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Impact of visual contact on vocal interaction dynamics of pair-bonded birds

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Animal social interactions usually revolve around several sensory modalities. For birds, these are primarily visual and acoustic. However, some habitat specificities or long distances may temporarily hinder or limit visual information transmission making acoustic transmission a central channel of communication even during complex social behaviours. Here we investigated the impact of visual limitation on the vocal dynamics between zebra finch, *Taeniopygia guttata*, partners. Pairs were acoustically recorded during a separation and reunion protocol with gradually decreasing distance without visual contact. Without visual contact, pairs displayed more correlated vocal exchanges than with visual contact. We also analysed the turn-taking sequences of individuals' vocalizations during an exchange with or without visual contact. In the absence of visual contact, the identity of a vocalizing individual was well predicted by the knowledge of the identity of the previous vocalizer. This property is characteristic of a stochastic process called a Markov chain and we found that turn-taking sequences of birds deprived of visual contact were Markovian. Thus, both the temporal correlation between the calls of the two partners and Markov properties of acoustic interactions indicate that, in the absence of visual cues, the decision to call is taken on a very short-term basis and solely on acoustic information (both temporal and identity of caller). Strikingly, when individuals were in visual contact both these features of their acoustic social interactions disappeared indicating that birds adapted their calling dynamics to cope with limited visual cues.
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While individual traits usually drive the probability of survival and breeding in a given environment, properties emerging from interactions between mates can also influence the success of a pair, overriding the influence of intrinsic individual quality (Ens, Safriel, & Harris, 1993; Ryan & Altmann, 2001). Many long-term monogamous species of birds show an increase in breeding success with pair bond duration, which is attributed to the improvement in partners' coordination over time (mate familiarity effect; Black, 2001; Black & Hulme, 1996; Forslund & Pärt, 1995). The strength of coordination and synchronization of behaviours within a pair may at least partly depend on the quality of communication between the individuals.

In birds, vocalization exchanges lie at the heart of pair bond formation and courtship (Marler & Slabbekoorn, 2004; Tobias, Gamarra-Toledo, Garcia-Olaechea, Pulgarin, & Seddon, 2011), but vocal interactions may also function in recognition of partners (Beer, 1971; Marzluff, 1988; Robertson, 1996; Vignal, Mathevon, & Mottin, 2008), pair bond maintenance (Beletsky & Orians, 1985), foraging behaviour (Evans & Marler, 1994; Gyger & Marler, 1988), vigilance against predators (Colombelli-Negrel, Robertson, & Kleindorfer, 2011; Krechmar, 2003; McDonald & Greenberg, 1991; Tobias & Seddon, 2009; Yasukawa, 1989), and incubation of eggs and nestling provisioning (Gorissen & Eens, 2005). Some species even exhibit highly synchronized vocal duets between mates (Benedict, 2008; Dahlin & Benedict, 2013; Farabaugh, 1982; Hall, 2004, 2009).

Mates can use acoustic communication while in visual contact or when visual contact is disrupted. Thus, there is a possibility that the amount of visual contact affects acoustic communication during contact maintenance. Some habitat characteristics or long

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distances between individuals may limit the efficacy of visual communication and therefore favour contact maintenance via acoustic cues. Female Steere's liocichlas, *Liocichla steerii*, are more likely to answer their mate's song and to engage in song duets in dense forest habitat than in open agricultural habitat (Mays, Yao, & Yuan, 2006). In the black-bellied wren, *Pheugopedius fasciatoventris*, birds answer their mate's song more often when the mate is close, and song answering facilitates approach and direct contact (Logue, 2007). In the common marmoset, *Callithrix jacchus*, visually occluded individuals engage in a reciprocal exchange of long-distance contact calls, a sequence called antiphonal calling (Miller & Wang, 2006), and the acoustic structure of the contact calls depends on the possibility of visual contact (Schrader & Todt, 1993). Thus, when visual contact is lost, acoustic communication seems to compensate for at least part of that loss and to become more accurate: partners respond to each other more systematically, more regularly and with specific acoustic signals. When visual contact is lost partners may be more motivated to find each other. Therefore, even if the predation risk is increased they may be more active acoustically because this becomes the central channel of communication. They may also concentrate more to hear, and find, each other or they may be more efficient because they only have one channel on which to focus.

To study the impact of the loss of visual contact on acoustic communication, we used the zebra finch, *Taeniopygia guttata*, a well-studied monogamous passerine that forms lifelong pair bonds (Zann, 1996). In the wild, partners are inseparable even outside the breeding season (McCowan, Mariette, & Griffith, in press), except during situations such as incubation when only a single bird can effectively incubate alone. Even during incubation they maintain a close relationship and will act as sentinel for each other while carrying out the relatively vulnerable task of sitting alone in the nest (Elie et al., 2010; Mainwaring & Griffith, 2013). When separated, zebra finch pairs show increased stress hormone levels as well as alterations in their behaviour that are reversed by reunion with the partner, responses considered characteristic of social bonding (Remage-Healey, Adkins-Regan, & Romero, 2003). Established pairs are able to respond quicker to an opportunity to breed (Adkins-Regan & Tomaszycki, 2007), and during chick rearing, nest visits are synchronized between partners, with highly synchronized pairs achieving greater reproductive success (Mariette & Griffith, 2012, 2015). In domestic birds, foster chicks raised by parents with similar personality traits show higher body mass and condition (Schuett, Dall, & Royle, 2011), suggesting that behavioural matching between partners could enhance parental care. The zebra finch is thus a good model species to study pair coordination and synchronization and how it potentially improves with pair bond duration. In addition, zebra finches use a large repertoire of calls during social interactions (Zann, 1996). Male and female can recognize their mates using calls only (Elie et al., 2010; Vignal, Mathevon, & Mottin, 2004; Vignal et al., 2008) and partners produce coordinated vocal duets at the nest during breeding that may help in maintaining the pair bond and coordinate brood care (Elie et al., 2010). During foraging, mates keep constant acoustic contact even when visually separated (Zann, 1996). Zebra finch mates thus remain highly coordinated in several situations in which calls are involved.

Our main prediction was that partners lacking visual contact would depend more on the acoustic channel and be better coordinated in their vocal interactions. We tested this hypothesis using a protocol of separation and reunion with a graded opportunity of contact which was composed of four stages: (1) partners were first separated in two acoustically isolated rooms; (2) they were allowed to be within acoustic contact at long distance and without visual contact; (3) they were reunited at close distance but still without visual contact; (4) partners were allowed to hear and see each other at close distance. The vocal activity of each bird was recorded throughout the protocol. We also recorded birds in a baseline condition: birds at close distance with both visual and acoustic contact, which allowed us to characterize 'classical passive' calling behaviour, i.e. without perturbation. Using automatic detection/extraction algorithms, we obtained the detailed calling activity and the temporal dynamics for each individual in each condition.

We studied three sets of measures to describe the calling behaviours in different conditions. First, we focused on the call rate and time spent calling which merely depict for each bird a global and general vocal activity. Next we performed an analysis of the dynamics of calling activity in which the temporal synchrony (or lack of it) in calling activity between mates was studied by computing the temporal cross-correlation between male and female calling signals. Then, to study the turn-taking sequences of the two partners with and without visual contact we chose to use Markov chains. This is a model in which the probability of being in one state (here who is calling) depends only on the probability of the previous state (who last called). This model has been previously used to characterize sequences of song syllables in birds (Kershenbaum et al., 2014), as well as human conversations: in face-to-face situations or on the phone when visual contact is not possible (ten Bosch, Oostdijk, & de Ruiter, 2004; Wilson & Wilson, 2005). Here we used this model for the first time to study the acoustic communication between partners from a new viewpoint, i.e. by exploring the dynamics of their acoustic exchanges.

The last two sets of measures, temporal cross-correlation and Markov chain dynamics, can together characterize important components of a pair's acoustic-dominated communication and we expected these components to be refined when visual cues were absent. Finally, we studied the impact of mates' history, i.e. previous breeding experience and origin (wild type or domestic), on the vocal interaction dynamics of different pairs.

METHODS

Experimental Procedure

Subjects and housing conditions

One group of zebra finches (25 pairs) was used for the separation/reunion protocol. In this first group, half were domestic birds bred in our colony (12 pairs); the other half were wild-type birds (13 pairs). The domestic birds had been bred in our facility for at least three generations (Tschirren, Rutstein, Postma, Mariette, & Griffith, 2009). The captive wild-type birds were either taken under licence from Sturt National Park (northwest New South Wales, Australia) in September 2007 using mist nets (Pariser, Mariette, & Griffith, 2010) or were direct descendants of these wild birds, and either first- or second-generation captive bred.

Domestic and wild-type birds were housed separately in two outdoor aviaries (10 × 8 m and 2 m high), each containing between 30 and 50 birds. Each aviary was provided with ad libitum commercial finch seeds, water, cuttlefish bones, grit, sprouted seed, two heat lamps and nestboxes.

We selected 20 pairs by directly observing the aviaries for 2 h on 3 consecutive days so as to detect pairs performing four specific behaviours (Zann, 1996): nestling rearing (birds raising chicks together), clumping (birds perching side by side in contact), allopreening (one bird preening the feathers of the other), nest sharing (birds sharing the same nest). Breeding activity in the two outdoor aviaries had been monitored for a year prior to the experiment. This allowed us to determine the previous reproductive success of the pair. The five remaining pairs (three wild type and two domestic) were formed by randomly putting together a male and a female in

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