DISCRIMINATORY APPROACH TO AUDITORY STIMULI IN GUINEA FOWL (*NUMIDA MELEAGRIS*) AFTER HYPERSTRIATAL/HIPPOCAMP-AL BRAIN DAMAGE

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ABSTRACT

Oades, R.D., 1980. Discriminatory approach to auditory stimuli in Guinea fowl (*Numida meleagris*) after hyperstriatal/hippocampal brain damage. *Behav. Processes*, 5: 227—249.

   Guinea fowl were trained to approach, feed and retreat from a food dish after hearing a species-specific food-trill. An ethogram including approach, search, locomotion and tension behaviour was recorded before and after operation for a training and a test regime of variations of the natural calls and other sounds. Experimental groups consisted of sham-controls and birds with lesions in the hyperstriatum/hippocampus anterior and posterior to the anterior commissure.
   Both the 'anterior' and 'posterior' groups showed impaired recognition of the stimulus variations as shown by increases of approach to the posterior group and of search behaviour by both lesion groups. The long approach of the posterior group was followed by a long period of arousal (high tension). This was more quickly habituated in the anterior group (search behaviour changed to low tension).
   It is hypothesised that in the anterior group, where activation is followed by a disengagement, there may have been changes in thresholds for matching learned specifications with new sensory input. The more generalised approach responses of the posterior group may show an impairment of the rules for the selection of input.

INTRODUCTION

   There are areas in the forebrain of birds and mammals that are likely to be involved in the use of polysensory information because they are directly connected to more than one sensory projection field. Prominent among these is the hippocampal complex of the limbic forebrain. There is much behavioural and neurophysiological evidence that the mammalian hippocampus takes part in the attentional processes associated with the recognition of sensory stimuli (reviews: Kemp and Kaada, 1975; Pribram and McGuinness, 1975; Oades, 1979). Pribram and Isaacson (1975) suggest that the hippocampal circuit determines whether inputs have occurred to which attention must be

given (p. 433) and thus also when a shift in strategy is required in order to execute an intention (p. 437).

In birds the situation has not been so intensively studied. Lesion damage to the hippocampus and the neighbouring accessory hyperstriatal areas does not affect simple discriminations (Hodos et al., 1973). But there are deficits on a pattern discrimination reversal (Stettner and Schultz, 1967). Examination of these results has led to the suggestion that the lesioned birds had an impaired ability to shift attention between aspects of the stimulus complex (Cohen, 1967; Stettner, 1974). There is some consensus that this area functions in the control of orientation to aspects of a stimulus (Salzen and Parker, 1975; Gentle et al., 1978).

Oades (1976a) has shown that lesions to the dorsomedial hyperstriatum and putative hippocampus in chickens decrease distractability on a runway task and incur behavioural deficits (e.g. passive avoidance) that parallel the behavioural deficits produced by hippocampal lesions in mammals. In an examination of the mechanism that might be affected by these lesions, Oades (1976b) showed that when faced with an array of red and yellow food grains and pebbles, the brain-damaged birds were less distracted by the pebbles than were the controls. Further the birds showed a persistence in the use of strategies for selecting a particular colour of food grain whilst feeding. Thus it seems that lesions can affect the shifting of attention and the use of learned specifications in the control of a search strategy. Attentional mechanisms include not only the selection of stimuli but their matching with learned specifications (e.g. recognition, cf. Broadbent, 1970).

There is further reason to suppose that processes, related to those for learning and retrieval, take place in the dorso-medial area. Lesions in the dorsal midline, rather than in the lateral hyperstriatum or neostriatum impair the ability of nutcrackers (*Nucifraga caryocatactes*) to find the places where they have stored food (Krushinskaya, 1966).

This current study addresses three questions.

(1) If attentional processes are damaged by limbic lesions they would not be expected to be restricted to the visual modality: does damage to the avian putative hippocampal complex affect performance on auditory tasks? Until recently it could be said only that some auditory responses may be recordable from the hyperstriatum (Adamo and King, 1967) and that damage here can affect orientation of the head to auditory stimuli (Adamo and Bennett, 1967).

(2) The putative hippocampus of birds may cover several functional subareas. Are there separable effects that result from non-overlapping lesions placed anterior and posterior to the anterior commissure on the performance of an auditory recognition task? The presence of acetyl choline is a characteristic of the mammalian hippocampus. Staining for acetyl cholinesterase in the forebrain of pigeons (B. Srebro, personal communication, 1978) suggests that the putative hippocampal area extends further posterior than the area *anterior* to the anterior commissure and dorsal to the septum described for

chickens (Oades, 1976a). Indeed Oades (1976b) did find that birds with damage to the parahippocampal area posterior to the anterior commissure showed a stability and persistence in their selection of food colour like those with more anterior damage and unlike those with lateral damage.

(3) Recent neurophysiological findings (review, Scheich, 1977) using species-specific vocalisations as stimuli in birds and mammals supports a hierarchical concept for central auditory analysis. Can this hierarchy be extended in anatomical terms from the primary auditory forebrain field (Field L of the neostriatum), that connects to the *posterior* parahippocampus and the anterior hyperstriatum/hippocampus?

Such an anatomical sequence may represent a hierarchy in terms of functional specialisation. Behavioural measures were taken to investigate whether brain damage to two separate but connected areas could result in two separable but related deficits. Such a result is not without precedent. For example Sahgal and Iversen (1978) showed that damage to the posterior and anterior inferior temporal cortex of monkeys interfered with their ability to categorise and to retrieve information, respectively, on a colour match-to-sample task. The current analysis of the behaviour of the Guinea fowl also leads to the hypothesis that separate processes have been affected by the two areas of lesion damage.

The Guinea fowl is the subject of these experiments because of an extensive background of experience with this bird in auditory analysis research in this laboratory. The task consisted of a time-limited, motivated approach (food reward) and withdrawal (punishment) from a species-specific call (food-trill). Natural variations of the trill-call and other sounds were used as test stimuli. An ethogram is shown to be a potentially useful tool in the analysis of an attentional situation where overt behaviour has formerly been overlooked.

MATERIALS AND METHODS

Preparation of animals

Results are reported from 17 adult Guinea fowl. All birds were trained and tested in their home chambers (48 × 130 × 120 cm high). They were maintained on a 12:12 h light:dark cycle at 23 ± 2°C at about 75% normal body weight. Water was continuously available.

The animals were prepared for operation under hypnodil anaesthesia (Janssen). The drug was injected into the pectoral muscle, 25 mg initially, followed by 10 mg every 0.5 h. The head was held between two ear bars of a stereotaxic apparatus with the bite bar 23 mm anterior and 23 mm below. The skin and bony horn were removed from the dorsal surface of the skull. Bilateral aspiration lesions were performed 1.2—3.7 mm (posterior) and 4.5—7.0 mm (anterior) with respect to a null point of the depression between forebrain and cerebellum over the blood sinus. Lesion depth were judged at 1.5 and

2.5 mm lateral to the mid-line, for the anterior group at 3.5 and 2.5 mm and for the posterior group at 4.5 and 3.5 mm, respectively. The lesion damage lay largely anterior and posterior to the plane of the anterior commissure.

After operation the exposed surface was covered by a cap of dental cement and the skin sealed with Histacryl tissue glue (Braun, Melsungen). Four days were allowed for recovery before testing recommenced. After behavioural testing all animals were perfused with saline and 10% formalin solution. The brains were serially sectioned (6 μm) and stained in cresyl violet for the recording of tissue damage (Fig. 1).

Histology

Histological examination showed that six birds belonged to the anterior and six to the posterior lesioned group. The lesions extend approximately 2 mm anterior or posterior to the plane of the anterior commissure. The bilateral extent of the lesion at five evenly-spaced intervals for all birds in each group is shown by the shaded area in Fig. 1; the maximum extent is shown by the hatched area.

The anterior lesion removed bilaterally the dorsal midline hyperstriatum accessorium and dorsal hippocampus; about 75% of the hyperstriatum intercalatum and 50% of the hyperstriatum dorsale (lateral part intact) were also damaged. The dorsomedial midline of the anterior hyperstriatum ventrale and the midline border of the neostriatum were damaged in four of six birds in the plane of greatest lesion damage.

The posterior lesion removed the dorsal and midline hippocampus bilaterally. The midline quadrant of the area parahippocampalis was damaged in anterior sections, but this became progressively more spared posteriorly. Damage to the dorsomedial and midline hyperstriatum ventrale anteriorly and the part of the neostriatum posteriorly that contains the anteromedial Field L was also sustained.

Data from two birds with lesions extending anterior and posterior to the anterior commissure showed characteristics of both groups during testing and were not included in the analysis. Three sham controls were exposed to the total operative procedure. The dura was cut, but no aspiration probe was applied.

Training

The birds were trained once a day to approach a dish to feed after hearing a food-trill and to stay away at all other times. Each session consisted of 20 repeated trills played from a Uher 4400 portable tape recorder at intervals of 1, 2, 3 or 4 min in a pseudo-random order. Each train-trill (Fig. 2) was the same example of a natural call given by a feeding Guinea fowl that no test animal had met. When a bird approached the food dish it was rewarded with 20—30 maize grains. Prior testing had shown single grains to be ineffective.
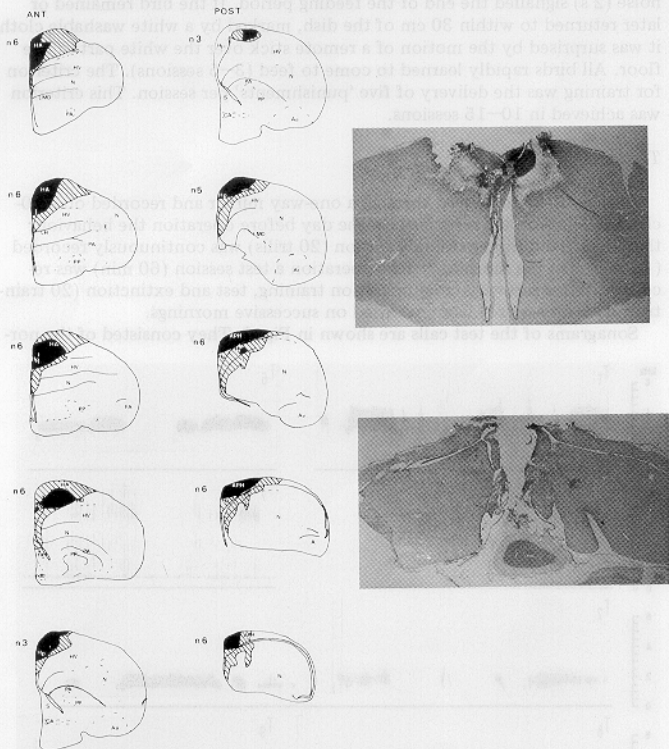
Fig. 1. On the left side of this figure brain damage sustained by the Al (ANT) and Pl (POST) groups of Guinea fowl are reconstructed on five evenly spaced serial sections from anterior (upper) to posterior (lower). This covers approximately 2 mm. Damage sustained by all members of the group is shaded. The maximum degree of damage sustained by any bird at the given plane is represented by the hatched area. The figure 'n' states the number of birds with damage at this plane. On the right-hand side of the figure, the two photographs show transverse sections in the plane of maximum damage for one example from the Al (upper) and the Pl group (lower). For further details see text (× 4.13).

Aa: Archistriatum, pars anterior; Ai: Archistriatum, pars intermedium; APH: Area para-hippocampalis; CA: Anterior commissure; FA: Tractus fronto-archistriatalis; HA: Hyperstriatum accessorium; HD: Hyperstriatum dorsale; Hp: Hippocampus; HV: Hyperstriatum ventrale; L: Field L; N: Neostriatum; PA: Paleostriatum augmentatum; PP: Paleostriatum primitivum; S: Septum.

The bird was allowed to feed for 45 s following the trill. A low frequency noise (2 s) signalled the end of the feeding period. If the bird remained or later returned to within 30 cm of the dish, marked by a white washable cloth, it was surprised by the motion of a remote stick over the white part of the floor. All birds rapidly learned to come to feed (3—5 sessions). The criterion for training was the delivery of five 'punishments' per session. This criterion was achieved in 10—15 sessions.

Testing

Behaviour was observed through a one-way mirror and recorded on a 10-channel Miniscript Z recorder. On the day before operation the behaviour that occurred during a training session (20 trills) was continuously recorded (45 min). On the morning before operation a test session (60 min) was recorded. After recovery from operation training, test and extinction (20 train-trills with no reward) were recorded on successive mornings.

Sonagrams of the test calls are shown in Fig. 2. They consisted of the nor-
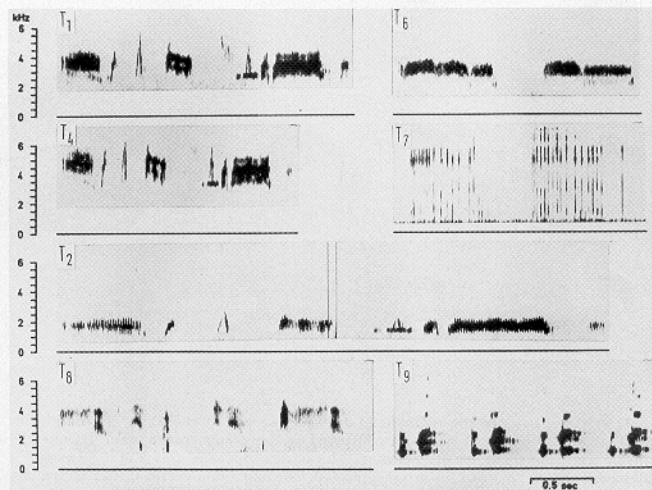

Fig. 2. This figure shows the sonagrams (frequency, kHz against time, s) for the train-trill (T) and test stimuli (T_{2-9}) that were presented to the Guinea fowl.

T_1, train-trill; T_4, fast trill; T_2, slow trill; T_8, novel trill; T_6, arousal trill; T_7, watch wind; T_9, iambus-song: for further details see text. (The difference between T_1 and T_6 is that for the former the carrier frequency is relatively stable and the elements are regularly repeated. In T_6 there are early fluctuations in the carrier frequency and the elements are repeated at about 150 cps at first, but slow to about 110 cps at the end.)

mal training trill (122 cps) filtered by 40 dB under 400 Hz (T_1, 55 dB), 3.15 KHz (T_3, 50 dB) or 8 KHz (T_5, 50 dB), played at slow speed (T_2, 63 cps, 60 dB) or fast speed (T_4, 160 cps, 66 dB), an 'arousal' trill (T_6, 127 cps, 64 dB), the winding of a watch (T_7, 29–53 cps, 61 dB), a novel food-trill (T_8, 127 cps, 54 dB) and an iambus-song call (T_9, 59 dB). The number in parentheses refers to the order of presentation and the average sound pressure level in the test chamber is given. No response to a test call was rewarded. The test programme consisted of nine test stimuli. Between each test stimulus two train-trills were played so that no effect of one test stimulus would effectively carry over to the next test stimulus. Time intervals between stimuli were 1, 2, 3 or 4 min in a pseudo-random order.

The behaviours recorded were feeding, move (move feet — M), peck floor, drinking, shake/feather ruffle, presence by dish, search (S), low tension (LT) and high tension (HT) postures. Search behaviour was characterised by the extension of the neck with the head still and/or with side to side movements of the neck below the body line (Fig. 3c). In high tension postures the legs were straighter and the neck was extended vertically. The head would sometimes turn but without sideways movement of the neck (Fig. 3a). In low tension postures the neck and legs were relaxed (Fig. 3b).

Analysis

Preliminary analysis showed that the data were not normally distributed. Variance of preoperative populations was considered (e.g. approach duration, $0.95 > P > 0.9$, Kruskal Wallis analysis of variance). Thus non-parametric tests appropriate for the behaviour of small samples were used (Ferguson, 1966; Siegel, 1956). Pre- to postoperative changes in the overt behaviour rather than absolute values were analysed. The data of the experimental groups were compared with preoperative and prestimulus conditions (related sample tests) and with sham-operates (unrelated sample tests). The probabilities given are for the performance between groups where Kruskal Wallis analysis of variance showed there to be changes; the Mann Whitney U test confirmed the groups responsible for the change (Siegel, 1956). Preoperative observation showed that overt behaviour occurred in phases (see *Overt behaviour*, p. 235). Thus a rank analysis for dominant behaviour in a phase was computed.

RESULTS AND DISCUSSION

Control measures of the incidence of the four main overt behaviours (M, S, LT, HT) were taken with undisturbed birds in the presence of a novel object (brown bottle) and birds with the novel object and food for 5 min under each condition. There were no significant differences between groups.

The pattern and sequence of behaviour associated with the train-trill will be described in the first section. The analysis concerns the 60 s after a stimulus. The occurrence of the behavioural components seldom reached prestimulus levels sooner.
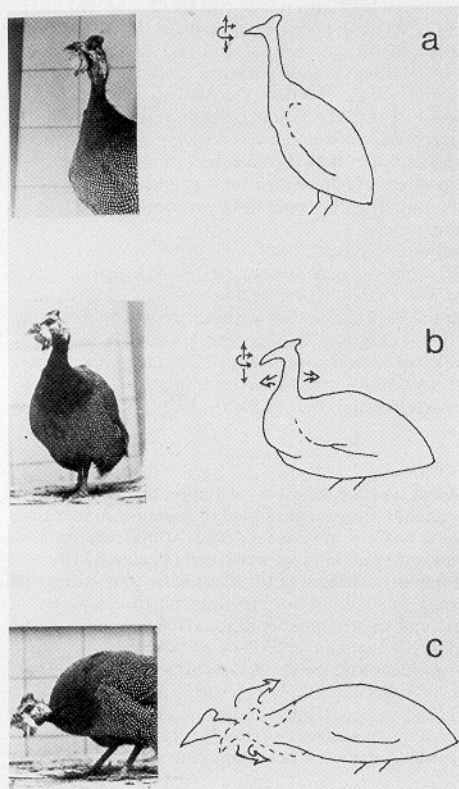
Fig. 3. This figure presents photographed examples of (a) high tension (HT), (b) low tension, (LT), and (c) search (S) behaviours of the Guinea fowl. Alongside each photograph is a diagram to show (a) extended legs, vertically extended neck, potential head movement; (b) relaxed (bent legs, withdrawn neck, potential head and neck movement; (c) bent legs, horizontally extended neck, potential neck movement. The grid pattern on the rear wall of the test chamber that assisted judgment of tension behaviours is also shown.

Training stimuli

Approach, leave and control measures

Results. Preoperative measures of the latency to approach and leave after the train-trill in the training and test regimes showed no significant differences. The high score for controls was due to one bird that otherwise performed normally (Table I). The latency for approach, postoperatively, increased for both lesioned groups with respect to the sham-controls ($P < 0.01$). The posterior group stayed longer by the dish than the sham-control group ($P < 0.05$).

The normal rhythm of feeding pecks could be interrupted by a bird raising its head before continuing to feed. The number of such feeding bouts did not differ between groups. 'Punishment' continued to be delivered outside the 1.5 min analysis period around a stimulus. There was no difference in the number of pre- and postoperative 'punishments' received by the three groups.

Discussion. The consistent proportion of feeding bouts suggests that the operation produced no major side effects on hunger or the coordination of the feeding pattern. No distraction from feeding was observed. With no change in the number of 'punishments' delivered nor of fearfulness shown in the presence of novelty one may conclude that motivation levels were stable and there was no gross interference with the retention of the task. The increased approach latency of the lesioned groups is discussed with search behaviour below.

Overt behaviour

After the train-trill there a rapid onset of feeding that lasted for about 30 s (Fig. 4, sixth 5-s period). The incidence of feeding rapidly decreased over the next 10 s. During these 10 s movement (M) sharply increased. The birds left the food area. Movement peaked between 45 and 55 s and then approached prestimulus levels. After feeding the probability of search behaviour (S) rapidly increased (Fig. 5, sixth to seventh 5-s period). This phase was followed by an increasing frequency of low tension (8—10) that was in turn superceded by a peak of high tension behavioural components (10—12).

After operation there were two points where the changeover between the dominant behavioural components was different between the groups (feed—S, LT—HT). Firstly, the posterior group fed longer than the anterior group (Fig. 4, $P < 0.03$) and then searched more than the anterior or control groups (Fig. 5, $P < 0.05$). This was reflected by the lower movement peak, with respect to prestimulus levels, shown by the posterior group ($P < 0.04$). Secondly, at the end of the behaviour sequence the anterior group showed more low and less high tension than the posterior and control groups (Fig. 5, $P < 0.016$).

Behaviour during extinction

There were no significant differences between groups in the length of time spent by the dish. There were no consistent tendencies across 20 extinction

TABLE I

Table I (A) shows the mean values (s) for latencies to approach and leave on pre- and postoperative training and test regimes after a 'train-trill' for birds with anterior (AI) and posterior lesions (PI) and sham controls (C). Table I (B) shows the mean changes (with SD) between regimes

(A) Approach/leave, mean latencies (s)

Regime:	Preoperative				Postoperative			
	'Train'		'Test'		'Train'		'Test'	
Group	Approach	Leave	Approach	Leave	Approach	Leave	Approach	Leave
AI	2.5	37.51	2.62	36.41	3.2	44.4	2.82	40.1
PI	2.57	41.91	2.74	39.82	3.39	51.62	3.01	49.61
C	3.8	40.52	2.61	44.45	2.7	40.86	2.74	43.52

(B) Approach/leave, change of latency (s)

Regime:	Approach		Leave	
	Pre- to postoperative		Pre- to postoperative	
Group	'Train'	'Test'	'Train'	'Test'
AI	+ 0.69[a]	+ 0.39	+ 6.88	+ 3.65
	± 0.8	± 0.7	± 7.1	± 4.8
PI	+ 0.82[a]	+ 0.27	+ 9.73[d]	+ 9.6
	± 0.6	± 0.2	± 11.8	± 6.2
C	− 0.79[b]	+ 0.13	+ 0.34[d]	− 0.93
	± 0.8	± 0.1	± 3.7	± 1.8

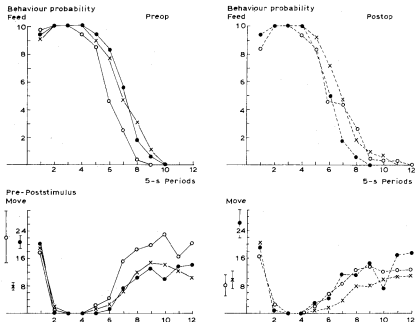a > b, $P < 0.01$; c > d, $P < 0.05$.

Fig. 4. For three groups of Guinea fowl this diagram shows the frequency of occurrence of feeding and movement (vertical axis) in successive 5-s periods (horizontal axis) for 1 min following a food-trill. The left-hand diagrams show preoperative and the right-hand diagrams show postoperative data. The symbols to the left of each diagram show the mean probability (with SD) for each behaviour taken from the 30 s preceding the trill stimulus. Each data point represents the mean for 20 trials. (Because of the possibility of several foot movements in a 5-s period, the vertical axis for M represents the mean of foot movements.)

Control group: preoperative ●——●, postoperative ●- - -●; anterior group: preoperative ○——○, postoperative ○- - -○; posterior group: preoperative ×——×, postoperative ×- - -×.

trials that distinguished the groups in the late stimulus period. This negative finding is important as it suggests that there is no gross impairment in the holding or removal of information from memory.

There was a high degree of search behaviour shown by both lesion groups initially. Further on the first trial, when reward was expected, both lesion groups showed an increased incidence of change between behavioural components with respect to prestimulus levels (+7.8). This measure could be an indicator of an internal state, for this level of change was only otherwise attained after the 'arousal'-trill (T_6, below).

Test stimuli

  Duration of approach

Results. Inspection of the duration of approach by controls (Table II) shows
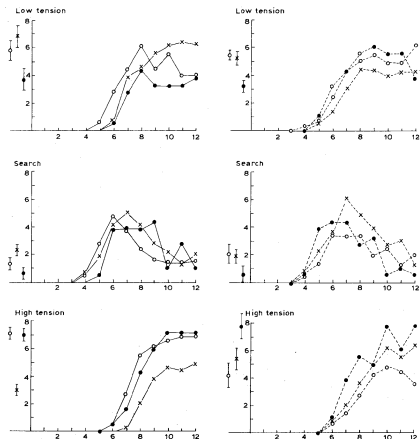
Fig. 5. For three groups of Guinea fowl this diagram shows the frequency of occurrence of search (S), low tension (LT) and high tension (HT) (vertical axis) in successive 5-s periods (horizontal axis) for 1 min after a food-trill. For further details see legend for Fig. 4.

that within this range there was no discernible effect of sound pressure levels. The attenuation of frequency in the filter-trills ($T_{1, 2, 3}$) had little effect. Most birds approached at first. The number of cycles per second in the stimulus was more important. The faster trills were more likely to elicit approach than slower trills or rhythms.

For the filter-trills and the 'novel' stimulus group ($T_{4, 7, 8}$) the anterior and sham-control groups spent a similar period by the dish that was less than half that for the posterior group. The third stimulus group ($T_{2, 6, 9}$) elicited mixed responses. To the slow trill (T_2) both lesion groups approached more than controls. All three groups approached the 'arousal'-trill (T_6) for a fairly long period. Only one bird from each lesion group and no control approached the iambus call (T_9).

TABLE II

Mean durations (with SD) of approach (s) to each of nine test stimuli, T_1—T_9, for birds with anterior (AI), posterior lesions (PI) and sham controls (C). The C group does not approach for as long as the two lesioned groups following T_1 (slow trill); The means are also shown for the two homogeneous groups T_1, T_3, T_5 and T_4, T_7, T_2, where the PI group approaches for longer than the AI or C groups

Stimuli Group	T_1	T_3	T_5	T_4	T_7	T_2	T_6	T_8	T_9
AI	17.7 ± 13	12.5 ± 8	13.8 ± 20	9.3 ± 11	7.7 ± 8	11.5 ± 12	21.5 ± 17	19.4 ± 22	7.9 ± 19
PI	33.9a ± 19	30.4b ± 19	25.4e ± 15	27.6d ± 16	18.3 ± 16	22.5 ± 18	22.3 ± 21	21.8 ± 14	2.2 ± 6
C	10.0 ± 13	11.0 ± 11	6.0 ± 10	10.0 ± 9	0 ± 0	5.0 ± 8	3.3a ± 5	20.0 ± 20	0 ± 0

	Mean T_1, T_3, T_5 f	Mean T_4, T_7, T_2 f
AI	14.6 ± 14	9.5 ± 10
PI	29.9a ± 17b	22.8a ± 17c
C	9.0 ± 10	5.0 ± 7

a = $P < 0.05$; b = $P < 0.04$; c = $P < 0.03$; d = $P < 0.02$; e = $P < 0.05$ with respect to preoperative levels; f = $P < 0.001$ Kendall coefficient of concordance.

Discussion. The posterior group continued to approach all stimuli except T_9 (song) longer than the anterior group (concordance $P < 0.001$). The posterior group had difficulty in distinguishing the test stimulus from the expected call, but the degree of generalisation extended only to the trill-like rhythms. As motivation levels and learning are relatively unaffected by the lesion, it is suggested that the selection of stimulus characteristics for the recognition process might have been impaired, (i.e. more information was allowed through for the matching process). When the received and expected stimulus are relatively similar the anterior group also had difficulty in making a selective distinction (e.g. to T_2).

Frequency of behavioural change

Results. I will first consider the frequency of change of the behavioural components shown by all three groups to all nine stimuli. The mean number of changes was 3.3 higher in the post-stimulus period than in the pre-stimulus period. After T_6 (arousal) the mean increase for all birds was 6.0. This increase for a call with clear communicative content was significantly more than for T_5 (filter-trill, $P < 0.025$) and T_2 (slow trill, $P < 0.05$) and twice as high as the average post-stimulus increase. This shows (cf. *Behaviour during extinction*, p. 235) that the frequency of behavioural change may be an indicator of communication received, at least in terms of arousal elicited.

The intergroup differences according to behaviour changes (Table III) distinguish the stimulus group $T_{1,3,5}$ from the other stimuli (concordance $P < 0.01$). The posterior group showed *less* behavioural change after T_1 ($P < 0.047$) and T_3 ($P < 0.02$) in the postoperative poststimulus period than the anterior group, and less, if compared to prestimulus levels, after T_5 ($P < 0.05$). After all other stimuli there were no marked differences, except for the iambus call (T_9). To T_9 the posterior group showed *more* behavioural change than the anterior and sham-control groups ($P < 0.025$). (The posterior group also showed non-significant increases to T_2 and T_6.)

Discussion. One may consider three categories of stimuli on the basis of approach duration and frequency of behavioural change. The first consists of filter-trills ($T_{1,3,5}$). The second consists of 'novel' signals ($T_{4,7,8}$) that differ in several respects from the train-trill (e.g. frequency of trill elements). The third category ($T_{2,6,9}$) possibly contains specific communicative properties separate from the train-trill (T_6 — arousal, T_9 — song and T_2, the slow trill has similarities with a warning trill — Maier, 1980).

One should consider what the responses may represent in terms of the nature of the stimuli. The arousal trill has structural properties similar to the train-trill, but it has other message properties (Maier, 1980). In all birds it elicited a high frequency of behavioural change (Table III). As approach behaviour seems to indicate that the stimulus has been recognised as similar to the learned stimulus, it is suggested that a high degree of behavioural change

TABLE III

The increases and decreases in the number of behavioural changes given in response to nine test stimuli (T_1–T_9) from pre- to post-operative regimes by anterior (AI) and posterior (PI) lesion and sham control (C) groups. The PI group shows a decrease compared to the AI group after the 'filter-trills', T_1, T_3, T_5, T_4, T_7, T_8, T_2, T_6, T_1 (concordance, $P < 0.01$) and an increase in comparison with AI and C groups after the 'iambus', T_2, T_9.

Stimuli: Group	T_1	T_3	T_5	T_4	T_7	T_8	T_2	T_6	T_9
AI	+ 4.0	+ 5.0	+ 0.8	+ 0.2	− 1.0	+ 1.0	− 0.3	+ 3.8	− 4.0
PI	− 1.3[a]	− 2.2[b]	0[a]	+ 2.3	+ 2.2	+ 0.5	+ 1.8	+ 4.3	+ 1.5[b]
C	+ 0.3	+ 1.3	+ 8.7	− 3.5	+ 1.3	− 0.5	0	− 1.7	+ 4.7

a = $P < 0.05$; b = $P < 0.025$.

represents to a lesser extent a similar 'activation'. When the anterior group did not approach, they showed a high frequency of behavioural change to test stimuli that were most similar in structure to the train-trill. In response to stimuli that have message content, the posterior group did not approach, but showed a high frequency of behavioural change.

High tension is reasonably seen as an alert posture that reflects a degree of arousal. It is compatible with a high frequency of behavioural change but not with approach. High tension was seen after the approach response for a short period in the anterior group and for a longer period in the posterior group when consummation did not follow. (In the training programme search is followed by low tension after consummation.) It is suggested that search and approach, frequency of behavioural change and high tension represent a progression from activation to arousal; (this parallels the so-called 'reasoning' process that has partly been attributed to limbic interactions by Pribram and McGuinness, 1975).

Overt behaviour

Results. The incidence of the four behavioural components (M, S, LT, HT) after the test stimuli showed a complex pattern of changes, but they broadly confirm that there were two similar groups ($T_{1,3,5}$ and $T_{4,7,8}$) and one mixed group ($T_{2,6,9}$) of test stimuli. For reasons of clarity of presentation, the data from each similar group are presented as means (Fig. 6 and 7). All differences are significant at a level of 5% or less.

(1) Filter-trills. (Fig. 6)

Two features are common to both lesion groups. The first emerges from a comparison of the train-trill (first extinction trial) and T_1. On the first extinction trial both lesion groups showed more search than they and controls did after T_1. Search continued longer for the posterior group. Secondly in response to the filter-trills the lesion groups showed less search than preoperative levels, but more than sham-controls. After the most filtered trill (T_5) they showed more high tension than preoperatively. The anterior group showed some differences. Correlating with a high frequency of behavioural component changes the anterior group showed more movement after the stimulus than preoperatively or sham-control levels. In response to T_3 these phases gave way to more low tension than in the posterior group.

(2) Novel stimuli. (Fig. 7)

By comparison with the filter-trills neither lesion group showed such large increases of search behaviour. But like their response to filter-trills they showed more search and less high tension than sham-controls. Nonetheless both groups showed less low tension than sham controls which might indicate a degree of novel stimulus-induced arousal, (shortly after the stimulus). There were also differences *between* the lesion groups. As with the training stimulus regime the anterior group showed more low tension, less high tension after a shorter search phase than the posterior group.
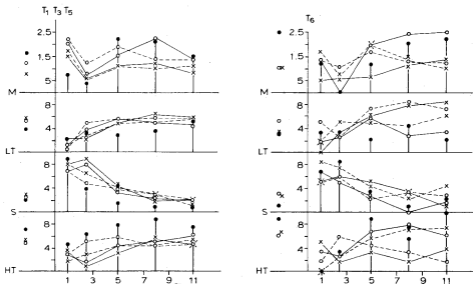
Fig. 6. The two diagrams show the frequency of occurrence of movement (M), search (S), low tension (LT) and high tension (HT) (vertical axis) during the minute (5-s intervals, horizontal axis) following the filter-trills ($T_{1,3,5,f}$, left) and the arousal-trill (T_6, right). Data are shown for three groups of Guinea fowl on pre- and postoperative sessions. Mean behavioural data are shown at intervals for clarity in showing early behavioural changes and for comparison with preoperative phases (see Figs 4, 5 and text). Prestimulus levels of behaviour are shown to the left of the vertical axis.

Control group: preoperative not shown, postoperative ●; anterior group: preoperative ○——○, postoperative ○- - -○; posterior group: preoperative ×——×, postoperative ×- - -×.

(3) Mixed stimuli.

These stimuli gave rise to stimulus-specific responses. In general the anterior group showed more low tension following any search behaviour than the posterior group, although both lesion groups showed more low tension than the sham controls. Specifically, the slow trill (T_2) elicited more search in the lesion groups than in the controls. The arousal trill (T_6) elicited much search behaviour in all groups (Fig. 6). The song (T_9) elicited very little search behaviour. Instead there was much high tension with the control groups showing the highest levels (Fig. 7).

Discussion. There are five main points to be made.

Firstly, the test stimuli were recognised as different from the training stimuli. This varied by degree with the nature of the stimulus. More search was observed on the first extinction trial than after the filter-trills. In turn this level of search was higher than that seen after the 'novel' stimuli. (This point assumes that search and approach represent an activated recognition process
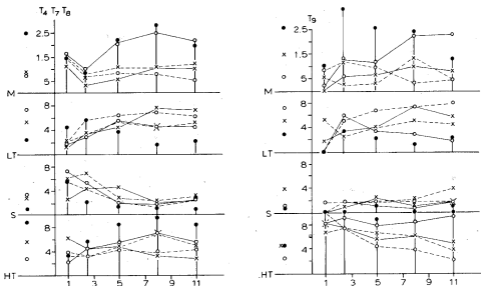
Fig. 7. The two diagrams show the frequency of occurrence of movement (M), search (S), low tension (LT) and high tension (HT) (vertical axis) during the minute following 'novel' stimuli (left) and iambus-song (right). For further details see legend for Fig. 6 and text (p. 240).

where recognition is seen as the matching of the received with the expected stimulus.)

Secondly, one must emphasise that the two organisation systems affected by the two lesions were not entirely contiguous with the brain damage. The lesion groups shared some impairment characteristics. After the filter-trills and 'novel' stimuli both groups showed more search, but later less high tension than sham-controls.

Thirdly, there were two categories of behavioural response to the test stimuli, the one shown by the posterior the other by the anterior group. After a test stimulus the posterior group showed a long approach and search period; the next phase was dominated by high tension components. The anterior group showed a shorter period of approach and search to fewer stimuli; they retreated sooner and showed low tension in the next phase and thereafter.

Fourthly, there were secondary characteristics that separated the two lesion groups. These depended on the nature of the test stimuli. Where the properties of the test stimulus were closest to the train-trills (i.e. filter-trills) the anterior group showed more behavioural changes. Where there was message content to the test stimulus, the posterior group showed more behavioural changes. Correlated with this reaction of the posterior group to $T_{2,6,9}$ was a higher level of high tension.

Lastly, there were two control measures that gave an approximate indication of the degree of generalisation and habituation to repeated stimulus pre-

sentation. In the first instance T_9 (iambus) elicited negligible search and approach responses from brain-damaged or intact birds. In the second instance lesioned groups showed less search after a filter-trill postoperatively than preoperatively. Nonetheless this level after operation was significantly higher than the sham-controls with the same experience.

In summary the anterior group appear to 'switch on' then 'switch off' approach and search responses quicker than the posterior and control groups. As such a measure is suggestive of a threshold change, I suggest the hypothesis that the learned stimulus specifications are activated more quickly following a stimulus and in the absence of a match (or consummation) deactivated more quickly (early mismatch, early decision to retreat).

The posterior group did not show these characteristics. They recognised the test for the training stimulus and approached. In the absence of consummation approach and search continued longer. They made a match for the physical characters of a test stimulus (train-trill similar to filter-trill) and for message content ($T_{2,6,9}$). The iambus did not elicit a strong approach response. The impairment resembles a specialised type of discrimination deficit. The hypothesis is that the rules for selecting input were damaged.

GENERAL DISCUSSION

There are three classes of measurement that may be indicative of changing central processes in response to auditory stimuli. Variations of these measures for two lesion groups (anterior and posterior hyperstriatum/hippocampus) and two control groups (preoperative and sham-operates) suggest that the central control of these processes has been differently affected. The first class of measurement consists of approach and departure latencies. The second is the frequency of behavioural change (of body tension, head and body movement). The third is the change of dominance of these tension and movement responses. The direction of change from one phase to the other (S-HT, S-LT) can be important. The tension components and locomotion are related. The following model is an interpretation based on observations of these measures.

A model

Previous work using visual task with chicks has shown that damage similar to the anterior lesions of this study induced a persistence in use of a strategy for selecting one class of input for response (Oades, 1976a, b). The current study confirms this and that more posterior damage can induce persistence associated with auditory and visual stimuli. This persistence, in comparison with controls, is seen as an 'activation' by the anterior group toward test stimuli that are similar to the training stimuli and as one of continued exploratory responses by the posterior group. On the basis of the detailed measures taken it is proposed that there are two types of 'persistence'. Further testing will be necessary to confirm this hypothesis.

The anterior group showed persistence, type I. The lowering of the threshold of activation for recognition units resulted in a degree of arousal towards filter-trills (high frequency of behavioural change) that was not seen with controls. Thus the anterior group persisted in 'reacting' to the test stimuli. A test stimulus that in a control bird should produce a slight mismatch, in the anterior group produced a stronger positive reaction (search and behavioural change) as their training-trill specifications had been activated. Approach was not prolonged for the lower threshold of activation gave rise to a matching decision similar to that of controls, that resulted in ending the approach phase.

Persistence, type II, was seen in the posterior group. Damage was more to the system that would select stimuli likely to match. The birds approached more stimuli, stayed longer and after the search phase showed more high tension arousal. They were deficient in the ability to disengage from the situation. Thus they showed a resulting perseveration of behaviour and generalisation of response.

In the formulation of this hypothesis the term recognition assumes a matching process between input and representations (specifications) of learned experience. The concept of matching has a long history of use in models of orienting and attention systems (Hebb, 1946; Sokolov, 1963; Bernstein, 1969; Velden, 1978). The term 'central specifications' comes from Andrew's (1976) reformulation of the term 'recognition units' (Treisman, 1960; Kahneman, 1973). A recognition unit is one of a population of central mechanisms each of which corresponds to a particular category of stimulus, in the sense that activation of the unit must occur before responses normally evoked by that category of stimulus are evoked by its presentation (Treisman, 1960; Andrew, 1976). That is to say, when a given activation threshold is reached, if there is a correct match, the animal will show consummatory and/or trained behaviour. If there is a mismatch the animal may disengage or retreat from the situation. It is suggested that it is this activation that has been affected by the anterior group. The threshold for a unit to be activated by an input has been changed. This threshold is reminiscent of the criterion value that signal detection theory has suggested must be exceeded for activation to ensue (Green and Swets, 1966).

The selection of stimuli affects the recognition process. There are rules for the selection of stimuli. Only a limited number of aspects of a stimulus complex go through to the matching process. A number of characteristics may have to be used of which no single one is sufficient by itself (cf. response set, Broadbent, 1970). It is suggested that this selection process has been impaired more in the posterior than in the anterior group as they approached and searched after more test stimuli than the controls. The impaired selection occurred at the level of fine call structure and was not a gross sensory deficit, for the iambus was not mistaken for a trill.

Conclusions

The results reported here support and extend the concept of a hierarchy for anatomical and functional specialisation for central auditory analysis (Scheich, 1977) that progresses from the sensory projections to Field L into the neighbouring hyperstriatum/parahippocampus for selection. This may extend to more anterior hyperstriatum for matching.

It may be significant that the posterior group received damage both to part of the auditory projection field and to the closely connected hyperstriatum. Units in the neostriatum bordering the hyperstriatum respond to species-specific calls (Bonke et al., 1979). This lesion will also have disrupted the infundibular connection to the parahippocampus (Benowitz and Karten, 1976). Kelley and Nottebohm (1978) have shown with autoradiographic methods that in the canary there may be connection from Field L to the overlying parahippocampus that projects forward to the anterior hyperstriatum. Although they thought that this labelling may have been due to isotope leakage, injections into the parahippocampus confirmed the postero-anterior connections. However, Field L does project to the hyperstriatum ventrale and a superficial dorsal area at the edge of the hyperstriatum (Zaretsky, 1978; Bonke et al., 1979).

The present study extends earlier work on the role of avian forebrain lesions in attention-related processes. It shows that areas potentially analogous to mammalian limbic structures are involved with the use of visual and auditory inputs. Having been trained to respond to one specific stimulus, birds with damage to the hyperstriatum/hippocampus anterior and posterior to the anterior commissure showed more search-related behaviour than controls after stimuli that varied from the trained stimulus. The anterior and posterior groups differed from each other in two principle respects. The anterior group reacted positively to the new stimulus and then disengaged rapidly (more low tension). The posterior group continued to approach more stimuli and after searching remained aroused (more high tension).

The finding of two neighbouring and connected brain regions with complementary functions in an attention system is not unique. Anterior and posterior inferotemporal lesions in monkeys impair the processes of retrieval and categorisation of information, respectively (Sahgal and Iversen, 1978). Also the closely bound hippocampus and septum of the rat mirror each other in some situations. Lesion of the hippocampus appears to impair the exclusion of redundant information in a conditioned association paradigm (Rickert et al., 1978), whereas septal lesions (Donovick et al., 1978) impair the ability to use redundant information provided to solve a maze problem (cf. discussion, Oades, 1979).

I should emphasise that the analysis of the observed behaviour of the Guinea fowl has led to the proposal of an hypothesis for the functional components of an avian attention system, but these components have received no direct test. Direct testing should involve interruption of input channels (e.g.

unilateral lesion of receptor or auditory pathways), repression of hypothetical central specifications (e.g. by cycloheximide and related drugs) and control of the individual's experience of specific sensory stimuli. Such testing should naturally include blind procedures for recording and analysis. Closer analogies with mammalian studies of the limbic system must await more detailed anatomical work. In the meantime the detailed analysis of behavioural components such as movement, search, and posture-tension have been shown to be useful tools for dissecting the possible role(s) of parts of the central nervous system in attention-related processes.

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