

Isolation-Dependent Enhancement of 2-[¹⁴C]Deoxyglucose Uptake in the Forebrain of Zebra Finch Males

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In a previous study (H. J. Bischof & K. Herrmann (1986), *Behavioral Brain Research*, 21, 215-221) we demonstrated that four forebrain areas of the zebra finch male are activated in situations which arouse the animal, for example when the birds are chased around the cage or when they are exposed to a female. These areas, the hyperstriatum accessorium-dorsale (HAD), a part of the medial neo-hyperstriatum (MNH), the lateral neo-hyperstriatum (LNH), and a portion of the caudal archi-neostriatum (ANC), show enhanced 2-[¹⁴C]deoxyglucose (2-DG) uptake according to the experimental situation. On the basis of these experiments, we examined whether the activation of the areas is correlated with motor activity and is influenced by different isolation times prior to a 2-DG experiment, where courtship of the male birds is elicited by exposing them to a female zebra finch. For this purpose, we isolated male zebra finches for 1 day, 1 week, or 8 weeks, respectively, before we injected the 2-DG and exposed the birds to a female. During the experiment, besides other activities, the number of song motifs performed by the bird and the frequency of changing perches was recorded. Our experiments demonstrate that there is a weak negative correlation between motor activity and 2-DG uptake, and a positive correlation between isolation time and 2-DG uptake. We suggest that long isolation blocks courtship behavior by some unknown mechanisms, and that the "internal drive" of the animal, which possibly corresponds with the activity of the four forebrain areas, is enhanced by isolation and by the fact that the birds do not perform the consummatory behavior. Our results also demonstrate that the 2-DG method can show up small differences in the internal state of an animal, which cannot easily be detected by behavioral measurements. © 1988 Academic Press, Inc

The metabolic rate and the neuronal activity of brain areas can be measured by the 2-[¹⁴C]deoxyglucose (2-DG) method (e.g., Nudo & Masterson 1986; Sokoloff, 1975; Theurich, Müller, & Scheich, 1984). Besides activity induced by sensory stimulation (e.g., Scheich, Bonke, Bonke,

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& Langner, 1979; Singer, 1981), effects of arousal on 2-DG uptake and hence neuronal activity of distinct brain areas have been demonstrated (Finkenstaedt & Ewert, 1985; Bischof & Herrmann, 1986; Gonzales-Lima & Scheich, 1984b; Müller & Scheich, 1986). Likewise, filial imprinting (Kohsaka, Takamatsu, Aoki, & Tsukada, 1979) and passive avoidance learning (Rose, 1985) can be demonstrated to enhance 2-DG uptake in certain forebrain areas.

Maier and Scheich (1983) demonstrated that the hyperstriatum accessorium and adjacent areas (HAD), the lateral neo-hyperstriatum (LNH), and the medial neo-hyperstriatum (MNH) are activated if young guinea fowl chicks are exposed to a sound of a certain frequency to which they were previously imprinted. Chicks which were naive or imprinted on another tone did not show this activation pattern. In other experiments on guinea fowls and domestic chicks, these results were confirmed and extended (Maier & Scheich, 1987; Wallhäusser & Scheich, 1987). Moreover, Müller and Scheich (1986) demonstrated that high activation of these areas occurs also in situations in which the birds are aroused by separating them from their companions.

We were able to confirm the results of Scheich and co-workers for another bird, the zebra finch (Bischof & Herrmann, 1986). We found that in these birds four areas were activated in arousing situations. Three of the areas, which we named HA, Nint, and Nlat, were identical to the areas HAD, MNH, and LNH described by Müller and Scheich (1986). The fourth area, a wedge-shaped part of the neo-archistriatum, was called A + Ncaud in our previous study. To simplify comparison and to unify the nomenclature, we adopt the names given by Müller and Scheich (1986) in this paper and call the fourth area ANC. (Fig. 1).

The activity of the areas HAD, MNH, LNH, and ANC of the zebra finch forebrain was high in experiments in which the birds courted a female for the first time in their life after an isolation period lasting from independence (Day 35 after hatching) to Day 100, or when we chased the birds around the cage for the entire time of the experiment. Hence, our results supported the assumption that the activity of the four forebrain areas is correlated with the arousal level of the birds.

Two questions remained open in this study. First, we could not directly prove that the activity of the four forebrain areas probably was not correlated to motor activity of the birds. Our argument was based on the fact that in the first courtship experiment the overall activity of the bird was much lower than in the chasing experiment, whereas the glucose consumption was comparable in the two cases. However, obviously the activity patterns of the birds were very different in the two situations, as the birds exhibited courtship behavior in the first experiment and fear reactions in the other. We therefore designed the present experiments

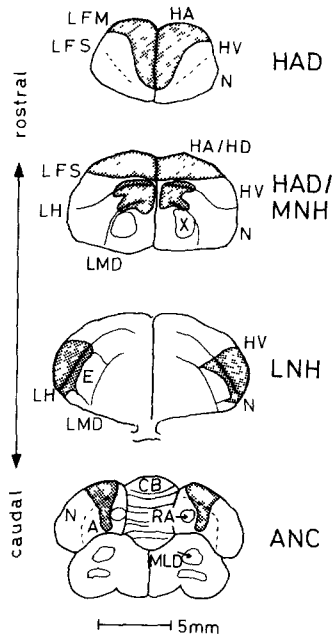


FIG. 1. Schematic drawings of selected transverse sections showing the position of the four areas (hatched). HAD, hyperstriatum accessorium/dorsale; MNH, medial neo/hyperstriatum; LNH, lateral neo/hyperstriatum; ANC, archi/neostriatum caudale; LFM, LFS, LH, LMD, laminae frontalis medialis, frontalis superior, hyperstratica, medialis dorsalis; HA, HD, HV, hyperstriatum accessorium, dorsale, ventrale; N, A, E, neo-, archi-, ectostriatum; RA, N. robustus archistriatalis; X, area X; MLD, N. mesencephalicus lateralis dorsalis; CB, cerebellum.

in a way which allowed direct comparison of behavior and 2-DG uptake in each experimental animal.

The fact that we obtained high levels of 2-DG uptake only in birds which courted for the first time in their life, and not in birds which were sexually experienced, gave rise to a second question which could not definitely be answered by the previous experiments. As the experienced birds were not isolated before the experiment, the effect obtained in the previous study could be due either to the isolation period of the first courtship group or to a special state of the birds in the first courtship situation. The answer to this question would be interesting, as zebra finches under certain circumstances can be reprinted in the first courtship, but not in later courtship events (Immelmann, unpublished), indicating a special arousal state of the birds during first courtship. Therefore, we isolated experienced male zebra finches for different amounts of time before giving them the opportunity to court a female in the 2-DG experiments.

MATERIAL AND METHODS

Twelve adult zebra finch males of about 100 days of age from the institute's stock were used for this study. The birds were kept together with a female for 4 weeks, which sufficed in all cases to establish a pair bond between the two birds. Subsequently, the birds were isolated for 1 day, 1 week, or 8 weeks, respectively ($n =$ four for each group). After the end of the isolation period, the 2-DG experiments were performed.

In all cases the tests were carried out in the cages in which the males were kept in during the isolation period. The room was artificially lighted at normal levels, and no precautions were taken to eliminate background noise, as this was constant throughout all experiments. At the beginning of the experiment the males, weighing between 10 and 11 g, were given an injection of 12 μ Ci 2-DG in 0.1 ml NaCl into the pectoral muscle and returned to the experimental cage. Four minutes later the female was placed inside the cage. In all experiments this female was the former cage mate of the male. The behavior of the birds was then monitored from a distance of about 3 m for 55 min. Pilot experiments demonstrated that at this time 2-DG uptake is still linear with the above mentioned amount of 2-DG injected. The following behavioral patterns were recorded by a computer-based event recorder system (for a description of these behaviors see Morris, 1954): bowing, zig zag dance, bill wiping, song motifs, copulations, and hopping from perch to perch. From these behaviors only two, namely the number of motifs of the sexually motivated courtship song and the motor activity measured by the frequency of hopping from perch to perch, are presented in the results, as the other behaviors occurred too rarely to serve as a basis for comparison between the three groups.

After the end of the experiment the males were immediately decapitated, and the brains were quickly removed from the skull and immediately frozen onto a cryostat head at -60°C . Transverse sections of 30 μm were cut at -17°C the next day. The mounted sections were quickly dried at 60°C on a hot plate and exposed to Kodak X-ray film at 4°C for 4 weeks. The film sheets were then processed by standard development methods. Sections were stained with thionin for identification of the labeled areas. Quantitative measurements of labeling densities were obtained by a computer-aided system which measured an adjustable rectangular section of the given brain area. This rectangle was adjusted in such a way that it optimally covered the area under measurement. For each brain, at least eight measurements were made in each of the four areas of both hemispheres.

Relative densities were calculated in order to compensate deviations due to factors such as the amount of glucose injected, time taken for removing the brain, or the time of exposure of the photographic paper.

These relative densities are based on a scale reaching from the measurement of the area with the constantly lowest density (area X, 0) to an area with a high, consistent density throughout all experiments (MLD, 100). Areas with higher densities than those of MLD, consequently, could reach values above 100. A mean of these measurements was calculated for each of the four areas in each bird and used for further calculations. A two-factorial ANOVA was then performed. If this test showed differences between groups, the source of the differences was then ascertained by a Student's two-tailed *t* test.

To ensure that the choice of the fix points of the scale had no influence on the results of our measurements, we additionally calculated relative densities based on scales with other fix points, as for scales between area X and field L, or area X as the only fix point. Although values of the densities varied according to the choice of the scale, the results did not differ from those obtained with the X-MLD scale in terms of the intergroup variations. As the calculations based on the X-MLD scale are compatible with those made in an earlier report (Bischof & Herrmann, 1986), this scale is used here too.

The significance of correlation between two variables was tested by calculating Spearman's ρ from the ranked data. The degree of significance was read from a significance table (Siegel, 1976).

RESULTS

1. Behavioral Data

Mean values and standard deviations were calculated for two different behaviors within each isolation group. The means for song motifs were 35.25 ± 13.46 for the 1-day isolation group, 36 ± 15.0 for the 1-week group, and 21.25 ± 10.55 for the 8-week group. Motor activity, in terms of frequency of changing perches amounted to 92.25 ± 35.16 for the 1-day, 94.25 ± 59.75 for the 1-week, and 33.25 ± 20.71 for the 8-week isolation group.

Although a tendency toward a negative correlation between isolation and activity is obvious, no statistically significant differences were obtained between groups, obviously due to the large individual differences between the activities of the male birds.

Figure 2 shows the distribution of the two behaviors over the time of the experiment. The diagrams again demonstrate that the overall activity is lower in the 8-week isolation group than in the others. In each case, the activity is fairly high at the beginning of the experiment and then slows down. A second maximum can often be observed in the second half of the experiment. This pattern is also observed in normally courting, not experimentally treated birds (Bischof, 1983). There is no evidence

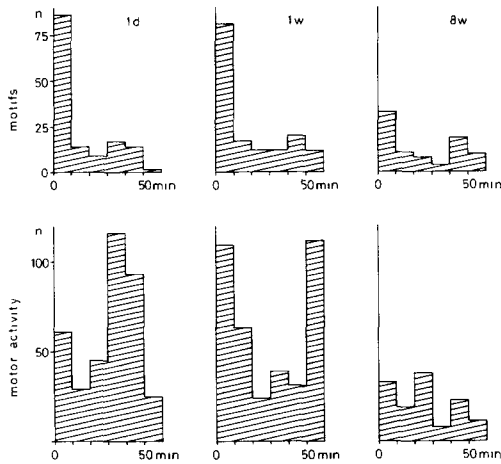


FIG. 2. Frequency of motifs and motor activity (hopping from perch to perch) of the male during the 2-DG experiments. Cumulated activity from four birds each for the 1-day (1d), 1-week (1w), and 8-week (8w) groups.

that the pattern is altered by isolation, apart from the decreasing tendency of the overall activity.

The calculation of Spearman's ρ reveals that the number of motifs sung by an individual bird correlates significantly with the measurement of motor activity, i.e., hopping from perch to perch ($\rho = .8374$, $p \leq .1$). This means that song activity can also serve as a measure of overall activity differences. Therefore, the calculations in section 3 are based exclusively on song motif measurements.

2. Isolation Dependence of Glucose Consumption

Figure 3 shows the relative densities of the four different telencephalic areas HAD, MNH, LNH, and ANC in birds isolated for 1 day, 1 week, and 8 weeks. In addition, two measurements from an earlier study (Bischof & Herrmann, 1986) were added: one from a "control" group where the birds sat alone in the cage for the experiment (columns c) and another from a group where the birds courted for the first time in their life (see Introduction) at the time of the experiment (columns 1c).

Comparing the groups the figure shows a trend of increasing density from group c to 1c in each brain area. The two-factorial ANOVA reveals that there are differences between the different isolation groups ($p = 5\%$, $F = 13.7$) as well as between the different brain areas ($F = 11.7$). However, there is only one difference which is always significant with the t test in all brain areas, that is the difference between the 1-week and the 8-week isolation groups, respectively. On the other hand, the difference between the 1-day and 1-week group is never significant. Ad-

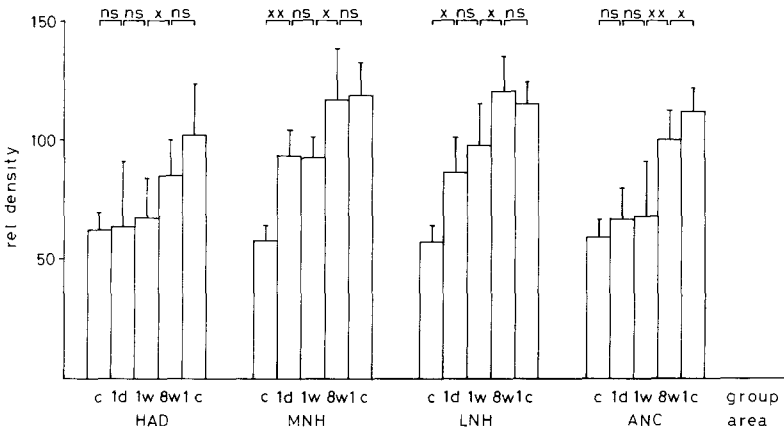


FIG. 3. Relative optical density of the four forebrain areas HAD (hyperstriatum accessorium/dorsale), MNH (neo-hyperstriatum intermedium), LNH (neo-hyperstriatum laterale), and ANC (archi-neostriatum caudale). c, control group; 1d, 1 day; 1w, 1 week; 8w, 8 week; 1c, first courtship group. C and 1c are adopted from a previous paper (Bischof and Herrmann 1986). ns, not significant. x, $p \leq .05$; xx, $p \leq .01$.

ditionally, the difference between the isolation group and the controls is significant in two areas, the MNH and LNH. In one area, the ANC, a significant difference between the 8-week isolation group and the first courtship group can be detected.

These results demonstrate that the activity of the four forebrain areas increases according to the length of isolation of the males before the experiment started. They indicate that in two brain areas (MNH and LNH) the glucose consumption, compared with that of control animals, is enhanced by courtship even after short isolation periods. Further, it seems that with the exception of the ANC there is no difference in glucose uptake between the 8-week isolation group and the first courtship group, which was isolated for about 7 to 8 weeks.

3. Activity Dependency of Glucose Consumption

For the analysis of the correlation between glucose consumption and activity we divided the 12 animals into three groups of four animals (low, middle, and high activity), according to their ranks based on the frequency of courtship behavior. We calculated the means and standard deviations of the relative densities of the four forebrain areas in each activity group.

Figure 4 demonstrates that in each area there is a tendency toward a negative correlation between activity and glucose consumption. However, this difference is not statistically significant, as revealed by the two-factorial ANOVA. As this might be an effect of inappropriate grouping,

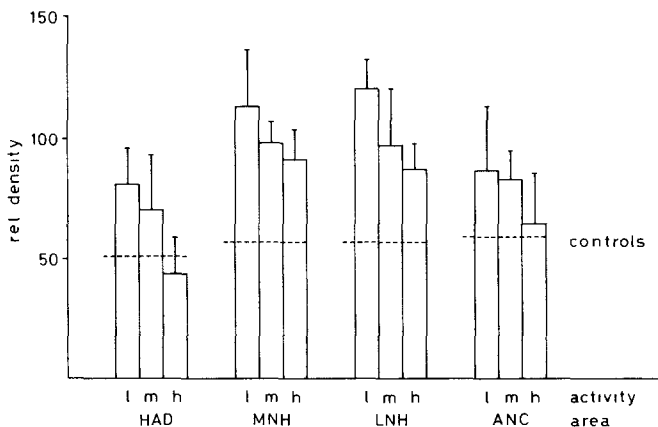


FIG. 4. Relative optical density of the same four forebrain areas as depicted in Fig. 2. l, low; m, middle; h, high activity. For other abbreviations see Fig. 3. controls: level of activity in the control group (data for controls from Bischof and Herrmann, 1986).

we performed a regression analysis of the data of the individual birds, estimating the relation between motifs sung in an experiment and a mean value calculated from the relative densities of all four forebrain areas (Fig. 5). The negative correlation, according to Spearman's ρ based on the ranked data, is significant at the 5% level ($\rho = -.528$).

These calculations demonstrate that there is a weak negative correlation between the activity of the bird and the glucose consumption in at least three of the four forebrain areas, namely HAD, LNH, and ANC. The

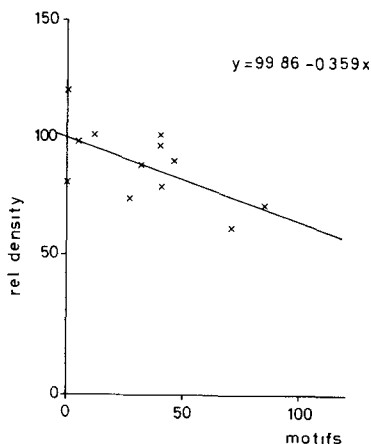


FIG. 5. Correlation between song motifs and relative density of the four forebrain areas (mean of all four areas).

same tendency can be observed in MNH. However, the trend is so small that it appears to have minimal functional significance.

DISCUSSION

Two main conclusions can be drawn from the results presented above: First, the glucose consumption and therefore the neuronal activity of the four forebrain areas HAD, MNH, LNH, and ANC is enhanced by isolating the male birds before exposing them to a female during the 2-DG experiment. Second, this enhanced neuronal activity is not or even negatively correlated with the male's behavioral activity measured in the 2-DG test.

Some further differences between the four areas were found, e.g., the neostriatal areas show significantly enhanced activity in the 1-day and 1-week isolation group, whereas in the other two areas a significant effect is detectable only after 8 weeks of isolation. However, we shall discuss only the main conclusions mentioned above, as too little information is available about the physiological function of the single areas (Bischof & Herrmann, 1986). In contrast, as mentioned under Introduction, there is good evidence that the four areas as a whole are activated by arousal and may be involved in the processing of behaviorally relevant information (Bischof & Herrmann, 1986; Müller & Scheich, 1986). This information in some cases gains its importance by imprinting (Maier & Scheich, 1983; Wallhäuser & Scheich, 1987).

This view of an influence of arousal is supported by anatomical evidence. At least three of the four forebrain areas have been demonstrated to receive projections from locus coeruleus and other unspecific nuclei of the brainstem (Bagnoli, Barselotti, Pellegrini, & Alesci, 1983 for HAD; Bischof, Herrmann, & Engelage 1987, for ANC; Wallhäuser & Scheich, 1986, for MNH). The reticular activation system is commonly regarded to be the source of unspecific activating pathways (Moruzzi & Magoun, 1949). For example, stimulation of the reticular formation enhances responses and the signal to noise ratio in the visual cortex of the cat (Singer, 1979). The same effect can be observed after application of noradrenalin (Kasamatsu & Heggelund, 1982) or in awake cats in comparison to sleeping animals (Livingstone & Hubel, 1981). Gonzales-Lima and Scheich (1984a) demonstrated that combined acoustic and reticular stimulation leads to a higher of 2-DG labeling than pure acoustic stimulation in parts of the inferior colliculus of rats. They further demonstrated that this enhanced activity can be conditioned by a series of simultaneous acoustic and reticular stimulations (Gonzales-Lima & Scheich, 1984b).

Our results clearly demonstrate that activation of the four forebrain areas is not dependent on the activity of the birds. The weak negative correlation between activity of the areas and behavioral activity may be due to a larger glucose consumption by the muscles of active birds, which reduces the amount of free 2-DG available for the brain areas.

Moreover, it is unlikely that the different arousal levels found in our experiments are a consequence of different arousal values of the stimulus for courtship, as in all experiments the male was exposed to its own female in its usual environment. Therefore, the source of the differences must be an internal factor which depends on the individual history of the bird. However, the external stimulus is necessary too, because in control birds, which are not exposed to a female, the activation of four forebrain areas is not enhanced by isolation. This was observed in the previous study (Bischof & Herrmann, 1986), where all control birds were isolated for several weeks before the experiment.

Therefore, it can be concluded that activation of the forebrain areas is controlled by two factors: an internal variable, which is influenced by isolation, and an external variable, possibly the occurrence of a releasing stimulus. This is exactly what Konrad Lorenz called the "principle of double quantification," which means, that a certain behavior is controlled by internal and external factors. He illustrated his idea by the famous "psychohydraulic model" (e.g., Lorenz, 1950). It is tempting to speculate that the neuronal arousal we see in our 2-DG experiments reflects the level of intrinsic energy, which was defined by Lorenz in this model of interaction of releasing mechanisms and motivation. However, Lorenz' model demands that this enhanced energy level leads to a higher rate of sexual behavior, if the releasing stimulus is presented after a longer time of isolation, or at least to a greater probability for the occurrence of the behavior.

This may be explained by the fact that isolation is not a normally occurring situation: one could speculate that such isolation for too long a time may lead to a blockade of courtship behavior. As a consequence of this blockade of the consummatory act, the Lorenzian "energy level" increases constantly. With this assumption, the results of our study can be explained: the "energy level," reflected by the activity of the "arousal" regions, is higher in the group isolated for a long time, whereas the frequency of behavior is constant.

It is not our intention to favor the Lorenz model rather than others (e.g., Deutsch, 1960). However, despite the drawbacks, which the model has in detail (e.g., Hinde, 1960), it illustrates very simply the principle of dual control of behavioral output by external stimuli and internal factors which together control the internal state of the animal and the resulting behavior. The compatibility of our data with the model demonstrates that the activity of the forebrain areas we have measured in our experiments not only may be related to the physiologically defined arousal level of the animal, but also reflects the "internal state" as it is defined by ethologists. If one accepts this, the DG uptake of these forebrain areas would be a physiological measure of this internal state which at

least in some cases may be more reliable and easier than to measure behavioral parameters.

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