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Lesions of a higher auditory brain area during a sensorimotor period do not impair birdsong learning

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Abstract

One important function of the nervous system is to form and retrieve memories to direct behavior. A prime example of memorization occurs in songbirds when they imitate the songs of another bird heard early in life. Although many brain areas required for song learning have been identified, their separate roles in memory formation and retrieval remain unclear. In juvenile male zebra finches, we test the role of a higher auditory cortical area in memory retrieval. The Caudal Medial Nidopallium (NCM) has previously been shown to be necessary for song memory acquisition and is thus a likely location for holding the memory of tutor song necessary for learning. We extensively exposed young birds to tutor song after which we performed large bilateral lesions in NCM using injection of ibotenic acid. We observed successful song copying in lesioned animals, comparable to song behavior in untreated control birds. Our results show that intact NCM is not required to guide vocal learning based on a previously formed song memory.

Introduction

We studied the organization of memory in the behavior of imitation learning based on observing and copying a conspecific's performance. We focused on birdsong development, which similar to speech development, involves perception and memorization of a sensory stimulus within a critical sensory period [1] [2]. Juvenile zebra finches start to sing subsong (soft vocalizations comparable to the babbling of human infants) typically at an age of 30 days post hatch (dph). Gradually they transform their subsong into a good imitation of the father's song, even if separated from the latter as early as 40 dph [3] [4] [5].

A key brain area that is important for tutor song memorization is the caudal medial nidopallium (NCM). Good tutor song copying correlates with increased NCM neural activation, assessed via either immediate early genes (IEGs) [6] [7] [8] or spiking responses [9] [10]. There is evidence that NCM holds a song memory in adult birds: tutor song recognition and recall of learned song are both impaired after irreversible lesions in NCM [11] [12], the impairment being memory specific because neither motor behavior nor auditory perception is significantly affected by the lesions. Evidence for a necessary role of NCM in tutor memory acquisition in juveniles comes from pharmacological manipulations: IEG suppression specifically during tutoring severely impairs tutor song learning [13], paralleling the IEG requirements for memory formation in rodents [14] [15] [16].

Objective

We investigated NCM's role in recalling of a tutor song memory. We studied the effects of very large irreversible NCM lesions in about 40 dph old juvenile zebra finches that had been extensively exposed to a tutor song prior to the lesions.

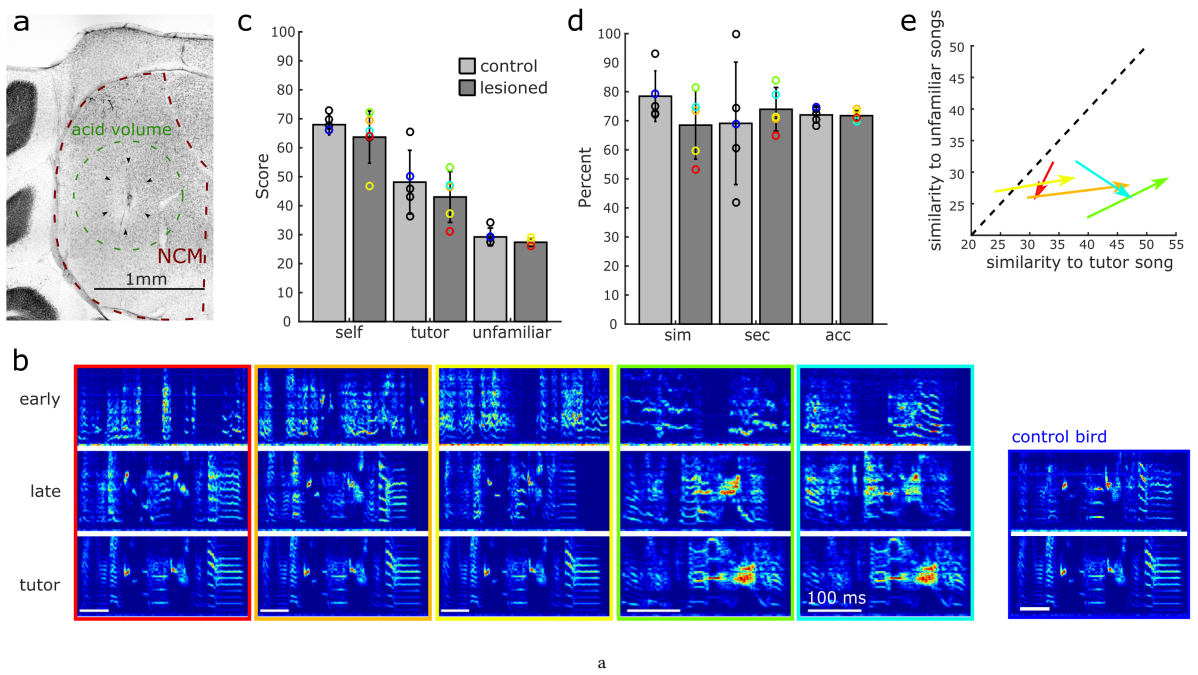


Figure Legend

Figure 1.

(A) Sample sagittal Nissl-stained brain section from an NCM-lesioned bird, confirming the lesion placement (black arrowheads) within NCM (dashed line). Dorsal is up, rostral is right. The green dashed line indicates the volume of the injected acid, providing a lower bound to the initial lesion extent.

(B) Example log-power song spectrograms (red: high sound intensity, blue: low sound intensity) from five NCM-lesioned birds (left) and from one non-lesioned control bird (right, same bird marked in blue in panels C and D). Initially, spectrograms in 43 days post hatch (dph) old juveniles (early, top) look different from spectrograms of tutor song (bottom). However, at 77 dph (late, middle), there is a good visual correspondence between juvenile and tutor song spectrograms. The spectrogram associated with the bird in a is outlined in red.

(C) Average scores of juvenile songs tested for similarity with themselves (self), with tutor songs (tutor), and with unfamiliar songs (unfamiliar). On average, all three similarity scores are indistinguishable between control birds (light gray bars) and NCM-lesioned birds (dark gray bars, mean \pm 1 standard deviation, t-test, $p > 0.05$), which reveals that NCM lesions do not impair song development. The circles represent scores in individual birds, the colors correspond to the colors of outlines delimiting the spectrograms in B.

(D) The songs in 77 dph NCM-lesioned birds and of age-matched control birds exhibit similar averages of percent similarity, of sequential match, and of accuracy relative to their tutors' songs (i.e., the 3 measures that define the similarity score in C): all three comparisons yield $p > 0.05$ (t-test).

(E) Between 43 and 77 dph, the songs in NCM-lesioned birds typically change (arrows) in the direction of higher similarity with their tutors' songs (horizontal) rather than with songs in unfamiliar birds (vertical).

A total of 26 male zebra finches (*Taeniopygia guttata*) from our breeding facility were used, 5 were lesioned, 5 were used as controls, 4 were used as tutors, and the other 12 were unfamiliar adult birds whose previously recorded songs were compared with those of the juveniles.

Birds

Birds were normally raised with both parents until 35–40 days post hatch (dph), giving them enough exposure to song for successful memorization [4]. At 41 ± 1 dph (range 40–42 dph, $N = 5$), birds received large bilateral excitotoxic lesions targeting NCM; lesions were made as previously described [12]. Thereafter, control and lesioned animals

were housed in sound attenuation chambers (IAC GmbH) on a 14/10 hours day/night schedule with ad libitum access to food and water.

Surgeries

Briefly, birds were anesthetized with isoflurane and head fixed in a stereotaxic apparatus. In each hemisphere they received 500 nl ibotenic acid solution (7 mg/ml in ddH₂O) delivered either in a single or in two injections between 1,500 and 2,500 μm ventrally from the brain surface (two injections to extend the lesioned area in the ventral direction). Injections were made at about 750 μm anterior to the bifurcation of the mid-sagittal sinus (751±48 μm, *N* = 5), and about 450 μm lateral from the midline (438±76 μm, *N* = 5). This same injection protocol was previously used in adults [12] and proved to be effective in lesioning a volume of NCM comparable in size to the injected amount of neurotoxic solution. The acid volume we injected per hemisphere (500 nl) is equally large as volumes injected in [13] (500 nl) and in [12] (500 nl), and much larger than volumes injected in [11] (110 nl). All birds resumed normal behavior within a few hours after surgery. After observing that lesions did not cause any major learning impairment, we decided that sham injections as controls would be unnecessary.

Histology

All birds with lesions were perfused at either 76 dph (*N* = 2) or 80 dph (*N* = 3). Birds were given an overdose of sodium pentobarbital, followed by perfusion via the left ventricle first with ringer solution, followed by 4% paraformaldehyde solution. To visualize cell bodies, sagittal sections were cut from fixed brains and Nissl stained with cresyl violet. In figure 1A, the volume of the injected acid is shown to indicate the initial lesion size. Based on the large volume and medial-posterior location of our injections we estimate that our lesions encompassed the regions targeted in previous NCM studies [9] [8] [11] [13].

Song motif selection and analysis

From all birds, we randomly extracted 20 song motifs recorded typically during the first few morning hours. All juveniles' song motifs were recorded at 76.6±2.5 dph (range 72–82, *N* = 27). For sufficiently developed songs (all adults and most of the juveniles), a stereotyped sequence of syllables (a song motif) was identified and only renditions of that sequence were extracted for the subsequent analysis. In poor learners and in birds in an early stage of song development, a stereotyped song motif could not be clearly identified; in these birds we extracted 'song motifs' as sequences (of comparable length) of syllables which represented most of the bird's vocal range (examples of such subsong "motifs" are shown in Figure 1b). Song motifs from juveniles and adults were compared to each other using Sound Analysis Pro (SAP) 2010b [17] and the results were further analyzed with custom Matlab scripts (Mathworks Inc). For each pair of birds, we assessed song similarity by averaging the 400 similarity scores (each ranging 0–100) resulting from pairwise comparison between each bird's 20 song motifs. The consistency of our choice of song motifs, as well as the stereotypy of such motifs (song crystallization), was tested by calculating for each bird the 380 similarity scores among its own 20 motifs, excluding comparisons of identical motifs. One of the 12 additional adult birds used to evaluate similarity to unfamiliar songs (that is, not a tutor) was discarded from the analysis because of low self-similarity (mean similarity score 54.8±8.0). For the remaining adults, average self-similarity scores ranged from 70.9 to 88.5 (mean 80.7±5.3, *N* = 15), which is well above all tutor-pupil similarities observed in our experiments and also above reports in the literature [5] [18] [13] [19] [20]; standard deviations of self-similarity scores ranged from 1.3 to 9.5 (mean 4.4±2.5, *N* = 15). To visualize songs we computed log-power sound spectrograms, which are time-frequency representations of sound intensity.

Note on Sound Analysis Pro (SAP)

SAP compares two songs using normalized sound features such as Wiener entropy, spectral continuity, pitch, and frequency modulation. Based on these features, SAP identifies segments in the pupil song that best match segments in the tutor song. The similarity score computed in SAP combines three different measures: percent similarity, sequential match and accuracy. Percent similarity corresponds to the fraction of segments in the tutor song for which a matching segment in the pupil song was found, or in other

words it reflects the fraction of the song that has been copied by the pupil. The accuracy measures the local similarity by comparing the song features frame by frame, and sequential match measures the temporal order of matching song segments. The similarity score is the sum of the partial similarities of the selected sections. The procedure is explained in detail in [17]. **Results & Discussion**

Birds were normally raised with their parents until about 40 days post hatch (dph), after which they were housed individually with no further exposure to tutor song. Hence, we made use of the fact that song learning is based on a memory of the father's song which had already been acquired before 40 dph. We investigated the role of NCM in recalling this memory to guide song learning during the sensorimotor period of birdsong development. If NCM stores the tutor song memory used as a template for learning, then the developed songs of NCM-lesioned birds would be impaired compared to the developed songs in control animals.

At 42 dph the juvenile birds received large bilateral lesions in NCM. Before the lesions, juveniles produced highly variable vocalizations (mean self-similarity score 38.0 ± 6.7 , range 26.1–41.7, $N = 5$ birds) with little resemblance to the tutor song (mean similarity score 33.0 ± 6.4 , range 24.0–39.8, $N = 5$ birds). At the end of the experiments, birds (76–78 dph) produced highly stereotyped song motifs (mean self-similarity score 63.7 ± 10.0 , range 46.7–72.4, $N = 5$ birds) comparable to song stereotypy in control birds that had not received any treatment (68.0 ± 3.5 , range 63.6–72.8, $N = 5$, $p = 0.34$, t-test, Fig. 1C). Most importantly, motifs of lesioned birds were good copies of their tutors' motifs: The mean similarity score in NCM-lesioned birds at 75 dph was 43.0 ± 8.8 (range 31.1–53.2, $N = 5$ birds) comparable to the mean similarity score in age-matched controls (48.1 ± 11.0 , range 36.2–65.6, $N = 5$ birds, $p = 0.44$, t-test, example in Fig. 1B, summary in Fig. 1C). None of the individual similarity measures (% similarity, sequential match, and accuracy) significantly discriminated by itself between lesioned and non-lesioned birds ($p = 0.17$, range 0.64–0.86, t-test, Fig. 1D).

We tested whether the observed increase in motif similarity between NCM-lesioned birds and their tutors could be explained simply by pupils' songs becoming more similar to wild-type zebra finch song rather than specifically to the tutors' songs. We calculated similarity scores between pupils' motifs and those of 14 unfamiliar adult birds, both at the beginning and at the end of the experiment. At 43 dph, the average similarity scores with unfamiliar songs was 27.81 ± 3.86 (range 22.79–31.76, $N = 5$ birds), and at the end of the experiments (76–78 dph) the average score was similarly low, 27.62 ± 1.40 (range 26.15–29.02, $N = 5$ birds, $p = 0.92$, t-test, Fig. 1E), significantly lower than the average similarity score with tutor song ($p = 0.002$, t-test). In comparison, the similarity between the controls' songs and the songs of unfamiliar adults was also significantly lower (29.2 ± 3.0 , range 26.1–34.2, $N = 5$ birds) than the similarity between the controls' songs and tutor songs (Fig. 1C, $p = 0.006$, t-test). This persistence of low similarity scores with unfamiliar songs demonstrates that songs in NCM-lesioned birds developed specifically toward their tutors' songs rather than nonspecifically toward generic zebra finch songs. In summary, despite the very large lesions made, birds successfully developed a good copy of their tutors' songs.

Conclusions

The observed post-lesion convergence of pupils' songs toward their tutors' songs reveals that NCM is necessary neither for retrieving a tutor song memory nor for long-term storage of that memory. Additionally, successful song learning in NCM-lesioned birds indicates that NCM is not necessary for any of the sensorimotor functions required for song learning. Given the reported involvement of NCM in tutor song memorization [13], we conclude that NCM's role in song memorization is restricted to the process of memory acquisition, after which the memory may be consolidated elsewhere in the song control system. At the very least, there must exist another song memory outside of NCM which birds can use to shape their developing songs.

Limitations

In [12] it was reported that the apparent lesion size visible after Nissl staining shrinks with time. We found a similar effect of the visible lesions at 75 dph (Fig. 1A) being much smaller than the injected acid volumes, which limited our ability to verify the extent of the initial lesion.

Additional Information

Methods

A total of 26 male zebra finches (*Taeniopygia guttata*) from our breeding facility were used, 5 were lesioned, 5 were used as controls, 4 were used as tutors, and the other 12 were unfamiliar adult birds whose previously recorded songs were compared with those of the juveniles.

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Supplementary Material

Please see <https://sciencematters.io/articles/201603000018>.

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Ethics Statement

All the experimental procedures were in accordance with the Veterinary Office of the Canton of Zurich.

Citations

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