2pAB12. A neuroethological analysis of the information in propagated communication calls.
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The detection and recognition of communication signals in natural soundscapes is a difficult task that animals and birds in particular excel at. We have used a neuroethological approach to quantify the recognition performance for propagated communication signals in the zebra finch, specifically regarding the information about individual identity. The propagated signals were analyzed using a regularized discriminant function analyses on a complete spectrographic representation of the signals. We found 1) a reduction in the informative frequency range a long distances yielding a frequency band sweet-spot, 2) that call duration and pitch are important parameters at short distances and 3) that frequency modulation gains are important parameters at longer distances. Operant conditioning experiments showed that female songbirds were able to discriminate male calls at up to 128m but not at 256m. Finally, neurophysiological recordings showed a similar pattern in that high neural discrimination for calls was observed at 16 m and that this information degraded as a function of distance. We are currently analyzing the tuning properties of neurons that showed the most invariant responses to propagated sounds and hypothesized that these will be tuned to the parameters that we found were the most informative in the discriminant function analysis.

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INTRODUCTION

As communication sounds propagate though the environment, the quality of the signal is systematically degraded. It has been very well documented that as a function of distance not only will the signal to noise ratio decrease but that the signal characteristics themselves can change as a result of absorption, scattering and refraction by the environment [1]. As a result the information bearing features in communication signals might be severely compromised. Nonetheless, animals and birds in particular, have been shown to be particularly adept at interpreting acoustical signals bearing information about the identity of the sender even when these signals are transmitted in very difficult listening situations [2]. Inspired by the acoustical discrimination prowess observed across the animal kingdom, bioacousticians have frequently studied the relationship between the nature of the signal degradation in particular environments and the evolution of robust communication signals in species that inhabit these environment [3]. Our study takes a similar ecological approach to study degradation of signals as a result of propagation but with the additional goal of understanding the neural mechanisms that are involved in recognizing the robust information bearing features in acoustical signals. For this purpose, we examined the effect of degradation on acoustical signals in zebra finches using a combination of acoustical analyses, behavioral studies and neurophysiological recordings. Zebra finches are gregarious songbirds of subarid regions of Australia, which form life-long pair bonds and breed in loose colonies[4]. It has been demonstrated that the long-distance call, which is emitted when a male-female pair is separated, bears an individual signature and is used for mate recognition [5]. In the work described here, we first studied the acoustical features that carry information about sender identity for calls recorded at various distances from the emitter. We then used these degraded calls in behavioral experiments to quantify the discriminability of these features. Finally, we recorded the neural activity of neurons in the primary and secondary avian auditory cortex to examine the match between the neural and behavioral discriminability and to understand the neural circuits involved in extracting the information bearing features.

THE ACTIVE SPACE OF THE ZEBRA FINCH INDIVIDUAL ACOUSTICAL SIGNATURE

Our first goal was to determine the active space of the zebra finch individual signal signature using acoustical and statistical techniques. We used a distance calls database recorded in the laboratory in soundproof boxes using a microphone placed 0.2 m above the bird cages. From this database, we selected 16 distance calls from 16 females and 16 males (16x16x2=512 calls). Our calls had a mean duration of 0.22 s ± 0.06 s for females and 0.13 s ± 0.05 s for males, and a mean fundamental frequency of 549.7 Hz ± 126.5 Hz for males and 803.3 Hz ± 164 Hz for males. The mean dominant frequency (maximum spectral energy peak) was 3042.7 Hz ± 445.9 Hz for the females and 3407 Hz ± 584 Hz for the males. Propagated calls were then recorded in an open field in the Loire region of France on a windless day (T=11°C). The call signals were broadcast using a MegaVox speaker (PB-35W) placed on a stool, 1.30 m high so as to avoid excessive ground reflection interference. We set the speaker volume to obtain a sound level of 70 dB SPL at 1 m (Velleman Sound Level Meter DVM 1326) as this corresponded to the average sound level measured from natural calls in the lab at the same distance. The propagated sounds were then recorded with a Schoeps microphone (MK4 cardioid, on a CMC6-U base) equipped with a Schoeps Basket-type Windscreen (W 20) and set 1.30 m high. We recorded the calls sequence at 2 m, 16 m, 64 m, 128 m and 256 m away from the source, twice for each distance. We then compared the signals from the two recording sessions for each call at each propagation distance to select signals that hadn’t been impaired by an unexpected sharp noise that was not relevant to our propagation study. These selected signals (256 in total for each sex and each distance) were then used

FIGURE 1. Spectrograms of the same distance call from a male zebra finch recorded at 2, 64 and 256 meters from the speaker.
throughout the whole analysis that followed. Figure 1 shows the spectrogram of a single call from a particular male zebra finch recorded at 2m, 64m and 258m.

To investigate the sound features that carry the information about the identity of the emitter and how this information changes as a function of distance, we used discriminant function analysis techniques. Traditionally, animal vocalizations are described in the field of bioacoustics with a small number of acoustical features (such as mean pitch, spectral mean, duration, etc). Linear Fisher Discrimination Analysis (FDA) is then performed on these features to investigate the presence of acoustical signatures for individual identity, sex, dominance status, etc [6,7]. Here we used a complete and invertible description of the sound: its full spectrogram. By using a complete description of the sound, we circumvented the use of a priori assumptions on the nature of the information-bearing acoustical features. There is, however, a complication with using a spectrographic representation: the dimensionality of the acoustical space (number of time points x number of frequency slices) is much higher than the total number of sound exemplars and classical FDA will be ill defined in such cases. To address this issue, we used a regularized version of FDA that can be thought as the equivalent of the PCA and ridge regression techniques that are used in regression analyses [8]. In the “PCA discriminant analysis,” the spectrogram of a call is represented with a small number of eigenvectors and the discriminant analysis is performed in that eigenvector space. Since this eigenvalue decomposition is a linear transformation, the inverse operation can then be applied to the discriminant functions in order to represent them in the spectrographic space. Figure 2 shows the first three discriminant functions that can be used to best discriminate the individual signature of female (left) and male (right) distance calls and how these functions changes with propagation distance.

As shown on that figure, while a large range of the frequency spectrum can be used to extract the individual signature at 2m, the frequency band that carries information shrinks as a function of distance and becomes restricted to a narrow range between 2 and 4 kHz at 256 m. The DFs also show that fine spectral cues appear to be useful at all distances; the fine alternation between positive and negative bands in the DF could indeed be used to separate calls based on their pitch. Finally, we also observed a sexual dimorphism in that the DFs for the male calls show much greater temporal structure that those obtained for female calls. This temporal structure is observed for example in the male DF1 obtained for 2m that shows temporal successions of negative (blue) and positive (red) weights along the temporal axis, a pattern that would be useful to distinguish calls based on their duration. More strikingly perhaps is the selectivity for downward sweeps that appears in the DF3 at 256 m. These sweeping sound features are clearly not present for female calls and are less crucial for discriminating male calls when the entire frequency range of the signal is available. The confusion matrices shown in figure 2 indicate that the determination of the caller identity degrades with distance but remains nonetheless possible to a certain extent even at 256 m. In figure 3, we quantify these results by showing the percent correct of classification on the validation data set as a function of distance. We also compare the quality of the discrimination obtained using our spectrographic representation of the sound to a more classical approach where distinct temporal and spectral features of each call are extracted before performing the FDA on this reduced set (n=10) of acoustical parameters. As shown in that figure, higher discriminability is obtained for male calls relative to female calls and this difference increases with...
propagation distance when the complete spectrographic representation is used. It is also noticeable that discriminability remains clearly above chance even at 256 m when using this representation.

![Graph showing percentage of correct classification as a function of distance for male and female calls using complete spectrographic representation (solid lines) or subset of spectral and temporal descriptors (dashed lines). Descriptors include mean, standard deviation, kurtosis, skewness, and entropy of the power spectrum and temporal envelope of each sound.](image1)

**FIGURE 3.** Percentage of correct classification as a function of distance for male (blue) and female (red) calls using either the complete spectrographic representation of the sounds (solid lines) or a subset of spectral and temporal descriptors (dashed lines). These descriptors include the mean, the standard deviation, the kurtosis, the skewness and the entropy of the power spectrum and the temporal envelope of each sound.

**INDIVIDUAL RECOGNITION MEASURED IN BEHAVIORAL EXPERIMENTS**

Our acoustical analysis shows that zebra finch calls retain information about identity over a range of propagated distances but that the quality of this information degrades and that the acoustical features that might be the most informative change as a function of distance. In the second part of this study, we performed behavioral experiments to determine whether birds could use this changing information. For this purpose, we designed an operant conditioning experiment where female birds could activate the call playback from either a familiar male or her own mate by sitting on perches found in side cages placed at opposite sides (see figure 4). We then counted the number of perching events for each side. On different days and in random order, the propagation distance and side of the mate was changed. The number of perching events was fitted using logistic regression with propagation distance and caller type as regressors. The coefficients in the logistic regression could be used to express the odds ratio as a function of distance as shown on figure 4. As shown on that figure, female zebra finches could discriminate the identity of the caller at 16 and 64 m but not at 256 m.

![Behavioral apparatus and graph showing odds ratios for perching on the Mate side of the cage.](image2)

**FIGURE 4.** Behavioral apparatus (left panel) used to test the discrimination of distance calls using an operant conditioning paradigm. The behavioral data was used to estimate the odds ratio for perching on the Mate side of the cage (right panel).
NEURAL DISCRIMINATION OF PROPAGATED CALLS

The third goal of our study was to analyze the neural representation of propagated calls in the zebra finch auditory system. More specifically, we wanted to see if we could use the measured neural activity to discriminate the identity of the caller and compare this neural discriminability to the behavioral discriminability measured above. We also wanted to determine the tuning properties of the recorded neurons and correlate the tuning with the neural discriminability and with the acoustical features that were the most deemed to be the most informative based on the acoustical analysis described in the first section of this paper.

Neural recordings were obtained in urethane anesthetized male and female zebra finches using electrode arrays. These arrays were lowered in the brain to target the avian primary auditory cortex known as the fieldL/CLM complex as well as secondary auditory areas CMM and NCM. As above, distance calls and their degraded and attenuated variants were used as stimuli. At each recording site, we played back 8 calls from 4 birds at all 5 distances. As exemplified on figure 5, neurons responded robustly to call playback with particular temporal patterns of spikes at short propagation distances. Neural discrimination for the identity of the caller was indeed almost perfect at 2 m even when from responses of single neurons. The neural discrimination decreased as a function of distance and was very low at 256 m, qualitatively matching the behavioral responses.

**FIGURE 5.** Spectrograms of stimulus (top row), spike raster (middle row) and post-stimulus histogram (bottom row) for the same call but recorded at 2, 16 and 128 m. In this example the characteristic patterned neural response observed at 2 and 16m was completely absent at 128m.

CONCLUSIONS

The distance call of the zebra finch is a complex acoustical signal that contains relatively robust individual signature. We have shown that this acoustical signature varies as a function of distance and that male calls are more robust to distortions due to propagation. Behavioral experiments show that birds are capable of using this information in order to recognize the call of their mate. We have started to examine neural responses to degraded calls and found neural discrimination values that match our behavioral results. In the near future, we will determine which auditory neurons show the most robust responses to deterioration from propagation and determine whether their tuning properties extract the signal features that we have shown are the most informative in our acoustical analysis.

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