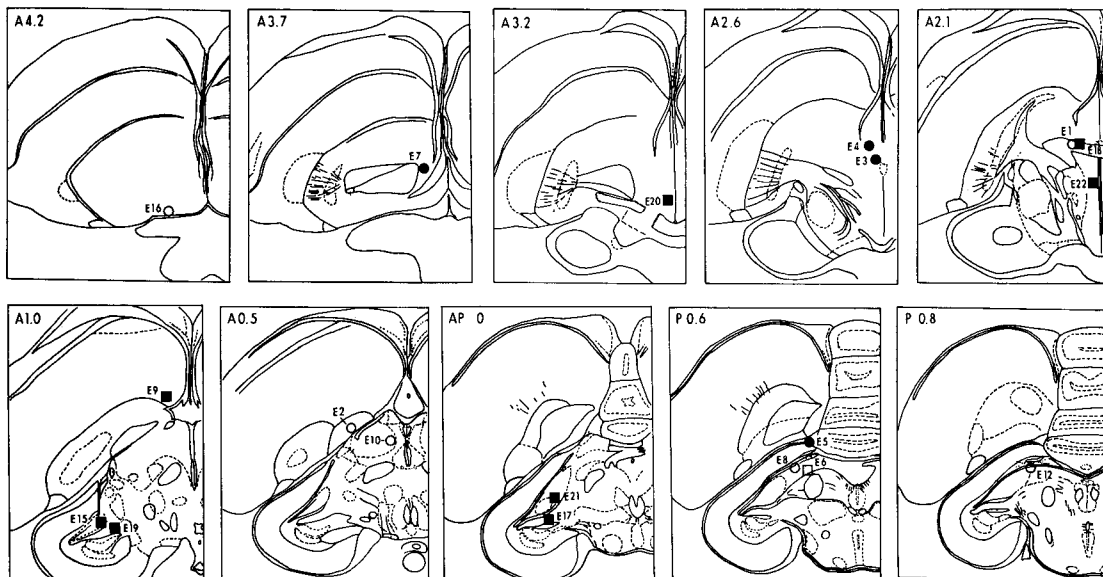


FIGURE 15. Locations of 19 electrode tips in brains of nine Steller's Jays. Squares indicate calling at thresholds from 29–200 μ a. Circles indicate absence of evoked calling. Filled squares and circles indicate elevation of the crest. Open symbols signify absence of crest elevation. Three of the 22 electrodes tested are not shown. Their locations were as follows: E13 was in the cerebellum. E11 was in either the optic tectum or archistriatum. E14 was in the neighborhood of the trigeminal sensory nucleus. Responses to stimulation are summarized in table 1. Data are plotted on atlas planes for Red-winged Blackbirds to enable direct comparison with that species. The AP numbers are for blackbirds, not jays. Anatomical structures are identified in Brown (1971).

for the Steller's Jay are in precise agreement with those for the Red-winged Blackbird. In both, a low-threshold region for calling evoked by ESB was found in TX (torus externus, which is the part of the torus semicircularis external to nucleus mesencephalicus lateralis dorsalis E6, 15, 21) and just below it in MLV (area mesencephalicus lateralis ventralis, E17, 19). And in both species responsive regions were found in the medial anterior hypothalamus (E20) and in or near the anterior commissure (E1, 18, 22). The failure of two electrodes in the torus (E8, 12) to evoke calling was surprising, but these seem to have been just outside the border of the responsive zone as delineated in the Red-winged Blackbird.

Other sites found to be negative for calling in jays were also negative in blackbirds. The calling evoked with E9 in the ventromedial neostriatum was not duplicated in the Red-winged Blackbird.

The histological data for calling evoked by ESB in the chicken are more abundant than for passerines. In the midbrain low thresholds are found in TX and MLV (Phillips et al. 1972) as in passerines. The responsive area in chickens seems to be larger and to extend somewhat more medially and ventrally (Peek and Phillips 1972) than in passerines, but this might be due to lack of data in some midbrain regions in passerines. The responsive regions in pas-

serines in the anterior hypothalamus and around the anterior commissure were also found in chickens. It can be concluded that the present data on evoked calling sites for jays are in good agreement with comparable data for Red-winged Blackbirds and chickens.

There was no evidence in the Steller's Jay that different calls were localized in different regions of the brain. Wahs were obtained with all vocalization electrodes. Additional types of calls (Rattle, Guttural, Shook) were obtained only along with Wahs and only from hypothalamic sites (except a few odd sounding Gutturals which might have been abbreviated Wahs from one midbrain electrode, E17). Although the sample of loci stimulated was small, it seemed that hypothalamic sites yielded more variability in evoked behavior from a single site than did mesencephalic sites. This is in agreement with results from Red-winged Blackbirds (Brown 1971) and chickens (Phillips et al. 1972). The finding of Potash (1970a) that various calls had different patterns of localization in the midbrain could not be verified in jays or blackbirds.

DISCUSSION

In 1964, I proposed a common factor in the motivation of different types of threat behavior in the Steller's Jay based on behavioral observations of jays and on studies using ESB

in mammals (Brown 1964a). This factor was termed agonistic arousal. It postulated a neural substrate for agonistic behavior and was applied primarily to threat behavior. Its existence was inferred from the observation of a graded series of behavior patterns of increasing intensity as threats. At one end of this series were various nonthreat behaviors in which the crest was typically not erected, such as resting, foraging, digging, storing, and being held in the hand. At the other end were fighting and aggressive sidling, in which the crest was maximally erect. Intermediate were various acts requiring some degree of physical exertion with or without agonistic overtones and characterized by intermediate crest angles. Vocalizations were placed on this gradient according to their characteristic crest angles and ranged from Song at low crest angles to Wah and Shook at high crest angles.

In the present experiments I wanted to see which elements of this graded series could be evoked by ESB and whether or not they were graded in accordance with intensity of ESB. It was found that crest erection could be evoked by ESB and that it was graded in accordance with intensity of ESB. The Wah could also be evoked by ESB, and its rate was also graded with intensity of ESB. However, none of the other vocalizations could be reliably and repeatedly evoked; of the others only the Rattle, Shook, and Gutturals were evoked at all and then only rather unreliably and in association with Wahs.

The failure to elicit most vocalizations and some of the other behaviors associated with the gradient of agonistic arousal was expected but is not understood. Possibly the lack of a suitable companion in most of the tests prevented certain displays and vocalizations. The narrow and restricted confines of the stimulation box may have contributed toward limiting the variety of evoked behaviors, but the jays did give Song, Shooks, Rattles, Gutturals, and calls equivalent to Too-leets while unstimulated in the stimulation box. Since a wide variety of stimulus pulse durations and frequencies was tried on the more suitable electrodes, it is not likely that evoked behaviors were missed because of failure to employ suitable stimulation parameters. Since both sexes and a variety of ages were tested, these factors are probably also not responsible. Some calls and behaviors might not be elicitable by ESB under any conditions in some species. The relatively small sample of brain areas stimulated might have been important in accounting for the small number of types of

calls evoked; however, in Red-winged Blackbirds such a sample would have been adequate to evoke the main types of natural calls that were obtained. Failure to evoke complete repertoires of vocalization during ESB in other species of birds even in extensive testing is a common result in such studies (e.g., Brown 1971; Phillips et al. 1972).

The neural system concerned with vocalization and associated displays has been described in birds as a descending system extending through forebrain and midbrain (Brown 1969, 1971). It is possible to evoke vocalization by stimulation at any level of this system but the threshold, character of the calls, and associated behavior vary depending on which part of the system is directly activated. Except for the anterior parts of this system, which are more concerned with reproductive behavior (Åkerman 1966; Brown 1969), the behaviors associated with evoked calling are mainly threat. Consequently, the posterior part of this system could be thought of as an agonistic arousal system since its activation induces agonistic calls (e.g., Wahs) and displays (crest erection, tail spreading). Anatomical and behavioral properties of this agonistic arousal system have been described in detail in studies on other species. The present experiments establish that the Steller's Jay fits the general picture obtained for other species of birds of a neural system in hypothalamus and midbrain concerned with agonistic vocalizations and related behavior, and they add the parameter of crest erection to its properties.

This study in conjunction with similar work on other species of birds confirms with neurobiological experiments the existence of the hypothesized neural system subserving agonistic arousal in the Steller's Jay with some of the main features which I hypothesized in 1964. They also identify it as the posterior part of the vocalization system which has been extensively mapped in other species. Many facets of the agonistic behavior of the Steller's Jay remain to be accounted for, however. The neuroanatomical relationships among the substrates for attack, threat, and escape are not at all understood, although some observations of attack and escape evoked by ESB have been made in birds (Åkerman 1966; Putkonen 1967; Phillips 1964; Maley 1969; Goodman and Brown 1966). The results that might be obtained with ESB in more natural environments, especially in various social situations, are still unknown.

The observation that the two electrodes (E3, 4) in or near the medial forebrain bundle

(MFB) evoked signs of "pleasure" and well-being calls to mind the well known association, perhaps fortuitous, of MFB with self-stimulation and other outward signs of "pleasure" in mammals (Olds 1962; Olds and Olds 1963). Unfortunately, the reliable reports of self-stimulation in birds (Goodman and Brown 1966; Goodman 1970; Andrew 1967, 1969) have failed, for birds, to convincingly implicate any one fiber system or brain region as the functional counterpart of the mammalian reward system. Only scattered and anatomically unrelated points have so far yielded self-stimulation. Andrew (1967) reported self-stimulation at one part of MFB in chicks and from the septomesencephalic tract (1969). Although MacPhail (1966, 1967) has claimed the lateral forebrain bundle in birds to be a reward system, his criteria of self-stimulation were not at all comparable with those used in mammals. The present data, though only tentatively suggestive, are at least consistent with the concept of MFB as part of a positive "reward" system in birds.

SUMMARY

Electrical stimulation of the midbrain and anterior brain stem was used to study the functional organization of agonistic behavior in the Steller's Jay. A system mediating agonistic arousal, as hypothesized earlier in a field study (Brown 1964a), was identified in the anterior hypothalamus, the region of the anterior commissure, the nonauditory part of the torus semicircularis, and the adjacent area mesencephalicus lateralis ventralis. Crest erection and calling were evoked and were graded in relation to intensity of activation in accordance with observations in natural populations. Bill-rapping or pecking was evoked with hypothalamic but not mesencephalic stimulation. Only Wahs were consistently and reliably evoked at all calling sites. Rattles, Gutturals, and Shooks were evoked inconsistently and unreliably with hypothalamic but not at all with mesencephalic stimulation (except Gutturals). Thresholds for evoked calling and crest erection were studied as functions of stimulus pulse duration, frequency, and current. Variation in pulse duration had relatively little effect on evoked behavior. Variation in pulse frequency had more conspicuous effects; at high frequencies an abbreviation effect and a telescoping effect were observed. Results are interpreted as supporting the existence of a system for agonistic arousal that is an important factor in the motivation of agonistic behavior in birds.

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