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Acoustic similarity to parental calls promotes response to unfamiliar calls in zebra finch fledglings

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Individual recognition, using acoustic, visual or olfactory individual signatures, is crucial for the coordination of social interactions and its occurrence has been demonstrated experimentally in many taxa. In this context, mistaking one individual for another is expected to be costly, for example through misdirected parental care or social punishment. To minimize the occurrence of such false responses, individual signatures should be distinct and selection should act on receivers to perceive these differences. However, it is largely unknown how precise signal perception is and whether similarity between individual signatures influences the occurrence of false responses. We used acoustic parent–offspring recognition in zebra finches, *Taeniopygia guttata*, to test how acoustic similarity between individuals affects a chick's response behaviour. In a playback experiment, fledglings were presented with calls of parents as well as calls of nonparents that varied systematically in their similarity to the parents' calls. The acoustic similarity between calls of parents and unrelated adults partly explained the response pattern of fledglings. Offspring preferentially responded to adult calls that were similar to their parents' call. The response pattern further seemed to incorporate a baseline responsiveness to conspecifics since most fledglings responded to very dissimilar adults. These findings demonstrate that the strength of response is related to signal similarity, which is potentially an important underlying mechanism shaping distinctiveness in signal design.

It is well established that birds and other taxa use contact calls to coordinate their social interactions and that these calls facilitate recognition between individuals (for a review see Kondo & Watanabe 2009). Individual recognition is selectively advantageous in a variety of repeated social interactions, for example to ensure that investments reach the correct recipient in parental care (Jouventin et al. 1999), or to enable mates to recognize one another (Vignal et al. 2008). Selection for individual recognition is expected to act on both the distinctiveness of individuals and the ability of the receiver to perceive differences between individuals (Tibbetts & Dale 2007).

Distinctiveness in identity traits can evolve through negative frequency-dependent selection, which promotes distinctive or rare signals/phenotypes (Dale et al. 2001; Sheehan & Tibbetts 2009, 2010). As soon as a 'rare' phenotype evolves, this might give the bearer a selective advantage by being more easily recognizable (Tibbetts & Dale 2007). This trait is then expected to spread, until the trait becomes common and a new rare phenotype evolves, resulting in large intraspecific variation in identity signalling traits (Tibbetts & Dale 2007). While negative frequency-dependent selection is expected to increase variation in the selected trait within the population, selection for distinctiveness is likely to be counterbalanced by the need for species recognition or sexual selection processes (Ryan & Rand 1993).

Comparative studies on penguins (Jouventin & Aubin 2002), gulls (Mathevon et al. 2003) and swallows (Medvin et al. 1993) suggest that the ability to perceive individual differences and the distinctiveness of signals are related to the degree of coloniality of a species, because coloniality also increases the risk of mistaking one individual for another. Distinctiveness, as well as the ability to recognize differences between individuals, is thought to have evolved to minimize the risk of costly false responses, i.e. recognition errors (Dale et al. 2001). Costs related to recognition errors could result in misdirected parental effort for parents, inability of parents and young to reunite, social punishment of young approaching unrelated adults or attraction of predators through increased unselective signalling (e.g. begging or contact calls).

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However, whereas the selective advantage of individual recognition is intuitive, virtually no study has addressed the potential costs of recognition errors.

While there is ample evidence that recognition, using various sensory pathways, exists between familiar (e.g. parents, group members) and unfamiliar individuals (acoustic, e.g. Charrier et al. 2001; Sharp et al. 2005; visual, e.g. Parr & De Waal 1999; Tibbetts 2002; olfactory, e.g. Bowers & Alexander 1967; Carazo et al. 2008), these studies also demonstrate that recognition processes are not perfect and that false responses occur. Specifically in zebra finches, *Taeniopygia guttata*, we (Jacot et al. 2010) have found that fledglings respond to nonparental calls and we proposed that such responses to nonparents could be recognition errors, related to acoustic similarity between parents and nonparents. Surprisingly however, few studies have specifically tested the effect of similarity on the precision of acoustic recognition processes (Fallow et al. 2011). Such studies are of crucial importance since costly recognition errors are likely to be an important driving force shaping distinctiveness in signal design.

In this study on captive zebra finches, we investigated how fledglings responded to nonparental adult distance calls that varied systematically in their overall acoustic similarity to the parents' distance calls. Zebra finches are opportunistic breeders with biparental care that nest in loose colonies of up to 100 pairs, and offspring are fed during an extended postfledging phase by their parents (Zann 1996). Acoustic recognition is an important component of the zebra finch's communication system; adult zebra finches of both sexes have been shown to recognize individuals of the other sex in a mate recognition context (Vignal et al. 2004, 2008). It has also been shown that young zebra finches preferentially respond to parental calls, suggesting that they are able to recognize their parents acoustically (Jacot et al. 2010; Mulard et al. 2010). One of the main calls used in social interactions is the distance call, a contact call used if birds are not close to each other or in visual contact (Zann 1996). Young fledglings use long tonal calls that gradually develop into a distance call at around the age of 30 days; these calls are most similar to female distance calls (Zann 1996).

A fledgling's response behaviour to unrelated adults may incorporate several, nonmutually exclusive components. First, it may reflect true recognition errors. Second, responding to unrelated adults may be part of social interactions where fledglings try to socialize with conspecifics. Third, it may reflect a fledgling's strategy to cheat on unrelated adults that are acoustically similar to their parents. This last hypothesis assumes that those similar unrelated adults produce offspring that are acoustically similar to the cheating fledglings and in turn will mistake them for their own fledglings. We used recently fledged zebra finches in a playback experiment, in which we visually and acoustically isolated fledglings from their parents and aviary members. As playback stimuli we used calls with known similarity between parent calls and calls of unrelated adults. This allowed us to test systematically a fledgling's response towards unrelated adults, depending on their acoustic similarity to its parents. First, we predicted that fledglings would react more strongly towards calls from their parents. Second, we predicted that responses to calls of unrelated adults would be less strong as acoustic similarity to parental calls decreased. In both predictions we expected that young birds would change the number of response calls and adjust call characteristics that are related to motivational status (Jacot et al. 2010).

METHODS

Subjects and Housing

Fledgling zebra finches used in the present study originated from a captive population held at the Max Planck Institute for Ornithology in Seewiesen, Germany. All fledglings tested in this study were descendants from birds breeding in aviaries that held six breeding pairs. Even though in this study we focused on recognition of social parents (recognition of the parent raising the fledglings), we also had information on the genetic origin of fledglings (Forstmeier et al. 2011). Of 120 fledglings in our study, 75 were within-pair offspring, 42 had been sired by extrapair fathers and three originated from dumped eggs. The sex of the offspring was determined using molecular methods (Griffiths et al. 1998). Temperature in the rooms was maintained at 23–25 °C and relative humidity from 40 to 60%. Rooms were illuminated by full-spectrum fluorescent light (Osram Lumilux T5 FH 28W/860 Daylight) and the light:dark period was 14:10 h. All birds received a millet seed mixture, cuttlefish, grit, water ad libitum on a daily basis and a multivitamin supplement once per week. All recognition trials were conducted between May and August 2009. Aviaries were checked twice a day for newly fledged birds. Nestlings were individually marked by numbered alloy bands.

Acoustic Similarity between Individuals

To calculate similarities between individuals, we used distance call recordings of 100 male and 94 female zebra finches (total number of calls: $N_{\text{males}} = 1576$, $N_{\text{females}} = 990$; number of calls/individual: mean ± SD: males: 15.76 ± 6.29; females: 10.53 ± 1.71). These calls had been recorded previously as described by Forstmeier et al. (2009), using the same playback-recording set-up as for our experiment (see below) from individuals that were unfamiliar to the tested fledglings. The calls were analysed with Sound Analysis Pro software (Tchernichovski & Mitra 2004) using standard settings. We extracted the following acoustic features to characterize the acoustic structure of each call: (1) call duration (ms), (2) variance in amplitude modulation (1/ms), (3) mean frequency (Hz), (4) mean frequency modulation (°), (5) variance in frequency modulation (°), (6) mean entropy, (7) variance in entropy, (8) mean pitch, (9) mean pitch goodness and (10) mean principal contour (for details see Tchernichovski & Mitra 2004; Reers & Jacot 2011).

To investigate the effect of acoustic similarity on the probability of a chick responding, we used stimulus calls with known similarity to parental calls. The acoustic similarities (i.e. the inverse of acoustic distances) between calls were calculated for both sexes from two separate linear discriminant function analyses using all 10 acoustic features ($N_{\text{males}} = 100$, $N_{\text{females}} = 94$; R-package: MASS, Venables & Ripley 2002). Using the discriminant scores for each call, the centre for an individual (i.e. the centroid) was calculated as the mean of each discriminant score for all calls from one individual (mean intraindividual variation in distance of calls to centroid: mean ± SD: males: 3.31 ± 1.29; females: 4.49 ± 2.24). In the next step, the 'most representative call' for each individual was then defined as the call with the shortest Mahalanobis distance to its centroid (distances to centre of group; mean ± SD: males: 0.86 ± 0.44; females: 1.43 ± 1.08; Mahalanobis 1936; Medvin et al. 1992).

In the following, we only use this one selected call from each of the 194 adults. As a measure of acoustic similarities between individuals, we calculated the Mahalanobis distances between the representative calls of all individuals, separately for each sex. For each individual parent we picked from the pool of other same-sex parents the five most similar calls (similarity 1, ranked 1–5 in distance; mean ± SD: male: 4.21 ± 3.50; female: 4.65 ± 2.77), five calls with intermediate similarity (similarity 2, ranked 40–44 in distance; mean ± SD: male: 11.72 ± 5.73; female: 11.83 ± 4.09) and five calls that were dissimilar (similarity 3, ranked 80–84 in distance; mean ± SD: male: 19.35 ± 6.73; female: 19.14 ± 4.85) as