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Learning to cope with degraded sounds: female zebra finches can improve their expertise in discriminating between male voices at long distances

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ABSTRACT

Reliable transmission of acoustic information about individual identity is of critical importance for pair bond maintenance in numerous monogamous songbirds. However, information transfer can be impaired by environmental constraints such as external noise or propagation-induced degradation. Birds have been shown to use several adaptive strategies to deal with difficult signal transmission contexts. Specifically, a number of studies have suggested that vocal plasticity at the emitter's level allows birds to counteract the deleterious effects of sound degradation. Although the communication process involves both the emitter and the receiver, perceptual plasticity at the receiver's level has received little attention. Here, we explored the reliability of individual recognition by female zebra finches (*Taeniopygia guttata*), testing whether perceptual training can improve discrimination of degraded individual vocal signatures. We found that female zebra finches are proficient in discriminating between calls of individual males at long distances, and even more so when they can train themselves with increasingly degraded signals over time. In this latter context, females succeed in discriminating between males as far as 250 m. This result emphasizes that adaptation to adverse communication conditions may involve not only the emitter's vocal plasticity but also the receptor's decoding process through on-going learning.

KEY WORDS: Acoustic communication, Vocal recognition, Perceptual plasticity, Propagation-induced degradation, Noise, Songbird

INTRODUCTION

As monogamy represents the dominant avian mating system (Emlen and Oring, 1977) and given the importance of sound communication in birds, interactions between paired mates based on reliable information transmission through the acoustic channel are critical to the fitness of most bird species (Falls, 1982; Kondo and Watanabe, 2009). Yet, vocal communication may be challenging because of the intrinsic nature of signal propagation and environmental noise (produced by other animals, wind or human activity). As sounds propagate through the environment, their quality is degraded, affecting the signal's amplitude as well as its temporal and spectral structures (Forrest, 1994; Wiley and Richards, 1982). As a result, the information-bearing features in communication signals can be severely compromised, reducing the signals' active space; that is, the

distance from the source over which the signal remains biologically relevant for potential receivers (Brenowitz, 1982; Marler and Slabbekoorn, 2004). How individuals cope with the environmentally induced degradation of sound signals could therefore play an important role in pair-bonding birds, specifically if mates have to recognize each other by voice at long range.

Birds have been shown to be proficient in communicating in difficult listening situations (Aubin and Jouventin, 2002; Aubin et al., 2014; Brenowitz, 1982; Klump, 1996; Park and Dooling, 1986). Individuals may alter their vocalizations, e.g. by modifying the amplitude and the pitch of songs and calls to increase the signal-to-noise ratio (Brumm, 2004; Mockford and Marshall, 2009; Nemeth et al., 2013; Slabbekoorn and Peet, 2003). Behavioural strategies such as choosing optimal emission and listening posts may also help counteract the deleterious effect of environmental constraints (Dabelsteen and Mathevon, 2002; Mathevon et al., 1996). In addition, songbirds show remarkable perceptual abilities to discriminate between noisy signals (Brémond, 1978; Hulse, 2002). However, only a small number of studies have examined individual discrimination in degraded calls (Aubin and Jouventin, 1998; Jouventin et al., 1999; Mathevon et al., 2008; Vignal et al., 2008). More specifically, a single study investigated the question of long-range individual recognition in a songbird living in an acoustically constraining environment: in the white-browed warbler *Basileuterus leucoblepharus*, a species from the Brazilian Atlantic forest, the individual signature encoded in the male song degrades rapidly during propagation, restricting individual recognition to neighbouring territorial males (Mathevon et al., 2008). Could discrimination be improved by learning? Phillmore et al. (Phillmore et al., 2002) showed that male black-capped chickadees *Poecile atricapilla* that learned to discriminate songs from conspecifics recorded at 5 m could transfer this knowledge to discriminate the same vocalizations mildly degraded by 25 m of propagation, suggesting that training at a given distance could improve discrimination performance at longer distances. However, the role of experience in the discrimination of individual voices degraded over a range of distances up to the limit of the active space remains unknown in songbirds. In this study, we investigated the ability of female zebra finches to individually identify males based on their propagated vocalizations. Furthermore, we examined whether training with increasingly degraded signals can help female subjects improve their discrimination ability.

The zebra finch *Taeniopygia guttata* Reichenbach 1851 is a small gregarious songbird from subarid Australia that pair bonds for life and lives in large flocks in open country with a scattering of trees and bushes (Butterfield, 1970; Zann, 1996). Because these birds are opportunistic breeders living in a very unpredictable environment (Zann, 1996), maintaining strong pair bonds between breeding events while living in large fission–fusion groups is of the utmost

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List of symbols and abbreviations	
GLMM	generalized linear mixed-effects model
LOR	$\log_2$ of the odds ratio
NoRe	non-rewarded
OI_{NoRe}	odds for interrupting the non-rewarded stimuli
OI_{Re}	odds for interrupting the rewarded stimuli
OR	odds ratio
PI_{NoRe}	probability for interrupting the non-rewarded stimuli
PI_{Re}	probability for interrupting the rewarded stimuli
Re	rewarded

importance. With the flock constantly on the move, topographic landmarks may be scarce and partners might not have a fixed nest site at which to meet each other: the use of a solid vocal recognition system could enable partners to avoid the cost of losing each other. Of all the zebra finch vocalizations, the distance call is used specifically between pair-bonded partners while foraging out of sight (Zann, 1996). Previous studies have shown that the distance call bears an individual signature, and that birds are capable of call-based recognition (Vignal et al., 2004; Vignal et al., 2008; Zann, 1984). The active space of the zebra finch distance call has been estimated based on naturalistic observations to extend up to 100 m (Zann, 1996); similar conclusions were reached using discrimination thresholds for masked signals in this species (Lohr et al., 2003).

In the present study, we predicted that zebra finches have a robust vocal recognition system that performs well even for distance calls propagated over long distances (i.e. more than 100 m). Additionally, we hypothesized that females could improve their ability to discriminate between male voices through experience. To test these hypotheses, we first explored the reliability of mate recognition by females at a range of propagation distances by assessing their preference for their mate's calls, using an operant choice apparatus (experiment 1). Then, to assess the role of experience and to further distinguish the discrimination process from the recognition process, we conducted forced-choice conditioning experiments (experiment 2) and compared the results of two different protocols. In both protocols of experiment 2, the females were asked to discriminate between the calls of two unfamiliar males. These calls had been propagated over the same distance: short, medium or long range. In the first protocol ('systematic-training' condition), the females learned to discriminate the calls of two males recorded at short range before being systematically challenged with the calls of the same males recorded at longer distances. In the second protocol ('no-training' condition), the females were challenged daily with a different pair of males played back at a randomly selected propagation distance, and thus did not have the possibility to learn from their previous experience in the task. To the best of our knowledge, this is the first study to examine the importance of learning in improving discrimination of individual vocal signatures following strong environment-induced degradation.

RESULTS
Signal degradation and the difficulty of individual discrimination at long ranges

To illustrate the increasing similarity between calls with propagation distance, we calculated the spectral correlation between the distance calls of males for every different pair that was used in both experiments. As one might expect, these correlation values were highly correlated with propagation distance ($r=0.73$, $P<0.001$), increasing to values close to 1 at 256 m (Fig. 1) where very little individual information in the degraded signal remains. This basic spectral analysis provides a coarse measurement of the increasing
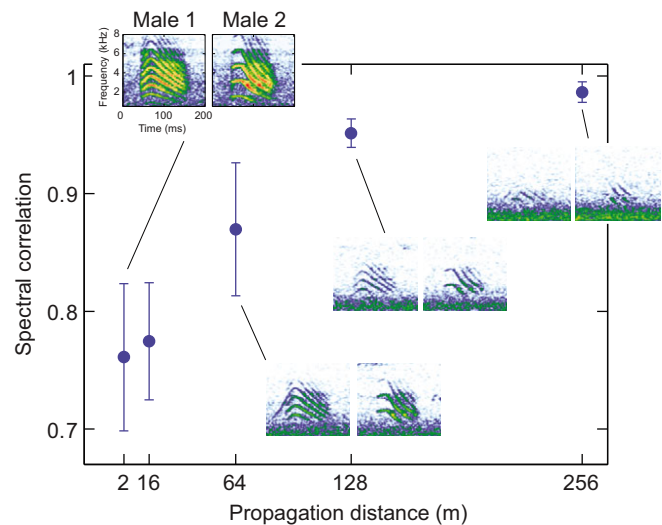

Fig. 1. Spectral correlations between the distance calls of males as a function of propagation distance. Correlations were calculated between the mean frequency spectrum of each male at a given distance; two examples are represented (error bars correspond to the s.d.). The correlation between male calls increases with distance along with propagation-induced signal degradation and the decrease of the signal-to-noise ratio. As an example, the spectrograms of the same calls from two males used as a rewarded–non-rewarded (Re-NoRe) pair are shown for each distance tested in experiment 2.

difficulty that subjects encounter when discriminating between male individuals at increasing distances. As illustrated by the spectrograms from the same pair of males displayed as an example in Fig. 1 (see inset), the progressive decrease in signal-to-noise ratio at long distances results in signals that are dominated by noise and have therefore very similar frequency spectra yielding high correlation values.

Experiment 1: preference test
The purpose of this experiment was to assess the preference of female zebra finches for variously degraded distance calls from their mate or from a familiar male (propagated at 16, 64 and 256 m), using an operant choice task with call playbacks as a reward. In the experimental apparatus (see Materials and methods), the subject could trigger the playback of a degraded distance call from either its mate or a familiar male (non-mate) by perching on either of two perches placed on opposite sides of the cage. Each subject was tested three times (for three distances), and each test consisted of two sessions between which the assignment of the mate and non-mate calls to each side was swapped. We hypothesized that females would prefer their mate's call, providing further evidence for individual recognition in zebra finches and its role in pair bond maintenance.

Using the side of the perching events (right/left) as a dependent variable, we found both an effect of the side assignment of mate and non-mate calls (logistic regression calculated across all subjects and all distances: $\chi^2_3=249$, $P<10^{-4}$) and an effect of distance ($\chi^2_9=3780$, $P<10^{-4}$). Females thus expressed a differential response to the mate side, and their perching probability was influenced by propagation distance. *Post hoc* tests showed a significant preference for the mate side at 16 and 64 m, but not at 256 m (16 m: $\chi^2_2=6.01$, $P=0.049$; 64 m: $\chi^2_2=8.74$, $P=0.013$; 256 m: $\chi^2_2=0.28$, $P=0.87$). We also noticed that session order had a significant effect on females' choice (16 m: $\chi^2_4=587$; 64 m: $\chi^2_4=38$; 256 m: $\chi^2_4=74$; all $P<10^{-4}$). The effect of

session order can be explained by the fact that birds seemed to persist in their preference behaviour from the first to the second session. Indeed, while the subjects could assess the side of their mate prior to the first session (see Materials and methods), they had to get used to the side reversal during the second session, which could result in a certain 'inertia' in changing the side preference, even when recognition occurred.

We estimated the mate effect for each bird and each distance independently using an odds ratio (OR) describing the preference for the mate side (probability of perching on one side when that side broadcasts mate calls divided by the probability of perching on the same side when it broadcasts non-mate calls; see Materials and methods). We chose the $\log_2$ of the OR (LOR), a measure often used to describe effects inducing a change in probability, to display our results (Fig. 2). An OR greater than 1 (or LOR>0) indicates a preference of the female for mate calls while an OR less than 1 (or LOR<0) indicates a preference for non-mate calls. If there is no preference, the OR is not significantly different from 1 (and the LOR is not significantly different from 0). As shown on Fig. 2, at 16 m the LOR for all but one of the tested females was greater than 0 (significant preference for mate: 5/10 subjects; significant preference for non-mate: 1/10 subjects). At 64 m, seven out of 10 females showed a LOR greater than 0 (significant preference for mate: 5/10 subjects), while three showed a LOR less than 0 (all non-significant). At 256 m, half of the females showed a LOR greater than 0 (significant preference for mate: 2/10 subjects; significant preference for non-mate: 2/10 subjects). Thus, the number of females showing a preference for their mate's calls decreased with increasing distance of propagation. Moreover, one can observe that the LOR confidence intervals at the longer distance were larger because of a reduced amount of total perching events, suggesting
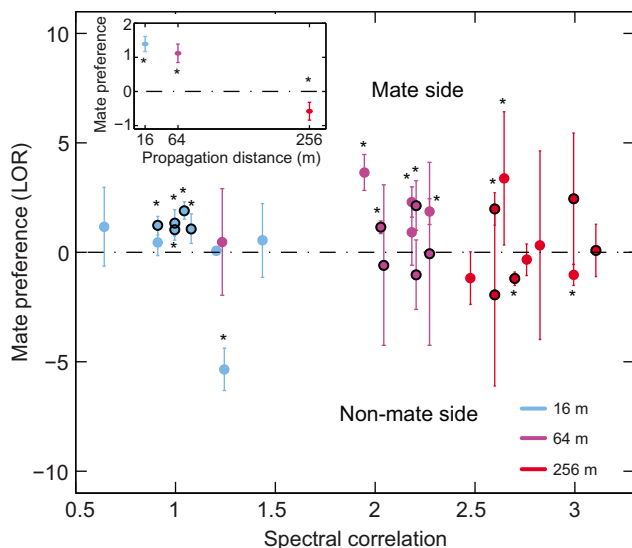
that male voices were less salient for the females. At longer distances, preference became more arbitrary; while a number of subjects showed a significant preference for their mate's calls at short and medium distances, the females' choice became more randomly distributed at 256 m, with a few subjects significantly preferring the non-mate calls.

Finally, in order to further investigate the effect of propagation distance on mate preference, we estimated the mate effect as described above but this time only for the five subjects that showed a significant preference for their mate at 16 m. For this subset, we also found an effect of the mate side ($\chi^2_3=262$, $P<10^{-4}$) and an effect of distance ($\chi^2_9=872$, $P<10^{-4}$). In Fig. 2, a bold black circle is used to show the data for these five subjects, and the inset shows the mean LOR at each distance. The effect of distance on the subjects' preference is clearly visible, with an almost linear decrease in the LOR with increasing distance. The fact that the LOR is significantly below 0 (preference for non-mate) at 256 m is because of the robust preference of a single subject for the non-mate: this subject had a high number of perching events relative to the other birds that caused the weighted mean of the LOR for all birds to be significantly negative.

Experiment 2: discrimination task

The purpose of this second experiment was, first, to further investigate the ability of female zebra finches to discriminate between two males while hearing variously degraded distance calls and, second, to test whether females could improve their discrimination through learning. Using a pecking key apparatus and a forced-choice operant procedure, we first assessed this ability in a 'systematic-training' paradigm: the tested females were asked to discriminate between the calls of the same pair of males from one day to the next, with increasing propagation distance (2, 64, 128 and 256 m). We compared this with a 'no-training' control condition: here, both the identity of males and the propagation distance were randomized over the four testing days. The birds triggered the playback of calls at will by pecking on a key. At any time they could choose to attend the full duration of the stimulus or peck again to interrupt the current stimulus and trigger the next one. Access to the feeder was only permitted when the bird chose to fully attend to the rewarded stimuli. The subjects were thus tested on their ability to interrupt the non-rewarded (NoRe) stimuli and refrain from interrupting the rewarded (Re) stimuli as this behaviour maximized their access to food (see Materials and methods).

For both protocols, we retrieved for each pecking event the stimulus type (Re/NoRe calls) and the subject's response (interruption/non-interruption). We first assessed the overall effect of stimulus type, distance and spectral correlation between the Re and NoRe stimuli by modelling the interruption behaviour using logistic regression (see Materials and methods). We performed these analyses for the systematic-training and no-training conditions separately. For both protocols we found: (1) that the females were interrupting the NoRe stimulus more than the Re stimulus, indicating that the birds were learning the task (for systematic-training: $\chi^2_5=120$, $P<10^{-4}$; for no-training: $\chi^2_5=145$, $P<10^{-4}$), (2) that distance significantly affected their interruption behaviour, indicating that performance in the task varied as a function of distance (for systematic-training: $\chi^2_6=27$, $P=0.0002$; for no-training: $\chi^2_6=49$, $P<10^{-4}$) and (3) that correlation between stimuli was significant, indicating that the task performance was affected by the degree of similarity between the two sounds (for systematic-training: $\chi^2_2=55$, $P<10^{-4}$; for no-training: $\chi^2_2=19$, $P<10^{-4}$).

To visualize the effect of distance on this discrimination task and to better analyse the differences between the two paradigms, we

Fig. 2. Mate preference. Results of the female preference tests between their mate's and a familiar male's calls having experienced different levels of propagation-induced degradation (experiment 1; *N*=10 females). The figure shows the mate preference estimates quantified by the $\log_2$ of the odds ratio (LOR) of correct choice. The LOR were estimated using a generalized linear model for each distance and each female (see Materials and methods). Positive values indicate a preference for the mate's voice. For visual clarity, the spectral correlations on the *x*-axis are Fisher transformed to obtain an unbounded correlation measure. The five subjects that showed a significant preference for their mate at 16 m are signalled for all distances by bold black circles. The inset shows the LOR of mate preference using these five subjects. *P<0.05. Error bars correspond to the 95% confidence intervals.

calculated, across subjects, the probability of interrupting each stimulus type (Re and NoRe) at each distance and for each paradigm separately. Statistical significance was assessed using logistic regression (see Materials and methods). In the systematic-training condition, the probability for interrupting the NoRe stimuli (PI_{NoRe}) was significantly higher than the probability for interrupting the Re stimuli (PI_{Re}) for all distances including 256 m (2 m: $\chi_1^2 = 14.6$, $P = 0.00013$; 64 m: $\chi_1^2 = 25.7$, $P < 10^{-4}$; 128 m: $\chi_1^2 = 39.8$, $P < 10^{-4}$; 256 m: $\chi_1^2 = 33.5$, $P < 10^{-4}$; Fig. 3A). These results indicate that the subjects were able to discriminate between the Re and NoRe stimuli at up to 256 m. The OR, defined here as the odds of interrupting the NoRe stimuli divided by the odds of interrupting the Re (OI_{NoRe}/OI_{Re}), can then be used to estimate the effect size of the differences in the probability of interruption. These ORs were relatively constant across distances (2 m: OR=1.83; 64 m: OR=2.23; 128 m: OR=2.1; 256 m: OR=2.2), showing that, apart from the slight improvement from 2 to 16 m as birds learned the task, their performance remained constant as the distance increased although the task became more

difficult. This preservation of performance appears to result from the experience gained in previous training days with the easier task.

In the 'no-training' condition, the PI_{NoRe} was significantly higher than the PI_{Re} at 2, 64 and 128 m but not at 256 m (2 m: $\chi_1^2 = 17.8$, $P < 10^{-4}$; 64 m: $\chi_1^2 = 99.8$, $P < 10^{-4}$; 128 m: $\chi_1^2 = 10.4$, $P = 0.0012$; 256 m: $\chi_1^2 = 0.28$, $P = 0.6$; Fig. 3B). Thus, contrary to the systematic training condition, females were not able to discriminate between the calls of two males at this longer distance. In this case the effect of distance was also reflected in the odds ratio (OI_{NoRe}/OI_{Re}) that decreased towards 1 as distance increased (2 m: OR=2.0; 64 m: OR=6.4; 128 m: OR=1.7; 256 m: OR=0.93). Without training, the task was, as expected, more difficult at longer distances.

DISCUSSION

Using two complementary approaches, we showed that female zebra finches are proficient in discriminating between the calls of two individual males at long distances, and even more so when they have the possibility to learn over time. This ability may be highly adaptive in this monogamous species, as losing the partner represents a high loss of investment as the birds might miss scarce opportunities to reproduce in their unpredictable environment. Our results underline the importance of considering the receiver's performance when studying acoustic communication in adverse conditions.

In the first approach, we aimed to determine whether female zebra finches were capable of discriminating between the calls of their mate and of a familiar male at different distances. The preference test showed that females significantly preferred the call of their mate at 16 and 64 m, but not at 256 m. The observation that a few subjects significantly preferred the non-mate calls at the longest tested distance (256 m) could be interpreted as a situation where the subjects were not able to discriminate the call of their mate, or even recognize these sounds as distance calls, but still managed to detect differences in the two playbacks and showed a significant preference for one (Lohr et al., 2003). With our second approach, we further investigated long-distance discrimination and assessed the zebra finches' discrimination abilities per se, disentangling the subjects' recognition process from the preference for their mate's calls and eliminating the potential impact of any previous social interactions with the males used as stimuli in the experiment. The discrimination task showed that female zebra finches are indeed able to discriminate between two male individuals at up to 128 m in a no-training context, but that when they have the possibility to learn from their previous experience, robust discrimination occurs even as far as 256 m.

In the field and laboratory-based calculations from discrimination tasks, the active space of zebra finches' distance calls has been estimated to be up to 100 m (Lohr et al., 2003; Zann, 1996). Here, we show that, with training, female zebra finches have the physiological ability to recognize acoustic signatures up to at least 256 m. As useful as laboratory experiments are in terms of reproducibility and measurement precision, they cannot completely mimic the conditions in nature, where birds might encounter more adverse propagation conditions (e.g. strong winds) or interference from other sound sources including other conspecifics. Nonetheless, our results suggest that wild zebra finches could benefit from repeated learning experiences and achieve recognition of their partner's degraded individual signature at distances greater than 100 m. This enhanced learned discrimination might also come into play in more adverse conditions, preserving discrimination at shorter distances. One should also note that laboratory experiments might underestimate natural discriminability: in our experiments, the
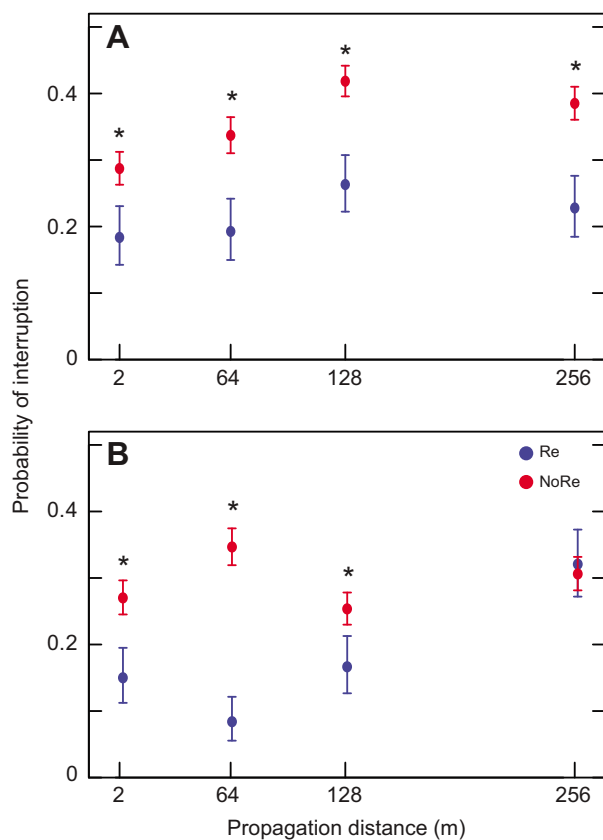

Fig. 3. Results of the discrimination tasks between calls of two different males performed by females (experiment 2). (A) Results for the 'systematic-training' condition (the same pair of males was used over all distances; females were challenged with increasing distance; N=5). (B) Results for the 'no-training' condition (pairs of males changed for each distance; distances presented at random; N=7). The figure shows the average probability of interrupting the rewarded (Re) and non-rewarded (NoRe) stimuli for each tested propagation distance (see Materials and methods). Significantly higher values for interrupting the NoRe stimuli compared with the Re stimuli indicate that female subjects were able to discriminate between the two sets of stimuli and responded accordingly to get access to food. Error bars represent 95% confidence intervals on the probabilities (binomial test). *Significance obtained from the logistic regression: $P < 0.002$.

signal, the echoes from reverberation and the noise all came from the same spatial location, the loudspeaker. In nature, these different sounds can come from spatially separated sources and spatial information could thus be used to further enhance discrimination (Bee, 2008; Dent et al., 2009; Maddox et al., 2012). A full recognition task in the natural context might also combine the tasks of discriminating one particular individual and determining its spatial location, i.e. its orientation and distance. Previous laboratory experiments showed that zebra finches can also discriminate between near and far signals (Phillmore et al., 1998; Radziwon et al., 2011) and have a rough sense of sound source azimuth (Park and Dooling, 1991). Further experiments both in the field and in the laboratory are needed to assess the performance for both localization and identification and in more complex listening conditions.

In the light of what could be considered a remarkable performance of individual discrimination in zebra finches, it is interesting to compare these measures with those obtained in other species. For the territorial white-browed warbler living in the dense environment of the tropical forest, the male's song loses its individual signature after less than 100 m of propagation; thus, the transmission of individual information is likely to be limited to nearby individuals, i.e. territorial male neighbours and the female partner (Mathevon et al., 2008). In the context of pair bond, females in this species would have access to the individual signature of their mate within the limits of their territory. As another example, female great tits incubating inside nest boxes still perceive subtle individual differences between their mate's song and a neighbour's song emitted from outside the box, despite the similarity between the songs and the sound degradation induced by the nest box (Blumenrath et al., 2007). In this case, females deal with short-range signal degradation but with a difficult discrimination task because of the signal similarity between individuals. Conversely, the ecological requirements of the zebra finch, especially its nomadic lifestyle outside of breeding events in an open environment, may call for perceptual abilities in individual recognition that are adapted to vocalizations being propagated at longer distances.

In our design, we chose to test females as they were shown to respond preferentially to their mate's voice (Miller, 1979; Vignal et al., 2008), whereas males' responses can change depending on the composition of the audience (Vignal et al., 2004). Testing males in the same tasks would be interesting. Although it is not certain that we could reliably test the males' abilities to recognize degraded calls using their preference for their partner's calls in an isolation context, using a conditioning experiment for testing male discrimination would certainly be insightful. Indeed, in zebra finches, the individual signature was found to be stronger in male distance calls than in female distance calls (Zann, 1984; Mouterde et al., 2014); discriminating between degraded calls of females could therefore be more difficult than for male calls.

In the complex task of recognizing individual voices in propagation-induced degraded calls, another interesting point is the extent to which learning takes part in the recognition process. Using field-reared and isolate-reared songbirds (*Poecile atriacapillus*), Phillmore et al. (Phillmore et al., 2003) showed that the discrimination of distance cues (i.e. the emitter's perception of its distance to the sender) is probably an innate skill. Conversely, the recognition of individual vocalizations appeared to require auditory contact with adult conspecifics during the subject's development. In the combined task of extracting information about individual identity in degraded calls, our indoor colony-reared subjects showed impressive abilities in the no-training context, and even greater capacities when given the opportunity to learn from one day to the

next. These results suggest that the zebra finches' vocal recognition system is highly efficient for degraded calls, and that it can be further improved through perceptual plasticity.

Further studies investigating which acoustic parameters birds can learn to rely on for discriminating degraded calls would be useful for a better understanding of the ongoing plasticity in the auditory system in adult songbirds. Moreover, studying plasticity at the level of the individual, as a means to adapt quickly to varying environmental conditions, is of primary importance in the current context of ever-growing anthropogenic noise. While the vocal plasticity of the sender has been the subject of a number of recent studies (Francis et al., 2010; Nemeth et al., 2013; Warren et al., 2006), the receptor's perceptual plasticity has received much less attention (Pohl et al., 2012; Slabbekoorn, 2013). The present study emphasizes that the adaptation to adverse communication conditions may also involve ongoing learning at the receiver's level.

MATERIALS AND METHODS
Experiment 1: preference test
Subjects
The subjects (*N*=10 adult male–female pairs) were raised in the ENES laboratory (14 h light/10 h dark photoperiod with adapted wavelengths, food and water *ad libitum*, temperature between 23 and 25°C). Prior to the experiments, the pairs were observed over a 2 month period of time to assess whether they were effectively mated. Every pair had thus been observed allopreening, building a nest and incubating eggs. The pairs were housed in separate cages (38×24×40 cm W×D×H) in the same room, having visual and vocal contact with each other.

Recording of distance calls and preparation of stimuli
To promote calling behaviour, the male and female of each pair were kept in separate cages and placed out of sight in two connected soundproof rooms. The males were recorded using a microphone (Sennheiser MD-42, Wedemark, Germany) placed 0.2 m above the cage and connected to a Marantz Professional Solid state recorder (PMD-670, Eindhoven, The Netherlands; sampling frequency: 44,100 Hz). Conditions of temperature, food and water availability were the same as in the aviary.

We isolated 10 distance calls from each male and normalized them by matching the maximum values of the sound pressure waveforms. These calls were used to create our propagated calls database. The propagated recordings were performed on an open flat field (Bellegarde-en-Forez, France, on the 1 March 2011 around noon, with cloudy weather, wind <5 km h^{-1}, temperature 10°C). We have shown that the effects of propagation on this French site are similar to those in the Australian desert with little vegetation (Mouterde et al., 2014). All 10 calls of each male bird were dispatched along a 4 min long audio sequence, in order to avoid any context effect (e.g. changes in the background noise). The call sequence was broadcast from a Marantz Professional Solid state recorder/player (PMD-671) connected to a MegaVox speaker (PB-35W, Anchor Audio Inc., Torrance, CA, USA) placed 1.3 m high so as to avoid excessive ground reflection interference. The volume of the Marantz player was set to obtain a mean sound level of 70 dB SPL at 1 m (Velleman Sound Level Meter DVM-1326, Gavere, Belgium) to match typical levels of the natural distance call in the zebra finch (Vignal et al., 2008). The call sequences were then recorded with a microphone (Schoeps MK4 cardioid, on a CMC6-U base, Karlsruhe, Germany) equipped with a Schoeps Basket-type Windscreen (W20) and set 1.3 m high. The microphone was connected to a second Marantz recorder/player (PMD-671; sampling frequency: 44,100 Hz). We recorded the call sequence 1 (for calibration), 16, 64 and 256 m away from the source, three to four times for each distance, enabling us to select from these three or four versions of each propagated call a signal that had not been impaired by unexpected transient sounds (e.g. birds or other animals calling in the vicinity, human-related activity). From these recordings, we thus isolated 10 different calls per male per propagation distance (10 calls × 10 males × 3 distances; total=300 calls). The background noise immediately preceding and following each call was replaced by silence; the call was then

ramped (relative amplitude gradually increased from silence to full volume over 10 ms using Goldwave) to avoid any switching noise at onset. To further remove irrelevant background noise, we also applied a high-pass filter above 500 Hz on the signals, following the lower frequency threshold of the zebra finch's audiogram (Okanoya and Dooling, 1987).

Estimating call acoustic similarity

To evaluate the difficulty of the discrimination task, we estimated the intrinsic similarity between the distance calls of males of every pair to be discriminated in the experiment by calculating the correlation between the mean frequency spectra of all sets of calls for each pair of males, at each distance (meanspec function, Seewave R package) (Sueur et al., 2008).

Experiment setup and protocol

Preference tests were conducted in a sound attenuation chamber (internal dimensions: 1.8×1.4×2.2 m W×D×H; Silence-Box, Tip-Top Wood, Saint-Etienne, France). Each female was housed alone in the chamber, in an experimental cage with a central body (30×34×34 cm W×D×H) where food and water were distributed *ad libitum* and which contained a single perch (see supplementary material Fig. S1). On each side of the cage, an opening (10×10 cm W×H) led to a side arm (20×10×26 cm W×D×H) containing a perch and equipped with infrared sensors that monitored when the bird entered the arm. Custom-written software was used to monitor the subject's activity on the perches and trigger playbacks as follows: a hop on a side perch broke the infrared beam and triggered the playback of a call from a loudspeaker (Bravo-Allroom, Audio Pro, Sweden) placed 20 cm away from the same side arm. Depending on the side arm, this call was randomly selected from the 10 calls available for the tested female's mate or from the 10 calls of a familiar male. Sound stimuli were broadcast by either of the two loudspeakers connected to an amplifier (Yamaha Natural Sound Stereo Amplifier, AX-396, Hamamatsu, Shizuoka, Japan) and a laptop. We calibrated the intensity of the sound stimuli by setting it at 70 dB SPL for the sounds recorded at 1 m (typical level of a natural distance call) and used that gain setting for all playbacks. Thus, stimuli used for the experiment (from 16 to 256 m) were emitted at the lower intensity level that matched the amplitude loss due to natural propagation.

The three propagation distances tested (16, 64 and 256 m) were representative of short, medium and long range. Each propagation distance was tested over a 3 day long trial and the female could choose between triggering either her mate's calls (mate) or calls from a familiar male (non-mate) recorded at the same distance. The identity of the familiar male was the same for the three trials of a given female, but different between females. The order in which the propagation distances were tested for each bird was randomized across subjects. The delay between the end of a trial and the beginning of the next trial for each bird was 21 days minimum. Each trial consisted of two experimental sessions (first session: mate's calls emitted from one side and non-mate's calls from the opposite side; second session: reversed positions) and started with a habituation period, enabling the subject to get used to the setup and learn which side arm was associated with which individual's calls (mate or familiar male) for the first session. Each experimental session lasted 17 h (1.5 days, spread over two consecutive days, each session being interrupted by the 10 h night time during which playbacks were turned off), which ensured that the subject's activity was recorded during the same amount of time for each mate/non-mate side assignment. The order of the side assignments was balanced across trials for each subject. After the end of the trial, the subject was returned to its mate in the colony room. The experimental protocol was approved by the Jean Monnet University's Animal Care Committee (authorization no. 42-218-0901-38-SV-09 to the ENES lab).

Data analysis

The perching events in the side arms were analysed as a binary response variable (perch right/left) using a series of logistic regression analyses. We first used a generalized linear mixed-effects model (GLMM) to test the main effect of the mate side (left or right) and the effect of distance on the females' perch choice (perch on the right or left arm). A random effect was used to control for the birds' potential bias for a particular cage side (see Appendix 1). We then estimated a GLMM for each propagation distance separately (16, 64 and 256 m) in order to examine the effect size and

significance of mate side for each distance; for these models, we also analysed the order effect of each session. We also performed a statistical test for each subject, which allowed us to examine the results un-weighted by the average number of perching events of each bird. Models were fitted using the lmer or the glm functions of R (v. 2.13.1, R Foundation for Statistical Computing).

The effect size of the presence of the mate, as assessed by the model, can be expressed by the OR, i.e. the ratio of the odds of perching on one side when it broadcasts mate calls divided by the odds of perching on the same side when it broadcasts non-mate calls (the value of this OR is right/left symmetrical and can be obtained from the perches either on the right or on the left; see Appendix 1). The higher the OR, the higher the female preference for her mate. In Fig. 2, we plotted the LOR obtained for each bird and each distance using the output of the GLMM model. Error bars were obtained from the standard error estimates of the regression coefficients obtained in the model fits. Finally, in order to clearly visualize the effect of distance on the subject preference, we also estimated the OR of mate preference at each distance using only the subset of females that showed a significant preference for their mate at 16 m (N=5).

Experiment 2: discrimination task

Subjects

Seven unpaired adult female zebra finches were used in this experiment. They were housed in the same single-sex cage at UC Berkeley's animal facilities (12 h light/12 h dark photoperiod with adapted wavelengths, temperature between 22 and 24°C, food and water *ad libitum*). All experimental procedures were approved by the Animal Care and Use Committee of UC Berkeley. Prior to the experiments, all subjects had previously been trained on the pecking test device and were familiar with the forced-choice procedure. The initial shaping sessions lasted for less than a week and two songs from different male zebra finches were used as Re and NoRe stimuli. For every subject, the experiment started on day 0 with a shaping test, using these same two songs as stimuli. This ensured that each subject started the experiments with the same just-prior experience with the apparatus, and having heard stimuli that were different from those used for the actual experiment.

Recording of distance calls and preparation of stimuli

To prepare the stimuli for these experiments, we used a distance calls database recorded between 2007 and 2008 from unpaired male zebra finches raised in the ENES laboratory. The recording procedure was similar to that of experiment 1, with the difference that here each bird was recorded in the presence of two females placed 3 m away and used as an audience to minimize stress, and was stimulated with distance call playbacks from previously recorded conspecific birds. This database was composed of 16 different call exemplars from 16 different males (16×16=256 calls).

We recorded the propagated calls of this database on 3 October 2010 in the afternoon, at the same location as explained above and using the same equipment (weather cloudy, no wind, temperature 11°C). We recorded the propagated calls 1 (for calibration), 2, 64, 128 and 256 m away from the source, twice for each distance, and processed the recorded calls (16 calls × 16 males × 4 distances; total 1024 calls) as explained for experiment 1.

Each acoustic stimulus used during the forced-choice discrimination task consisted of a sequence of six distance calls randomly selected from the 16 available calls of the same male individual for the same distance, and randomly distributed within a 6 s window.

Experimental apparatus

The forced-choice task apparatus (see supplementary material Fig. S2) consisted of a modular test chamber (interior dimensions 31×24×29 cm; Med Associates Inc., St Albans, VT, USA) placed in a soundproof booth (Acoustic Systems, MSR West, Louisville, CO, USA; interior dimensions 76×61×49 cm). The experimental panel consisted of a pecking key placed 20.5 cm above the floor and accessible through a wooden perch. Below, a feeder containing seeds could be made accessible or not to the subject, depending on its appropriate response to the playback. Acoustic stimuli were broadcasted by a computer connected to an amplifier (Technics, Matsushita Electronics SA-EX140, Osaka, Japan) and a loudspeaker (Bose model 141, Framingham, MA, USA) placed 20 cm from the test chamber (sound level

calibrated as in experiment 1 to match the natural intensity levels at each propagation distance). The computer was also connected to the test chamber apparatus to record pecking events, play sounds and activate the feeder in real-time with a single customized program written in MATLAB.

Conditioning procedure
Every male call used for the playbacks was unknown to the female subjects prior to the experiments. Both protocols (systematic-training and no-training) consisted of four tests conducted for four consecutive days. One test consisted of three, 30 min-long trials separated by two 90 min-long rest periods. The pecking key's light was used to distinguish the trial period (pecking light on) from the rest period (pecking light off). The 30 min countdown for each trial started when the subject pecked the key for the first time. When pecking the key during a trial (see supplementary material Fig. S3), the female triggered the playback of calls from either of two males randomly selected from our database: the Re male (with a probability of 0.2) or the NoRe male (with a probability of 0.8). She could then go to the feeder and wait until the end of the 6 s playback to get a reward for the Re stimuli, or interrupt it by pecking again to trigger a new stimulus. Because the time windows for pecking (the 3×30 min trials) were limited and most stimuli were NoRe, the subjects were motivated to interrupt the NoRe stimuli until they obtained a Re stimulus, at which point waiting until the end of the playback would ensure them access to seeds for 10 s. Interrupting the playback of a Re stimulus eliminated the possibility of reward following this playback.

To motivate the subjects to use the pecking key for food reward, they were fasted for 20 h prior to the beginning of the experiment and maintained in a fasted state (85–90% of their free-feeding mass) for the whole experiment by only giving them 1.5 g of seeds after each daily test. Every day, the subject's mass was monitored before starting the test and it was returned to its cage in the colony room after the test. As approved by the Animal Care and Use Committee of UC Berkeley, our criterion for interrupting the fast was a loss of mass greater than 15% of the initial mass recorded before the fasting started. No bird was taken out of the procedure following this criterion.

Systematic-training condition
In the systematic-training condition, a different pair of Re and NoRe males (chosen at random) was assigned to five female subjects and the same assignment was then used for all propagation distances tested: a given female was always tested with the same pair of males. In addition, each female was successively challenged as follows: day 1, distance calls propagated at 2 m; day 2, 64 m; day 3, 128 m; day 4, 256 m. We hypothesized that this cumulative training from short to long distances would help females to increase the active space of the male signals, i.e. to discriminate between the males in spite of increasing sound degradation.

No-training control condition
In the no-training condition, we randomly selected four pairs of males from our database and used them as stimuli for all subjects (N=7 females; the same five as in the systematic-training condition and two additional ones). For a given female, the pair of males and the propagation distance (2, 64, 128 and 256 m) used were randomly assigned across the four testing days. Thus, the subjects were all tested with the same males and the same propagation distances, but not in the same order, both parameters being balanced across subjects. Thus, all subjects had to learn to discriminate between a different pair of males every day and therefore had no cumulative training for one set of stimuli from one day to the other. This test provided insight into the baseline capacity for discrimination of degraded calls.

Data analysis
For both protocols, we retrieved for each pecking event the stimulus type (Re/NoRe) and the subject's response (interruption/non-interruption). The interruption behaviour of the subject was used as the dependent response variable. Using logistic regression, we tested the effects of the stimulus type, the distance and/or the spectral correlation (i.e. the acoustic similarity) between the Re and NoRe sounds (see Appendix 2). Subject identity was used as a random factor to take into account potentially different biases in average interruptions across conditions for each bird. Spectral correlations between sound stimuli were calculated as explained for experiment 1. As

described in Results, we found that all three factors (stimulus type, distance, stimulus correlation) were significant. Then, to both visualize the results and serve as *post hoc* tests, we analysed the data for each distance separately and without taking the correlations into account. For each distance and each stimulus type, we calculated the probability of interrupting the stimulus averaged across birds. This average probability was obtained from the total number of pecks and the total number of interruptions across birds. Note that this average probability gives higher weight to the birds that pecked more. This is appropriate as our confidence for the probability of interruption for birds that pecked more is higher; also, very similar results were found by first estimating the probability for each bird and then calculating the average. Statistical significance was obtained from the logistic regression that predicted interruption probability and used stimulus type as the regressor and bird as a random factor. Using bird as a random factor also allowed us to exclude outlier effects (where one bird would dominate the data). This was not the case in our data as performing the logistic regression without the random effect yielded identical statistical results. If the random factor is excluded, the logistic regression is identical to an exact binomial test for proportion. In Fig. 2, the statistical significance (shown as *) is obtained from the linear regression with the random effect and the confidence intervals for the probabilities shown for the exact binomial test.

APPENDIX 1
Experiment 1: preference test
The perching events in the side arms were analysed as a binary response variable (perch right/left) using a series of logistic regression analyses. The omnibus test consisted of a GLMM with a binomial distribution to test the main effect of the mate side (left or right) and effect of distance (expressed as a factor). A random effect was used to control for the birds' potential bias for a particular cage side. The logistic regression equation can be written mathematically as:

$$\log\left[\frac{p_R}{p_L}\right] = k_{0,i} + k_{1,i}\text{Mate} + (k_{0,i,j}), \tag{A1}$$

where p_R and p_L are the probability of perching right and left, respectively, Mate is a binary variable (1=right, 0=left), i is the index for distance and j is the index for birds. The term in parentheses is the random effect. The effect of mate is assessed by comparing the deviance of the full model above with the model that can be written as:

$$\log\left[\frac{p_R}{p_L}\right] = k_{0,i} + (k_{0,i,j}). \tag{A2}$$

Similarly the effect of distance can be assessed by comparing the deviance of the full model with deviance obtained in the model that can be written as:

$$\log\left[\frac{p_R}{p_L}\right] = k_0 + k_1\text{Mate} + (k_{0,j}). \tag{A3}$$

The deviance is equivalent to the sum of square errors in linear regression and can therefore be used to estimate the goodness of fit of a model. Differences in deviance are used to compare models: a parameter is significant when the deviance of the full model is significantly lower than the deviance of the model not including that parameter. We estimated the statistically significant differences in the deviance models by using likelihood ratio tests.

As stated in Materials and methods, we also estimated GLMM for each propagation distance separately (16, 64 and 256 m) in order to examine the effect size and significance of Mate side at each distance; for these models we also analysed the order effect of each session. We also performed a statistical test for each bird.

The effect size of the presence of the mate, as assessed by the model, can be expressed as an OR: the ratio of the odds of perching

on the right when the mate is on the right divided by the odds of perching on the right when the mate is on the left. The odds of perching on the right when the mate is on the right are:

$$\frac{p_{\text{R|Mate}}}{1 - p_{\text{R|Mate}}} = e^{k_0 + k_1} \ . \tag{A4}$$

Similarly, the odds of perching right when the mate is on the left are:

$$\frac{p_{\text{R|NoMate}}}{1 - p_{\text{R|NoMate}}} = e^{k_0} \ . \tag{A5}$$

The odds ratio for the effect of mate on the right side is then simply:

$$\text{OR} = \frac{e^{k_0 + k_1}}{e^{k_0}} = e^{k_1} \ . \tag{A6}$$

Repeating this calculation for the left side, one finds exactly the same answer:

$$\text{OR} = \frac{e^{-k_0}}{e^{-k_0 - k_1}} = e^{k_1} \ . \tag{A7}$$

The error bars in Fig. 2 were obtained from the standard errors of k_1 obtained in the model fits.

APPENDIX 2
Experiment 2: discrimination task

The omnibus test that took into account all the regressors can be written as:

$$\log\left[\frac{p_1}{1 - p_1}\right] = k_{0,i} + k_{1,i}\,\text{StimType} + k_{0,i,c}\text{Corr}$$
$$+ k_{1,i,c}\,\text{StimType} \times \text{Corr} + (k_{0,j}) \ . \tag{A8}$$

Here, i is the index for distance, StimType is the binary variable to distinguish Re versus NoRe stimuli (0 for NoRe, 1 for Re), Corr is the spectral correlation between the Re and NoRe stimuli and j numerates the bird. Then, the average and bias-corrected odds of interrupting the NoRe stimulus are:

$$\text{OI}_{\text{No Re}} = \frac{p_1}{1 - p_1} = e^{k_0} \tag{A9}$$

and of interrupting the Re stimulus are:

$$\text{OI}_{\text{Re}} = \frac{p_1}{1 - p_1} = e^{k_0 + k_1} \ , \tag{A10}$$

where $k_0 = k_{0,i} + k_{0,i,c}\text{Corr}$ and $k_1 = k_{1,i} + k_{1,i,c}\text{Corr}$. The OR is then $\text{OI}_{\text{NoRe}}/\text{OI}_{\text{Re}} = e^{-k_1}$.

To test for the significance of the stimulus type, distance and stimulus correlation, this full model was compared with models not taking into account each of these respective effects. Statistical significance for these model comparisons was obtained from likelihood ratio tests. We also fitted models separately for each distance and without taking into account stimulus correlations. These simple models can be written as:

$$\log\left[\frac{p_1}{1 - p_1}\right] = k_0 + k_1\,\text{StimType} + (k_{0,j}) \tag{A11}$$

with a bird-specific bias as a random effect and:

$$\log\left[\frac{p_1}{1 - p_1}\right] = k_0 + k_1\,\text{StimType} \tag{A12}$$

without the random effect.

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