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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 large distances may temporarily hinder or limit visual information transmission making acoustic transmission a central channel of communication even during complex social behaviours. Here we show the impact of visual limitation on the vocal dynamics between zebra finches partners. Pairs were acoustically recorded during a separation and reunion protocol with gradually decreasing distance without visual contact. Without visual contact, pairs display more correlated vocal exchanges than with visual contact. We also analysed the turn-taking sequences of individuals’ vocalisations during an exchange with or without visual contact. We show that in the absence of visual contact, the identity of a vocalising individual is well predicted by the knowledge of the identity of the previous vocaliser. This property is characteristic of a stochastic process called a Markov chain and we show here that deprived of visual contact, turn-taking sequences are 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 clues the decision to emit a call is taken on a very short-term basis and solely on acoustic information (both temporal and identity of caller). Strikingly, when individuals are in visual contact both these features of their acoustic social interactions disappear indicating that birds adapt their calling dynamics to cope with limited visual cues.

Keywords: Markov chains, pair-bond, turn-taking, visual contact, vocal communication, zebra finch
Whilst 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, vocalizations exchanges lay 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 partner’s recognition (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; Yasukawa, 1989; McDonald & Greenberg, 1991; Tobias & Seddon, 2009), 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 the visual contact is disrupted. Thus, there is a possibility of the amount of visual contact affecting acoustic communication during contact maintenance. Some habitat characteristics or long 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 compared to 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 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 in the acoustic channel because it becomes the central channel of communication. They also may concentrate more to hear each other in order to find each other, or they may be more efficient because they only have one channel to focus on.

In order 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 of the breeding season (McCowan, Mariette, & Griffith, in press), except during situations like incubation where only a single bird can effectively incubate alone. Even during incubation they maintain a close relationship and will act as sentinel for each other whilst 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 emit 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
where calls are involved.

Our main prediction is that partners lacking visual contact will depend more on the acoustic channel
and show a better coordination in their vocal interactions. We tested this hypothesis using a protocol
of separation and reunion with 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, i.e. birds being at close distance with both visual and
acoustic contact, that allowed us to characterise ‘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 dynamic 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, in order 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 emitting a call)
depends only on the probability of the previous state (who emitted the last call). This model has
been previously used to characterize sequences of songs syllables in birds (Kershenbaum et al.,
2014), as well as human conversations: in face-to-face situation or on the phone when visual contact
is not possible (Ten Bosch, Oostdijk, & de Ruiter, 2004; Wilson, M. & Wilson, T. P., 2005). Here
this model is used 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 chains dynamics – can
together characterize important components of a pairs acoustic-dominated communication and we
expect them to be refined when visual cues are absent. Finally we studied the impact of mates’
history - previous breeding experience and pairs’ origin (wild type or domestic) – on the vocal
interaction dynamics of different pairs.

MATERIALS & METHODS

Experimental Procedure

Subjects and housing conditions

The birds used for this study were zebra finches (*Taeniopygia guttata*).

One first group of birds (25 pairs) was used for the separation/reunion protocol. In this first group,
half of the animals 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 et al. 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 X 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 three consecutive days during two hours so as to detect pairs using 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 one), 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 (3 wild type and 2 domestic) were formed by randomly putting together a male and a female in the same individual cage for one month prior to the experiment. One week before the beginning of the experiment, the effectiveness of these five pair bonds was verified by observing clumping and allopreening.

All pairs were caught in the aviaries and then housed in individual cages (1 pair per cage, height = 40 cm, width = 75 cm, depth = 47 cm) stored in the same rearing room for the duration of the experiment.

Another group of birds, naive to the experimental protocol, was used for the protocol in baseline condition. This group was part of the colony of European Domestic zebra finches bred at the ENES laboratory, University of Saint-Etienne and comprised 11 pairs. Finch seed, cuttlefish bone and water were provided ad libitum and salad once a week. The temperature was maintained around 23–25 °C and the photoperiod was 14L/10D. Pairs were bred in private cages (dimensions 40x40x25cm) put in a same room.
Pairs from both groups of birds had been formed at least one month before the experiment and we checked if partners actually behaved as a pair using regular proxies (clumping/alopreening) used to identify pairs in this species (Zann 1996).

Separation – reunion protocol

The day before the experiment, each pair was moved from the rearing room to the experimental room and placed in a separation cage. The morning of the experiment, two webcams (logitech HD pro C910) and two microphones (AKG C 417 Clip-on Microphones, one per half cage) connected to a recorder (zoom H4n) were activated to monitor the birds’ locomotor and vocal behaviours during the whole experiment. Two sessions were run in the same morning in two different experimental rooms, allowing us to record two pairs per day. Each day, the first session began at 8:00 am and the second session at 10:00 am. Each session lasted one hour. Wild type and domestic pairs were randomly chosen to be recorded during the first or the second session. Partners were physically separated using two partitions placed in the middle of the experimental cage, which allowed separating the cage into two separate sections. The newly independent sections were then moved in two other independent rooms separated by 6 m and two heavily insulated doors: each partner was then placed in a new room, visually and acoustically isolated from its mate (Fig.1).

After 30 minutes of separation (Isolated), the doors from the independent rooms were opened for 10 minutes, allowing acoustic contact at long distance between the birds but preventing visual contact (Far No Visual). This situation was suitable for the exchange of distance calls between partners. Each bird was then removed from its room and placed back in the first experimental room so that partners were both moved and placed in the same room again, at close distance but without visual contact, for 10 minutes (Close No Visual). Finally, the partitions were removed and both acoustic and visual contact were permitted during 10 minutes (Reunion).
**Determination of pair history**

We had two pieces of information about the pairs’ history: the origin of the pair as wild-type (Wild) or from domestic stock (Dom), and the previous breeding experience of each pair (as the breeding experience of wild-type birds with their potential previous partner in the wild was unknown), stating whether pairs successfully reared offspring (Offspring) or not (No Offspring).

**Pair recordings in baseline condition**

In this second protocol we recorded pairs in a baseline condition. The day before the experiment, each pair was moved from the rearing room to the experimental room and each bird was placed in a cage, with one microphone per cage. Microphones (Audio Technica AT8531) were connected to a recorder (zoom H4n). We recorded vocal exchanges during a long period (6 hours) (9-10 am to 15-16 pm) to have the opportunity to study vocal dynamic in a baseline condition.

**Call extractions**

Vocalizations were extracted from recordings using in-house software. These programs were written in python (www.python.org) by authors H.A.S. and M.S.A.F using open-source libraries. This software accuracy was tested, confirmed and used in a previous study (Elie, Soula, Mathevon, & Vignal, 2011). All methods are described in this previous study and we summarize them here.

Vocalization detection is a pipeline of three stages. The first process was a simple threshold-based sound detection based on a high-pass filtered energy envelope (1024 samples FFT; 441 Hz sampling; cut-off frequency: 500Hz). During the second stage, each sound whose peak was extracted was reconstructed by exploring the two sides and keeping area with energy higher than 10% of the peak. Thus, each event was either lengthened or shortened to obtain the same amplitude range during the event. This allows a good estimate of the call duration. The third stage simply merged overlapping waveform segments. Together, the three stages produced start, end, and duration values for each sound event detected in the recording.
Two additional stages were added for this study in order to assign each call to its emitter and also remove cage or wing noises. The first additional stage removed double calls, i.e. calls emitted by one bird and recorded by its microphone but also recorded by the microphone of the other bird of the pair (only in Far No Visual, Close No Visual and Reunion conditions) by using energy and delay differences. The second stage removed cage or wings noises using a machine learning process. We trained a supervised classifier using a data set composed of 4500 random extracted sounds from all of our data. Each sound was classified by one expert (MSAF) as “call” or “non-call”. The classification was performed on the spectrogram of the sounds sliced in equal parts using 55 parameters. More precisely, the spectrogram matrix was first reduced to the frequencies of interest – between 500Hz and 8kHz. To obtain the same size for all calls that have different durations, we sliced the temporal axis into 5 parts. We sliced the frequency range into 11 parts. The average value was taken to compute each entry of the reduced matrix (of size 11 by 5). This matrix will be seen as a vector of 55 parameters. We trained a Random Forest classifier (Breiman, 2001) with 1500 sounds. This classifier had an overall rate of error below 10% of the remaining 3000 sounds. We then applied an important manual verification to the extracted call sequences. This procedure allowed us to extract two types of calls from the zebra finch repertoire: tet calls i.e. soft and short harmonic stacks with almost no frequency modulation (Zann, 1975; 1993), and distance calls i.e. complex sound consisting of a harmonic series modulated in frequency as well as amplitude (Zann, 1996). Because we were interested in the dynamic of the exchange only, we decided to pool the two types of calls in the following analyses.

Ethical note

The first group of birds was bred at the ENES laboratory, University of Saint-Etienne with the Autorisation du ministère français de la recherche, licence number 42-218-0901-38 SV 09. The second group was bred at the Macquarie University with the Animal Research Authority reference number 2010/053-5.
Data Analysis

We separated the analysis into the three parts described below: vocal activity, cross-correlation and Markov analysis.

**Vocal activity**

We calculated general parameters such as call rate (number of calls per minute), cumulative number of calls (total number of calls emitted from the beginning of the experiment at a given time), and time spent calling (duration between the first and the last vocalization as a percentage of total recording time). We also looked at the correlation between male and female call rates (Fig. 2(c)): for each pair we have the male call rate on the x-axis and the female call rate on the y-axis, and therefore each point represents a pair.

**Cross-correlation: Temporal analysis of male-female calling activity**

We computed the cross-correlation between male and female calling signals. A calling signal is a temporal description of the calling emission and is defined as a function of time \( t \) that is 1 if the bird is emitting a sound at \( t \) and zero otherwise. The sampling frequency was set to 200Hz (5ms bins).

For example if, for one part of a calling signal of 75ms, we obtain 0 0 0 1 1 1 1 1 1 1 1 0 0, it means that during the first 15 ms (3*5ms) the bird is silent, then this bird emits a call of 50ms (10*5ms) length, before it goes back to silence for 10 ms. \( S_{\text{male}} \) stands for the male signal and \( S_{\text{female}} \) for the female signal. We computed the cross-correlation (cc) of these two signals (\( S_{\text{male}} \) and \( S_{\text{female}} \)) with the following formula:

\[
cc(T) = \left< (S_{\text{male}}(t) - \text{mean}(S_{\text{male}}))(S_{\text{female}}(t+T) - \text{mean}(S_{\text{female}})) \right>.
\]

With the normalization step, we have: \( CC(T) = cc(T)/cc(0) \)

where \( CC \) is the normalized cross-correlation, \( T \) the time delay, and \( S_{\text{male}} \) and \( S_{\text{female}} \) the male and female signals as functions of \( t \) (time).
To compare cross-correlation between conditions, we computed the extreme of CC as a function of the delay T. One maximum (peak) at positive time values gives information about the delay of the male’s answer to the female’s call and conversely for a maximum at negative time values. We measured several parameters on the normalized cross-correlation functions: maximum peak height, each peak height and time (for both negative and positive time delays), the area under curve, as well as the duration with curve above 0.1. The area under curve is an indicator of the variability in answer delays. The duration with curve above 0.1 is the total time interval where the cross-correlation is higher than 0.1 and represents the temporal correlation duration of vocal exchanges.

**Markov analysis: Sequential analysis of male-female calling activity**

As we found a strong correlation in partners’ vocal activities, we expected that the vocal dynamic within pairs would present a long-term memory. To test this hypothesis we used Markov chains, a model in which the probability of being in one state (here emitting a call) depends only on the probability of the previous state (who emitted the last call), *i.e.* a model with a very short term memory. Consequently, if the vocal dynamic present a long-term memory the Markov model would be a poor predictor of the data.

Calling sequences were simply transformed into an array of M (Male call) and F (Female call) indicating the emitter’s identity (e.g. MMFMFMFF). Assuming two states M and F, the call sequence can be viewed as a stochastic process that "jumps" from state to state. With the Markov hypothesis the emitter identity depends only on the previous emitter according to a transition probability (for example the probability of having an M (male call) after a F (female call)). More precisely, a Markov matrix of size 2*2 depicts the probability of jumping from one identity to the other: in this matrix, an entry at line i and column j is the probability when emitter is i (M or F) that the next emitter will be j (M or F). By construction, this matrix reproduces both the average number of calls for each individual but also the first order transition. Sequences that induce cyclic pattern like MMMFMFMFMFMF - always three M followed by F - are not Markovian because the
sequence memory is longer than one step (here it is four steps). On the other hand, sequences with a perfect alternation (MFMFMFMF) are Markovian because the probability of having an $i$ depends only on the previous state: 1 if the previous state was $j$ and 0 if the previous state was $i$. Totally random sequences of M and F would be Markovian, because the probability of having an $i$ after a $j$ (equal to 0.5) does not depend on previous states. In the latter case, by chance, we could obtain long series of M (or F) but the likelihood of such sequences occurring randomly will decrease exponentially (with the length of the series). Therefore, the statistics of series of M and F would follow a particular structure if the sequence was Markovian (here the statistic is the autocorrelation, see below).

To assess whether or not, the calling sequences are akin to a Markov model, we produced artificial call sequences based on characteristics given by the real sequence Markov matrix. To take the variability of sequences into account in this comparison, these artificial sequences are the same length as our real sequence. Therefore we can compare the artificial sequences statistics (see below) with the real sequence counterpart: we computed the real sequence autocorrelation over a signal consisting of 0 (presence of male call) and 1 (presence of female call). We then compared it to the theoretical autocorrelation of a Markov chain analytically computed as $\lambda^T$ were $\lambda$ is the second eigenvalue of the Markov matrix (the first eigenvalue is 1) and $T$ is the time delay. For each time step, we located the real data's autocorrelation value in the empirical distribution of all autocorrelation values from the artificial sequences. We tested if our autocorrelation value (from the real sequence) was likely to belong to this distribution. For that we used the cumulative distribution and obtained the p-value corresponding to our real autocorrelation value. If the p-value was higher than $\alpha$ (5%) then there was no reason for rejecting the Markov model as a good approximation of this sequence.
All statistical tests were performed using R software (R Core Team, 2014) and python (www.python.org).

Vocal activity

For the general parameters of vocal activity (call rate and time spent calling), as the distributions did not allow to group all factors in a single model, we used independent tests for each factor. A fit to the Normal distribution was tested using the Shapiro test. When comparing two groups, if normality was confirmed, homoscedasticity was tested using the Fisher, and if not, the Fisher test with permutation from the “RVAideMemoire” package was used (allowing non-normal data).

When comparing more than two groups, the Bartlett test was used when normality was confirmed (we always had at least 4 individuals per group), or Bartlett test with permutations in the other case (non-parametric, “RVAideMemoire” package).

We had four paired conditions (Isolated, Close No Visual, Far No Visual and Reunion with the first zebra finch group), and one unpaired condition compared to the others (Baseline, with the second zebra finch group). First, when comparing between paired conditions we use either Student test for paired data (if only two means compared) or ANOVA for repeated measures (if homoscedasticity) or Friedman test (if heteroscedasticity) to test global differences between all four conditions.

Wilcoxon pairwise signed rank test was then used for posthoc pairwise comparisons. Then, when comparing between two unpaired groups, if normality was confirmed we used either Student test (if homoscedasticity) or Student test with Welch correction (if heteroscedasticity). If normality was not confirmed, Student test with permutations (if homoscedasticity) or Man-Whitney-Wilcoxon test (if heteroscedasticity) were used.

Linear model selection

From the most complex model (interactive model), simplifications were performed. When comparing models we chose to use the AICc (second order information criterion) that takes into account sample size by increasing the relative penalty for model complexity with small data sets.
The AICc converge to AIC when sample sizes increase. For each parameter, statistics resulting from the best model are presented, i.e. the model with the lower AICc. P-values were computed using multiple comparisons between conditions with Tukey contrast (‘glht’ function of ‘multcomp’ R package).

Correlation between male and female general activity
We performed linear models including all factors (condition = 5 levels: Isolated, Far No Visual, Close No Visual, Reunion, Baseline, Offspring = 2 levels: Offspring (previous breeding experience), No Offspring (no previous experience) and Type = 2 levels: Wild (wild type) and Dom (domestic)) and the pair identity as random factor. We selected the following linear models: female call rate ~ male call rate * condition + 1|pair and female time spent calling ~ male time spent calling * condition + 1|pair. As the interactions between the two factors were significant, we studied the influence of male call rate and time spent calling in each condition separately. Detailed results of the models are shown in Table A1.

Probability of emitting at least one call
The probability of emitting at least a call was studied using a generalized mixed model with a binomial family, with a 0/1 response (0 if the bird did not emit one call during the recording, 1 if the bird emitted at least one call). The following model was selected: probaOneCall ~ condition * Offspring + 1|pair. As the interaction between the two factors was significant, we studied the influence of Offspring on the probability of emitting a call in each condition separately. Detailed results of the model are shown in Table A2.

Markov analysis
For each time step we had the success or failure for our real data to belong to the theoretical
distribution of Markov (0 if data did not belong to the distribution, 1 if data belong to the
distribution). Birds from the baseline group had all the same previous breeding experience
(Offspring) and they were all domestic, so we could not include them in a global model with
Offspring and TYPE factors. As a consequence we first built a model including the condition as a
factor (markov fit ~ condition + 1|pair, generalized linear mixed models with binomial family). This
model was validated and it was thus possible to interpret the results. However we also wanted to
know if the previous breeding experience (Offspring/No Offspring) and the type (Wild/Dom) had
an influence on the Markov fit. We built generalized linear mixed models with binomial family
including all factors (condition, Offspring, TYPE) and selected the following: markov fit ~
condition * TYPE + 1|pair. As the interaction between factors was significant, we studied the
influence of TYPE in each condition. All binomial models were checked as explained in Model
validation section. Detailed results of the models are shown in Table A3.

Model validation

Before being interpreted each model was checked, paying particular attention to their residuals. For
binomial models, we used five relevant plots from custom-written codes (Collett, D., 1991;
Atkinson, A.C., 1981) to test the validity. First, with the graph of standardized deviance residuals
we checked the residuals mean homogeneity, and with the graph of absolute value of standardized
deviance residuals we checked the residuals variance homogeneity. For both plots we only checked
if the residuals were between -2 and 2: because of the binary nature of date (and contrary to
classical linear models), non-homogeneously distributed residuals are no necessarily reflecting an
inappropriate model. The model hat matrix was then extracted and its diagonal coefficients ($h_i$)
enabled us to check the general influence of observations on the model fit to data. The threshold for
$h_i$ values is $2*\text{mean}(h_i)$. The Cook’s distance gave us information about the influence of each
observation on the parameter estimation, and had to be lower than $4/n$ with $n$ the number of
observations. Finally, we build the half-normal plot (Atkinson, A.C., 1981) i.e. standardized deviance residuals as a function of the half-normal distribution quantiles with simulated envelope. If data points were included in the envelope, the linear predictor was correct.

RESULTS

Vocal activity: Call rate increases with decreasing distance and with visual contact opportunity. The five conditions triggered different vocalization behaviours of the pairs as they significantly affected both call rate and time spent calling (Friedman test: call rate: $\chi^2_3 = 37.75, P < 0.001$; time spent calling $\chi^2_3 = 43.41, P < 0.001$). Call rates in the Close No Visual and Reunion conditions were higher than in all other conditions (Fig. 2(a)). Time spent calling was higher in the Close No Visual condition than in the Isolated and Far No Visual conditions (Fig. 2(b)), and was even higher when visual contact was possible (Reunion and Baseline conditions) (see Table 1).

Birds in Isolated and Far No Visual conditions displayed low levels of vocal activity (Fig. 2(a) and 2B). Some pairs did not emit calls at all (1 of 25 in Isolated and 10 of 25 in Far No Visual), but most pairs did, and for pairs that emitted at least one call, even though calls were few, they were spread over a large percentage of the recording time (62 ± 36 % for Isolated and 63 ± 35 % in Far No Visual). Compared to the Close No Visual and Reunion conditions, visual contact in Baseline condition was associated with significantly lower call rates (Fig. 2(a)), but high percentage of time spent calling (Fig. 2(b)). In all conditions, there was no difference between the sexes either in call rate or in time spent calling (Table 2).

Vocal activity: the correlation between male and female vocalizations increases with proximity but vanishes with visual contact. We computed the correlation coefficient ($R^2$) between the call rates and time spent calling of the male and the female of each pair in each condition (linear models with significant interactions, male
call rate * condition: $F_{4,66}=5.47, P = 0.001$ and male time spent calling * condition: $F_{4,66}=4.58, P = 0.002$) (Fig. 2(c) and Fig. A1). Correlation increased significantly between the isolation condition (Table 3, Isolated, $R^2$ call rate = -0.02 [-0.41, 0.37], $R^2$ time spent calling = 0.35 [-0.052,0.65]) and conditions allowing acoustic contact only (Table 3, Far No Visual $R^2$ call rate = 0.76 [0.53, 0.89], $R^2$ time spent calling = 0.89 [0.77,0.95], and Close No Visual $R^2$ call rate = 0.89 [0.77, 0.95], $R^2$ time spent calling = 0.99 [0.99,1.0]). Thus, without visual contact, the closer male and female are, the higher the correlation of their vocal emissions. This suggests that an increase in acoustic contact probability after a separation leads to a more correlated vocal activity. This correlation was lower when visual contact was allowed (Table3, Reunion $R^2$ call rate = 0.21 [-0.20, 0.56], $R^2$ time spent calling = 0.83 [0.66,0.92], and Baseline $R^2$ call rate = 0.46 [-0.19, 0.83], $R^2$ time spent calling = 0.21 [-0.45,0.71]).

Thus, pairs showed correlated vocal activities during vocal exchanges without visual contact. This correlation decreased with visual contact, and could sign a return to a baseline condition.

Cross-correlation: Pairs’ temporal coordination is different in acoustic or visual contact.

The cross-correlation of mates’ calling signals significantly differed between the five experimental conditions (Fig. 3). The vocal coordination was lower when visual contact was allowed (Reunion and Baseline conditions). Without visual contact, the cross-correlation was higher but varied according to the distance between mates. In the Far No Visual context, two peaks on the cross-correlation plot (Fig. 3) indicate that male and female answered each other alternatively: the left peak (with a negative time value) reflects the fact that on average the female answered the male with a 600ms delay, and the right peak (with a positive time value) tells us that on average the male answered the female with a 350ms delay. In the Close No Visual context, one unique peak indicates that one partner (here the female) answered the other with a 40ms delay. Illustrations of these results are shown in figure A2, with an example of call emission dynamic for one pair.
Among all pairs, the number of peaks of the cross-correlation differed between the Far No Visual and Close No Visual contexts (exact binomial test: $P = 0.007$), with two peaks being more likely in the Far No Visual condition and one peak in the Close No Visual condition.

**Markov Analysis: Mates call sequence statistics are Markovian only without visual contact**

Here most pairs’ vocal exchanges followed very closely a Markovian pattern when visual contact was not allowed (Fig. 4). The fit to Markov of the call sequence was lower when visual contact was possible as the Reunion and Baseline conditions each differed from both the Close No Visual and the Far No Visual conditions. This difference in the Markov fit was significant between conditions (generalized linear model with binomial family, Table 4). In other words, without visual contact the decision to emit a call is taken on a very short memory: the identity of an emitter is well predicted by the knowledge of the identity of the previous emitter only.

**Mates’ history modifies vocal coordination**

Our results suggest that pairs correlate their vocal exchange and we wanted to assess if this capacity was related to the history of the pair for some of the three measures described above – Vocal activity, Cross-correlation and Markov analysis. For the first group of birds (corresponding to the Isolated, Close No Visual, Far No Visual and Reunion conditions) we had information about the prior breeding experience of pairs (Offspring/No Offspring indicating whether the partners had a breeding experience together or not) and their type (Dom for domestic or Wild for wild-type).

**Vocal activity:** In the Far No Visual condition, pairs with successful breeding experience (Offspring) were more likely to emit calls than other pairs (No Offspring) (Fig 5(a), generalized linear model with significant interaction between condition and Offspring factors, $z = -3.21, N=50, P = 0.001$). So, when separated and able to hear each other, pairs with prior breeding experience were more likely to start a vocal exchange.
Cross-correlation: Besides, among pairs starting a vocal exchange in the Far No Visual and Reunion contexts, pairs with breeding experience presented more regularity in their delay of response to each other than unexperienced ones (cross-correlation maximum peak height for No Offspring vs Offspring, student test with Welch correction: $t_{12.77} = 2.23, N = 25$ pairs, $P = 0.004$ in Far No Visual and $P = 0.044$ in Reunion). In the Reunion context, temporal correlation of vocal exchanges was longer for experienced pairs (duration with a cross-correlation higher than 0.1, Wilcoxon exact rank sum test: $W = 104, N = 25$ pairs, $P = 0.054$).

In the Far No Visual context, temporal correlation of vocal exchanges was longer in wild-type pairs than in domestic pairs (duration with cross-correlation value higher than 0.1: student test with permutations: $t = 2.2, N = 13$ pairs, $P = 0.049$).

Markov fit: The difference in the Markov fit was significant between conditions, but this difference was not the same between the wild and domestic groups. Figure 5(b) shows that wild-type were more likely to fit better a Markov dynamic than domestic (Far No Visual: $z = 2.77, N = 12, P = 0.005$; Close No Visual: $z = 3.73, N = 23, P < 0.001$; Reunion: $z = 2.92, N = 25, P = 0.003$). Wild-type pairs show $78.5 \pm 33.3\%$ points in time fitting Markov whereas domestic pairs show $58.2 \pm 33.7\%$ points fitting Markov.

**DISCUSSION**

Our experiment revealed a strong correlation between mates’ vocal activities that was stronger when birds were in acoustic but not visual contact. The temporal cross-correlation between a pair’s vocalisations was higher when only acoustic contact was allowed (in both reunion and baseline conditions). We also found using a Markov analysis that the turn-taking sequence of the two partners was more predictable when pairs were unable to see one another. Both the temporal correlation and Markov property reveal that without visual clues the decision to emit a call is taken
on a very short-term basis and solely on acoustic information, indicating that birds adapt their
calling dynamics to cope with limited visual cues.

Taken together, these results show that partners possibly compensate the lack of visual contact by
improving vocal interaction to maintain an equivalent level of contact maintenance. This could also
indicate a slow return to the baseline situation, due to the close and assured presence of the partner.

This high correlation of vocal emissions in acoustic contact only between partners probably
indicates that the probability of response of one individual is strongly dependent on the actual
emission of the other. Assuming this is the case, we proposed a sequential analysis and studied the
turn-taking sequence using Markov chains paradigm. As we showed, most turn-taking sequences
showed Markov-like dynamics when acoustic contact is possible.

Similar vocal activity between partners when only acoustic contact is allowed could indicate an
assortative mating on partners’ vocal profile, silent birds and talkative birds being mated together.
However, calling behaviours of the male and the female are strongly different in other conditions.
Thus, the similar behaviours when no visual contact is possible could more likely indicate an
adjustment of behaviour. This similarity between mates through an adjustment of behaviour has
been described previously. For example in black-bellied wrens (*Pheugopedius fasciatoventris*),
even if females are able to sing different types of songs, they match the song-type of their mate
during duets (Logue, 2006). A study of vocal learning in budgerigars (*Melopsittacus undulatus*)
also showed that males imitate the contact calls of their newly assigned female (Hile, Plummer, &
Striedter, 2000).

Vocal activities of partners during acoustic contact showed a strong correlation of call rate and time
spent calling and high coordination (temporal cross-correlation). These data could fit some of the
characteristics used to define vocal duets (Farabaugh, 1982; Hall, 2004; Wickler & Seibt, 1982),
especially in long distance acoustic contact. In our study, vocal exchanges between partners when
acoustic contact only is possible could thus be seen as duet-like exchanges that participate in pair
bond maintenance after a separation. However it has to be noted that coordinated calling activity
does not necessarily imply a duet or a conversation. In some social contexts, birds can adjust the
timing of their calls only to reduce vocal costs, and the resulting vocal activity of the group is then
coordinated. For example, between parental feeding visits, barn owl (*Tyto alba*) young siblings
optimize communication and adjust their call timing to avoid signal interference (Dreiss, Ruppli,
Faller, & Roulin, 2015).

When partners are only in acoustic contact, turn-taking sequence dynamics are not distinguishable
from a Markov chain. This is an unexpected result. Indeed, Markov chains are systems that display
exponentially decreasing autocorrelation due to short-term memory. Yet, we found a strong
correlation in partners’ vocal activity. Long time correlation can usually be explained by oscillating
behaviours (one individual repeating the same pattern with a long period such as a sequence of
MMMFMMF – 3M’s followed by a F) or by long-term memory (one or both individuals recall
patterns of emission far back in time). In the context of a new acoustic contact after separation this
does not seem to be the case and very short memory (Markov-like dynamics) seems to be the rule
when no visual contact is possible. In this condition, the birds’ decision to emit a call seems to
depend only on the previous emitted call, and this indicates the presence of a discussion rather than
a proper rhythm of calling emission for each partner.

There is some relationship to human discussion behaviours. In social science, conversation experts
suggest that humans agree with implicit conversational rules that determine the optimal moment to
alternate the speaker (Duncan, 1972; Sacks, Schegloff, & Jefferson, 1974). Turn-taking involves
highly coordinated timing, with short response times and dynamics depending only on the last
emission (Choudhury & Basu, 2004; Takahashi, Narayanan, & Ghazanfar, 2013; Wilson, M. &
Wilson, T. P., 2005). Ten Bosch et al. (2004) studied the differences in turn-taking behaviour
between face-to-face and phone conversations in humans. Phone conversations (thus relying only
on acoustic cues) show shorter pauses than face-to-face dialogues, and furthermore the variability in pauses duration is larger in face-to-face dialogues. This was also the case in our study of zebra finches: during acoustic contact, delays of response between partners are extremely precise whereas in visual contact the answer delay is much more variable. This confirms that for birds such as for humans, the context of conversation seems to be an important factor for the timing aspects of turn-taking. A possible explanation for this phenomenon is that in face-to-face conversations individuals have several ways to convey information and to let know to their partner they are still involved in the conversation, without having to use acoustic signals. During the conditions allowing visual contact (reunion and baseline) it would be interesting to focus on visual signals between partners in addition to acoustic ones. We found that a turn-taking sequence made of acoustic signals only is not Markovian in this case, but a sequence made of both visual and acoustic signals could reveal that birds’ decision to emit a signal (visual or acoustic) depends only on the previous emitter, *i.e.* that this new type of sequence is Markovian.

Our results suggest that pairs very well coordinate their vocal exchange and we wanted to assess if this capacity was related to the history of the pairs. In our experiment some individuals remained silent during long distance acoustic accessibility and this can be explained by the protocol: whenever one individual emitted a call the other one could hear it and start a vocal exchange. On the other hand, there was no reason to detect that the other was within earshot without trying and emitting a call. We show that the pairs’ history did indeed play a role when such a contact opportunity emerges: experienced pairs were more likely to start calling to elicit answer from partner than inexperienced ones. This may be explained by several causes. It is possible that experienced pairs show more reliable vocal recognition between partners. A study in mandarin voles (*Microtus mandarinus*) and root voles (*Microtus oeconomus*) suggests that the intensity of mate recognition by sniffing or licking is related to familiarity degree (Zhao, Y., Tai, Wang, Zhao, X., & Li, 2002). Comparing discrimination of mate versus non-mate calls of birds from experienced pairs and inexperienced
pairs would test this hypothesis. In this study, the acoustic contact between pairs occurred after a
separation, thus it represents a vocal reunion in a non-reproductive context and could contribute to
pair bond maintenance. Inexperienced pairs are quieter in this context perhaps because their bond is
weaker and partners are less motivated to maintain contact. It is possible that previous breeding
experience allowed partners to exhibit many vocal exchanges, especially during duets at the nest
(Elie et al., 2010) and this could have led to a talkative and coordinated pair. As mate separation
results in an increase in corticosterone concentrations in zebra finches (Remage-Healey et al.,
2003), it is possible that the stress of isolation and visual separation differs between experienced
and inexperienced pairs and provokes different levels of vocal activity. This remains to be
investigated.

We showed that vocal interactions of wild-type birds fit better with a Markov model than domestic
ones when in acoustic contact. It has been shown that even if there is no evidence for a bottleneck
due to domestication of zebra finches, captive populations have lost some of the genetic variability
present in the wild (Forstmeier, Segelbacher, & Mueller, 2007). Our two groups of birds thus have
genetic differences that could explain their different call dynamics. Parameters used in previous
studies to compare wild and domestic zebra finch behaviour have not revealed any significant
difference between these populations (Tschiren et al., 2009). Besides, to our knowledge, no element
could explain vocal dynamic differences between wild and domestic zebra finches. However,
Honda and Okanoya (1999) showed that White-backed Munia (Lonchura striata) and its domestic
strain, the Bengalese Finch (Lonchura striata var. domestica) present differences in both the
acoustical properties and the temporal aspect of their songs. This could also be the case in zebra
finch call dynamics. Additional experiments are needed on this point.

Here we confirm that classical metrics like mean or coefficient of variation are not always sufficient
for the study of animal vocal interaction sequences (Kershenbaum et al., 2014). We show that short-
term memory model like Markov can explain vocal exchanges dynamics in a particular context (no visual contact), but long-term memory dynamics should be studied in various contexts in the future.

Zebra finches form life-long pair bonds, with low levels of extra-pair paternity (Birkhead, Burke, Zann, Hunter, & Krupa, 1990; Zann, 1996; Griffith et al. 2010), and show high coordination of pair activities during and outside reproduction (Mariette & Griffith 2012; Mainwaring & Griffith 2013). Thus, zebra finches show one of the strictest social and reproductive monogamy in birds. Here we show that, without visual cues, a form of synchronization and coordination of the pair is expressed through the strong correlation of partners' calling activities. This coordination decreases with visual contact as birds’ vocalizations return to an individual baseline dynamic.

This study provides new insight into the question of how birds can adapt their calling dynamics to cope with limited visual cues. Without visual contact, pairs’ vocal activity is highly correlated and the decision to emit a call is taken only on acoustic information and on a very short-term basis. That way, this calling dynamics may increase the amount of information by decreasing the uncertainty when visual contact is not possible and when acoustic transmission becomes the only channel of communication.

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REFERENCES


Figure 1: Protocol design
Schematic describing the separation/reunion protocol. Cages were acoustically and visually separated (Isolated) then visually separated at long distance via the doors opening (Far No Visual), visually separated at short distance (Close No Visual), and then visually reunited (Reunion). We also recorded zebra finch pairs in a baseline condition (visual and acoustic contact at short distance) during 6 hours.

Figure 2: Call rate and time spent calling analysis
(a) Call rate (mean number of calls per minute) per recording and for each sex. For the Isolated, Far No Visual, Close No Visual and Reunion conditions, N=25 pairs, and for the Baseline condition, N=11 pairs. Bars are means, and Confidence Interval 5% for non-normal data are given. Different letters indicate significant differences (posthoc test after Friedman test for paired data and student tests for independent data). Pairwise tests yield no significant differences either between sexes. (b) Time spent calling in each condition and for each sex (duration between the first vocalization and the last as a percentage of total recording time). For the Isolated, Far No Visual, Close No Visual and Reunion conditions, N=25 pairs, and for the Baseline condition, N=11 pairs. Bars are means, and Confidence Interval 5% for non-normal data are given. Different letters indicate significant differences (posthoc test after Friedman test for paired data and student tests for independent data). Pairwise tests yield no significant differences between sexes. (c) Correlation of male and female call rates. Linear regression of female versus male call rates depending on the condition. Isolated $R^2 = -0.02 [-0.41, 0.37]$, Far No Visual $R^2 = 0.76 [0.53, 0.89]$, Close No Visual $R^2 = 0.89 [0.77, 0.95]$, Reunion $R^2 = 0.21 [-0.20, 0.56]$, Baseline $R^2 = 0.46 [-0.19, 0.83]$. 
Figure 3: Mean cross-correlation between male and female signals for each condition, over all pairs.

Figure 4: Percentage of fit to Markov model for male/female call sequences. Fit to Markov model as the percentage of points in time statistically close to the theoretical Markov autocorrelation values. Bars are means, with Confidence Interval 5% for non-normal data. Different letters indicate significant differences (posthoc test after Friedman test for paired data and Wilcoxon test or student test with permutations for independent data).

Figure 5: Influence of mates history on vocal coordination.

(a) Probability to remain silent in Far No Visual condition in experienced (Offspring) vs non-experienced pars (No Offspring). Bars are means, with Confidence Interval 5% for non-normal data. (b) Percentage of fit to Markov model of wild-type (Wild) vs domestic (Dom) birds. Fit to Markov model as the percentage of points in time statistically close to the theoretical Markov autocorrelation values. Bars are means, with Confidence Interval 5% for non-normal data.

Figure A1: Correlation of male and female time spent calling

Linear regression of female versus male time spent calling depending on the condition: Isolated $R^2 = 0.35 \ [0.05,0.65]$, Far No Visual $R^2 = 0.89 \ [0.77,0.95]$, Close No Visual $R^2 = 0.99 \ [0.99,0.1]$, Reunion $R^2 = 0.83 \ [0.65,0.92]$, Baseline $R^2 = 0.21 \ [-0.45,0.72]$.

Figure A2: Example of cumulative number of calls for one male and one female and associated call timing for each condition.

(a) Cumulative number of calls. The inset shows that for the Baseline condition, we present a minute from a burst period, i.e. when the call rate is high. When visual contact was not possible (dotted lines), the cumulative numbers of calls for the male and the female were highly correlated, with period where both the male and the female are calling (see the arrow). When visual contact is
allowed, curves of cumulative number of calls were no longer correlated. (b) Call timing. When visual contact is prevented, male and female alternate their calls with a very regular answer delay. This alternation is not the same at short (Far No Visual) or long distance (Close No Visual). This alternation of calls disappeared when visual contact is allowed. Figure A2 shows an example of the cumulative number of calls emitted during one minute in each condition for a single pair. In the Baseline condition, we extracted this minute from a period when the call rate was high (a). When visual contact was prevented and only acoustic contact was possible (Far No Visual and Close No Visual, dotted lines), the cumulative number of calls of the male and the female were highly correlated, with periods where both partners were calling (arrow on A) and periods where both partners remained silent. In these conditions, graphs of call timing show that male and female alternated their calls (b). In the Far No Visual context the graph shows a regular alternation of partners call, whereas in the Close No Visual context the female answered the male almost systematically after a short delay. This alternation of calls disappeared when visual contact was allowed (Reunion and Baseline) and curves of cumulative number of calls were no longer symmetrical. Call timings were also different, with more variable delays of response to the partner.
Separation/reunion protocol

- **Isolated** (30 min)
  - Separation and isolation

- **Far No Visual** (10 min)
  - Acoustic contact at long distance

- **Close No Visual** (10 min)
  - Acoustic contact at short distance

- **Reunion** (10 min)
  - Acoustic & visual contact at short distance

Baseline condition

6m
Figure 2:

(a) Call rate (calls/min)

(b) % time spent calling

(c) Female call rate (calls/min) vs Male call rate (calls/min)
Figure 3:

The graph shows the cross-correlation over time for different conditions:
- **Isolated**
- **Far No Visual**
- **Close No Visual**
- **Reunion**
- **Baseline**

The x-axis represents time in milliseconds (ms), ranging from -1000 to 1000. The y-axis represents the cross-correlation, ranging from -0.1 to 0.5. The graph clearly illustrates the differences in cross-correlation across the various conditions.
Isolated  Far No Visual  Close No Visual  Reunion  Baseline

Markov fit (%)
Figure 5:

(a) Percentage of silent pairs

(b) Markov fit (%)

Figure A1:

Female time spent calling (%)

Male time spent calling (%)

Isolated
Far No Visual
Close No Visual
Reunion
Baseline

Dom Wild

Offspring
No Offspring
Figure A2:

(a) Cumulative number of calls over time for the baseline condition (6h).

(b) Graph showing the cumulative number of calls over time for different conditions with male and female subjects.

Legend:
- Far No Visual
- Close No Visual
- Reunion
- Baseline
Table 1: P-values of statistical tests on differences in call rate and time spent calling between conditions (Isolated, Far No Visual, Close No Visual, Reunion and Baseline)

<table>
<thead>
<tr>
<th></th>
<th>Isolated</th>
<th>Far No Visual</th>
<th>Close No Visual</th>
<th>Reunion</th>
<th>Baseline</th>
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<tbody>
<tr>
<td><strong>Call rate</strong></td>
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<tr>
<td>Isolated</td>
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<tr>
<td>Far No Visual</td>
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<td></td>
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<td>$P = 0.59$ (1)</td>
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<tr>
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<td></td>
<td>$P = 0.29$ (2)</td>
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<td><strong>Time spent calling</strong></td>
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<tr>
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<tr>
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<td>Reunion</td>
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<td>$P = 0.001$ (1)</td>
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<tr>
<td>Baseline</td>
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<td>$W = 18,$</td>
<td>$t_{24.8} = 2.45,$</td>
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<td>$P &lt; 0.001$ (3)</td>
<td>$P &lt; 0.001$ (4)</td>
<td>$P = 0.02$ (3)</td>
<td>$P = 0.42$ (2)</td>
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Call rate: (1) Pairwise Wilcoxon signed rank test after Friedman test: $\chi^2_3 = 37.75$, $N = 25$ pairs, $P < 0.001$ for global difference between conditions, (2) Student test, $N = 36$ pairs, (3) Student test with Welch correction, $N = 36$ pairs, (4) Student test with permutations, $N = 36$ pairs; Time spent calling: (1) Pairwise Wilcoxon signed rank test after Friedman test: $\chi^2_3 = 43.41$, $P < 0.001$ for global difference between conditions, $N = 25$ pairs, (2) Student test, $N = 36$ pairs, (3) Student test with Welch correction, $N = 36$ pairs, (4) Wilcoxon exact test (rank with ties), $N = 36$ pairs
Table 2: Differences in call rate and time spent calling between sexes

<table>
<thead>
<tr>
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<th>Close No Visual</th>
<th>Reunion</th>
<th>Baseline</th>
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<td>$t=-1.79$, $N=50$</td>
<td>$t=-0.8$, $N=50$</td>
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<td>$t_{48}=-0.46$, $N=50$</td>
<td>$t=-0.62$, $N=22$</td>
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<td><strong>time spent</strong></td>
<td>$P=0.071$ (1)</td>
<td>$P=0.41$ (1)</td>
<td>$P=0.82$ (2)</td>
<td>$P=0.64$ (2)</td>
<td>$P=0.58$ (1)</td>
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<td><strong>calling</strong></td>
<td>$t=-0.86$, $N=50$</td>
<td>$t=-0.44$, $N=50$</td>
<td>$t=-0.013$, $N=50$</td>
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<td>$P=0.64$ (1)</td>
<td>$P=0.99$ (1)</td>
<td>$P=0.45$ (1)</td>
<td>$P=0.82$ (2)</td>
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P-values of statistical tests in each condition (Isolated, Far No Visual, Close No Visual, Reunion and Baseline). (1) Student test with permutations, (2) Student test
Table 3: Correlation coefficients ($R^2$) between males and females for call rate and time spent calling

<table>
<thead>
<tr>
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<th>Reunion</th>
<th>Baseline</th>
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<td>$t_{23}$=53.0, $P$&lt;0.001</td>
<td>$t_{23}$=7.28, $P$&lt;0.001</td>
<td>$t_{23}$=0.63, $P=0.54$</td>
</tr>
</tbody>
</table>

Correlation coefficients and $P$-values are given for the five conditions (Pearson’s correlation test).
Table 4: Differences in Markov fit between conditions

<table>
<thead>
<tr>
<th></th>
<th>Isolated</th>
<th>Far No Visual</th>
<th>Close No Visual</th>
<th>Reunion</th>
<th>Baseline</th>
</tr>
</thead>
<tbody>
<tr>
<td>Isolated</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Far No Visual</td>
<td>$z = 11.23$</td>
<td>$z = 1.59$</td>
<td>$z = 1.59$</td>
<td>$z = 7.74$</td>
<td>$z = 1.55$</td>
</tr>
<tr>
<td></td>
<td>$P &lt; 0.001$</td>
<td>$P = 0.483$</td>
<td></td>
<td>$P &lt; 0.001$</td>
<td>$P = 0.512$</td>
</tr>
<tr>
<td>Close No Visual</td>
<td>$z = 14.2$</td>
<td>$z = 1.59$</td>
<td>$z = 14.2$</td>
<td>$z = 7.74$</td>
<td>$z = 1.55$</td>
</tr>
<tr>
<td></td>
<td>$P &lt; 0.001$</td>
<td>$P = 0.483$</td>
<td>$P &lt; 0.001$</td>
<td>$P &lt; 0.001$</td>
<td>$P = 0.512$</td>
</tr>
<tr>
<td>Reunion</td>
<td>$z = 7.74$</td>
<td>$z = 1.59$</td>
<td>$z = 1.59$</td>
<td>$z = 7.74$</td>
<td>$z = 1.55$</td>
</tr>
<tr>
<td></td>
<td>$P &lt; 0.001$</td>
<td>$P = 0.483$</td>
<td>$P &lt; 0.001$</td>
<td>$P &lt; 0.001$</td>
<td>$P = 0.512$</td>
</tr>
<tr>
<td>Baseline</td>
<td>$z = 1.55$</td>
<td>$z = 1.59$</td>
<td>$z = 1.59$</td>
<td>$z = 7.74$</td>
<td>$z = 1.55$</td>
</tr>
<tr>
<td></td>
<td>$P = 0.512$</td>
<td>$P &lt; 0.001$</td>
<td>$P &lt; 0.001$</td>
<td>$P &lt; 0.001$</td>
<td>$P = 0.512$</td>
</tr>
</tbody>
</table>

P-values of generalized linear model with binomial family are given for each condition (Isolated, Far No Visual, Close No Visual, Reunion and Baseline).
<table>
<thead>
<tr>
<th>Model</th>
<th>Formula</th>
<th>Fixed effects</th>
</tr>
</thead>
<tbody>
<tr>
<td>Call rate</td>
<td>female call rate ~ male call rate * condition + 1</td>
<td>pair</td>
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<tr>
<td>Time spent calling</td>
<td>female time spent calling ~ male time spent calling * condition + 1</td>
<td>pair</td>
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</tbody>
</table>

Detailed results are shown for the call rate and time spent calling (111 observations on 36 pairs). Call rate random effects standard deviation: intercept=2.74, residual=6.06. Time spent calling random effects standard deviation: intercept=0.002, residual=20.75
Table A2: Detailed model results for the probability of emitting at least one call.

**probaOneCall ~ condition * Offspring + 1|pair**

Fixed effects:

|                                | Estimate | SE   | z value | Pr(>|z|) |
|--------------------------------|----------|------|---------|----------|
| (Intercept)                    | 1.8877   | 0.8498 | 2.221   | 0.026    |
| condition Far No Visual        | 0.9544   | 1.0095 | 0.945   | 0.344    |
| condition Close No Visual      | 0.9545   | 1.0095 | 0.945   | 0.344    |
| No Offspring                   | 0.7339   | 1.0995 | 0.668   | 0.504    |
| condition Far No Visual : No Offspring | -4.5790 | 1.4243 | -3.215  | 0.001    |
| condition Close No Visual : No Offspring | -0.9545 | 1.3181 | -0.724  | 0.469    |

Detailed results are shown for the Far No Visual and the Close No Visual conditions (78 observations on 25 pairs). Random effects (pair) variance=2.24, standard deviation=1.50.
Table A3: Detailed model results for the Markov fit of calling sequences.

**markov fit ~ condition + 1|pair**

Fixed effects:

|                      | Estimate | SE    | z value | Pr(>|z|) |
|----------------------|----------|-------|---------|----------|
| (Intercept)          | -2.2927  | 0.3308| -6.931  | < 0.001  |
| condition Far No Visual | 4.0761  | 0.3628| 11.235  | < 0.001  |
| condition Close No Visual | 4.6465  | 0.3267| 14.221  | < 0.001  |
| condition Reunion    | 2.1112   | 0.2729| 7.736   | < 0.001  |
| condition Baseline   | 0.9677   | 0.6260| 1.546   | 0.122    |

**markov fit ~ condition * Type + 1|pair**

Fixed effects:

|                      | Estimate | SE    | z value | Pr(>|z|) |
|----------------------|----------|-------|---------|----------|
| (Intercept)          | -2.2795  | 0.5123| -4.450  | < 0.001  |
| condition Far No Visual | 3.3426  | 0.5061| 6.604   | < 0.001  |
| condition Close No Visual | 3.7069  | 0.4648| 7.975   | < 0.001  |
| condition Reunion    | 1.5910   | 0.4442| 3.581   | < 0.001  |
| Type Wild            | -0.3842  | 0.8030| -0.478  | 0.632    |
| condition Far No Visual : Type Wild | 2.2228  | 0.9593| 2.317   | 0.020    |
| condition Close No Visual : Type Wild | 3.2109  | 0.9654| 3.326   | < 0.001  |
| condition Reunion : Type Wild | 1.3740  | 0.7335| 1.873   | 0.061    |

For the first model, detailed results are shown for all conditions (107 observations on 32 pairs), random effects (pair) variance=1.40, standard deviation=1.18. For the second model, detailed results are shown for the Isolated, Far No Visual, Close No Visual and Reunion conditions (78 observations on 25 pairs), random effects (pair) variance=1.33, standard deviation=1.15.