

Human-like brain hemispheric dominance in birdsong learning

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Unlike nonhuman primates, songbirds learn to vocalize very much like human infants acquire spoken language. In humans, Broca's area in the frontal lobe and Wernicke's area in the temporal lobe are crucially involved in speech production and perception, respectively. Songbirds have analogous brain regions that show a similar neural dissociation between vocal production and auditory perception and memory. In both humans and songbirds, there is evidence for lateralization of neural responsiveness in these brain regions. Human infants already show left-sided dominance in their brain activation when exposed to speech. Moreover, a memory-specific left-sided dominance in Wernicke's area for speech perception has been demonstrated in 2.5-mo-old babies. It is possible that auditory-vocal learning is associated with hemispheric dominance and that this association arose in songbirds and humans through convergent evolution. Therefore, we investigated whether there is similar song memory-related lateralization in the songbird brain. We exposed male zebra finches to tutor or unfamiliar song. We found left-sided dominance of neuronal activation in a Broca-like brain region (HVC, a letter-based name) of juvenile and adult zebra finch males, independent of the song stimulus presented. In addition, juvenile males showed left-sided dominance for tutor song but not for unfamiliar song in a Wernicke-like brain region (the caudomedial nidopallium). Thus, left-sided dominance in the caudomedial nidopallium was specific for the song-learning phase and was memory-related. These findings demonstrate a remarkable neural parallel between birdsong and human spoken language, and they have important consequences for our understanding of the evolution of auditory-vocal learning and its neural mechanisms.

left-brain activation | hemispheric specialization | *Taeniopygia guttata* | language evolution

There are remarkable similarities between the acquisition of human speech and avian song learning. Like human infants, songbirds learn their vocalizations from an adult tutor during a sensitive period early in life, and in both cases, there is a transitional "babbling" phase that precedes adult vocalizations (1–3). Such vocal imitation has been demonstrated in humans, certain marine mammals, bats, and three avian taxa (songbirds, parrots, and hummingbirds), but it seems to be absent in our closest relatives, apes (1, 4). Furthermore, the regions of the songbird brain involved in vocal production and auditory perception are analogous to the brain regions that are important for producing and understanding speech in humans (1, 2, 5).

The caudomedial nidopallium (NCM) of songbirds (Fig. 1A) is thought to be the avian equivalent of the human auditory association cortex in the temporal lobe, including Wernicke's region (1, 6) (Fig. 1C). In addition to a general role in auditory perception (7), the NCM is involved in auditory memory (8). Specifically, the NCM is thought to contain (part of) the neural substrate of the memory of the tutor song (1, 6–13). In contrast, the premotor nucleus HVC (a letter-based name; Fig. 1B) plays an important role in song production and sensorimotor learning

(14–17), and may thus be functionally analogous to Broca's area in the human frontal lobe (1, 2, 6) (Fig. 1C). Thus, similar to the functional dissociation between Broca's and Wernicke's areas in humans, vocal production and auditory perception and recognition are subserved by distinct regions in the songbird brain (9). It is well documented that human speech- and language-related neural activity occurs predominantly in the left hemisphere. Left-sided dominance of temporal lobe activation (including Wernicke's area) could already be demonstrated in neonates who were exposed to speech (18). In addition, in older babies who are in the early babbling phase, exposure to speech evokes a left-dominant activation pattern of Broca's area (19).

To investigate whether there is lateralization in the NCM and HVC in songbirds, we measured brain activation in response to tutor song exposure in both juvenile and adult zebra finches (*Taeniopygia guttata*). First, we exposed juvenile male zebra finches that were in the middle of their sensorimotor song-learning (babbling) phase (mean age of 56 d, range: 54–59 d) to songs of their father, songs of an unfamiliar conspecific, or silence. After stimulus exposure, the birds were perfused and the brains were processed with immunocytochemistry to label Zenk, the protein product of the immediate early gene *ZENK* (an acronym of *zif-268*, *egr-1*, *ngf-1a*, and *krox-24*) (20). The degree of expression of Zenk is a marker for neuronal activation (7, 20). We quantified the number of Zenk-immunopositive neurons bilaterally in the NCM and HVC as well as in the hippocampus, a brain region that has not previously been implicated in birdsong.

Results

The juveniles had already learned parts of their father's song, as measured in the morning before stimulus exposure [similarity score: $58.5 \pm 4.1\%$ (SEM) to the tutor song, which was significantly greater than similarity to an unfamiliar conspecific song: $44.9 \pm 2.8\%$ (SEM); $t(11) = 2.5$, $P = 0.029$]. There was no significant difference between the mean similarity score in the tutor, novel, and silence groups [$F(2,11) = 0.074$, not significant (n.s.)]. Fig. 2 contains representative photomicrographs of Zenk expression, whereas the mean number of Zenk-immunopositive neurons for the different groups is shown in Fig. 3. Because the Zenk expression values were not normally distributed, we first log-transformed the data. An overall repeated-measures ANOVA revealed a significant effect of brain region [$F(2,11) = 4.592$, $P = 0.035$] and a significant interaction between brain region and hemisphere [$F(2,11) = 22.617$, $P < 0.001$]. We

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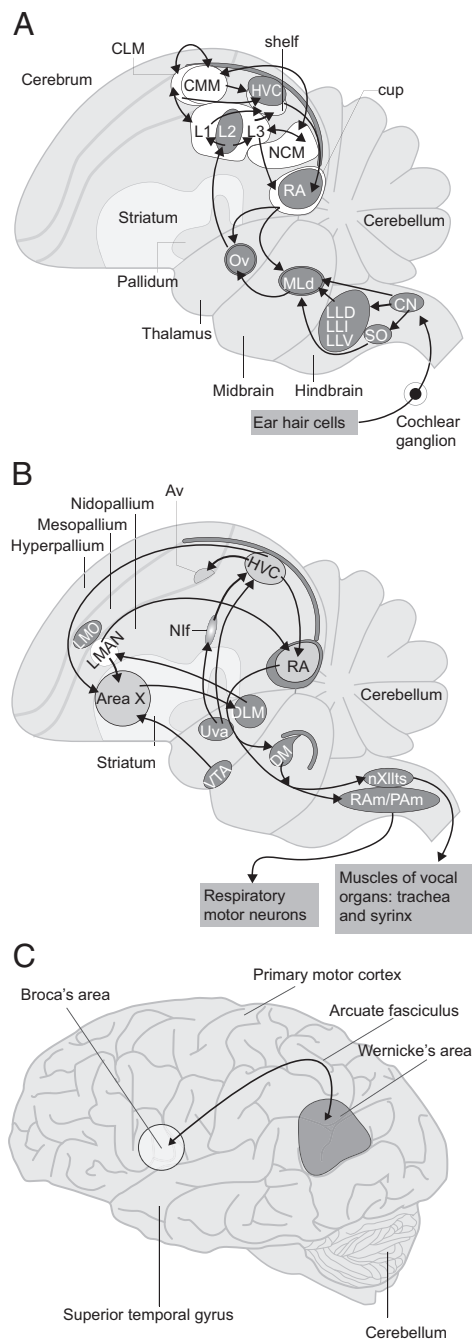


Fig. 1. Schematic side views of the songbird (A and B) and human (C) brain. (A) Regions depicted in a light shade show increased neuronal activation when the bird hears song. The NCM and CMM regions are assumed to contain the neural substrate for tutor song memory. (B) Nuclei HVC, Av, RA, LMAN, and Area X show increased neuronal activation when the bird is singing. (C) In the human brain, Broca's area is most importantly involved in speech production, whereas Wernicke's area is mainly involved in speech perception and understanding. Modified from Moorman et al. (20). Area X, area X of the striatum; Av, avalanche; CLM, caudolateral mesopallium; CMM, caudomedial mesopallium; CN, cochlear nucleus; DLM, medial subdivision of the dorsolateral nucleus of the anterior thalamus; DM, dorsomedial subdivision of the nucleus intercollicularis of the mesencephalon; L1, L2, and L3, subdivisions of field L; LLD, lateral lemniscus, dorsal nucleus; LLI, lateral lemniscus, intermediate nucleus; LLV, lateral lemniscus, ventral nucleus; LMAN, lateral magnocellular nucleus of the anterior nidopallium; LMO, lateral oval nucleus of the mesopallium; MLd, dorsal part of the lateral nucleus of the mesencephalon; Nif, interfacial nucleus of the nidopallium; nXIIIts, tracheosyringeal portion of the nucleus hypoglossus (nucleus XII);

conducted subsequent analyses on the results for each of the three brain regions. There was a significant effect of hemisphere in the NCM in juveniles [$F(1,20) = 13.284, P = 0.002$]. Moreover, there was a significant interaction between stimulus and hemisphere [$F(2,20) = 4.400, P = 0.026$]. In particular, responsiveness to the father's song was greater in the left NCM than in the right NCM [paired t test, $t(7) = 3.314, P = 0.013$; Bonferroni-corrected $\alpha = 0.01667$], but there was no such left-sided dominance in response to novel song or in silence. Thus, lateralized neuronal activation in the NCM of juveniles was memory-specific. In view of this result, we subsequently investigated whether the degree of lateralization was related to the quality of song imitation. We only had song recordings from the preexperimental day for five of the juveniles in each of the tutor and silence groups and six juveniles in the novel group; thus, the results shown in Fig. 4 are preliminary. Nevertheless, we found that the lateralization ratio ($[L - R]/[L + R]$; *Materials and Methods*) was positively correlated with the degree of song similarity between tutor and tutee in the juvenile zebra finches that were exposed to tutor song ($r = 0.900, P = 0.037; n = 5$) (Fig. 4). There was no significant correlation in the novel and silence groups. In addition, there was a significant difference between the correlations in the three experimental groups (Fisher r -to- z transformation, Q value = $6.689 > \chi^2 5.99$). The absolute level of activation in the left NCM in the tutor group was not significantly correlated with song similarity, suggesting that the strength of song learning was related to lateralization specifically, and not to absolute left-sided neuronal activation.

In the HVC of the juvenile male zebra finches, we found that neuronal activation was significantly greater in the left hemisphere than in the right hemisphere [$F(1,14) = 46.061, P < 0.001$]. However, there was no significant effect of stimulus in the HVC [$F(2,15) = 1.114, n.s.$]. This means that the left HVC was activated spontaneously, irrespective of the stimulus presented, and even though these birds had not sung for at least 4 h before neuronal activation was measured. The levels of neuronal activation in the hippocampus did not differ between stimulus groups or hemispheres.

In a separate experiment, we investigated lateralization of neuronal activation in response to song in adult songbirds. These birds showed significant imitation of the song of their fathers [song similarity to the tutor song: 69.2 ± 3.44 SEM, which was significantly greater than similarity to an unfamiliar conspecific song: 45.5 ± 3.57 SEM; $t(14) = 5.809, P < 0.001$]. There was no significant difference between the mean similarity score in the tutor and in silent groups [$t(13) = 0.302, n.s.$]. The mean number of Zenk-immunopositive neurons for the two groups is shown in Fig. 3, whereas Fig. 5 contains representative photomicrographs of Zenk expression patterns. Although there was a significant difference between the response to father's song and to silence in the NCM [$F(1,30) = 5.191, P = 0.040$], there was no significant interaction between stimulus and hemisphere, and there was no significant difference between neuronal activation in the left and right NCM. Similar to the results in juveniles, in the adult zebra finches, there was left-sided dominance in the HVC irrespective of the stimulus presented [$F(1,30) = 5.789, P = 0.032$]. In the hippocampus, we found basal levels of neuronal activation that did not differ between stimulus groups or hemispheres.

Discussion

By comparing neuronal activation patterns in response to song playback, we revealed left-hemispheric dominance in both a

Ov, nucleus ovoidalis; PAm, nucleus para-ambiguus medullaris; RA, robust nucleus of the arcopallium; RAm, nucleus retroambiguus medullaris; SO, superior olive; Uva, nucleus uvaeformis; VTA, ventral tegmental area.

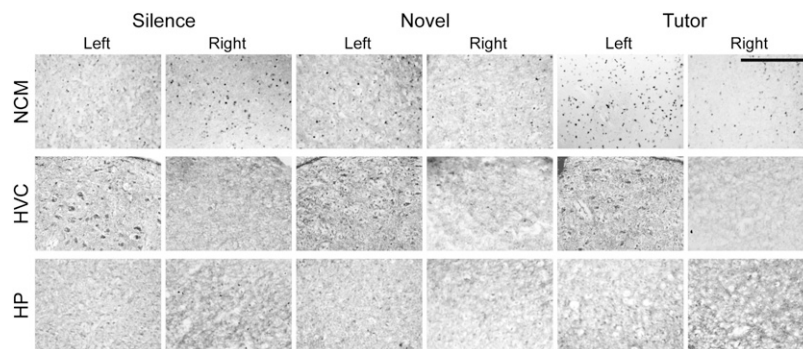


Fig. 2. Photomicrographs of juvenile zebra finch brains showing Zenk immunostaining. Representative images at the level of the NCM, HVC, and hippocampus (HP) are shown for the silence, novel, and tutor stimulus groups. (Scale bar: 0.2 mm.)

Wernicke-like region (NCM) and a Broca-like region (HVC) in zebra finches that is similar to the brain lateralization associated with human speech and language. We found left-sided dominance in the NCM of young zebra finches that were exposed to their father's song, reminiscent of the early left-sided dominance of temporal brain regions that is found in human infants (21, 22). Moreover, we demonstrated that the lateralized response in the NCM is memory-specific, because lateralization only occurred when the juveniles were exposed to their father's song and not when they were exposed to unfamiliar conspecific songs or to silence. Similarly, in a functional MRI (fMRI) study in 2.5-month-old infants, exposure to the mother's voice was shown to elicit greater neural activation than exposure to an unfamiliar voice in the left temporal lobe but not in the right temporal lobe (23). Repetition of speech stimuli decreased the initial strong response in the left temporal lobe but did not affect activation in the right hemisphere (23), showing memory-specific activation in

the left temporal lobe. Thus, the present results in songbirds are similar to memory-related left-sided dominance of Wernicke's area in human infants. In human adults who are exposed to speech, Wernicke's area in the left hemisphere is more active than the corresponding area in the right hemisphere (22). Furthermore, the left superior temporal sulcus shows a suppressed response when the same sentence is repeated (24), similar to repetition suppression in young infants (23). In contrast, in our experiment in adult zebra finches, we found no significant difference in neuronal activation between the left and right NCM. In other studies, lateralization of auditory processing in the NCM was found in adult zebra finches (25–29), although the direction of lateralization that was found differs among studies. Apart from the different methodology that was used in these studies (electrophysiology, aromatase inhibition, or fMRI), in contrast to the present study, memory-related lateralization was not investigated.

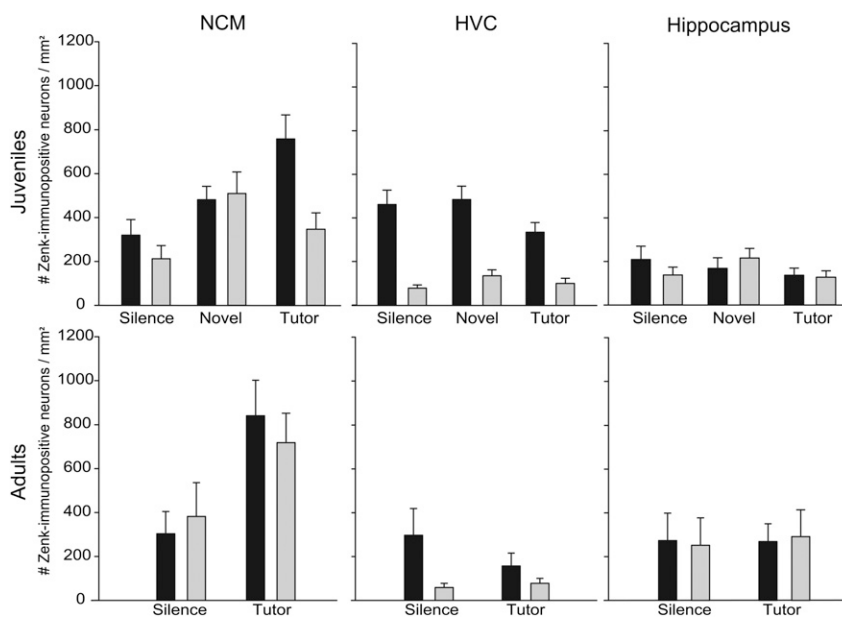


Fig. 3. Zenk expression in the brains of juvenile and adult male zebra finches. (Left to Right) Mean number of Zenk-immunopositive neurons per square millimeter is shown for the different brain regions. (Upper) Results for juvenile male zebra finches are shown. There is left-sided dominance in the NCM of juveniles in response to tutor song but not to novel song or silence. In the HVC, there is left-sided dominance irrespective of the stimulus presented. The levels of neuronal activation in the hippocampus did not differ between stimulus groups or hemispheres. (Lower) Results for adult male zebra finches. The mean activation level is higher in the NCM of adult zebra finches that were exposed to tutor song than to silence, but there is no difference between the hemispheres. There is left-sided dominance in the HVC, irrespective of the stimulus presented, similar to the juveniles. The levels of neuronal activation in the hippocampus did not differ between stimulus groups or hemispheres. Black bars represent the left hemisphere, and gray bars represent the right hemisphere. Error bars represent the SEM.

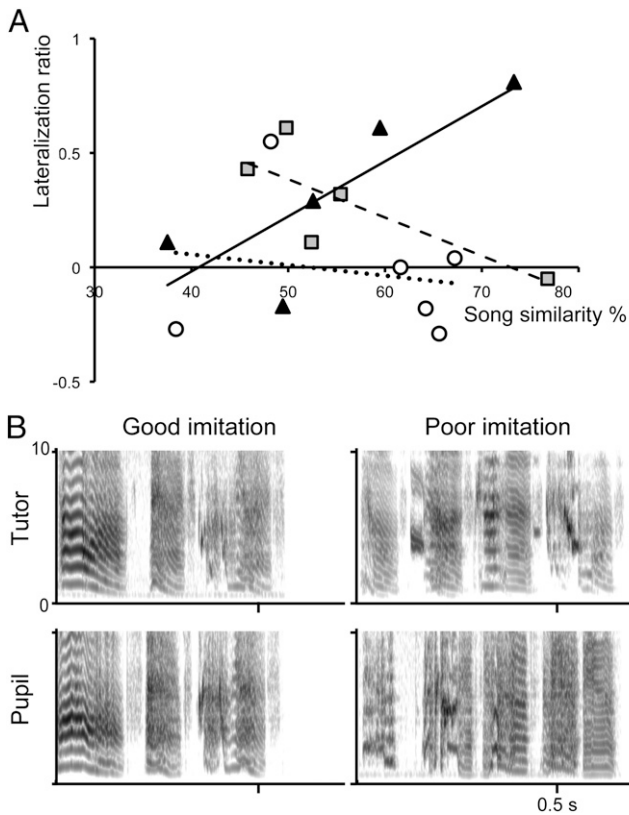


Fig. 4. Correlation between lateralization ratio and degree of song similarity. (A) Lateralization ratios ($[L - R]/[L + R]$) were calculated for each subject from the number of Zenk-immunopositive cells per square millimeter in the NCM of juvenile zebra finches and were correlated with song similarity scores. In the birds that were exposed to tutor song (\blacktriangle), the correlation was significant (solid line, plotted by linear regression, $R^2 = 0.67$). There were no significant correlations in the novel (\circ , dotted line) or silence (\square , dashed line) group. (B) Spectrograms of juveniles that produced a good or poor imitation of their tutor's song. (Lower Left) Juvenile had a song similarity of 73.3% with its tutor. (Lower Right) Juvenile had a song similarity of 49.4% with its tutor.

The left-sided dominance of HVC activation in adult and juvenile male zebra finches in the present study was not caused by exposure to the stimulus songs or by the subjects singing themselves. The unexpected activation of the left-sided HVC in the silence group might reflect off-line song processing. Most birds

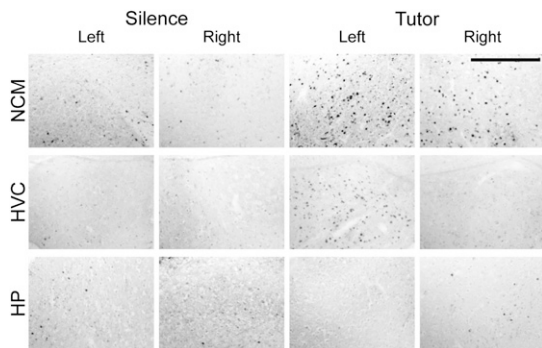


Fig. 5. Photomicrographs of adult zebra finch brains showing Zenk immunostaining. Representative images at the level of the NCM, HVC, and hippocampus (HP) are shown for the silence and tutor stimulus groups. (Scale bar: 0.2 mm.)

were kept in the dark until the stimulus was presented, and they may have slept. Electrophysiological studies have demonstrated that the HVC shows spontaneous neuronal activity during sleep, similar to the activity recorded during singing (30–32). Thus, in the present study, a similar process may have occurred, which would then be limited to the left hemisphere. To investigate further what causes spontaneous left-sided activation in the HVC, our experiment could be repeated in, for example, canaries (*Serinus canarius*), where, less ambiguously than in the zebra finch, neuronal activation related to song production is found to be lateralized to the left HVC (33, 34). Although there are several reports of HVC lateralization in zebra finches, most of them were concerned with neural activity during song production, or only perception (and not memory-related activation) was studied.

In 3-mo-old human infants (19) or 4- to 12-y-old human children (35) who were exposed to speech, left-sided dominance of Broca's area was found. In human adults, Broca's area in the left hemisphere was activated during syntactic processing of speech (22). Also, in adults who learned a new language, Broca's area in the left hemisphere was activated (36). The left-sided dominance of the HVC in juvenile and adult zebra finches is similar to lateralization of Broca's area in humans in this respect. However, fMRI studies did not show spontaneous lateralized responsiveness in Broca's area in either infants or adult humans (37–40).

There are conflicting reports on lateralization in nonhuman primates, which do not show vocal learning. In macaques, left-sided dominance of the superior temporal gyrus was found for species-specific sounds (41, 42), but others found no lateralization in either the Broca- or Wernicke-homolog (43). In contrast, right-sided dominance of the superior temporal gyrus for species-specific sounds was reported for chimpanzees (44). In the visual domain, memory-related left-hemispheric dominance has been reported for filial imprinting in domestic chicks (45), similar to the present results in juvenile zebra finches. In an extensive series of studies, Horn and collaborators (45) found that the left intermediate and medial mesopallium (IMM) shows greater memory-related activation (measured in a number of ways, including the size of the postsynaptic densities and NMDA receptor binding) than the right. Horn (45) has suggested that the left IMM acts as a permanent store, whereas the right IMM relays to an additional storage system dubbed S', which lies outside the IMM and is important for temporary memory storage between 4 and 6 h and at least 26 h after imprinting training (45).

Minagawa-Kawai et al. (46) suggested that human language lateralization might arise as a result of both preexisting left-right biases for aspects of generic auditory processing and left-sided language-learning mechanisms. In the present study, the left NCM showed greater activation for memory-specific auditory stimuli in juveniles specifically. An interesting possibility is that there is a temporal left-sided dominance associated with song memory formation early in development, which disappears once the memory is formed. That we do not see any lateralization in adult zebra finches could indicate that there is no lateralization bias for general auditory perception, or at least it is not manifest as cellular activation. To test whether it is the case that lateralization is dependent on the song-learning phase, this experiment should be repeated with different developmental groups included in the experimental design. Additionally, it would be interesting to investigate the effect of lesions to the left NCM on song memory compared with right-sided lesions, an experiment that, ideally, should also be conducted in several age groups.

In conclusion, in addition to the behavioral, genetic, and neural parallels that were found between adult songbirds and adult humans (1), our findings suggest that perception of human speech and birdsong shows similar patterns of lateralized brain

activation. Brain lateralization may be a corollary of the auditory-vocal learning that arose in humans and songbirds as a result of convergent evolution (47).

Materials and Methods

Animals. The 22 juveniles in the present experiment had been used in a previous study (13) that was only concerned with the left side of the brain. In addition, 15 adult male zebra finches were used that were bred at the Central Animal Facility of Utrecht University and raised by both parents until 72 d posthatching. The adult males were separated from their tutors at 78 d posthatching and kept in aviaries until the start of the experiment. Preceding the experiment, all birds were housed individually in soundproof chambers for 48 h. Mean age at the day of the experiment was 56 d (range: 54–59 d posthatching) for the juveniles and 37 mo for the adults. Experimental procedures were in accordance with European law and approved by the Animal Experiments Committee of Utrecht University.

Stimuli. As stimuli, we used 10 songs from the same animal. These songs were repeated in random order for a total of 90 song presentations. The playback of the total stimulus lasted an hour. For tutor stimuli, songs of the fathers of the experimental males were used. Novel stimuli were songs of conspecific males that were not present in the aviary during the life of the subjects. The rms amplitude of all songs was equalized, and the average duration of songs used was 2.1 s (sound files were constructed using Praat software; ref. 48).

Experimental Design. On the day of the experiment, the lights were turned on at 6:00 AM. For most juvenile birds ($n = 19$) and all adult birds, the lights were turned off at 8:00 AM to prevent them from singing. The other juvenile birds ($n = 3$) were kept in a room with the lights on but did not sing. At that time, the songs of the young males were recorded to analyze their similarity to the tutor song. Between 11:00 and 12:00 PM, the juvenile birds were exposed to tutor song, novel conspecific song, or silence. The adult birds were exposed to tutor song or silence at 1:30 PM. A more detailed protocol is provided in the study by Gobes et al. (13).

Immunocytochemistry. Thirty minutes after the end of exposure to the stimulus set, the experimental subjects were anesthetized with 0.06 mL of sodium pentobarbital (i.m.) and subsequently perfused with PBS, followed by fixation with 4% paraformaldehyde/PBS. Brains were dissected out and postfixed in 4% paraformaldehyde at 4 °C for 6 h. Parasagittal 20- μ m sections were made on a cryostat and mounted on poly-L-lysine-coated slides. The brains were stained immunocytochemically for *egr-1* (Zenk). A more detailed protocol is provided in the study by Gobes et al. (49).

Image Analysis. Quantification of Zenk-immunopositive cells was performed for NCM, HVC, and hippocampus as described previously (cf. 13, 49, 50). Digital photographs were taken using a Leica DFC 4206 camera and the

Leica Application Suite program on an Axioskop (Zeiss) with a 20 \times objective. The images were taken at the extreme caudal pole of the medial NCM, the center of the HVC nucleus, and the point of the hippocampus at which the curve is most pronounced (cf. 50). Image analysis was performed with a personal computer-based system using KS400 version 3.0 software (Zeiss). A program was developed in KS400 to quantify the number of immunoreactive cells semiautomatically. Counts of three sections for each region in both hemispheres per animal were averaged for further statistical analysis. Image analysis was performed blinded as to the experimental history of the subject.

Song Analysis. For the juveniles, five songs were randomly selected from the last 10 songs that were sung on the day of the experiment just before 8:00 AM; the birds did not sing from the moment the lights were turned off. We recorded the songs of the adult experimental birds between 1 and 12 mo before the experiment. The songs from the tutors and birds were filtered and equalized using Praat software. Sound Analysis Pro (51) was used to assess the fidelity of tutor song imitation of the experimental subjects by calculating the “percentage similarity,” which is a measurement of syllable copying. Based on multiple features (Wiener entropy, spectral continuity, pitch, and frequency modulation), this comparison provides an objective quantification of song similarity (52). Sound Analysis Pro has a “floor effect,” because zebra finch songs always resemble each other somewhat on these features. We thus compared songs from birds in the main experiment with songs from five unfamiliar nontutor birds to investigate whether our zebra finches had learned from their song tutors specifically or if similarity was attributable to general song characteristics.

Statistical Analyses. We log-transformed the data because the values in the left-sided NCM were not normally distributed (z values for skewness and kurtosis >1.96) and the variances were not equal (Levene test, $P = 0.013$). We conducted repeated measures ANOVA to compare the effect of stimulus exposure on the Zenk response in the left and right NCM, HVC, and hippocampus. To test for lateralization effects within the stimuli groups, post hoc paired t tests with Bonferroni corrections for multiple testing were performed. A lateralization ratio was calculated by dividing the difference in Zenk expression levels between the two hemispheres in a brain region by the total amount of Zenk expression of the two hemispheres: $[L - R]/[L + R]$. This lateralization ratio enabled us to look at true lateralization levels not influenced by differences in absolute neuronal activation. We tested for a correlation between the lateralization ratio and song similarity percentage using Spearman’s rho correlation test. Data were analyzed using SPSS 20.0.0 (IBM Corporation).

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