Proc. Natl. Acad. Sci. USA
Vol. 80, pp. 3860–3864, June 1983
Neurobiology

Acoustic imprinting leads to differential 2-deoxy-D-glucose uptake in the chick forebrain

(ontogeny/plasticity/learning/avian brain)

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Communiated by Theodore H. Bullock, March 21, 1983

ABSTRACT **This report describes experiments in which successful acoustic imprinting correlates with differential uptake of D-2-deoxy[^{14}C]glucose in particular forebrain areas that are not considered primarily auditory. Newly hatched guinea chicks (*Numida meleagris meleagris*) were imprinted by playing 1.8-kHz or 2.5-kHz tone bursts for prolonged periods. Those chicks were considered to be imprinted who approached the imprinting stimulus (emitted from a loudspeaker) and preferred it over a new stimulus in a simultaneous discrimination test. In the 2-deoxy-D-glucose experiment all chicks, imprinted and naive, were exposed to 1.8-kHz tone bursts for 1 hr. As shown by the autoradiographic analysis of the brains, neurons in the 1.8-kHz isofrequency plane of the auditory "cortex" (field L) were activated in all chicks, whether imprinted or not. However, in the most rostral forebrain striking differences were found. Imprinted chicks showed an increased 2-deoxy-D-glucose uptake in three areas, as compared to naive chicks: (*i*) the lateral neostriatum and hyperstriatum ventrale, (*ii*) a medial magnocellular field (medial neostriatum/hyperstriatum ventrale), and (*iii*) the most dorsal layers of the hyperstriatum. Based on these findings we conclude that these areas are involved in the processing of auditory stimuli once they have become meaningful by experience.**

Early experience of young animals with a particular sensory stimulus may have deterministic behavioral consequences. Subsequently, the animal prefers the familiar stimulus over novel ones. Since its first description by Lorenz (1) this phenomenon is known as "imprinting." Its most conspicuous difference from other forms of learning is that imprinting takes place only during a restricted developmental period of life and that the imprinting effect is considerably resistant to other experience [for recent theories see, e.g., Hess (2) and Immelmann *et al.* (3)]. This and particular prerequisites for imprinting to occur (e.g., previous, generalized sensory experience, social conditions, complexity of stimuli, and so on) were in the past extensively studied at the behavioral level. Visual stimuli were used almost exclusively, although for many species auditory stimuli are essential (2). Our own experiments with guinea chicks showed that this species imprints successfully on tone bursts (unpublished data).

Some experimental data are available on underlying substrates of imprinting in the brain (4–10). Yet, propositions concerning biochemical and physiological mechanisms of imprinting are at a preliminary stage. Imprinting supposedly modifies the responsiveness of hitherto undefined neurons to the imprinting stimulus. A useful approach to localize and further investigate such changes at a multiunit level is experiments with D-2-deoxy[^{14}C]glucose (d[^{14}C]Glc). This substance is taken up like glucose by active neurons and, because it is not metabolized, it is accumulated. Hence, on autoradiographs of brain sections, areas of enhanced neuronal activity can be recognized (11).

The present dGlc experiments were undertaken to reveal areas of enhanced activity in the brains of guinea fowl chicks (*Numida meleagris meleagris*). These birds have the advantage that we know their vocal repertoires thoroughly (12, 13). Furthermore, differential dGlc uptake into auditory areas in response to various acoustic stimuli has been studied previously (14–16).

Chicks imprinted either with 1.8-kHz or 2.5-kHz tones and naive controls were exposed to 1.8-kHz tones in a 1-hr session while injected with dGlc. In autoradiographs, known auditory areas were similarly labeled in imprinted and control chicks. However, three particular areas in the rostral forebrain showed extensive labeling almost exclusively in brains of successfully imprinted chicks. These results have several implications for the concept of imprinting mechanisms.

MATERIALS AND METHODS

Experimental Animals. These were 27 young guinea chicks kept in the laboratory from hatching (28th breeding day) to 7 days of age. They were bred in our laboratory in an incubator at a temperature of 37 ± 0.5°C. Newly hatched chicks were allowed to stay at least 4 hr or the first night in the incubator. Afterwards, four to eight chicks always lived together in small cages (room temperature, 25–30°C; day/night cycle, 12 hr/12 hr). Commercial chicken food and water were available ad lib.

Imprinting Procedure. Two groups of chicks (group I, 12 chicks, and group II, 5 chicks) were imprinted in two 1-hr sessions each, the first at the day of hatching and the second the following day (day 1). Imprinting was carried out in a diffusely lit room. Cage mates were placed together with a stuffed guinea hen in a box with hay while the imprinting stimulus was played from a tape recorder. The stimulus was a rhythmic tone burst of either 1.8 kHz (group I) or 2.5 kHz (group II), the rhythm corresponding to the maternal contact call or "iambus" (12). The 1.8-kHz frequency is prominent in the contact call (formant), whereas 2.5 kHz is found in several guinea fowl calls, but not in the contact call. The frequency band of chick calls is between 2 and 3.5 kHz (13).

Testing Procedures. To test whether the imprinting procedure had been successful chicks were submitted to approach and discrimination tests. These tests were performed in a Y-maze with loudspeakers behind two branches. These branches had a small, separate box at their ends. There, the stuffed hen could be placed hidden from the view of the chicks unless they entered the box. Chicks started a trial run in the third branch.

In a "pretest," the imprinting stimulus was played behind one box while the stuffed hen sat in front of this box (i.e., was

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Abbreviations: dGlc, 2-deoxy-D-glucose; HA, hyperstriatum accessorium; HD, hyperstriatum dorsale; HV, hyperstriatum ventrale; LH, lamina hyperstriatica; N, neostriatum; E, ectostriatum.

visible to the chicks). Two trials were performed, one on each side. They were stopped as soon as the chicks either jumped on the hen or entered the box or, if no response occurred, after 10 min. In this pretest half of the eventually successful chicks ran past the hen straight into the box with the loudspeaker.

In the "approach test," the imprinting stimulus was played behind the box where the stuffed hen was sitting (now invisible to the chicks). Stimulation from behind the right and the left box was balanced for each chick. The trial was scored correct if the chick first entered the box from which the stimulus was played. The chick was picked up after 30 s spent in the box and brought back to its cage mates. Should a chick first enter the silent box, the trial was scored as an error. However, the chick was allowed to correct its choice before it was sent back to its mates. Unsuccessful trials were stopped after 10 min. Each test consisted of three or four trials spaced at 30-min intervals. A chick had completed a test successfully if all three or three of four trials were correct.

In the "discrimination test," again the imprinting stimulus was played behind the box where the stuffed hen was sitting. Simultaneously, however, the alternative stimulus (either 1.8 kHz in group II or 2.5 kHz in group I) was played behind the empty box. Due to slightly different intervals between tone bursts (395 ms for 1.8 kHz and 415 ms for 2.5 kHz, respectively) the phase of the two stimuli changed, which made them easier to localize. Right–left counter balancing, the number of trials, and scoring were the same as for the approach test. Each chick was tested for approach on days 2 and 3 and for discrimination on day 4. On days 5, 6, and 7 one or two discrimination trials were given to confirm the observed preference. The dGlc experiments took place on day 7.

Experiments with d[^{14}C]Glc. Seven-day-old chicks (either imprinted chicks or naive controls who had never heard either stimulus) were injected with dGlc intraperitoneally and intramuscularly (18 μCi/40 g in sterile saline; 1 Ci = 3.7×10^{10} Bq). Each chick was placed in a cardboard box covered with a fine cloth and placed in a soundproof chamber. Under diffuse illumination the 1.8-kHz stimulus was played for 1 hr. At the end of this period, the chick was decapitated, and the brain was removed, frozen, and processed according to the procedure given by Scheich *et al.* (14). In short, at a temperature of −15°C serial transverse sections of the whole brain were cut at 30 μm, placed on microscope slides, and immediately dried at 50°C. Every third section was placed in contact with Kodak NMB x-ray film in Kodak X-Omatic cassettes and exposed for 3 wk. Reference sections were stained for Nissl substance.

Densimetric Analysis. Areas of interest in at least three autoradiographs from each chick between brain levels B and C as shown in Fig. 2 were analyzed with an image processor. The system included a commercial television camera mounted on a microscope. The output of the camera was AD-converted with 8-bit resolution and the signals were stored in a HP 21 MX computer in a linear matrix with 256 × 256 picture points. In all autoradiographs, a reference-density measurement was made in a comparable area of low and even background labeling medioventral to the ectostriatum. The measured density of each point in areas of interest was transformed into a ratio of that measurement relative to the background. (Ratios were used rather than absolute densities to compensate for individual differences of dGlc incorporation into the brain and of x-ray film development.) The obtained ratios were divided into five classes, the same for all data: (*i*) less than the labeling density of background given as 1.0; (*ii*) between 1.0 and <1.2 times the labeling density of the background; (*iii*) between 1.2 and <1.5 times the labeling density of background; (*iv*) between 1.5 and <2.0 times the labeling density of background; and (*v*) >2.0 times the labeling of background, which was the class of strongest labeling. The two-dimensional distribution of points belonging to these labeling classes was plotted in different shades of gray on a screen and was reproduced further by a hard-copy unit of a Tektronix 4012 display terminal (see Fig. 3). In addition, an elongated rectangular window was superimposed on the screen in areas of strongest labeling. The density of picture points across the width of the window (0.15 mm on the real brain section) was integrated and the values were plotted as a profile along the window. The results of profile analysis are presented in Table 1.

RESULTS

General Behavior. For each chick, the essential measure of imprinting success was the amount of correct trials. But some consistently observed behavioral observations are given here because they may be helpful in an adequate interpretation of the imprinting results. During imprinting, chicks appeared to be at ease: they sat beneath the hen and gave "soft peeps." Soft peeps are the chick contact calls and occurred in the home cage while walking or feeding. If a chick was separated from the group it produced sequences of loud "distress calls," as do chicks when first placed into the Y-maze (distress calls are commonly given in any disagreeable situation, such as separation, hunger, or pain). In the pretest when the stuffed guinea hen was visible to the chicks in front of the correct box, half of the imprinted chicks snuggled up to or jumped on the hen. But the other half disregarded the hen and ran straight into the box with the loudspeaker.

There were typical differences between imprinted and nonimprinted animals in the approach as well as in the discrimination test. Imprinted chicks first localized the simulus by moving the head. Then, they walked straight forward to the correct box, entered, and jumped on the hen, where they stopped distress calling but gave soft peeps. These chicks might already give soft peeps, as soon as they heard the familiar tone stimulus. If an imprinted chick entered the wrong box ($P = 0.14$), this error was usually corrected rapidly by running to the other box. Nonimprinted chicks showed nondirected walking, while giving loud distress calls. The movement was stereotyped: the chick ran many times, back and forth along one wall of the Y-maze or entered and left a box many times. Such a chick rarely stayed near or jumped on the hen in the box.

Approach Test. On day 2, 11 of 12 (group I) and 4 of 5 (group II) chicks performed the approach test successfully. The 2 unsuccessful chicks were discarded. On day 3, 2 chicks of group I failed; the 13 remaining chicks were successful. Five of them made no error either in the first or in the second test.

Discrimination Test. The discrimination test on day 4 was performed successfully by 11 chicks; the 2 unsuccessful chicks of day 3 and 1 additional chick of each group failed. These data showed that chicks could be imprinted on either 1.8 kHz or 2.5 kHz—i.e., the preference of a given stimulus was the result of imprinting rather than of an inborn preference of a particularly important frequency.

dGlc Labeling. Autoradiographs of 14 experienced chicks (10 of group I and 4 of group II) and of 10 naive controls (group III) were analyzed. Structures were named according to the pigeon atlas of Karten and Hodos (17) and the chicken atlas of van Tienhoven and Juhasz (18). In all brains, the nuclei (n) of the auditory pathway were labeled: n. angularis and n. magnocellularis (n. cochlearis complex), n. laminaris (medial superior olive), n. mesencephalicus lateralis dorsalis (inferior colliculus), n. ovoidalis (medial geniculate body), and, in the forebrain, field L (the primary auditory projection area) and a caudal part of the hyperstriatum ventrale (HV), a higher-order auditory field (19–21). In addition, increased dGlc uptake was found in two visual nuclei, n. rotundus (n. lateralis posterior

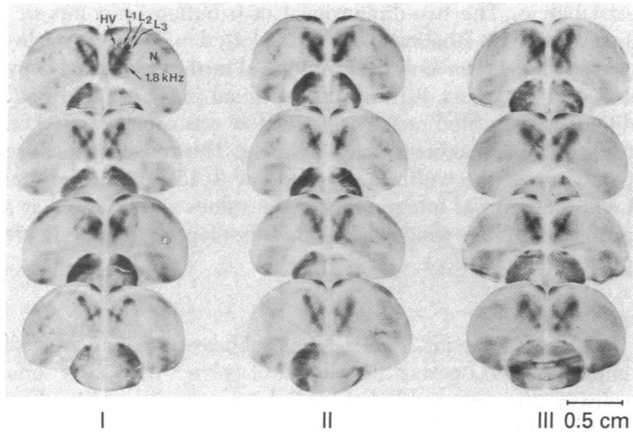

FIG. 1. Autoradiographs of dGlc labeling in field L of the caudal neostriatum (N) (transverse plane) in 12 chick brains frozen after 1 hr of 1.8-kHz tone stimulation. The input layer L_2 and the 1.8-kHz isofrequency plane were strongly labeled in all chicks. Sections of four birds were chosen from each group: group I, chicks imprinted as well as stimulated with 1.8 kHz; group II, chicks imprinted with 2.5 kHz and stimulated with 1.8 kHz; and group III, naive control chicks stimulated with 1.8 kHz.

thalami) and the ectostratium (E) (parastriate cortex) (22, 23).

No difference was found in the labeling of known auditory areas between imprinted and naive chicks—i.e., whether a given stimulus was associated with specific experiences or not. Fig. 1 illustrates this fact for field L in the N and for the overlaying HV. Field L consists of three layers, L_1, L_2, and L_3 in mediolateral sequence (24). The input layer L_2 showed a distinctly higher background activity than L_1 and L_3. The stripe across L_1, L_2, and L_3 and part of the HV, perpendicular to the input layer L_2, was produced by the 1.8-kHz tone stimulation. As known from other experiments, stripes produced by different frequencies show the same orientation but are found ventrally (higher frequencies) or dorsally (lower frequencies) from the 1.8-kHz stripe (14, 16).

In the rostral third of the forebrain, distinctly different patterns of dGlc uptake were found between the imprinted chicks and the naive controls. These differences are illustrated in Fig. 2, in which the essential results of each group are illustrated by autoradiographs from one representative chick. In each of these chicks, five transverse planes of the forebrain (planes A–E = anterior–posterior) were chosen. In the control chick, most forebrain areas showed rather homogenous labeling. Contrasts between particular areas were weak, except for strong labeling in the visual E. In imprinted chicks, contrasts were dramatically enhanced. They were most pronounced in the chick imprinted as well as stimulated under dGlc with the 1.8-kHz tone burst. Strong labeling was found in imprinted chicks in the following areas: (*i*) part of the lateral N (Fig. 2) and HV, rostral, and dorsal to the visual E; (*ii*) a wedge-shaped magnocellular area at the medial edges of both hemispheres, which includes part of the N and HV above and below the LH; and (*iii*) the dorsorostral forebrain roof, including the HA and the hyperstriatum intercalatus superior [a primary visual input area within the HA (25)] and small parts of HD. The most distinct region of dGlc uptake occurred in the rostral part of all three areas (Fig. 2 *A–C*), whereas differences eventually disappeared more caudally in the brain (plane E and following).

To quantify the dGlc uptake in different areas a densimetric analysis was performed as described in *Materials and Methods*. The intensity measurements in densely labeled areas were obtained as ratios relative to the background. The background labeling (mean ± SEM) measured in absolute values was virtually the same in all groups—namely, 126 ± 21 in group I, 136 ± 14 in group II, and 117 ± 32 in group III. (A value of 255 means that the full light was transmitted and a value of 0, that no light reached the camera system—i.e., extreme labeling.) Thus, plots of analyzed autoradiographs and profiles from different chicks are comparable (Fig. 3 and Table 1). In Fig. 3, such plots of three naive control chicks (*A–C*), four successfully imprinted chicks (*E–H*), and an unsuccessful experienced chick (*D*) are given. The plane of all plots corresponds to plane B in Fig. 2.

The densimetric analysis confirmed the correlation between successful imprinting and high-density labeling of distinct areas in a quantitative way (Table 1). Nine of 10 successfully imprinted chicks (6 of 7 group I chicks and all 3 group II chicks) but only 3 of 10 control chicks showed high-density labeling. High-density labeling was defined by the following criterion: labeling density in at least some parts of all three identified areas should be >1.5 times the labeling density of the background. Three chicks with the utmost labeling (i.e., most extensive regions of >2.5 times the labeling density of background) belonged to group I, in which chicks heard the same stimulus during imprinting, testing, and the dGlc experiment. It is interesting that the three chicks of group I who failed in the discrimination test were those with extremely weak label-

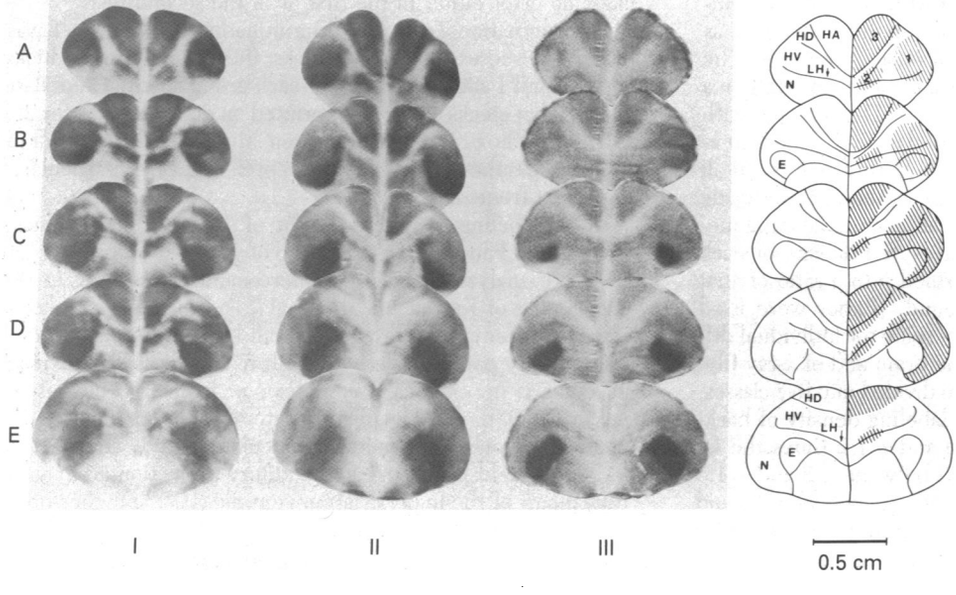

FIG. 2. Autoradiographs of dGlc labeling in three rostral forebrain areas. Equidistant (0.4 mm) serial sections of one representative case from each group (I, II, and III) are shown. Five transverse planes of the forebrain are shown on the left (A–E). Anatomical structures: HA, hyperstriatum accessorium; HD, hyperstriatum dorsale; and LH, lamina hyperstriatica. In the scheme, areas labeled in imprinted chicks are marked with stripes: 1, lateral N/HV; 2, medial N/HV; and 3, HA.

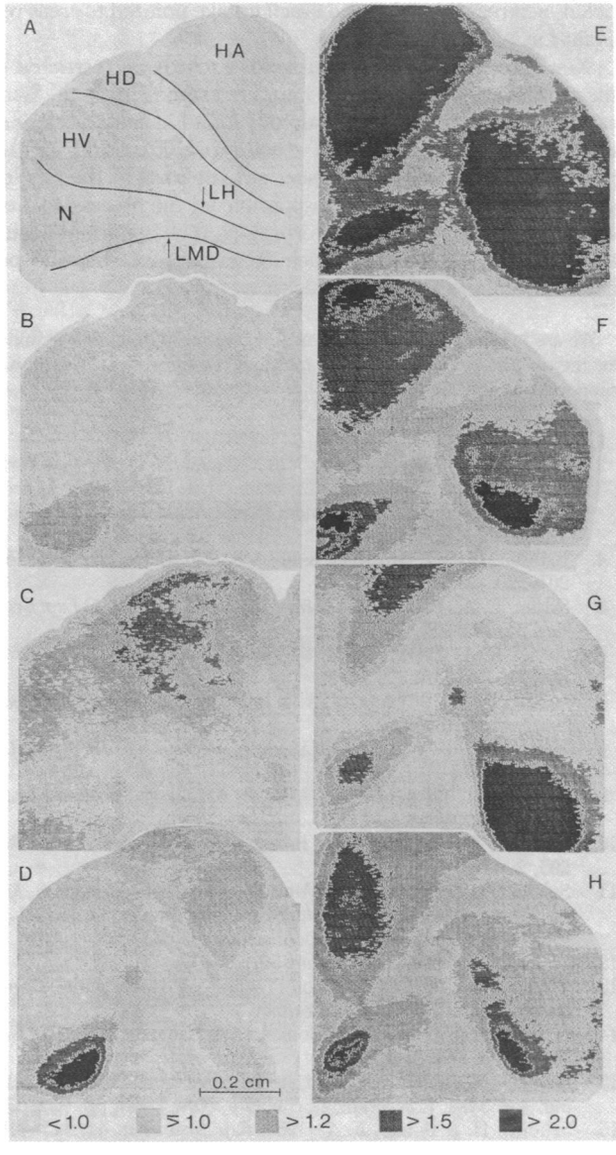

FIG. 3. Densimetric analysis of autoradiographs corresponding to plane B in Fig. 2. (*A–C*) Analyses of three naive control chicks; (*D*) an unsuccessfully imprinted chick; and (*E–H*) analyses of successfully imprinted group I chicks (*E* and *G*) and group II chicks (*F* and *H*). Different shades of gray correspond to five density classes: (*i*) labeling density less than background, which is given as 1.0; (*ii*) between 1.0 and 1.2 times the labeling density of background; (*iii*) between >1.2 and 1.5 times the labeling density of background; (*iv*) between >1.5 and 2.0 times the labeling density of background; and (*v*) >2.0 times the labeling density of background.

ing in the HA and medial N/HV, resembling control chicks (Table 1).

DISCUSSION

Guinea chicks are acoustically imprintable until 4 days after hatching. However, chicks, once imprinted, were still found to approach and prefer the imprinting stimulus at least until the age of 2 wk (unpublished data). Hence, day 7 was chosen for the dGlc experiment to avoid incidental imprinting of naive control chicks during stimulation. On the other hand, imprinted chicks should still be reactive to the imprinting stimulus.

In agreement with earlier results (14–16), auditory areas up to the level of field L and the HV were strongly labeled with

Table 1. Correlation between successful imprinting and high-density labeling

Group	*n*	Lateral N/HV	Medial N/HV	HA
I	3	>3.5/<6.5*	>3.5/<6.5*	>2.5/<4.0*
	3	>2.0/<2.5*	>2.0/<2.5*	>1.7/<2.5*
	1	<1.5	<1.25	<1.25
	3†	<2.2	<1.25	<1.25
II	2	>2.5/<3.5*	>2.5/<3.5*	>2.0/<2.5*
	2	>2.0/<2.5*	>2.0/<2.5*	>1.7/<2.5*
III	3	>2.0/<2.5*	>2.0/<2.5*	>1.5/<2.5*
	1	<1.25	<1.25	<1.5
	6	<1.25	<1.25	<1.25

Labeling density is given relative to the background, which is given as 1.0.
*High-density labeling.
†These chicks failed in the discrimination test.

dGlc in response to tone bursts in all chicks (Fig. 1). According to the tonotopic organization, as shown in microelectrode and dGlc studies (14, 24), a 1.8-kHz frequency plane was labeled in field L and in the HV. This labeling pattern allowed for control of whether or not the 1.8-kHz stimulus was perceived by a chick during the dGlc experiment. The similarity of labeling in the two areas in imprinted and naive chicks indicates that in those sensory areas physical parameters of stimuli were analyzed independently of their behavioral meaning to the receiver.

In contrast, high-density labeling in three rostral forebrain areas was well correlated with preceding imprinting experience. These three areas—namely, the HA, the lateral N/HV, and the medial magnocellular field (medial N/HV)—were *not* reported to receive primary acoustic projections (19–21).

The HA includes a primary visual projection area, the hyperstriatum intercalatus superior. Therefore, labeling might be assumed to be due to the light stimulation. However, the hyperstriatum intercalatus superior was not labeled in otherwise homogeneously labeled autoradiographs of controls who received the same light stimuli. Further, the hyperstriatum intercalatus superior represents a small part of the HA only (25), and labeling was neither restricted to nor concentrated in this region.

Similarly, although adjacent to the visual E (23), the lateral N/HV was strongly labeled only in chicks who also showed strong labeling in the other two areas.

On the other hand, dense dGlc labeling of two visual nuclei—namely, n. rotundus and E (22, 23)—could be the result of diffuse light stimulation during the dGlc session, for it is found in all chicks.

In higher-order brain areas, differential neuronal responsiveness may depend on whether a stimulus evokes specific attention, is recognized, and has a particular meaning, as shown by unit recordings in mammals—e.g., by Ridley and Ettlinger (26), Berger *et al.* (27), Pfingst *et al.* (28), and Mountcastle *et al.* (29). Similarly, differential responsiveness might have developed in the three described areas as a result of imprinting, in which an otherwise meaningless stimulus became familiar and meaningful.

Homologies between avian neostriatal and hyperstriatal structures and mammalian cortical areas have already been studied, but mainly for sensory areas (30–32), whereas particular homologies between the three areas of interest and mammalian parietal, temporal, and frontal cortices or limbic structures have not yet been established. Therefore, because information about anatomical connections and physiological properties in any of the three areas as yet is poor, functional sug-

gestions as given below can only be preliminary.

Recognition of the imprinted stimulus may be crucial for differential neuronal activity because strongest labeling occurred in six of seven successfully imprinted chicks of group I. These chicks heard their imprinting stimulus during the dGlc experiment. Rather high-density labeling was found too in all chicks of group II who, during the dGlc experiment, experienced the alternative stimulus of the discrimination test. Hence, the chicks might have recalled this stimulus, or there was a generalization to stimuli similar to the imprinting stimulus. (Note that the rhythms of both stimuli were virtually the same.) In contrast, the three chicks of group I who failed in tests (i.e., chicks who already had difficulties in recognizing the imprinting stimulus during behavioral tests) showed almost no labeling in two of the three areas. Similarly, 7 of 10 naive controls showed no labeling.

However, in three control chicks labeling density was comparable to group II chicks. Because chicks lived together socially, especially experimentally naive chicks might have been imprinted to one another, some of them possibly to fellow peep calls. During the dGlc experiment, these controls then could have generalized the peep call experience to our mother-like synthetic calls, as was shown in behavioral tests for ducklings by Gottlieb (33, 34).

Instead of stimulus recognition, either the attention paid to a particular stimulus or the behavioral intentions evoked by such a stimulus may be assumed to be crucial for differential neuronal responsiveness and thus the high-density labeling observed. Again, many cases with high-density labeling would be predicted in group I and probably group II, but few cases in group III, because only prolonged responsiveness leads to enhanced dGlc uptake, and persistence of both functions depends on the animal's interest in a particular stimulus. Recognition of a imprinted (i.e., meaningful) stimulus supports this interest. However, interest is rapidly lost if a stimulus is meaningless.

Although in our chicks high-density labeling was found in response to an acoustic imprinting stimulus, the question arose whether or not different sensory modalities might produce similar labeling. In fact, Kohsaka *et al.* showed a similar increase of dGlc uptake in the medial and lateral N/HV of chicks after visual imprinting (9). In both experiments, brain activity was tested when the chicks were already successfully imprinted. Hence, medial and lateral N/HV may be multisensory or limbic structures that are responsible for selective attention to, recognition of, or behavioral interpretation of a significant stimulus. No labeling occurred in the HA in the visually imprinted chicks (9). Recently, E. Weber in our laboratory recorded evoked potentials in the HA of imprinted chicks in response to imprinting tones. Thus, one could speculate about HA as an associative area with special requirements for auditory stimuli.

Because neuronal responsiveness was *not* tested during the imprinting process itself, the highly labeled areas presented here may or may not be the same as those where information was processed or stored (or both) during imprinting.

Probably, the lateral N/HV is an area involved in the imprinting process as well as in information retrieval. In chicks, lesions in that area drastically decreased visual imprintability and retention, as reported by Salzen *et al.* (5–7). But whether acoustic imprinting was similarly affected was not tested.

The most caudal region of the medial N/HV was claimed to be involved in visual imprinting by Bateson *et al.* (4), Horn *et al.* (8), and McCabe *et al.* (10). During imprinting, they found enhanced uracil uptake there (4, 8) and, if the area was lesioned, decreased imprintability and retention (10). This area was labeled neither in our experiment nor in that of Kohsaka *et al.* (9). This is no contradiction, for it is assumed that in the dGlc experiments areas relevant for information recall were labeled, whereas the enhanced uracil uptake pointed to areas relevant for information storage.

None of the functions discussed is exclusively restricted to the processing of imprinting or imprinted stimuli, or both. Some cases of similar labeling were already found in subadult guinea fowls in response to playback of species-specific calls (D. Bonke, personal communication). Hence, at least parts of the labeled areas may be more generally responsible for the processing (i.e., attention, recognition, and interpretation) of important acoustic stimuli, mainly those, which by experience, became behaviorally significant to the chicks.

We are indebted to Mrs. M. Hansel, G. Kunze-König, and I. Röder for the preparation of autoradiographs and the figures. This work was supported by the Deutsche Forschungsgemeinschaft, SFB 45.

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