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Spine Morphology of Neurons in the Avian Forebrain Is Affected by Rearing Conditions

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An area of the caudal forebrain of male zebra finches, the Archi–Neostriatum caudale (ANC), which is active during arousal (Bischof & Herrmann, 1986, 1988), shows rearing-dependent changes in neuron morphology (Rollenhagen & Bischof, 1991). We demonstrate here that rearing conditions also affect the shape of spines of one of the four ANC neuron types. This neuron type was examined in birds reared under five different conditions—in isolation (1), caged (2), in the aviary (3), and with social contact (4) or chasing (5) after an isolation period. Our results show that social experience determines the proportion of the three types of spines (thin, mushroom, and stubby) of the investigated neuron type. Rearing conditions and short social contact also affect the spine stem length of the thin spine type. Long-term isolation results in a reduction in number and elongation of shafts of thin spines, along with an increase of stubby-and mushroom-shaped spines. Short-term social contact or arousal enhances the number of mushroom-and thin-shaped spines and reduces the length of spine stems of thin spines. We suggest that isolation prevents the ANC neuron from reaching full development. The increase of mushroom and thin spine types due to social contact indicates that the stubby-shaped spines are replaced by, or transformed into, mushroom-shaped spines, and the mushroom-shaped spines are replaced by, or transformed into, thin spines. These results confirm and extend the experimental background for our hypothesis (Rollenhagen & Bischof, 1991) that social contact is necessary for development of normal morphology of ANC neurons.

Studies in mammals indicate that social deprivation during rearing reduces the receptive surface of neurons in certain brain areas, for example the branching index in the cortex (Greenough & Volkmar, 1973; Withers & Greenough, 1989), hippocampus (Fiala, Joyce, & Greenough, 1978), and cerebellum (Floeter & Greenough, 1979) of rats. The number of spines is also reported to be reduced in rats reared in isolation (e.g., Bennett, Diamond, Krech, & Rosenzweig, 1964; Beaulieau & Colonnier, 1987). Several studies demonstrate changes of spine shape as well. In socially deprived fish (Coss & Globus, 1978) or in fetal retarded humans (Purpura, 1974), for instance, spine stems are elongated in comparison with those found in normally grown animals. Other spine changes are observed with visual deprivation (Globus & Scheibel, 1967) or undernutrition (Schönheit & Haensel, 1988, 1989).

The effects of different rearing conditions on spine number have also been reported for birds. Wallhäusser & Scheich (1987), for example, demonstrated that spine density of neurons in the medial neostriatum/hyperstriatum (MNH) of the forebrain is affected by rearing conditions in chicks. In zebra finches, an area of the caudal forebrain, the Archi–Neostriatum caudale (ANC), which is activated during the first courtship encounter after a period of isolation or by chasing the birds around the cage (Bischof & Herrmann, 1986, 1988), also shows changes in neuron morphology that depend on rearing conditions (Rollenhagen & Bischof, 1991).

Within ANC, neurons can be separated into four "stellate" neuron types. The classifications of neurons depends on shape, size of the soma, thickness of the dendrites, and spine density. One of the ANC neuron types (Fig. 1) is characterized by a soma of 5–10 μm in diameter, dendrites of 1.2–1.4 μm in diameter at the primary sections, a relatively low spine density, and a radius of the dendritic field of about 100 μm. This neuron type has fewer spines in male zebra finches isolated from Day 40 to Day 107, compared to birds reared socially in cages or aviaries (Rollenhagen & Bischof, 1991).

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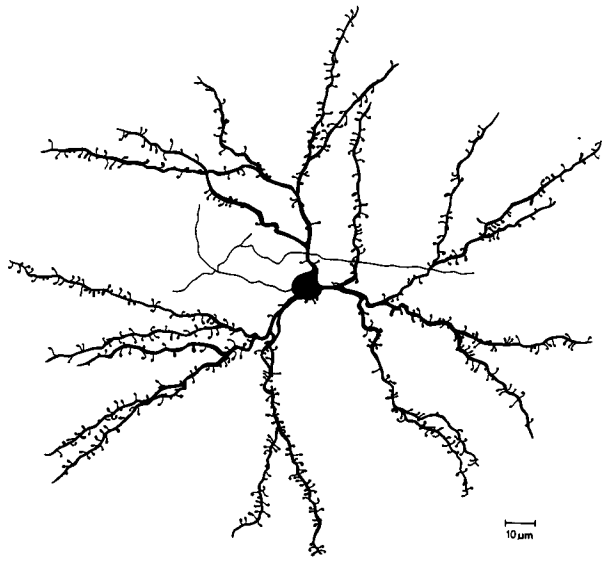

FIG. 1 Camera lucida drawing of an ANC type I neuron. Bar = 10 μm. See text for explanations.

We also demonstrated that a short period of social contact (7 days) after isolation, raises the spine density to the level observed in socially reared animals. Comparison with another brain area (the sensory field L) showed that this effect is not found in all brain regions. The enhancement of spine density as a consequence of social rearing may therefore be a special feature of associative areas like the ANC (Rollenhagen & Bischof, 1991). The experiments in mammals (see above) suggest that rearing conditions could also affect the shape of spines of ANC neurons. The present study has examined this question in zebra finches.

MATERIALS AND METHODS

Golgi-impregnated material from 17 male zebra finches used for a previous study were reexamined (Rollenhagen & Bischof, 1991). The birds, after reaching independence from their parents, were reared under five different conditions:

1. "Isolates": reared in a single cage from Day 40 to Day 107 without visual and social contact (n = 4);
2. "Cage": reared in a cage with three other males and one female (n = 4);
3. "Aviary": reared in an aviary with a flock of conspecific males and females (n = 4);
4. "1W♀": reared like those in group 1, except that the birds were given contact to a female between Day 100 and Day 107 (n = 4);
5. "Chasing": reared like those in group 1, except that the birds were chased around the cage for 1 h per day between Days 100 and 107 (n = 4). This group was included because we wanted to test whether arousal initiated in absence of the visual or vocal cues, which are characteristic of the presence of a social partner, would have similar effects compared to the arousal induced by social partners.

At Day 107 the birds were sacrificed, 100-μm transverse sections were taken after processing the brains according to a modification of the Bubenaite Golgi method described elsewhere (Herrmann & Bischof, 1988). Five to ten fully impregnated ANC type I neurons (Rollenhagen & Bischof, 1991; Fig. 1) from each bird were analyzed from drawings made with the help of a drawing tube attached to a Zeiss microscope at a magnification of 1250× under oil. For the measurements only those of the most peripheral (terminal) sections of the dendritic tree which were parallel to the surface were selected. Terminal sections were chosen because other studies show that these are most strongly affected by early experience (Wallhäusser & Scheich, 1987; Herrmann & Bischof 1988; Patel, Rose, & Stewart, 1988). These terminal sections (20 for each bird) were marked during drawing and the length was measured with the help of a graphics tablet. The number of spines/10 μm was counted for each group of spine types (see Results) separately. No attempt was made to correct for hidden spines (Feldman & Peters, 1979). Because the diameter of the dendrites (0.83 μm) does not change between the groups, the underestimation is likely to be the same for all groups, thus not causing artificially high differences. The length of the spine stems of one spine type (thin, see below) was measured. The spine stem, by our definition, is the thin stalk between the surface of the dendrite and the larger bulbous swelling of the spine. Since not all spines were parallel to the section plane, our measurements are an underestimation of the real length.

For both the spine type and the spine length measurement, the data collection was performed "blind," that is, coded slides were not uncoded until all measurements had been made.

For statistical analysis, a mean value was calculated for each animal. These means were used to determine the mean value in each rearing group. Differences between the rearing groups were then tested by Kruskal and Wallis H test and subsequent Mann–Whitney U tests. As the computed calculations of significance provided by statistical packages are incorrect for n's below 5, the significances were drawn from a table provided by Siegel (1976).

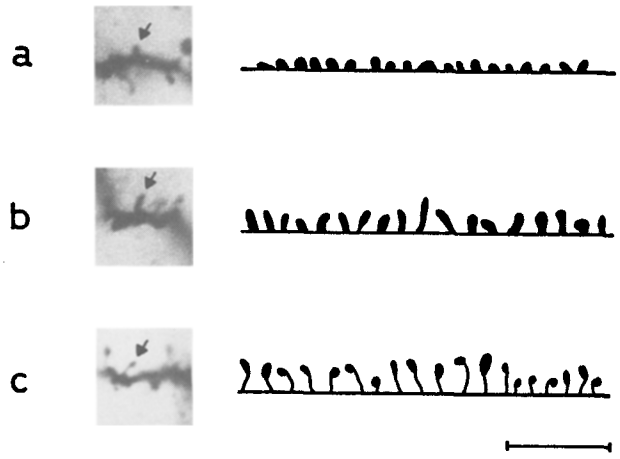

FIG. 2 A sample of spine drawings and photographs showing the different spine types: (a) stubby, (b) mushroom, (c) thin. Bar = 10 μm.

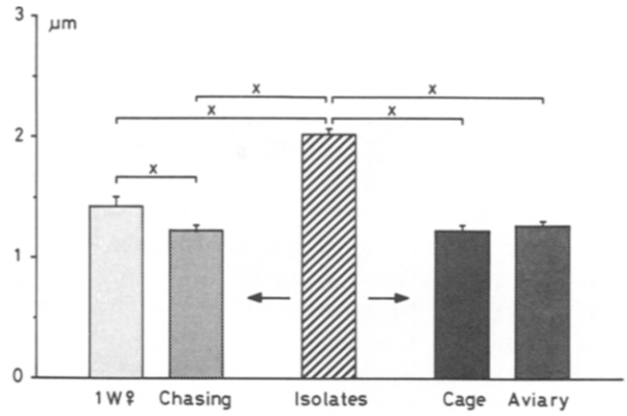

FIG. 4 Mean spine stem length of the "thin" spine type of birds reared under the five different rearing conditions (see text). Isolated birds have significantly ($H = 14.612349$, $p < .01$) longer spine stems than zebra finches of all other rearing groups. "x", Significant differences ($p \leq .028$).

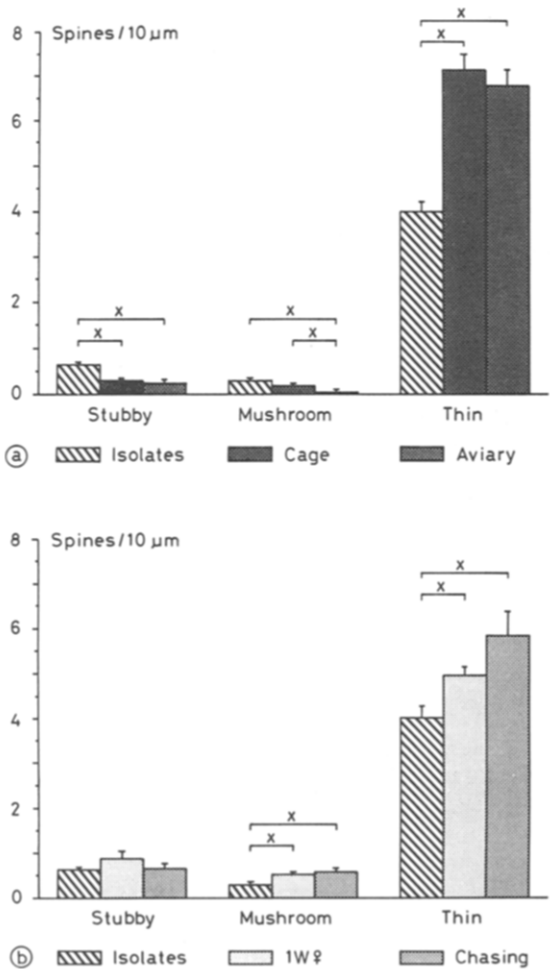

FIG. 3 Mean spine number/10 μm of the three different spine types (a) showing the long-term effects of isolation and (b) the short-term effects of social contact or "arousal" (see text). Significant differences ($p \leq .028$) are indicated by "x".

RESULTS

Our study shows that the spines of the neuronal type examined can be classified into three different types (classification after Peters & Kaiserman-Abramov, 1970; Schönheit & Haensel, 1989):

1. Thin: spines with a slender spine stem and a bulbous terminal expansion ("swelling");
2. Mushroom: spines with a thicker spine stem ending in a larger spine head;
3. Stubby: short spines without any distinct spine stem and spine head.

Figure 2 shows a sample of spine drawings depicting the classification of the spines into three types. Thin and mushroom were identified by the possession of a "thin" or "thick" spinestem. Stubby-shaped spine types were characterized by absence of spine stems.

The counts of the different spine types show that thin spines are most frequent on the dendrites of the ANC neurons in all experimental groups. The proportion of the three spine types, however, changes significantly ($p \leq .01$; Kruskal and Wallis H test; $H = 15.31$ (stubby), $H = 16.60$ (mushroom), $H = 14.50$ (thin)) with social experience.

Two effects can be separated: first, a long-term effect of isolation, and second, a short-term effect of social contact or "arousal."

Long-Term Effects (Figs. 3a, 4)

"Long-term effects" are the changes occurring due to differential rearing from Days 40 to 107. The ANC neurons of isolated birds have significantly

fewer thin spines than those of cage-reared (z = 2.309401, $p \leq .028$) or aviary-reared (z = 2.309401, $p \leq .028$) animals. In contrast, neurons of isolated birds show a significantly higher proportion of stubby-shaped (z = 2.309401, $p \leq .028$) and mushroom-shaped (z = 2.323272, $p \leq .028$) spines when compared to aviary-reared animals. Whereas the number of stubby-shaped spines of isolated birds is also significantly (z = 2.309401, $p \leq .028$) higher when compared to cage-reared birds, there is no significant (z = 0.577350, $p \leq .686$) difference in the number of mushroom-shaped spines of isolated and cage-reared birds (Fig. 3a).

When percentages are considered in place of absolute values, our calculations (Table I) reveal that mushroom shaped spines increase in isolated birds, when compared with those of cage reared birds.

In addition, rearing birds in isolation affects the length of the spine stems of the thin spines (Fig. 4). When compared with the socially reared groups (1.2 ± 0.05 μm cage and 1.25 ± 0.03 μm aviary), the isolated birds have significantly longer spine stems (2.01 ± 0.05 μm; z = 2.309401, $p \leq .028$ compared to cage and z = 2.309401, $p \leq .028$ compared to aviary).

Short-Term Effects (Figs. 3b, 4)

In order to estimate the short-term effects, the isolated group was compared with the groups that were exposed to a female or chased around the cage, respectively, for 7 days after an isolation period of 60 days. It is conceivable that birds of each of the three categories mentioned above had similar values before the "7-day" treatment was given to two of the groups.

Seven days of social contact with a female after a period of isolation leads to a significantly higher proportion of mushroom-shaped spines (z = 2.323272, $p \leq 0.028$) than that seen in the isolated birds. Likewise, the number of mushroom-shaped spines is significantly enhanced after chasing the birds around the cage (z = 2.323272, $p \leq .028$). No significant difference can be obtained for the stubby-shaped spines between chased birds (z = 0.145204, $p \leq 1.114$) and those that have had social contact to a female (z = 2.0220726, $p \leq .058$) when compared with those of isolated birds. In comparison with isolated birds, the number of thin spines is significantly higher in birds after social contact with a female (z = 2.309401, $p \leq .028$) or after being chased (z = 2.309401, $p \leq .028$) around the cage. Seven days of social contact or chasing the birds around the cage after isolation results in a decrease in spine stem length (1.41 ± 0.08 μm/1W♀ and 1.21 ± 0.04/Chasing) to values also observed in socially reared animals (1.21 ± 0.05 μm cage and 1.25 ± 0.03 μm aviary; the difference between chased and socially reared birds is not significant (z = 0.145204, $p \leq 1.114$ compared to cage and z = 1.306840, $p \leq 0.342$ compared to aviary; Fig. 3b).

After 7 days of social contact with a female, the spine stem length is slightly higher when compared to cage-reared (z = 2.02726, $p \leq .058$) or aviary-reared (z = 2.178067, $p \leq .058$) birds (Fig. 4).

DISCUSSION

Our results clearly demonstrate that rearing conditions affect the percentage and density of the three different spine types and the length of the spine stems of the thin spines. As stated above we can distinguish two effects, a long-term effect of isolation and a short-term effect of social contact or arousal after an isolation period. We will discuss these effects consecutively.

In zebra finches raised in isolation from Days 40 to 107 the frequency distribution of the different spine types shifts toward a higher proportion of stubby-and mushroom-shaped spines, whereas the proportion of thin spines is reduced (Fig. 3a). Thin spines are the predominant spine type in adults (Peters & Kaiserman-Abramov, 1970; Connor, Diamond, & Johnson, 1980;), and synaptic contacts are presumably only built on spine heads of this spine type (Peters & Kaiserman-Abramov, 1970; Schönheit & Haensel, 1984). A reduction of the proportion of thin spines and an increase in the proportion of stubby-and mushroom-shaped spines probably indicates an immature stage of development (Marin-Padilla, 1974; Purpura, 1975; Schönheit & Haensel, 1984, 1989). These ideas can also be applied to our findings, suggesting that ANC neurons in isolated birds are not fully developed to the mature stage typical of socially reared birds. This view is further supported by the second long-term effect revealed by our study, namely the fact that the stems of the thin spines are longer in isolated than in socially reared birds (Fig. 4). Elongated spine stems have been found in mammals during development or retardation (e.g., Marin-Padilla, 1972, 1974; Purpura, 1975, 1983). It has been suggested that the efficiency of synaptic transmission by thin spines is dependent on the length and diameter of the spine stems (Chang, 1952; Purpura, 1975; Fifkova & van Harreveld, 1977). According to this idea, the thin spines in isolated birds would be less effective in transmission than thin spines in socially reared birds.

TABLE 1
Means and Standard Deviations of Spine Densities (counts/10 μm) for Each Individual Bird Used in This Study

	Rearing condition				
	Isolates	Cage	Aviary	1W♀	Chasing
Total spine density	5.19 ± 0.33	7.77 ± 0.44	7.04 ± 0.51	6.07 ± 0.43	7.81 ± 0.36
	4.68 ± 0.28	7.62 ± 0.39	6.99 ± 0.34	6.08 ± 0.36	8.46 ± 0.42
	5.42 ± 0.32	7.91 ± 0.33	7.52 ± 0.34	7.55 ± 0.43	6.03 ± 0.39
	4.72 ± 0.37	6.19 ± 0.30	6.56 ± 0.24	8.93 ± 0.55	6.96 ± 0.28
Median	5.04 ± 0.17	7.70 ± 0.50	7.04 ± 0.19	7.40 ± 0.27	7.38 ± 0.70
Percentage	100	100	100	100	100
Stubby	0.59 ± 0.10	0.27 ± 0.10	0.45 ± 0.14	0.70 ± 0.13	0.54 ± 0.12
	0.60 ± 0.10	0.29 ± 0.11	0.24 ± 0.09	0.92 ± 0.27	0.90 ± 0.17
	0.68 ± 0.12	0.28 ± 0.10	0.23 ± 0.15	1.24 ± 0.25	0.73 ± 0.19
	0.73 ± 0.14	0.17 ± 0.07	0.17 ± 0.07	0.87 ± 0.15	0.50 ± 0.09
Median	0.64 ± 0.04	0.28 ± 0.04	0.23 ± 0.08	0.89 ± 0.16	0.64 ± 0.12
Percentage	12.70	3.64	3.27	12.03	8.67
Mushroom	0.15 ± 0.32	0.36 ± 0.12	0.03 ± 0.01	0.57 ± 0.11	0.42 ± 0.13
	0.31 ± 0.28	0.17 ± 0.25	0.03 ± 0.02	0.49 ± 0.13	0.58 ± 0.23
	0.26 ± 0.10	0.12 ± 0.28	0.11 ± 0.09	0.61 ± 0.10	0.62 ± 0.14
	0.35 ± 0.11	0.16 ± 0.06	0.01 ± 0.01	0.40 ± 0.07	0.58 ± 0.10
Median	0.28 ± 0.06	0.17 ± 0.07	0.04 ± 0.01	0.39 ± 0.01	0.58 ± 0.06
Percentage	5.60	2.21	0.57	7.16	7.86
Thin	4.42 ± 0.29	7.17 ± 0.46	6.64 ± 0.53	4.81 ± 0.28	6.74 ± 0.42
	3.77 ± 0.23	6.87 ± 0.32	6.99 ± 0.36	4.97 ± 0.36	6.87 ± 0.46
	4.22 ± 0.28	7.53 ± 0.36	7.50 ± 0.38	5.51 ± 0.43	4.95 ± 0.31
	3.54 ± 0.28	5.84 ± 0.25	6.24 ± 0.29	4.98 ± 0.36	4.98 ± 0.26
Median	3.99 ± 0.25	7.17 ± 0.49	6.81 ± 0.36	4.97 ± 0.20	5.87 ± 0.55
Percentage	79.20	93.12	96.73	78.28	83.71

Taken together with the fact that the overall spine density is essentially reduced in isolated animals, our results show that isolation prevents the ANC type I neurons from full development; they are left in a premature stage until adulthood. In the second part of our study we compared the effects of two different treatments following isolation between Day 40 and Day 107: first, exposing to a female for 7 days, and second, chasing the birds round the cage for 1 hour at each of 7 consecutive days. We have shown previously (Rollenhagen & Bischof, 1991) that both treatments increase the spine density of ANC neurons of previously isolated birds to values obtained in socially reared animals. This study shows that the number of mushroom-shaped and thin spines is increased and that the length of the stems of the thin spines is reduced by this treatment compared to isolated animals.

Phenomena like this are quite common during development. Coss and Globus (1978), for example, showed that social stimulation after isolation shortens the spine stem length of tectal interneurons in fishes. Retardation of development as a consequence of some sort of deprivation, e.g., undernutrition, is quickly compensated if the deprived factor is provided (reviewed in Bateson, 1980). Our study shows that such compensation of developmental retardation occurs not only during development, but also in adult birds, at least in certain brain areas. However, we have shown previously that 7 days of social contact are not sufficient to repair all effects of isolation (Rollenhagen & Bischof, 1991). While the number of spines reaches the values obtained in socially reared birds (Rollenhagen & Bischof, 1991, confirmed in this study, see Table I), the complexity of the dendritic tree remains in the isolated stage. Whether longer social experience also enhances this feature is a question that is currently being investigated.

Another issue that needs to be considered is the question of whether the three types of spines arise separately from each other or, as some authors suggest (Peters & Kaiserman-Abramov, 1970; Schönheit & Haensel, 1984), are stubby and mushroom spines replaced by or transformed into thin spines. Table 1 shows that in the cage-or aviary-reared animals the percentage of stubby-and mushroom-shaped spines is smaller than in isolated animals, whereas the percentage of thin spines is higher. One could interpret this finding to show that in socially

reared animals the mushroom-and stubby-shaped spines are replaced by, or transformed into, thin spines. As the absolute number of spines also increases, this cannot be the only source of the increase in thin spines. New spines must have also arisen. We cannot decide from our study whether these arose as mushroom-or stubby-shaped spines and then transformed into thin spines, or whether thin spines can also arise directly. It is interesting that with short-term social contact after isolation (i.e., 1W♀ and Chasing groups) the percentage of mushroom-and stubby-shaped spines is not reduced as in the case of long-term social rearing. But, in fact the percentage of mushroom shaped spines is enhanced. This again could indicate that mushroom and stubby spines are precursors of thin spines, although it does not really prove it.

The results of this study confirm and extend the experimental background for our hypothesis (Rollenhagen & Bischof, 1991), namely that social contact is necessary for development of normal morphology of ANC neurons. ANC neurons in isolated birds are less complex, have fewer spines, and longer stems of the thin spine type than ANC neurons of socially reared animals. Effects of isolated rearing can be repaired partly by short periods of social contact. Our chasing experiment probably allows us to be more accurate in defining which factors mediate the effects of social rearing. Chasing is probably not a normal social contact, although it may belong to social interactions in the wider sense. We interpret this result as to show that it may be one endogenous component of social contact, namely the enhanced arousal level of the animals, which mediates the effect on ANC neuron morphology. This is supported by 2-deoxyglucose experiments (Bischof & Herrmann, 1986, 1988), which demonstrate very high activation under exactly the same conditions as have been employed in the present experiments.

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