

Persistence of the Pattern of Feeding in Chicks with Hyperstriatal Lesions

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Abstract. Chicks with dorsal midline hyperstriatal lesions (DMHA) were trained to prefer red to yellow food before being presented with a choice from a plain floor (experiment 1) or a pebble-encrusted floor (experiment 2). On both tests DMHAs showed a relatively stable pattern of choice compared to controls. In experiment 1, controls decreased their intake of non-preferred yellow food on day 1, but this sharply increased on subsequent tests. In experiment 2, controls increased the number of pebbles pecked, and thus, the length of a run of pecks on non-preferred food changed with respect to DMHAs. Chicks with more lateral lesions gave patterns distinct from controls and DMHAs showing an initial disruption of the trained preference. The choice of chicks with more ventral or posterior lesions could not be distinguished from controls. The lack of lability of the trained feeding behaviour of DMHA-lesioned chicks is interpreted as consistent with the suggestion that the DMHA may have functions which are similar to the 'hippocampus' of mammals.

Introduction

A continuation of the feeding responses to the preferred (by training) of two coloured foods from the home cage floor has been shown for chicks injected with testosterone in comparison with the responses of oil-injected controls [ROGERS, 1971; ANDREW, 1972a, b]. ROGERS [1971] stated that 'Once a male chick treated with testosterone begins to respond to a given stimulus, it will persist in responding to the same sti-

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mulus for longer than will a control chick, and it will be less easily distracted by other perceptual inputs'.

OADES [1976] has reported that chicks with dorsal midline hyperstriatal lesions (DMHA) continued to run to drink in a shocked passive avoidance situation in contrast to control birds which learned to withhold the trained running response. DMHAs were also unable to withhold responding on a DRL 10 schedule after food reward to the same extent as controls and were less distracted by novel stimuli in a runway task than control birds [OADES, 1976]. In these situations DMHA chicks were described as continuing with the trained pattern of behaviour for longer than sham-operated birds. The DMHA includes *part* of the area which has been described as hippocampal in an anatomical context [VAN TIENHOVEN and JUHASZ, 1962] and is close to or part of the area for which a 'limbic' function has been suggested [KARTEN *et al.*, 1973].

For a parallel between the behaviour of DMHA chicks [OADES, 1976] and hippocampal rats in a passive avoidance [ISAACSON and WICKELGREN, 1962] and in a distractibility runway [WICKELGREN and ISAACSON, 1963] to be supported, the hypothesis should predict the effects of DMHA lesions on the choice behaviour of chicks. A situation in which a choice from two coloured foods available over the floor of the home cage approaches one which chicks would encounter in a more natural context. DMHA chicks would be expected to persist in selecting and responding to the preferred colour by training and to be less distracted by irrelevant pebbles stuck to the floor, as has been described for testosterone-injected chicks (Ts) [ANDREW and ROGERS, 1972].

In this food choice situation a food-deprived chick is introduced to a floor where there is an array of food grains of two different colours. From training one colour is preferred, but both will be accepted as food. An analysis of the order in which the coloured grains are pecked provides a method for describing the nature of the pattern of responding of the chick. This test has the advantage of providing a number of targets as would be encountered in the natural situation, and a floor on which the length of a sequence of pecks on one colour indicates the ability of a chick to avoid switches of attention to distracting stimuli. It is useful that there is a choice between food grains, in that this provides two stimuli of similar food value and familiarity which differ largely according to colour.

In the first experiment two choice tests were performed on 3 successive days, as it was expected that the birds with lesions would show a

more stable pattern of choice over successive tests (persistence of the trained pattern of responding), whereas controls would change. In this 'priming' situation DMHA and control chicks were given brief exposures to one colour of food on a plain floor to test the potentially biasing effect on the pattern of responses to red and yellow food on the succeeding food choice test. This experimental situation attempts to test the degree of persistence shown by chicks, when 50 pecks of one colour of food are obtained immediately before the food choice is made available. These tests were carried out over a period of 3 days to see if longer overnight exposure to the non-preferred food might exert a stronger effect. During the course of these tests both groups tended to peck more of the originally non-preferred food, but the effect was much more pronounced in controls. The most pronounced differences were found on the 3rd day of testing.

In the second experiment pre- and post-operative tests were conducted on a pebble floor [ANDREW and ROGERS, 1972]. An increased persistence of feeding responses includes decreased distractibility by irrelevant stimuli, coupled with an increased ability to sustain attention on a particular localised stimulus. This increased persistence of search for a particular type of food is most easily seen when a test floor, which is covered with distracting stimuli (glued-down pebbles of approximately the same size and appearance as food grains), is used. DMHAs showed a lack of distractibility relative to controls by not pecking as many pebbles, and they showed a more stable pattern of responding in comparison with controls which changed their feeding pattern (mean run length).

Preliminary data are also presented to show that lesions more lateral or posterior to the DMHA result in different effects on the feeding pattern.

Materials and Methods

General Procedure

Male domestic fowl chicks (Warren sex-link, Southdown, Uckfield, England) were individually housed in cages 21×21×30 cm high. The home cage consisted of three aluminium sides covered with brown paper to avoid reflection. The fourth side was made of perspex to permit observation. The cages were illuminated continuously by a 40 W bulb from above. The temperature was maintained at 27±2 °C. Water was continuously available in a small perspex dish and food was scattered over the floor of the cage which was covered by a white absorbent paper towel.

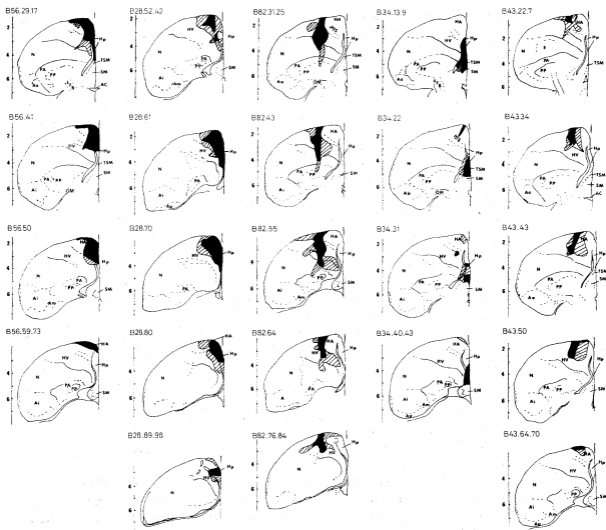


Fig. 1. 4-5 diagrams are shown in vertical columns to show the unilateral (hatched) and bilateral (shaded) extent of the five types of lesions to the brain of the chick discussed in the text. The diagram of the anterior transverse section is at the top of each column. Code and lesion method see text.

DMHA (B56). This group shows damage to extend 2.3-3.3 mm between the planes of the anterior (AC) and the posterior commissure. The lesion principally involves the DMHA and 'hippocampus' (Hp) with slight damage to the other hyperstriatal areas toward the midline (e.g. hyperstriatum ventrale, HV). Aa = Archistriatum anterior, Ai = archistriatum intermedium, Am = archistriatum mediale, HA = hyperstriatum accessorium, HIS = hyperstriatum intercalatum superior, LFB = lateral forebrain bundle, N = neostriatum, OM = occipito-mesencephalic tract, PA = paleostriatum augmentatum, PP = paleostriatum primitivum, SM = medial septum. **Posterior DMHA (B28).** Damage extends 1.9-2.9 mm starting pos-

The chicks were operated on day 10 of life. Details of the modified mouse-stereotaxic instrument, the electrodes, the anaesthesia and histological procedures have been given in ANDREW [1973] and ANDREW and OADES [1973].

Lesions

The DMHA and dorso-lateral hyperstriatum (DLH) chicks received lesions by aspiration. Suction was created by water running from a tap through a T tube and applied to the surface of the brain through a fine glass pipette. The size of the lesion was approximately determined in the horizontal plane by pricks delivered to the skull with a needle in the electrode implanter of the stereotaxic apparatus. The depth of the lesion was gauged with reference to a mark 5 mm from the tip of the pipette. The suction in the pipette was monitored during the operation by dipping it into a nearby beaker of water. After operation surface blood was removed with a small piece of absorbent paper, and the skin was stitched with a surgical needle and thread.

The antero-posterior (A/P) coordinates used on the stereotaxic apparatus were as follows: DMHA 15–18 mm A/P, 1 mm lateral to midline, 4 mm deep; posterior DMHA 14–16 mm A/P, 1 mm lateral to midline, 4 mm deep; and DLH 15–18 mm A/P, 2 mm lateral to midline, 4 mm deep.

Bilateral electrolytic brain lesions were made by a constant current generator delivering 0.1 mA for 20 sec with bipolar electrodes. These lesions were intended to cut the tractus septomesencephalicus (TSM) in the ventral hippocampus. The following coordinates were used: TSM 15.35–16.35, in the midline, 4.8 mm deep.

Superficial hyperstriatal cuts were performed with a scalpel blade in the A/P planes of the DMHA with the intention of cutting any connecting fibres between the lateral and midline hyperstriatum. The coordinates were as follows: cut in the lateral hyperstriatum (cut-HA) 15–18 mm A/P, 5 mm lateral to midline, depth superficial (c 1.5 mm).

All control birds were sham-operated. A sham operation consisted of the delivery of the anaesthetic and an incision to the skull, skin and dura. All operated birds were given a minimum period of 24 h recovery prior to exposure to the test situation. The planes in which sections (12 μ m thick) of the brain were cut for histological examination were designed to coincide with those represented in ANDREW'S

terior to the plane of the AC and disappearing posterior to the plane of the posterior commissure (maximum between the pallial and posterior commissure). The DMHA, 'hippocampus' and midline HV show damage as in B56. Ap = Archistriatum posterior. DLH (B82). Damage is located in the lateral-medial HA extending ventrally to the HV and posteriorly for 2.6–3.4 mm in the planes of the DMHA lesion, but leaving the 'hippocampus' intact. TSM (B34). Damage is restricted to the 'hippocampus', usually between the planes of the AC and pallial commissure (occasionally to the posterior commissure). There is very slight neostriatal and hyperstriatal involvement in a few birds. Damage extends 1.7–2.9 mm. Cut-HA (B43). Damage is restricted to the HA dorsal and lateral to the ventricles. It starts near the plane of the AC or pallial commissure and extends posteriorly for about 2.5 mm. E = Ectostriatum.

stereotaxic atlas for the brain of the young chick [ANDREW, 1973; ANDREW and OADES, 1973]. All the slides were examined for the absence of tissue, tissue collapse and degeneration of the TSM and tractus occipitomesencephalicus. No chick showed bilateral degeneration of the occipito-mesencephalic tract.

Each individual bird was numbered (and received a letter prefix, e.g. B61). For representative birds the diagrams (fig. 1) are arranged vertically with the anterior plane shown first at the top of each column. Each diagram of a section has a second figure following the code for the individual bird. This number refers to the slide (in the series which was cut for each bird) from which the diagram was taken. The first and last diagrams for each bird may have an additional figure which represents the first (anterior) and last (posterior) slide in the series where histological damage was recorded. This allows for the length of the lesion to be calculated in the A/P axis (4 sections/slide). A figure elsewhere in the diagram refers to the reference section in the stereotaxic atlas.

Experimental Procedure

Red and yellow foods were soaked, dyed and dried according to the method described by ANDREW [1972a]. The floor of the home cage (which was also the test cage) was laid with clean absorbent paper every day and before testing.

In experiment 1, all birds were maintained on red food from day 1 until day 10. That yellow food was accepted at all on testing may to some extent be attributable to the presence of some partly dyed grains (yellow grains had been removed) and other grains which had cracked, displaying some yellow facets inside. The feeding behaviour of 18 DMHAs (B62-B81) with 21 controls and 7 DLHs (B82-B90) with 10 controls were considered. Each test consisted of the presentation of a clear perspex floor over which were evenly spread 200 grains of red and 200 grains of yellow food. This food choice was presented once in the morning and once in the afternoon for up to 3 days in succession to each chick. Immediately prior to each test a 'priming' floor with only one food colour was presented to each chick. The colour of the priming food was red before the morning test and yellow before the afternoon test. 50 pecks were recorded from the priming floor to test the stability of the search behaviour, shown by the pecking responses on the choice floor in the short term. 100 pecks were recorded in the choice situation. ROGERS [1971] made a computer simulation of this situation to investigate the effect of the removal of the coloured grains in varying proportions on the distribution and availability of these colours. She showed that a run of pecks on a single colour up to 100 out of 400 red and yellow grains from random locations on the floor of the home cage would not significantly alter the proportions available. The stability of the pattern of responding after longer experience of yellow, non-preferred food was tested over the period of 3 days, with yellow food experience in the intervening overnight periods (about 14 h/night).

In both experiment 1 and 2 all chicks had been deprived of food for a period of 4 h prior to testing. The colour of the food toward which each chick directed most pecks (yellow or red) was termed preferred and the other non-preferred. All chicks showed a red preference on the first test. Preferred food may be assumed to be red unless otherwise stated. ROGERS [personal commun.] and the present author found that the mean run length of pecks (MRL) on non-preferred

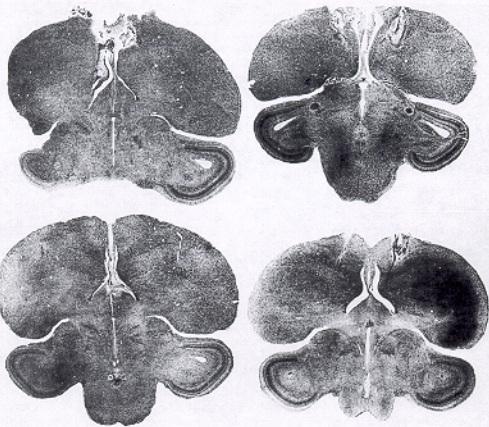


Fig. 2. These photomicrographs show representative transverse sections of the chick brain in planes showing the maximum extent of the four following types of lesion. *a* DMHA; the dorsal 'hippocampus' and about $\frac{1}{3}$ of the HA are absent toward the midline. More extensive HV damage is largely unilateral in this oblique section. *b* DLH; from the disrupted lateral quarter of the HA damage descends ventrally into the HV. The midline structures remain intact. This picture shows damage slightly posterior to the usual plane of DLH damage (similar to DMHA). *c* TSM; most damage is sustained by the ventral 'hippocampus' and dorsal midline septum. *d* cut-HA; up to $\frac{1}{4}$ of the lateral HA is disrupted bilaterally. Damage extends ventrally just into the HV.

food was the more sensitive measure of a change in the number of pecks. The mean was used to characterise each individual, since a figure sensitive to a single long run or a number of very short runs of pecks is needed.

In experiment 2, chicks were maintained on red food for 8 days, and on day 9 they had experience of yellow food for 4-5 h. The following groups were tested: 16 DMHAs (B28-B33, B52-B61) with 21 controls, 9 TSMs (B34-B42) with 9 controls and 9 cut-HAs (B43-B51) with 8 controls. The test floor consisted of a piece of clear perspex on which small stones were cemented and over which red and yellow foods were evenly spread. The stones were coloured similar to the food by the method used by ANDREW [1972a]. The chicks were exposed to the test floor with coloured foods for 5 min on day 9. All birds were tested on the pebble floor once before and once after operation. As in experiment 1, 100 pecks were recorded on an Esterlyne Angus pen recorder. Observation was carried out at close quarters at the level of the home cage floor so that all the targets could be seen clearly.

The following three categories of chicks were not considered: chicks which did not show 50 pecks on priming, those which did not show an initial red preference, and those DMHAs which showed only slight or restricted damage to the midline structures.

Statistics

All statistical comparisons were between groups of scores, one from each individual involved for each experimental test. Two-tailed Mann-Whitney rank tests [SIGEL, 1956] were applied unless otherwise stated, since data were either non-parametric or far from normal in distribution. In the tables presented the asterisks and stars which are used to indicate significant differences appear twice in each table to clearly show the two figures which are compared.

Results

Experiment

DMHAs

A difference in the MRL of yellow non-preferred food is found between DMHAs and controls between the first two tests on day 1. Significantly more controls decrease their MRL on non-preferred food with respect to DMHAs ($0.002 < p < 0.02$, table I). After a night when only yellow food was available in the home cage, the change of MRL on yellow, non-preferred food between the preceding afternoon's yellow prime test and the red prime test the next morning moves in the opposite direction. Controls now show a longer MRL on yellow, non-preferred food than DMHAs ($0.025 < p < 0.05$, table I). The MRLs (non-preferred food) of controls on the yellow prime test are significantly lower than the MRLs on the red prime test, day 1 ($p < 0.01$, Wilcoxon matched pairs test). The increase of MRL on yellow, non-preferred food which occurs across

Table 1. Influence of priming as measured by MRL yellow and yellow pecks in the first ten feeding responses from a plain floor

Birds	Day 1 red prime		Day 1 yellow prime		Day 2 red prime	
	MRL yellow	yellow pecks in 10	MRL yellow	yellow pecks in 10	MRL yellow	yellow pecks in 10
DMHAs	2.0±0.5	2.0±1.0	2.0±0.6 change 0* (MRL) change 0*** (yellow pecks)	2.0±1.2	2.0±0.8 change 0** (MRL) change +1.0 (yellow pecks)	3.0±1.6
Controls	2.0±0.6	4.0±1.5	1.0±0.5 change -0.95* (MRL) change -2.0*** (yellow pecks)	2.0±1.2	2.0±0.3 change +1.0** (MRL) change 0*** (yellow pecks)	2.0±1.6

The median MRL on yellow food and the median number of yellow pecks made in the first ten feeding responses (with SD) are recorded from a plain floor food choice test of red and yellow foods presented to DMHA and control chicks. The first food choice test was preceded by 50 pecks on red food, the second test by 50 pecks on yellow food and the third test (day 2) by 50 pecks on red food again. The data are derived from 13 DMHAs and 16 controls on day 1 and 11 DMHAs and 15 controls on day 2. Data from birds which did not record 50 pecks on the priming presentations are not included.

* $0.002 < p < 0.02$; ** $0.025 < p < 0.05$; *** $p = 0.05$.

Two similar symbols show the two figures compared.

a night of yellow food is also significant ($p < 0.01$). There are no significant changes of MRL for DMHAs over these tests.

The strongest effect of the priming exposure on chicks is likely to be seen in the first ten pecks of the choice tests. Table 1 shows the changes in the number of yellow pecks in the first ten responses. On day 1, controls show a significant decrease between red and yellow prime tests ($p = 0.05$), whilst the DMHAs by comparison make a similar number of yellow pecks on both tests. However, after the longer experience of yellow food overnight no significant differences for either group appear on the red prime test, day 2. (It should be noted that controls are giving higher yellow, non-preferred food scores – non-significant – than DMHAs on the first red prime test, day 1. Thus, it is the size of the decrease in the number of yellow pecks between tests by which controls differ from DMHAs).

It is important to emphasise that there are no significant differences in the percentage of yellow food pecked by DMHAs or controls on each

Table II. Percentage of yellow food taken on a plain floor

Birds	Food choice day 1		Food choice day 3 yellow prime
	red prime	yellow prime	
DMHAs	19.9±8.4	19.0±9.3	48.3±15.2*
Controls	24.5±11.8	18.4±14.8	66.0±15.6
DLHs	32.2±6.3**	39.6±16.8***	54.8±13.6
Controls	13.1±5.8**	13.3±8.4***	46.6±18.8

The mean percentages (with SD) of yellow non-preferred food taken on post-operative food choice tests on a plain floor are recorded. The data are taken from tests conducted on day 1 and 3 on separate batches of chicks. The first food choice test on each day was preceded by 50 pecks on red preferred food, the second test by 50 pecks on yellow, non-preferred food. All choice tests were from red and yellow food. The first batch of chicks contained 18 DMHAs and 21 controls, the second 7 DLHs and 10 controls. DMHAs do not differ from controls until day 3, when controls take a significantly higher proportion of yellow food. DLHs take a higher percentage of yellow food than controls when tested on day 1.

* $p=0.002$; ** $p=0.05$; *** $0.025 < p < 0.05$.

Two similar symbols show the two figures compared.

of the first three priming tests (which were conducted on days 1 and 2 of testing). Priming exposures have influences on the MRLs of controls on these early tests, but the measures of the percentage of yellow food taken have not changed significantly. Thus, if a chick is able to modify its pattern of search or response for coloured foods as a result of a limited priming exposure to yellow food (non-preferred training) then further experience should increase this tendency. Thus, 7 DMHAs and 10 controls were given a second night's experience of yellow, non-preferred food also for the reason that controls showed a non-significant increase in the percentage of yellow food taken on day 2 and that the influence of priming on the first ten responses may have been masked by overnight yellow food experience between day 1 and 2.

The MRL on yellow food tends to increase for controls with respect to DMHAs ($p < 0.1$, day 2) as the MRL on red food decreases ($p < 0.1$, day 2). Indeed many controls are starting to change their preference to yellow food. On the yellow prime test, day 3, 2 of 10 controls and 4 of 7 DMHAs are still maintaining a red preference. DMHAs seem to show a

decrement compared to controls in their ability to change preference which is shown by a very significant difference in the percentage of yellow food taken ($p = 0.002$, table II). This suggests that a degree of learning by controls has occurred which is in addition to earlier changes of their patterns of responding (day 1). It is emphasised that differences in the percentages of food taken differ between DMHAs and controls only on day 3 of testing.

DLHs

These show an immediate difference from controls (and the DMHAs reported above) on their first choice test. They take a significantly higher percentage of yellow, non-preferred food ($p = 0.05$, table II) on the first red prime test and on the yellow prime test on day 1 ($0.025 < p < 0.05$). These differences obscure any influence which the priming may have on initial pecking. It would seem that as well as taking a higher percentage of yellow food than either DMHAs or controls (or Ts) [unpublished data] that the pattern of feeding responses may also differ. Thus, there are no significant differences between DLHs and controls, according to the measures of MRL yellow or MRL red food on the two priming tests on day 1. However, yellow is still the non-preferred colour on day 1, but to show that DLHs are still capable of showing runs of pecks on both colours of food and not pecking at random, responding was analysed in terms of sequences of ten pecks on the same food colour (table III). DLHs show more sequences of ten pecks on yellow, non-preferred food than controls on day 1 ($0.001 < p < 0.01$, χ^2 test.)

Following day 1 there is a continued and striking increase in the amount of yellow food which DLHs accept. For many DLHs yellow food becomes preferred food by day 3. Compared with controls they increase the percentage of yellow food pecked markedly on day 2 (red to yellow prime test, $p = 0.05$) and slightly on day 3 (red to yellow prime test, $p = 0.1$).

Experiment 2

DMHAs

In this experiment all birds were tested on a pebble floor, once before and once after operation. All birds had a red food preference ($\geq 50\%$) on the first test. It was stated that one of the advantages of this food choice test from a floor is that it provides a measure of the ability

Table III. Feeding responses on day 1, measured by MRL yellow and the number of sequences of ten yellow pecks

Birds	Food choice test, day 1			
	red prime		yellow prime	
	MRL yellow	sequences of ten yellow pecks	MRL yellow	sequences of ten yellow pecks
DLHs	2.3 ± 0.7	0.6*	3.5 ± 0.6	0.9*
Controls	2.0 ± 0.5	0*	1.0 ± 0.6	0*

The median MRL on yellow, non-preferred food (with SD) and the mean number of sequences of consecutive responses to yellow, non-preferred food shown by 7 DLHs and 10 controls on two plain floor food choice tests are recorded. The tests were preceded by 50 priming pecks on red and yellow food, respectively. There are no significant differences between the MRLs. However, DLHs do show more sequences of ten pecks on yellow food than controls which may be taken to show that the feeding responses of DLHs are patterned rather than random.

* $0.001 < p < 0.01$ χ^2 test. Two similar symbols show the two figures compared.

of the chick to avoid responding to other features of its environment. Some of these features in this situation are pebbles.

It was predicted that DMHAs would not be expected to peck more pebbles postoperatively, whereas controls would tend to be relatively more distracted showing more variable and exploratory responses. Controls show a significant increase in the number of pebbles they peck on the second test (6.8 ± 3.3) compared to the first test (3.2 ± 2.1 , $p = 0.05$, 1-tail test). By contrast DMHAs show less variability and do not show a marked increase on the second test (4.7 ± 1.8) of pebble pecks. This resembles a report [ANDREW and ROGERS, 1972] that controls significantly increased the percentage of pecks which they directed at pebbles in comparison with Ts on the post-injection test. The Ts show no significant increase in the percentage of pecks given to pebbles. It seems that the birds (DMHAs and Ts), which are alleged to be showing a persistence in their pattern of feeding responses, do not increase the number of pebbles pecked, whereas controls do increase the percentage of pecks which are delivered at pebbles.

The stability of the trained pattern of feeding responses of DMHAs as measured by the MRL is maintained postoperatively on a pebble floor (table IV) as well as on the plain floor (experiment 1). This is also

Table IV. MRL yellow, non-preferred food on a pebble floor

Birds	Pre-operative test	Post-operative test
Controls	2.15 ± 0.5	1.7 ± 0.3*
DMHAs	3.0 ± 0.4	3.05 ± 0.5*
Posterior DMHAs	2.55 ± 0.4	2.45 ± 0.4
Controls	1.4 ± 0.2	1.85 ± 0.7
TSMs	1.7 ± 0.2	1.7 ± 0.5
Cut-HAs	2.0 ± 0.6	3.0 ± 0.5

The MRL on yellow, non-preferred food (and SD) are recorded on a food choice test between red and yellow foods from a pebble-encrusted floor pre- and post-operatively from the following batches of chicks: controls 9; DMHAs 10; posterior DMHAs 6; controls 8; TSMs 9, and cut-HAs 9. All birds had been trained to prefer red food but also to accept yellow food. They were deprived of food for 4 h before test. Tests were given on day 10 and 11 of life. Red food was provided overnight. DMHAs maintain an MRL on non-preferred food at a more stable level than controls. This level is higher than controls in the experiments cited. The data from TSMs and cut-HAs do not differ significantly from control data, but the former remain stable like the DMHAs, whereas the latter tend to increase in a manner reminiscent of DLHs.

* $0.002 < p < 0.02$. Two similar symbols show the two figures compared.

true for the 'posterior DMHAs' where the lesioned area extends posteriorly (from the planes where the septum end) in the dorsal midline towards the plane of the posterior commissure (fig. 1). However, the posterior planes of damage in these birds overlap with an area which, if lesioned, results in distractible behaviour in a runway like controls [OADES, 1976]. Thus, this 'posterior DMHA' group of chicks shows damage which crosses the posterior limit of the DMHA.

The stability of the scores of the DMHAs (which are seen by both the measures of MRL as well as percentage) allow the more variable controls to show a level of responding which differs significantly post-operatively ($0.002 < p < 0.02$, table IV). The performance of DMHAs on a pebble floor food choice test is thus consistent with that on a plain floor.

TSMs and Cut-HAs

In table IV a comparison of MRL yellow, non-preferred food for TSMs and cut-HAs may be seen. There are no significant differences between these or other measures attempted.

In both groups the hyperstriatum accessorium received only slight damage. In the TSMs this was largely brought about by the lowering of the electrodes. In the cut-HAs a short longitudinal bilateral cut was made with a scalpel blade which would have interrupted superficial fibre tracts that may run towards the midline. The difference of the lesions lies with the moderate damage sustained in the 'hippocampus' by the TSMs. In the cut-HAs this structure is mostly intact.

The TSMs give pre- and post-operative scores similar to DMHAs (stable); however, they do not show any changes in the number of pebbles pecked. In other experiments reporting the behaviour of DMHAs [OADES, 1976] there has been no correlation of the DMHA deficit with damage to the TSM. Therefore, it seems reasonable to regard the present TSM birds as a control population despite some similarities with DMHA behaviour. The sham-operated controls show slight decrease (of MRL and percentage yellow food), but cut-HAs show a slight increase of both of these measures. As this result on a pebble floor is unlike the behaviour of DMHAs (or Ts) [ROGERS, 1971] the longest run on yellow, non-preferred food was investigated to see if the means were being skewed in this way by continued responding to non-preferred food after a switch from preferred food. Cut-HAs show a significant increase for the longest run on yellow, non-preferred food (9.0 ± 1.6) compared with their pre-operative score (5.0 ± 1.3 , $p = 0.035$, sign test). Controls do not show a similar increase in the mean length of the longest run, but do increase their variability as would be expected (2.0 ± 0.8 to 3.0 ± 2.6). The lesion damage of cut-HAs is lateral in the hyperstriatum similar to but less extensive than the DLHs. These results are also suggestively similar to those obtained from DLHs on the plain floor.

Discussion

The behaviour of the DMHAs show two factors. The first is that their behaviour would change. The second is that the change of behaviour would occur significantly slower than for controls (and for most birds lesioned in other sites). DMHAs can distinguish and respond to the changes. It is their ability to change which shows a deficit.

No behavioural study involving avian hyperstriatal lesions has reported major visual deficits [HODOS *et al.*, 1973; BENOWITZ, 1972; STETTNER and SCHULTZ, 1967; MCPHAIL, 1971], although some pattern

vision may be involved with the thalamofugal projection area [PRITZ *et al.*, 1970; MAIER, personal commun.].

In experiment 1 there are no significant differences between DMHAs' MRL on yellow, non-preferred food after short (priming), and longer term (overnight) experience of yellow food. This is in marked contrast to the controls which showed (i) a decrease after priming (day 1, yellow prime) and (ii) a longer term increase (day 2-3) in MRL yellow on a plain floor. In similar situations controls are reported to significantly increase their MRL yellow food on the yellow prime test, day 1 [ROGERS, 1971], in contrast to (i) and to continue to increase on day 2 [ANDREW and ROGERS, 1972] which supports (ii). On days 2 and 3, DMHAs tend to accept more yellow food than on day 1, but this is very much less than the amount that controls will accept (MRL and percentage yellow food).

In summary, on day 1, controls are shifting their responses towards preferred food, away from the colour of the food used in priming. This apparently paradoxical effect has been found before [ANDREW, 1972b]. On days 2 and 3 the effect of priming is masked by the greater influence of the colour of the food experienced overnight. Controls are shifting their responses away from the preferred food (by training exposure) toward the colour to which they have been most recently exposed. These events show some similarity (DMHAs not reversing their preference) with an extinction presented in an operant conditioning situation by BENOWITZ and LEE-TENG [1973]. They found that chicks with ablations of the dorso-medial hyperstriatum were able to retain a pre-operatively acquired discrimination, but were impaired in the subsequent reversal.

Considering the influence on intact chicks of the priming and overnight exposures to yellow, non-preferred food, experiment 1 demonstrates firstly, the influence of the sensory experiences and secondly, the change of a pattern of responding. On these plain floor food choice tests controls change their MRLs over the first three tests (percentage steady), then they change according to both measures (increase) over the next three tests. The priming or overnight exposures to yellow food could influence the feeding pattern by affecting the central rules for selection or the tests for matching the food seen with the characteristics of the food remembered.

Considering in particular the change of MRL on non-preferred, yellow food on day 1, the decrease shown by controls may reflect the observation of ROGERS [1971] that birds, which did not eat yellow food on

the priming experience, avoided yellow food more in the following test. She observed that this effect would last for the next 2 days. Only two birds from the present study showed such a lasting effect. Thus, it is possible to suggest (as above) that the central criteria for matching the food seen with the food remembered, may become stricter after repeated examination of yellow, non-preferred food in the priming situation. Similar results have been found for some Ts [ANDREW, personal commun.; 1972b]. On the longer overnight exposures controls have to feed on yellow food to avoid near starvation. Yellow food is palatable, and they have accordingly altered the relative values they have learned to ascribe to red and yellow food. They will now peck a greater proportion of yellow, non-preferred food (this is supported by a lack of difference between DMHAs and controls on the measure of the first ten pecks after the red priming on day 2).

In view of the influence of the experimental regime on the behaviour of controls lability may be seen as the ability to alter the rules for selection or to make available alternatives to the changes experienced in the external environment. This will affect the likelihood of a change of the pattern of responding to all environmental stimuli in the short (priming) and long (overnight) term. Thus for example, after a DMHA lesion, a chick which sees a yellow, non-preferred food grain is as likely to peck it as it was prior to the operation. Controls may change the proportion of yellow food pecked, depending on the details of the individual's experience during and between tests. Considering chicks with DMHA lesions, the feeding patterns do appear less labile and less sensitive to changing experience. They show stable measures of MRL and percentage of yellow, non-preferred food on the first three tests on the plain floor, and only slowly increase the amount of yellow food taken during the second three tests.

More marked are the changes of feeding pattern which occur by day 3 after 2 nights of yellow food when many controls (in contrast to DMHAs) have changed their preferred food to yellow. Intact birds seem to modify or change their description of food features after a long period of exposure (e.g., 2 nights, 28 h) to a new stimulus or environment which is long enough for some learning about the new features to occur. It takes longer for DMHAs to change their pattern of responding as much as controls. This is most easily accounted for by the same deficit as was shown in the earlier tests by DMHAs - that they cannot withhold the trained/learned patterns as well as intact chicks.

In common with the cut-HAs of experiment 2, DLHs take more yellow food on the first food choice after operation. This effect is much more marked for DLHs with their more extensive lesions than for the cut-HAs. The DLHs were tested on a plain floor, the cut-HAs on a pebble floor, but no other groups of brain damaged, control (or Ts) take more yellow food on the first priming test on a plain floor or on the pebble floor test after operation/injection.

The results appear to show that DLHs have difficulty in retaining the preoperatively acquired discrimination. BENOWITZ [1972] reports a result which may be similar to the effects observed for the DLHs. He described the retention of a task (methanthranilate avoidance) to be impaired by lesions, extending far laterally from the midline dorsal hyperstriatum of chicks.

On the evidence of the cut-HAs lateral damage does not appear to make chicks more distractible on the pebble floor test. DLHs are as successful as all other chicks at pecking food. They also show runs of pecks on red and yellow food. DLHs are unlikely, therefore, to have a sensorimotor deficit. But an increased responsiveness to yellow food cannot be completely excluded.

In experiment 2, controls became more distracted by pebbles and responded more to pebbles on the second test. Associated with this change was an increased variability of response. In contrast DMHAs pecked a similar number of pebbles before and after operation which also suggests that the 'central mechanism', which allows pebbles to be pecked, has not been directly altered by the lesion. This result also contributes to the evidence against a visual deficit being the cause of the difference in the pecking behaviour of the DMHA and control groups.

From the distractibility hypothesis it might be expected that controls would make shorter runs on one colour of food from the pebble floor, but at the same time make more of them. However, this does not seem to occur in the present case, for the percentages of the foods taken follows the measures according to MRL. It has already been argued that the MRL on non-preferred, yellow food is the most sensitive measure of the pattern of search in the food choice situation. The pattern of search thus measured is able to change without the measures of the percentage of preferred or non-preferred food taken, changing. Thus for example, the MRL on non-preferred food may decrease in length, but increase in frequency. Over 100 pecks the percentage of non-preferred food taken may remain stable; only when the change of the MRL is sufficiently

Birds	Food choice pebble floor	TSM degeneration				Hyperstriatum ventrale degeneration				Behavioural score post-operative MRL yellow
		severe	moderate	slight	intact	severe	moderate	slight	intact	
<i>DMHAs</i>										
B55		*						*		3.1
B56		*						*		3.0
B58		*						*		3.4
B52			+					*		1.3
B53			+					*		2.3
B57			+						*	3.2
B59				+					*	2.7
B60				+				*		5.3
B54					*			*		2.8
	plain floor									MRL yellow (yellow prime, day 1)
B74		*						*		0
B75		*						*		0
B76		*						*		10
B77		*						*		5
B78		*						*		2.2
B72		*							*	2.0
B81			*				*			1.0
B80			*					*		2.0
B79			*					*		1.3
B73				+				*		1.8
<i>DLHs</i> plain floor										
B89				*				*		20
B83				*		*				100
B82				*		*				32
B85				*		*				40
B86				*		*				12
B87				*		*				50
B80				*				*		0
B90				*				*		38
B88				*					*	30

The above are estimates for the degree of degeneration of the TSM and hyperstriatum ventrale for a sample of chicks sustaining DMHA and DLH lesions. For each chick one of the scores recorded in the behavioural test is also given. 9 DMHAs from the pebble floor, 10 DMHAs from the plain floor and 9 DLHs from the plain floor food choice tests provide the data for the samples. There is little (e.g. B83) or no evidence to support a correlation between the degree of damage sustained by the TSM nor the hyperstriatum ventrale with the recorded behavioural deficits. * = Degeneration/no degeneration in anterior and posterior planes of the serial sections; + = degeneration restricted to the posterior planes of the serial sections.

large or the frequency does not change, must the percentage of preferred or non-preferred food change. An interpretation which would seem to be consistent with these results is that controls, having been distracted by a pebble, would revert to a grain of the trained preference. Such behaviour has been recorded from Ts [ROGERS, 1971] after a switch of attention between clumps of food grains (containing both colours) and would therefore not be expected to be characteristic of controls in these experiments. However, unpublished data suggest that distraction makes the next colour pecked less predictable for controls than for DMHAs, because some controls may increase their MRL on yellow food on the second test with respect to DMHAs and to their pre-operative levels.

It should be noted here that these measures of feeding behaviour are sensitive to batch differences. This effect has been recorded to a varying extent by other workers. Thus, comparing the groups of controls of ANDREW and ROGERS [1972] and ANDREW [1972a], male groups are found to differ in their MRLs by $\frac{1}{4}$ peck (3.4–3.67) and control females by $1\frac{1}{4}$ pecks (1.2–2.4) on their MRL on non-preferred food.

The small groups of TSMs and cut-HAs reported in this study do not provide evidence that the severing of major pathways to and from the DMHA are responsible for the effects of the DMHA lesion. Further evidence on the potential role of the TSM is given in table V. There is little or no correlation between the proportion of the TSM degenerating after DMHA lesion and the behavioural scores obtained by these birds.

The DMHA lesion may extend laterally to about 1.5 mm from the midline. In the ventral direction damage extends to include the hyperstriatum accessorium, hyperstriatum intercalatum and dorsale at the lateral limit. Some damage to the hyperstriatum ventrale becomes more extensive toward the midline ventricles (but this remains relatively slight with respect to the volume of the hyperstriatum ventrale). Towards the midline slight neostriatal damage occurs in some birds, but this is not regarded as significant. This damage and the removal of the parahippocampus and 'hippocampus' is largely restricted in the A/P axis to that tissue lying dorsal to the septum. Damage starts at or slightly anterior to the plane of the anterior commissure and extends through the plane of the pallial commissure toward but seldom as far as the posterior commissure. The posterior limit to the extent of the active area has been passed by the plane of the posterior commissure.

The ventral limit to the active area has not been thoroughly investigated. It seems that the hyperstriatum ventrale does not have a strong

role in the mechanism discussed [MCPHAIL, 1971] as behavioural deficits depend more on the absence of the dorsomedial areas and not in proportion to the amount of hyperstriatum ventrale damaged (table V). Hyperstriatum ventrale damage was restricted to near the ventricles, more extensive disruption was unilateral.

In the midline, in between the ventricles, the limit is approximately half-way down the 'hippocampus'. Only the dorsal 'hippocampus', close by the dorsal limit of the ventricles, may be participating in the effects of the DMHA lesion. The reason for this is that the ventral limit of the active area is given by the dorsal limit of the TSM lesions. The TSM lesions damaged the ventral and medial 'hippocampus' and dorsal septum. This ventral and medial area may, thus, possibly provide a non-participatory break in the neural substrate between the DMHA and the septum, both of which, if damaged, give rise to behavioural differences from controls [OADES, 1976].

The DLH lesion was produced in an attempt to see how far laterally tissue damage would cause behavioural deficits like the DMHA. The lesion damage occurs in the same A/P coordinates as the DMHA. The lesions removed up to half of the hyperstriatum accessorium (lateral) and a quarter of the hyperstriatum ventrale (midline). The hyperstriatum intercalatum and dorsale show surprisingly slight damage, but no inference can be made on their functional contribution.

Finally, a discussion of this series of experiments should be seen in comparison with areas of potentially similar function in mammals. No direct comparison can be made between the food choice situation and any which have been presented to hippocampal mammals. But the development of preferences and a pattern of responding (to two acceptable foods) may be indirectly compared, in the complexity of choice, to maze learning and probability learning. The low frequency of exploration of novel alleys, whilst hippocampal rats run a multiple maze [MEANS *et al.*, 1971; COHEN, 1970], may be comparable to the low frequency of yellow, non-preferred pecks shown by DMHA chicks. Intact and neocortically lesioned rats, exposed to novel alleys, explore more than those with hippocampal damage. Sham-operated chicks, exposed to yellow, non-preferred food, peck such food more than DMHA chicks and show a greater variance in their responses.

Probability-learning tasks also suggest perhaps that hippocampal damage does not reflect a simple deficit of exploration, predicted by O'KEEFE and DOSTROVSKY [1971], but to the mechanism enabling a

change of the pattern of responding in the presence of a novel stimulus. An integral aspect of a response or learning set is the ability to modify and to change patterns of response. STEVENS and COWEY [1973] report a specific deficit on probability-learning tasks from animals with ventral hippocampal damage. It is tentatively suggested that changes in the sensitivity of intact chicks (compared to DMHAs) to priming with non-preferred food (changed number of yellow pecks during the first ten pecks) may be evidence that DMHAs have suffered damage to the ability to change their behaviour, comparable to that attributed to ventral hippocampal function.

KIMBLE [1968] has discussed evidence supporting a hippocampal role in the generating of internal inhibition. ISAACSON [1974, p. 195] has remarked that animals with 'Hippocampal lesions . . . had trouble moving beyond hypotheses related to the attribute originally guiding behaviour'. Thus, it may be suggested that the lack of lability of the patterns of behaviour of DMHAs in comparison with controls is a result of a deficit in the inhibition of the current behaviour.

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