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Research report

The effect of social environment on singing behavior in the zebra finch (*Taeniopygia guttata*) and its implication for neuronal recruitment

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Abstract

Previous studies found that complex social environment increases new neuronal recruitment in brains of adult male zebra finches, in comparison with exposure to a simple social environment. These experiments could not determine, however, whether this increase was due to greater amounts of auditory input (amount of auditory information the male is exposed to), or auditory output (amount of song it produces). To answer this question, we raised male zebra finches to adulthood in a controlled environment, and were then exposed them to either a single unfamiliar female (simple social environment) or to 45 unfamiliar zebra finches of both sexes (complex social environment). Their singing behavior was monitored in these new social environments. Birds which were exposed to a simple social environment sang significantly more than birds which were exposed to a complex social environment. This supports the hypothesis that increased neuronal recruitment in birds exposed to a complex social environment correlates with processing and storing of auditory input, and not with song produced by the bird.

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Keywords: Social environment; Singing; Zebra finch; Songbird; Neuronal recruitment**1. Introduction**

A previous study [5] showed that exposure of adult male zebra finches (*Taeniopygia guttata*) to a new complex social environment (large heterosexual group) increases new neuronal recruitment in their brains, in comparison with other individuals, which had been exposed to a new simple social environment (male-female pairs). This increase was observed in nidopallium caudale (NC), high vocal center (HVC) and Area X—three regions that are involved in vocal communication. The same outcome was replicated for NC in a later study [1]. The results support the hypothesis that new neurons enhance the brain's ability to acquire new long-term memories [6], and that regulation of new neuron survival by extent of circuit use may be a general mechanism for ensuring that neuronal replacement is closely attuned to environmental change. In our previous study we interpreted that the increase in neuronal recruitment in group-housed birds resulted from the richer auditory environment to

which they were exposed, in comparison with the pair-housed birds.

However, this is not the only possible interpretation, because an increase in neuronal recruitment can also be a result of more singing in males which were exposed to a new social setting. There is an indication that neuronal survival in HVC is greater in singing than in non-singing birds [4], an effect that in this region seems to be mediated by brain derived neurotrophic factor (BDNF; [4,7]). Our previous study did not distinguish between the two possibilities—quantity of singing to which the males were exposed vs. quantity of singing which the males produced. Therefore, the aim of the present study was to monitor singing behavior of males exposed to the two social settings – complex and simple – in order to determine whether the differential patterns which were previously observed in neuronal recruitment can be explained by either input of vocal stimulus (quantity of singing heard by the male) or by output of such stimulus (quantity of singing the male produces). Our results show that contrary to the higher output hypothesis, males exposed to complex social environment (large heterosexual group) sang significantly less than males in simple social environment (pair situation). These results support the hypothesis that an increase

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in neuronal recruitment in group-housed birds results from a richer auditory environment, rather than higher song production.

2. Materials and methods

2.1. General

The present study is an extension of a previous one [5] and therefore the experimental design that we used here is the same as the one described there. Three outdoor breeding colonies at the Meier Segals Garden for Zoological Research at Tel-Aviv University, Israel, provided our subjects. Juvenile zebra finches were banded at fledging with one numbered plastic ring for individual identification and kept in their breeding colonies until the age of 45–60 days, when they became independent and could also be sexed by their plumage. Only males were used in our experiments.

All cages and aviaries describe below were exposed to natural illumination conditions that changed seasonally (10.1–14.7 h of light per day). The range of mean daily temperature was from 12 to 30 °C. Our birds are able to breed any time of year under these conditions. For this reason and because individuals for each of the experimental groups were obtained at all times of the year, seasonal changes in temperature and photoperiod were unlikely to have affected the outcome of our study.

2.2. Experimental design

At 45–60 days each experimental male was randomly allocated to its future experimental group and then banded with three additional plastic rings, randomly chosen, so that it had a unique color combination of total of four rings, for its individual identification. The experimental males were removed from their native colony; each one of them was put in a standard cage (65 cm × 35 cm × 45 cm), together with three other unrelated individuals, to avoid stress that, in this very sociable species, might result from isolation. The three strangers consisted of another juvenile male of the same age, and two adults (a male and a female over 150 days old). Each such cage was visually isolated from the outside environment, and placed by itself, so that the experimental bird that was kept in it could only hear or see the three zebra finches with which it was housed.

The birds we used in our experiments were kept under the above conditions until the age of 5–7 months, well after male zebra finches normally reach sexual maturity (at about 80 days). After this period each male was placed in a large outdoor aviary (1.5 m × 1.5 m × 2 m) where they encountered either of two social environments: simple (with one stranger adult female), or complex (40–45 adult stranger birds of both sexes). Experimental birds stayed in the new social environments for 40 days. The walls of these aviaries were covered with burlap and the aviary had a roof of opaque plastic. Distance between aviaries was about 50 m. Because of all these conditions birds in any given aviary could not hear nor see those in other aviaries. The interior arrangement – perches, food and water dishes – was the same for all aviaries. In these aviaries, as well as in the previous standard cages, nest boxes were not provided.

2.3. Measuring singing behavior

Song of zebra finches can be divided to two types: directed and undirected [9]. Directed song is sung during courtship and therefore might indicate pair bonding, while undirected song is sung in all other occasions. The two song types are distinguished by behavioral characteristics: during directed song, the male stands close to a specific female (not more than 20 cm) and directs its posture towards that female at all times; during undirected song the posture of the male is not directed specifically towards any other bird [9]. In all observations described below, we recorded, for each song type, the following parameters: number of song bursts, their duration, and number of repetitions of the basic phrase in the song. Total duration of songs (measured as described below under Section 2.4), was later chosen as the parameter measuring song quantity and for statistical analysis. We did not use number of songs to measure song quantity because some of the birds sang many but short songs, while others few but long ones. Therefore, although the singing “quantity” (total duration) of both types of singers was equal, if judged by the number of songs, the formers sang more

than the latter. For the same reason we also did not use the number of basic phrases as the measure for song quantity. In addition, some of the birds added calls in the middle of their singing, or used long opening phrases which both made their song longer, but did not change the number of basic phrases they use.

2.4. Observations

Eighteen observations were made on each of the 34 experimental birds, before and after the exposure to the new social environment (see below for details). Observations on each bird were evenly distributed in all hours of the day, to avoid any possible effect of time of the day on data collected on singing behavior of the observed bird. Observations were carried out by 10 people. To minimize the possible effect of individual differences between observers on the results, each experimental bird was observed by four people: one observer conducted six observations out of the total 18, and each of the others conducted four. In addition, each observer observed birds from both experimental groups. Each observation was preceded with five minutes during which the observer was silently present at his/hers observation spot, to allow the birds to get used to the observer's presence. Then, for 15 min, the observer monitored the bird's singing behavior and used an audio device to make notes in real time, by indicating the onset and end of each singing event. Using these notes we could determine the various song parameters specified above.

2.4.1. Observations prior to the exposure to the new social environment

Five of the 18 observations were randomly carried out on singing behavior of each bird during the 8 days prior to its exposure to the new social environment, while it was still in the standard cage with three other individuals. During these observations the observer sat 2 m away from the cage. Data collected from these observations enabled us later to ensure that variables which were unrelated to our tested hypothesis (such as age, or pre-assignment to a future experimental group), did not affect the singing behavior of the birds (see below for details).

2.4.2. Observations after the exposure to the new social environment

Thirteen observations were made after the males were introduced into their new social environment in the aviaries. These observations were made through a narrow slot (5 cm × 25 cm) which was cut in the burlap cover of the aviary, to minimize any disturbance which the observer's presence might cause to the birds. Our hypothesis was that if singing behavior changes as a result of its exposure to a new social environment, then this change will be more pronounced soon after the exposure than later, when habituation to the new environment can occur. Therefore, during the first few days after the exposure to the new environment, singing behavior was recorded more intensively than at later stages, as follows: *Day 0*: an observation was carried out immediately after the bird was exposed to its new social environment, between 11:00 to 13:00. *Day 1*: Two observations were made—in the morning (7:00–11:00) and in the afternoon (13:00–15:00). The rest of the observations were evenly distributed at all hours of the day. *Days 2, 3, 5, 10, 13, 17, 20*: One observation was made on each of these days. *Day 23 or 24*: One observation was made on one of these 2 days which was randomly chosen. *Day 27 or 28*: One observation was made on one of these 2 days which was randomly chosen. *Days 33–39*: One observation was made on one of these 3 days which was randomly chosen.

2.5. Body mass

At the end of the experiment all experimental birds were weighted. This was used as an indirect evidence for overall health.

2.6. Statistical analysis

2.6.1. General

Observations in which a clear distinction between directed and undirected singing was uncertain, were not included in the analysis of each song type but were included in the analysis of both song types. Therefore, sample sizes for the different statistical analysis differ, and are specified separately for each case.

2.6.2. Controlling for confounding variables

Our main goal was to test whether exposure to different social environments (complex or simple) affects singing behavior of adult zebra finch males. However, prior to this data analysis we wanted to ensure that other factors did not affect the singing behavior of the birds. Therefore, we first tested if the following variables had any effect on singing behavior of our birds.

2.6.2.1. Age. Birds were either 5 or 7 months old when exposed to the new social environment. Although both of these ages are well beyond sexual maturity, we wanted to ensure that this age difference did not affect singing behavior. To do this we used data from the five observations which were carried out in the standard cages, before the exposure to the new social environment (see above). For each bird we averaged the duration of each singing type (total, directed and undirected) during these five observations. Then we compared, for each signing type, the data obtained from birds that were 5 months old with those obtained from birds that were seven months old. Since the data were not normally distributed (Kolmogorov–Smirnov test), we analyzed them by using Mann–Whitney *U*-test for non-parametrical data.

2.6.2.2. Pre-assignment to future experimental groups. In the standard cages, prior to the social change, each bird was already assigned to its future social environment. To ensure that this pre-assignment was random and did not cause any bias in the distribution of birds across the two experimental groups, we used data from the five observations which were carried out in the standard cages, before the exposure to the new social environment. For each bird we averaged the duration of each singing type (total, directed and undirected) during these five observations. Then we compared, for each signing type, the data obtained from birds that were later exposed to a simple social environment with those obtain from birds that were later exposed to a complex one. Since the data were not normally distributed (Kolmogorov–Smirnov test), we analyzed them by using Mann–Whitney *U*-test for non-parametrical data.

2.6.2.3. Observer's presence. We do not know whether the five minutes prior to each observation, during which the observer was silently present at his/hers observation spot, were enough for the birds to get used to the observer's presence. Therefore, we tested whether there were any consistent differences in singing duration between the two halves of the observations. To do this we compared, for each bird and in all observations (those carried out on standard cages as well as those carried out on aviaries), total singing duration between the two halves of the observation. This comparison was made by using Wilcoxon test for non-parametrical paired data.

2.6.3. Testing the effect of new social environment on singing behavior

As explained above, a total of 13 observations were carried out in the aviaries, within the 40 days during which the experimental birds were exposed to a new social environment. Two of these observations were made on Day 1 after exposure. For the statistical analysis, data from these two observations were pooled for each bird and for each of the tested singing types (total, directed and undirected). Accordingly, for each bird, we had data from 12 observations, which were divided into three groups, each consisting of four observations, as follows: Days 0–3, Days 5–19, and Days 20–39 from exposure to social change. We used these data, after applying the square root transformation, to test the following questions: (1) Does social environment affect singing behavior; (2) Does acclimation to a new social environment (days elapsed since exposure to the change) affect singing behavior? To test these questions we analyzed the data of singing duration for each of the tested singing types (total, directed and undirected) and in both experimental groups (simple, complex) by using ANOVA with repeated measures, where the three observation groups (see above) were taken as the three repeated measures. Post hoc comparisons were carried out by the Bonferroni (HSD for unequal *N*) method.

2.6.4. Body mass

Two-way ANOVA was used to test for possible differences in body mass between experimental groups.

3. Results

3.1. Controlling for confounding variables

As shown below, differences in singing behavior between treatment groups were not a byproduct of differences in age, initial group composition, or observer's presence.

3.1.1. Age does not affect singing behavior

Prior to the exposure to the new social environment, birds were either 5 or 7 months old. Their singing duration (of total, directed and undirected singing) did not differ significantly (Mann–Whitney *U*-test; total: $U_{0.05(2),14,17} = 87$, $P = 0.20$; directed: $U_{0.05(2),12,14} = 79$, $P = 0.8$; undirected: $U_{0.05(2),12,14} = 53.5$, $P = 0.12$). From this we infer that these age groups did not affect singing behavior. Therefore, in further statistical analysis, data were pooled from both ages in each group. Even if there is a weak effect of age that we could not detect, the two groups did not differ in the age of the birds, and therefore it is unlikely to be the cause of the main effect of social environment on singing behavior.

3.1.2. Birds were randomly distributed to the two experimental groups

We wanted to ensure that assignment of each bird, prior to its exposure to a new social environment, was random. For this we followed the procedure explained in Methods and found no significant differences in singing duration between birds that were later exposed to a simple social environment and birds that were later exposed to a complex one. These non-significant differences were found in total, as well as in directed or undirected singing (Mann–Whitney *U*-test; total: $U_{0.05(2),15,16} = 111$, $P = 0.72$; directed: $U_{0.05(2),12,14} = 71.5$, $P = 0.52$; undirected: $U_{0.05(2),12,14} = 75.5$, $P = 0.66$). From this we infer that distribution of the birds to the experimental groups was random and did not cause any future bias.

3.1.3. Observer's presence does not change singing behavior of the birds during observations

Prior to the exposure to the new social environment, as well as after the exposure, duration of total singing (directed and undirected) did not differ significantly between the first and the second half of the observation (Wilcoxon; prior to exposure: $T_{0.05(2),16} = 22$, $P = 0.18$; complex: $T_{0.05(2),9} = 22$, $P = 0.95$; simple: $T_{0.05(2),9} = 9.5$, $P = 0.12$). From this we infer that the observer's presence had no effect on singing duration of the birds during observations, and therefore, for statistical analysis, we pooled the data from the entire observation (15 min).

3.2. Social environment affects singing behavior

Birds which were exposed to a simple social environment sang significantly more than birds which were exposed to a complex social environment, both in total singing (Fig. 1A; repeated measure ANOVA: $F_{(1,28)} = 8.07$; $P = 0.008$), and in undirected one (Fig. 1C; repeated measure ANOVA: $F_{(1,20)} = 5.22$; $P = 0.03$). Direct singing was not significantly different between

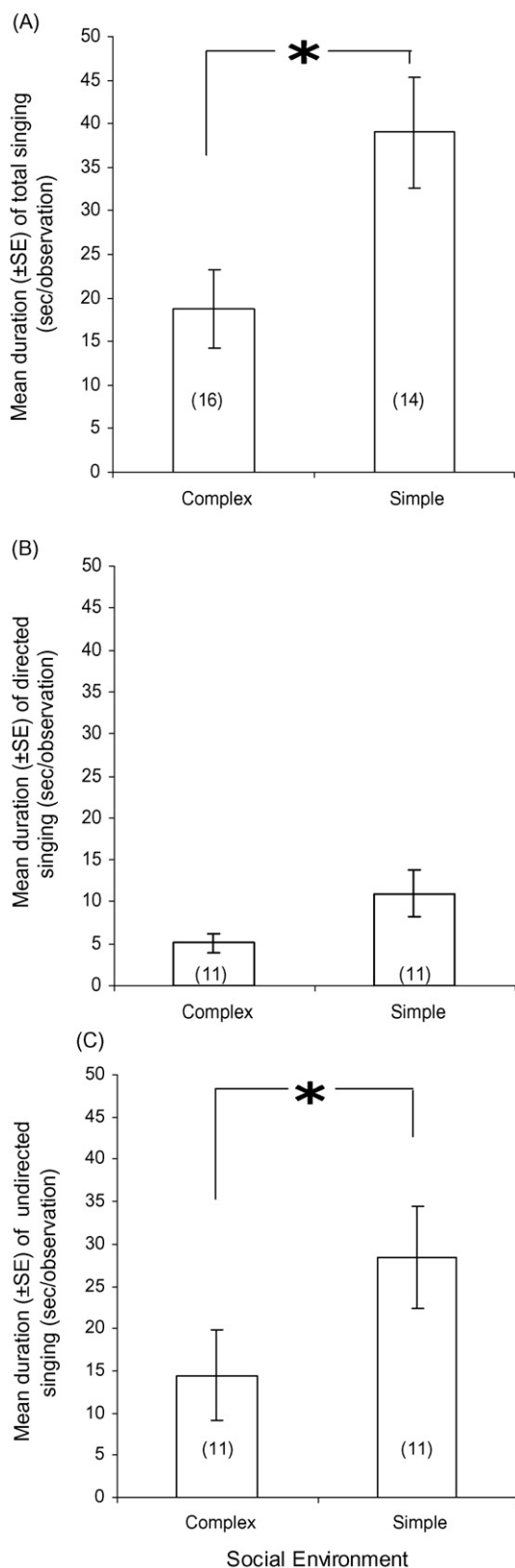


Fig. 1. Mean duration (second/observation \pm S.E.) of total singing (A); directed singing (B); and undirected singing (C), of males which were exposed to different social environment (complex or simple) (* $P=0.008$ in (A) and 0.03 in (C); (N) number of birds).

the two experimental groups, but a non-significant trend, consistent with more singing in simple environments can still be observed (see Fig. 1B; repeated measure ANOVA: $F_{(1,20)} = 3.87$; $P = 0.063$).

3.3. Acclimation to new social environment and singing behavior

Our repeated measure ANOVA model allowed us to test the possible effect of acclimation to the new social environment (days elapsed from exposure to the change) on singing duration, in each of the tested singing types (total, directed, undirected) and in both experimental groups (simple, complex). Since in all singing types no interaction was found between days elapsed from the change and experimental group, data were pooled for the two social environments. The results show that total singing duration increases with time elapsed from social change (Fig. 2A; repeated measure ANOVA: $F_{(2,56)} = 4.56$; $P = 0.015$). Similar analyses carried out separately for direct and undirected singing indicated a similar but weaker trend (Fig. 2B and C; repeated measure ANOVA: directed: $F_{(2,40)} = 2.65$; $P = 0.083$; undirected: $F_{(2,40)} = 3.4$; $P = 0.043$).

3.4. Body mass

No significant differences were found in body mass between experimental groups (mean body weight was 13.2 ± 1.0 g; $N = 34$).

4. Discussion

4.1. Social environment affects singing behavior

The main and somewhat surprising finding of this work is that male zebra finches sing significantly more when they are exposed to a simple social environment, than when they are exposed to a complex one. This significant difference is found when testing the duration of total singing (Fig. 1A), as well as when testing the duration of only undirected singing (Fig. 1C). A similar, though not significant, tendency is found when only directed singing is tested (Fig. 1B). We also found that there is a gradual and significant increase in singing duration as a function of days elapsed from the change in social environment (Fig. 2). This gradual increase suggests that males may need to acclimate to the new social environment before expressing their full potential of singing behavior.

4.2. Implications for neuronal recruitment in the adult brain

The greater significance of our finding is in shading more light at the causes for increased neuronal recruitment which was observed in brains of adult zebra finch males that were introduced to a new complex social environment [5]. As we described in Section 1, this previous study showed that birds placed in a complex social environment recruited significantly more new neurons in their brains than birds kept in pairs. This

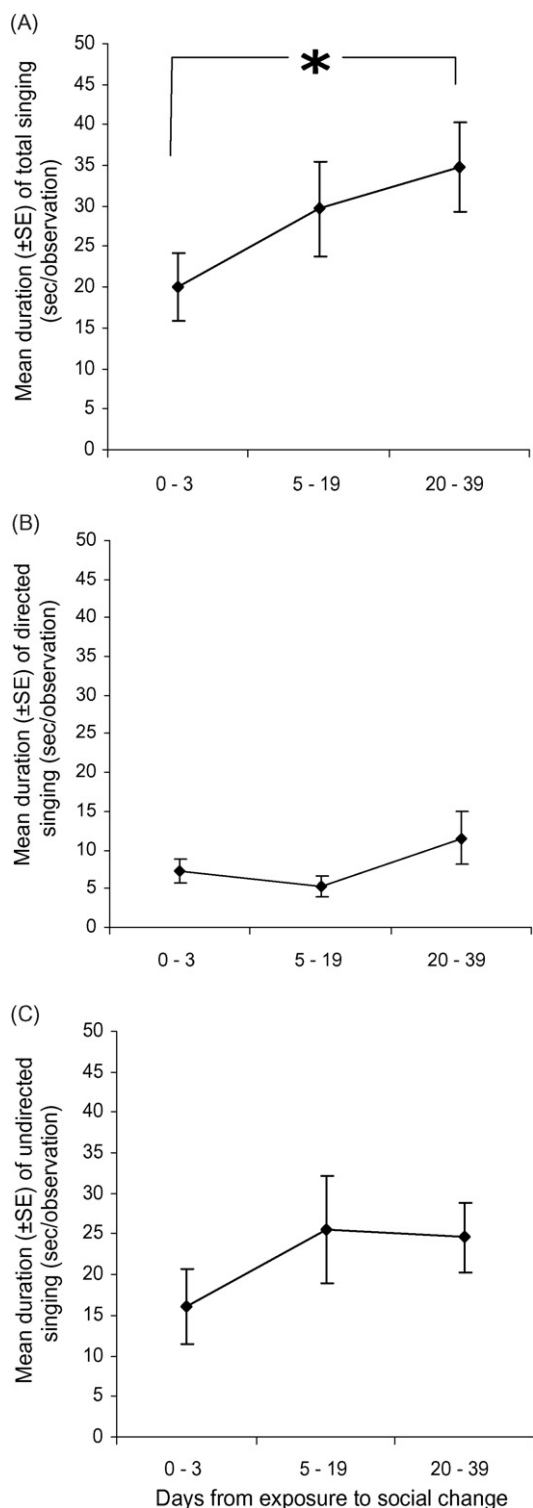


Fig. 2. Mean duration (second/observation \pm S.E.) of total singing (A); directed singing (B); and undirected singing (C), as function of days from exposure to social change. Data of both experimental groups (birds exposed to social and simple environments) is combined ($^*P = 0.01$; N for total and directed singing = 30; N for undirected singing = 22).

difference was found in three brain regions which are known to be involved in vocal communication: nidopallium caudale (NC), high vocal center (HVC) and Area X. The explanation to these findings was that the increase in neuronal recruitment observed

in brains of birds that were placed in a complex social environment resulted from the richer auditory input to which they were exposed, in comparison with the poorer auditory input in the simple environment.

However, this might not be the only possible interpretation, because increased neuronal recruitment can also result from an increase in singing when males are exposed to a new complex social setting. For example, there is an indication that neuronal survival in HVC is greater in singing than in non-singing birds [4]. In Lipkind et al. [5] singing behavior of the experimental males was not documented, and therefore it was not possible to distinguish between the two possibilities. The main goal of our study was to complete the picture, by adding a behavioral aspect to the neurobiological one. If singing behavior is the main positive effect on neuronal recruitment, than it could be expected that males which are exposed to a complex social environment (and had been found to have high neuronal recruitment in their brains) will sing more, while males which are exposed to a simple social environment (and had been found to have lower neuronal recruitment in their brains) will sing less. However, our results show the reverse relation: birds in a complex environment sing less than birds in a simple environment. This outcome rejects the possibility that higher neuronal recruitment is caused by increased singing and supports the suggestion offered in Lipkind et al. [5], that it is due to the richer auditory input in a complex social environment: when being placed in such an environment, birds are exposed to richer new auditory information, in comparison with birds which are placed in a simple environment, where auditory input is poorer. Increased neuronal recruitment in brains of the former group, in regions which are involved in vocal communication, is thought to enable them to process and acquire the large amount of new auditory information, which might be important to their survival.

Nevertheless, it should be acknowledged that alternative hypotheses for the relation between singing behavior and neuronal recruitment cannot be completely ruled out. This is because the social dynamics in a large group must be very different from those of a single pair of birds. For example, in a complex social environment other factors, such as the question of who the song is directed at, and its possible use for manipulating the behavior of other individuals, also play a role. Or perhaps neuronal recruitment might be affected not only by song duration (as measured in this study), but also by its complexity. Obviously, such factors are very hard to be reliably documented when observing an aviary containing many birds, as was the case in our study. Therefore, for reasons explained in Section 2, we did not analyze them, and do not have the tools to discuss these possibilities here.

Another factor to be considered when discussing our results and their implication on neuronal recruitment is the possibility that a pair situation might be stressful to a social bird such as the zebra finch. To our knowledge, there is no evidence for an effect of stress on neuronal recruitment in birds, as was recorded in mammals [3]. Moreover, body mass of our birds at the end of the experiment did not differ between groups, and was also similar to that of wild birds [9]. From this we infer that all birds in our study remained in good general health.

Therefore, taken together, we conclude that the higher neuronal recruitment observed by Lipkind et al. [5] in brains of group-housing birds, in regions which are involved in vocal communication, is probably due to the rich auditory input in this environment, and enables the processing of this large amount of new information.

4.3. Possible reasons for differential singing in different social environments

The outcome that males which are exposed to a simple social environment sing significantly more undirected songs than males exposed to a complex one (Fig. 1C) might be explained by agonistic activities, which are more common in the latter than in the former ([5]; Adar, unpublished data). These agonistic activities might interfere with singing, or take time which otherwise could have been used for singing. Another possible explanation is stress, which is caused by agonistic activities [8] and might have a negative effect on singing behavior. Thus, a male in a complex social environment, which presumably is more stressed compared with a male in a simple social environment, would sing less.

Undirected singing is produced in several events: near the nest, as well as in wide social contexts, and also when the male is alone. Zebra finches live in large flocks, and therefore our experimental manipulation of keeping a male with only one female ('simple environment') was probably not natural. As a result, it could be that these males were more motivated to look for other finches than males which were kept with many more conspecifics ('complex environment'), and that this higher motivation was expressed by more undirected singing in the formers compared with the latter. Support for this suggestion comes from a few cases in our study in which males from the simple environment group were left without the female. Their scores were not included in the statistical analysis, but they seem to sing even more undirected songs than males from the same group that had female partners. Another supporting evidence comes from a study conducted in the wild [2], which showed that during the non-breeding season the male sings more when its mate is absent, compared with when the female is near. If the female returns or the male forms a pair with another female, his undirected singing decreases again. From all this we conclude that a male with less social and coupling options is more motivated to sing undirected songs, probably for self advertising and for finding social companions, than a male which is surrounded by other male and female zebra finches.

Directed singing did not differ significantly between males exposed to a complex social environment and males exposed to a simple one (Fig. 1B). This can be explained by the fact that directed song is produced while courting a female, and experimental males from both groups had the opportunity to do so. We could not determine actual pair bonding which resulted in breeding, because, as mentioned above, nest boxes were not available in the aviaries. However, there were indications that some males (though not all), from both groups, formed pair bonds with females. These indications are based on observing

behaviors as alopeening between an experimental male and a female, and sometimes mating.

The significant difference in total singing (directed and undirected; Fig. 1A) between males in a simple social environment and males in a complex one is probably due to pooling undirected singing which is more commonly produced and showed a significant difference between the two experimental groups, and directed singing which is less produced and did not show a significant difference between the two groups, but did show the same tendency as the undirected singing.

4.4. Overview

The aim of our study was to determine whether differential neuronal recruitments, which were previously observed in brains of birds that were exposed different social environments, can be explained by either input of vocal stimulus or by output of such stimulus. We found out that birds which were exposed to a simple social environment sang significantly more than birds which were exposed to a complex one. This supports our hypothesis that increased neuronal recruitment in the latter correlates with processing and storing of auditory input, and not with song produced by the bird.

However, as discussed above, other factors (such as who the song is directed at, possible use of song for manipulating the behavior of other individuals, effect of song complexity on neuronal recruitment) might also be important. Such aspects were not included in our present study, and it would be interesting to investigate them in future studies. In addition, we believe that the current study emphasizes the importance of combining behavioral observations with neurological ones, in order to fully understand which environmental factors might affect observed changes in the brain. Furthermore, the present study demonstrates how important it is to try conducting, as much as possible, neuroethological research in the correct behavioral context for the investigated species.

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