Neuroethology of female preference in the synchronously singing bushcricket *Mecopoda elongata* (Tettigoniidae; Orthoptera): why do followers call at all?

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Summary

Imperfect synchrony between male calls occurs in the acoustically interacting bushcricket *Mecopoda elongata*, and males establishing the temporal leadership attract more females in choice experiments. An asymmetrical representation of leader and follower signals in pairs of direction-selective neurons of the auditory pathway was suggested to represent the neural basis for the preference of females. We investigated the time–intensity trading effect, which occurs when the temporal advantage of the leader signal is compensated, and can be reversed, by an additional sound pressure level of the follower. In behavioural arena trials the intensity trading of the preference of females for leader signals depends on the playback level; a higher sound pressure level (SPL) is needed for compensation at higher playback levels. We studied the simultaneous neuronal representation of leader and follower signals, and the time–intensity trading function in the pair of omega-neurons in the CNS. Consistent with the behavioural data, the representation of leader and follower signals can be reversed with an additional loudness of the follower, and the steepness of the trading function depends on the playback level. We also implemented data on the neuronal representation of synchronized signals in individual receivers into computer-based agents, which performed phonotaxis in a virtual sound field. Results of these simulations closely resemble those obtained from real females with respect to the overall preference under the various time–intensity trading conditions. Furthermore, in combination with the observed trading functions these simulations demonstrate, that under more realistic field conditions the ultimate success of followers in attracting females is much higher than suggested from arena trials. We discuss the evolutionary consequences for male calling strategies in synchronously calling Orthoptera.

Key words: sensory bias, acoustic synchrony, bushcricket, female choice, neuroethology, simulation, time–intensity trading.

Introduction

Synchronous signalling is a behavioural phenomenon that has been well documented for visual and acoustic signals in, e.g. fireflies (Buck and Buck, 1966; Lloyd, 1973); fiddler crabs (Backwell et al., 1998); anurans (Wells, 1988; Tuttle and Ryan, 1982; Grafe, 1996; Grafe, 1999; Greenfield and Rand, 2000); orthopterans (Walker, 1969; Sismondo, 1990; Greenfield and Roizen, 1993; Snedden and Greenfield, 1998; Hartbauer et al., 2005) and spiders (Kotiaho et al., 2004). Adaptive explanations for the evolution of synchrony, such as predator avoidance, increased attraction of mates, or the preservation of species-specific signal patterns have found little empirical support (but see Kotiaho et al., 2004), so that synchrony and alternation are more often considered an epiphenomenon resulting from male–male competition in choruses (Greenfield et al., 1997).

However, in all these interactions between two or more signallers, synchrony is imperfect, in that one signal leads the other by some amount of time, from a few milliseconds to several hundreds of milliseconds, resulting in 'leaders' and 'followers' within choruses. With only few exceptions females show a strong preference for leading signals, when given the choice between leader and follower signals (Klump and Gerhardt, 1992; Greenfield, 1994; Galliart and Shaw, 1996; Grafe, 1996; Snedden and Greenfield, 1998; Römer et al., 2002). Sexual selection by female choice would thus exert a strong selection pressure on males to adopt a mechanism that avoids signalling shortly after a neighbouring male. The inhibitory resetting mechanism as suggested by Greenfield and Roizen (Greenfield and Roizen, 1993) serves such a function: it initiates the inhibition of calling right after perceiving a neighbour's signal by resetting the phase of the endogenous oscillator, such that the next call is delayed. Examples for this mechanism are synchronous song interactions in males of the bushcricket *Neoconocephalus spiza* (Greenfield and Roizen, 1993) and the snowy tree cricket *Oecanthus fultoni* (Walker, 1969).

Males of the bushcricket *Mecopoda elongata* also synchronize (or under some conditions alternate) their chirps

with their neighbours in an aggregation (Sismondo, 1990). Using playback experiments and simulations of song oscillator interactions Hartbauer et al. (Hartbauer et al., 2005) investigated the mechanisms that result in synchrony, and in particular the probability for the leader role in synchrony. The phase response curve of the song oscillator in *Mecopoda* is different from other rhythmically calling or flashing insects, in that only the disturbed cycle is influenced in duration by a stimulus. In contrast to *Neoconocephalus* or *Oecanthus*, where leader and follower roles regularly switch with successive song interactions, in *Mecopoda* there are sustained leader- or follower chirps of one male, when the intrinsic chirp periods of two males differ by 150 ms or more. Indeed, a major predictor for the leader role of a male is its intrinsic chirp period, which varies in a population from 1.6–2.3 s. Faster singing males establish the leader role more often than males with longer chirp periods.

Ultimately, female response preferences will strongly determine the timing interactions of males in a given species. Surprisingly, however, even in *M. elongata*, with no indication of frequent switching between leader and follower roles, there is also a strong preference by females for leading chirps (Römer et al., 1997). The fact that males with longer endogenous chirp periods do call at all and couple their calls as followers with those of a faster male deserves an explanation. It has been suggested by Römer et al. (Römer et al., 2002) that a sensory bias within the central nervous system of females represents the proximate mechanism of the female preference for leading calls in *Mecopoda*. If a female is equidistant from two males spaced apart in the field, she receives leader and follower chirps from opposite directions, and both leader and follower signals will activate sensory receptors and interneurons of their respective auditory side. A feature of some prominent interneurons in grasshoppers, crickets and bushcrickets is a contralateral inhibition, which gives the leader signal a temporal advantage to suppress the representation of the follower signal on the opposite side more strongly than the follower signal can do *vice versa*. The result is an asymmetrical representation of leader and follower signals within the CNS (Römer et al., 2002), and with a decision rule in the female 'turn to the side more strongly activated' (Schildberger, 1994) the phonotactic approach of the female will be to the leader signal. Römer et al. have also shown that the stronger representation of the leader signal in the discharge of interneurons can be compensated and even reversed by an increase in loudness of the follower signal, depending on the temporal advantage of the leader (Römer et al., 2002). The aim of the present study was to further explore the possibility that a sensory bias is responsible for the female choice of this species, and to demonstrate that under circumstances that are relevant under field conditions, males producing follower signals may indeed be successful in attracting females. This was addressed using neurophysiological and behavioural methods. In addition, we used simulation tools to quantify the success of leader and follower males in attracting females when considering more complex field conditions.

Material and methods

Animals

Experiments were performed on females of the bushcricket *Mecopoda elongata* L. (Orthoptera, Tettigoniidae; Mecopodinae) that were originally collected in the field in Malaysia. The animals were reared in crowded colonies at a temperature of 27°C, 70% relative humidity, on a 12 h:12 h light:dark cycle. They were fed *ad libitum* with fish food, oat flakes and fresh lettuce. The taxonomic relationships within the genus Mecopoda are uncertain, and there are probably several sibling species that could only be distinguished by their song patterns, but not morphologically. In our population males produce songs identical to the songs of 'species S' described (Sismondo, 1990). The male advertisement call consists of chirps 200–300 ms in length, each chirp composed of 10–16 syllables of increasing amplitude (Hartbauer et al., 2005). The chirp period for each male is highly constant and varies between males from 1.6 to 2.3 s at an ambient temperature of 27°C. Neighbouring males mainly synchronize their calls.

Behaviour

All behavioural experiments were done in the first 8 h of the dark cycle. The preference of females was tested in phonotactic arena trials. The arena (2 m×2 m) was on the floor of a room with the walls and ceiling covered with acoustic foam, so that echoes at any position of the orienting female were well below 30 dB SPL (sound pressure level) in the frequency range 5–50 kHz, and thus below hearing threshold of the insect. Two speakers (DynAudio D21/2 Skanderborg, Denmark) were positioned 10 cm above the floor at a distance of 160 cm from each other, with the speaker axes intersecting at the release point of the female, 190 cm from each speaker. Females were physically, but not acoustically, isolated as last instar nymphs from males, and were first tested behaviourally 2 weeks after their last moult. For a phonotactic trial a female was placed in a small wooden box (10 cm×10 cm×15 cm) at the release point and was accustomed to the experimental condition for 10 min without acoustic stimulation. Then the acoustic stimulus was broadcast and the approach of the female was monitored with an infrared-video camera (Eneo: VK-1313/IR12-24, Röderberg, Germany) mounted at a height of 2 m above the centre of the arena. Experiments were carried out in complete darkness; infrared illumination of the arena was established with a headlamp mounted above the arena. A phonotactic trial was considered successful at one of the two speakers, when the female had reached a radius of 30 cm around the speaker. Trials in which females had not left the starting box after 10 min of acoustic stimulation were stopped and the female was tested again the following day. If not otherwise stated, one female was used only once for a behavioural experiment.

Video recordings were digitised with a video card and the phonotactic pathway reconstructed frame by frame using ImageJ software (version 1.32j; http://rsb.info.nih.gov/ij/). The software automatically detected the object (female) against the

background, so that the position of the female (centre of gravity of the object) could be monitored in each frame. From these data, also the time taken to the target and the velocity were calculated.

Playback stimuli were based on a recording of the song of an acoustically isolated male, using a ½" microphone (type 2540; Larson & Davis, Provo, UT, USA) and sound level meter (CEL 414). The recording was digitised with a custom-made AD/DA board at a sampling rate of 250 kHz. One representative chirp of duration 250 ms was selected for further playback experiments and imported into Cool Edit software. Using the identical chirp on both channels of the software a basic sound file was produced, where different leader–follower relationships were created by temporally shifting one channel relative to the other. Stimuli were played back in continuous loops from the output channels of the AD/DA hardware, *via* a stereo amplifier (NAD stereo power amplifier 214, Pickering, ON, Canada) and attenuator (KAY Elementrics Corp., Lincoln Park, NY, USA; 837 attenuator) for each channel. The leader or follower role of a speaker was frequently reversed among different trials to control for a possible bias towards one side of the arena. As a further control for such a bias, experiments with the two signals broadcast at the same time (delay 0 ms) and the same SPL were performed. Since eight females chose the right and eight the left speaker, a bias in the arena can be excluded.

Experiments with leader and follower signals were conducted at three different absolute sound pressure levels, namely 57 dB SPL, 62 dB SPL and 72 dB SPL for the leading signal. For time–intensity trading experiments the follower signal was delayed by 140 ms and its intensity was increased, whereas the SPL of the leader signal was kept constant. All sound pressure levels were measured at the releasing point of the female in the arena, using a ½" microphone (type 2540; Larson & Davis) and sound level meter (CEL 414), and are given as root mean square (RMS), fast reading (rel. 20 μPa). Since the chirp consists of 13 syllables of increasing amplitude, and the last, most intense syllable of the chirp is only 30 ms long, we compared, *via* an oscilloscope, the last syllable amplitude with that of a reference 7 kHz pure continuous tone. All SPL values thus refer to the last syllable.

Neurophysiology

Neurophysiological experiments were carried out to quantify the simultaneous representation of the leader and follower stimulus in a prominent pair of interneurons in the afferent auditory pathway, the so-called omega-neurons (Römer, 1985; Molina and Stumpner, 2005). The methods of the preparation and for obtaining extracellular action-potential recordings of the neurons have been described in detail (Römer et al., 2002). In short, the prothoracic ganglion was surgically exposed in a ventral side up preparation, and an extracellular tungsten electrode was placed close to the anterior omega-tract, where the segments of the two bilaterally homologous cells cross the ganglionic midline. Action potentials recorded from the two cells differ in amplitude and shape; usually the soma-contralateral cell exhibits the larger AP amplitude with faster rise and fall times, so that a custom-made spike-discrimination algorithm could correctly assign each spike to one of the two cells with a high probability. The preparation was placed in an anechoic chamber, 50 cm equidistant from two speakers (Technics, type EAS-10 TH 400A, Hamburg, Germany) at a position 90° laterally on opposite sides.

Prior to each binaural stimulation experiment the threshold of each omega neuron was determined with unilateral stimulation, using the conspecific chirp as stimulus. This was done to accurately compensate for differences in hearing thresholds on both auditory sides of each preparation, which were in the order of 0–8 dB. Using the threshold of each neuron as a reference, in the binaural stimulation experiment the sound pressure levels were adjusted to between 0 and 30 dB above threshold, respectively. Furthermore, a monaural intensity response function was measured between 0 and 30 dB above threshold. In the time–intensity-trading experiments, the same playback values as in the behavioural experiments, namely 57 dB SPL, 62 dB SPL and 72 dB SPL, were used for the leading signal. The SPL of the follower stimulus was varied relative to the leader stimulus, between –10 and +15 dB, in increments of 2 or 5 dB. All binaural experiments were performed with time delays of either 0 or 140 ms. A total of 23 animals were examined for neurophysiology.

At the end of each binaural stimulation protocol, which included 72 different stimulus configurations, each repeated 10 times, we repeated the measurement of an ipsilateral intensity response function. If the results of the last measurements deviated by more than 10% from the first one, the whole experiment was discarded. Action potential recordings were stored digitally on a DAT recorder (TEAC; RD-120 width unit) transformed by a sampler, CED power 1401, and evaluated with the Spike2 software (Cambridge Electronics Design, Cambridge, UK).

We considered binaural discharge differences (number of action potentials/chirp) as crucial for phonotactic decisions of females, for the following reasons. (1) The quality of pattern copying appears not to be relevant at all for *Mecopoda*, since unpublished song interaction experiments with males using unmodulated sound pulses of 300 ms duration and white noise as carrier had the same effect as conspecific chirps. The same is true when only the last three syllables of a chirp are being presented. Both types of signal produce a spike pattern in afferent fibres and interneurons, including omega-neurons, rather different to the conspecific chirp. (2) Instantaneous firing rates as a measure of the representation of leader and follower stimuli also turned out not to be useful. Maximum firing rates are elicited with the last, intense syllables, and can be almost identical in the response to leader and follower, although the spike number is not. This is due to the AM pattern of the chirp with syllables increasing in amplitude, and the representation of the softer onset syllable of the follower signal can be suppressed by reciprocal inhibition of the leader signal, without significantly affecting maximal firing rates at the end of the response.

Since inter-individual differences in binaural discharge differences as a result of different thresholds, or the degree of excitation and/or inhibition would reduce the ability to compare results between individuals, we standardized the responses. First, the average response of both cells [(response of left + response of right cell)/2] was calculated for four intensity values above threshold (5, 10, 15, and 20 dB), each taken from the monaural intensity characteristic with ipsilateral stimulation (l and f=responses of left and right cell to monaural stimulation, respectively). For any binaural stimulation the difference of the excitation (L–F) of both omega cells was calculated relative to this average value according to the following formula:

$$v = (L–F) / [(l+f) / 2] . \qquad (1)$$

v could take positive values, which refer to a neuronal dominance of the leader signal, or negative values, for a dominance of the follower signal.

Simulation

In addition to behavioural and neurophysiological experiments, we also used simulations of female phonotaxis. The main aim of the simulations was to analyze the differential success of leaders and followers, when the time difference and the amplitudes of their signals are varied as a result of the effects of sound attenuation over distance, and the speed of sound propagation. However, the simulation does not provide direct comparison of trajectories of live females with those of agents, because they do not operate on neuronal results achieved at different stimulation angles, and do not include a changing heading of the agent in the simulated sound field (see below). Despite these limitations, by changing the parameter values in the simulation and making the above comparison we could nevertheless find hints for orientation and decision rules used by females. The simulation was implemented in Matlab (version 6.5.0, Math Works, Inc.). The source code for the Matlab simulation is available at: stradnej@stud.uni-graz.at.

The dimensions of the surface for the two-dimensional simulation area were variable; the area was drawn in a coordinate plane with the point (0/0) representing the centre of the surface. The two positions representing the location of the two singing males, as well as the SPL of their signal, could be chosen by the user. For each location in the coordinate system the SPL of both signals was calculated, using the formula of geometric spreading of sound (6 dB/doubling of distance relationship):

$$L = L_0 + (–8.6562 \times \ln x) , \qquad (2)$$

where L is the intensity in dB SPL at the calculated point, L_0 the intensity of the male in dB SPL at a distance of 1 m and x the distance of the calculated point from the male. In addition, the time delay between the chirps of the two males was calculated for each location in the simulated area. The time delay between the emitted calls of both males was set to either 0 or 140 ms (for correspondence with the neurophysiological and behavioural experiments), and the actual time delay at each

location of the arena was calculated for both signals based on the speed of sound propagation of 344 m s^{-1}.

Thus, each location in the area was defined by the difference of two parameters: the difference in the SPL of leader and follower signal and their time difference. In a first series of simulations, the distance between the two singing males was set to 1.6 m and the time delay of the leader and follower signal was 140 ms. An agent, representing a female in the simulation, started the simulation at a distance of 1.90 m to both males. Importantly, for each simulated agent we implemented the neural data of a different neurophysiological preparation, so that agents moved according to the same rules (see below), but their movement was based on data of different individuals. The movement of an agent was exclusively phonotactical, i.e. by arriving at a given patch within the arena, it responded to the combination of time–intensity differences of the two signals. Differences in the neuronal representation of both signals (as examined in the previous neurophysiological experiments) on each patch in the simulated arena were used by the agent for the following movement. The decision rule was always to move into the direction of the stronger neuronal representation of one signal. The movement was simulated with one step over five patches after perceiving one synchronized chirp. Since males produce a chirp every 2 s and a patch has a length of 1 cm, the average speed of the agent was about 2.5 cm s^{-1}.

After each step, the agent could decide anew to which of the two sources it should orient. Two implemented variables affected the movement of the agent. One was the variable indecision, based on the parameter v. Since the agents had an implemented rule 'turn to the side which is stronger stimulated' when reaching a patch in the arena with a certain time–intensity relationship between both signals, a threshold had to be defined when the responses can be considered asymmetrical, i.e. one is significantly superior over the other. Ideally, equal representation of both signals is given with v=0.0, and any slight deviation as a result of one more action potential in one cell should cause the agent to move into this direction. However, noise in the sensory system causes some variability in response to the very same stimulus, which leads to a random deviation from v=0.0. Thus, in order to eliminate random decisions in the implemented rule of the agents, the variable indecision allowed the setting of the threshold for orientational movements, so that only a deviation, of e.g. $v > \pm0.1$, caused a decision to move into a particular direction. If the neuronal discharges do not deviate by more than this threshold criterion the agent moves randomly into one direction.

When the variable indecision was set to 0.1, the agent interpreted a value of v between –0.1 and +0.1 as neural equilibrium at the actual patch and, therefore, moved randomly to the left or right with a random angle between ±45°. The agent moved into the direction of the leader, if v was higher than +0.1 and otherwise ($v < –0.1$) into the direction of the follower. We simulated three types of directional responses, based on those reported for other Orthoptera (Römer and Rheinlaender, 1989): first, a movement with an angle that precisely correlated with the stimulus angle. Second, the angle of movement correlated

to the stimulus angle, but with a variation of ±20° in either direction (Hardt, 1989; Murphey and Zaretzky, 1980), and third a correct lateralization, with a fixed angle of movement between 45° and 90° to the correct side (von Helversen and Rheinlaender, 1988). In the simulation, the degree of directional movement of the agent was based on the variable angle of movement. It was thus possible to simulate a phonotaxis based on a very precise localization, where the stimulus angle=angle of movement, or a rather inaccurate lateralization.

In a second series of simulations, the phonotactic movements of agents were simulated in a larger arena. The values of the parameter for the experiments were taken from previously described tests. Agents started in a semicircular arena with a radius of 7 m, at different distances to the centre (0, 1.4, 2.8, 4.2 and 5.6 m), where two males produced synchronized leader and follower calls at a distance of 10 m from each other. Again, each patch was defined by a time–intensity parameter combination of the two signals according to geometric spreading of sound and the speed of sound propagation. An agent started 100 times from each starting point in response to the same signal combination, and the success of leader and follower in attracting agents was counted as number of agents being attracted to the signal. The decision of the agents to move towards one sound source was again based on the differential representation of the signals in their simulated afferent auditory pathway, as explained above. The neuronal threshold of the two auditory sides in the agents was set to the average value obtained in neurophysiological experiments. Thus, for example on a patch defined by the amplitude of 72 dB SPL those values of the neurophysiological experiments were incorporated into the simulation, which were obtained at 20 dB above threshold. Intermediate values of time–intensity parameter combinations, for which no neurophysiological experiments had been conducted, were interpolated.

Results

Behaviour

When given a simultaneous choice between two synchronous chirps of identical amplitude, with one signal leading the other by 140 ms, females exhibit a strong preference for the leader signal. Fig. 1A shows the reconstruction of the phonotactic path of ten females in the arena; nine females moved to the speaker broadcasting the leader signal, one moved to the follower signal. A total of 18 females were tested; of these 15 preferred the leader signal (binomial test: *P*<0.01). There was some variation in the phonotactic approaches between females with respect to the speed and actual path taken. The fastest female took only 27 s for the approach (average time = 60.83±31.36 s, ± s.d.). The phonotactic path of some females was almost straight to the speaker with only little meandering, whereas others deviated considerably from a direct path (Fig. 1A).

When the two signals were presented in a strictly alternating fashion, one following the other after 1 s, females randomly chose one of the speakers (Fig. 1B). Of ten females tested, five
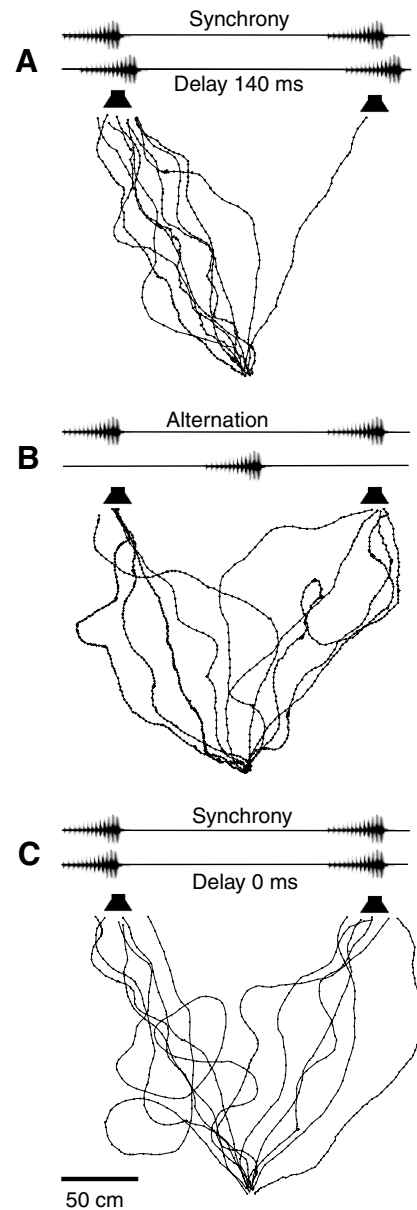

Fig. 1. Phonotactic path of ten female *M. elongata* towards two speakers broadcasting either synchronous chirps with a time delay of 140 ms of the follower (A), chirps regularly alternating after 1 s (B), or chirps presented in perfect synchrony with no time delay at all (C). Females prefer the leader of two identical chirps (left speaker in A), and approach both alternating signals and those in perfect synchrony with no preference.

chose the left and five the right speaker. Again, there was some variation regarding the speed of approach and the path taken to the target, but females moving to alternating signals took about two to three times longer than those moving to synchronous signals (153.4±102.3 s compared to 53.1±15.6 s; paired *t*-test *P*<0.01, *N*=10). The mean speed of females towards alternating signals was 2.03±1.3 cm s^{-1} s.d. compared to the synchronous signal situation with a time delay of 140 ms (3.74±1.2 cm s^{-1}; paired *t*-test, *P*<0.001). The mean distance covered during the

approach was 209±41 cm s.d. for alternating signals and 182.7±13.1 cm for synchronous signals, but the difference was not significant (paired *t*-test, *P*=0.073). When females were presented perfectly synchronized signals with no time delay, they randomly preferred one or the other speaker with a pattern of movement almost identical to the one with alternating signals (compare Fig. 1C with 1B).

In a time–intensity trading experiment we tested whether the preference of females for leading chirps can be compensated by an increased loudness of the follower signal (Fig. 2). However, the increase in loudness of the follower signal to compensate for the temporal advantage of the leader depended on the absolute SPL of the leader signal. At an intensity of 57 dB SPL the follower signal was increased by 2 dB, but most females still preferred the leader (binominal test; *P*<0.05; Fig. 2A). A 4 dB advantage of the follower resulted in almost equal choice for the leader and follower signal (nine *versus* seven), whereas with a 6 dB advantage females significantly preferred the follower signal (13 *versus* four). When the same trading experiment was performed at 62 dB SPL (Fig. 2B), even an advantage of 8 dB for the follower was not sufficient to compensate for the temporal advantage of the leader. With a further increase by 2 dB for the follower (total 10 dB louder than leader), the preference now switched to the follower. Finally, at 72 dB SPL, even a 10 dB advantage of the follower was not sufficient to shift female preference to the follower (eight *versus* nine leader/follower choices).

Neurophysiology

The neuronal representation of leader and follower signals was investigated neurophysiologically by simultaneously

recording the responses of the pair of omega-neurons. Whereas the threshold varied considerably between different preparations, there was only little binaural threshold asymmetry observed, as evident in the difference in hearing threshold of the left and right omega-cell, when each was stimulated from their respective ipsilateral side. On average, both cells differed in their threshold by only 3.2±2.4 dB (± s.d.).

In a series of time–intensity-trading experiments we investigated under which conditions the disadvantage of the follower signal in the neuronal representation could be
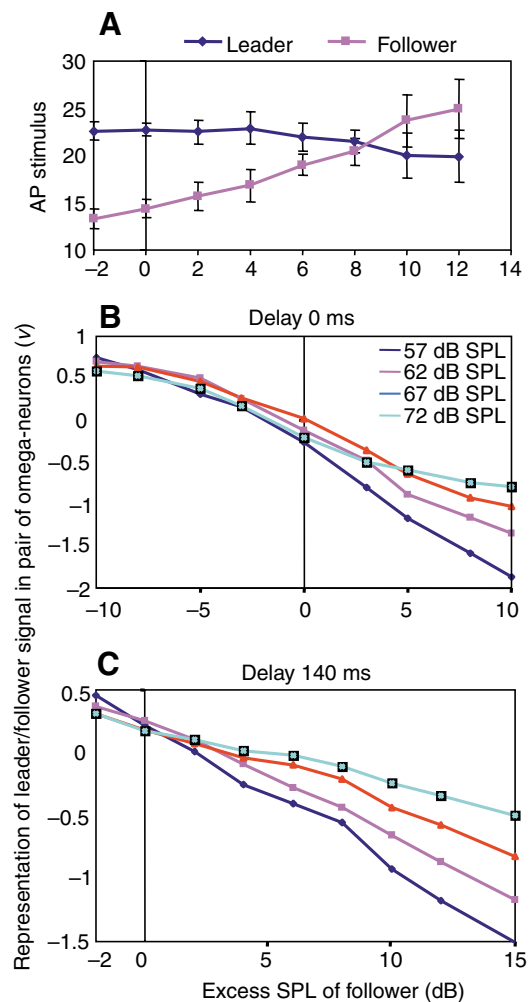
Fig. 3. (A) Representation of leader and follower signals in the pair of omega-neurons of one preparation (playback levels 67 dB SPL; time delay 140 ms). (B,C) Results of similar experiments at four different playback levels of 57, 62, 67 and 72 dB SPL, when there is no time delay of both signals (B), and with a time delay of 140 ms (C); *N*=13. The value of *v*=0 is a standardized measure for equal representation of both signals, positive values refer to a dominance of the leader, negative values of the follower signal. Note that with a time delay of 140 ms for the follower, *v* is shifted to positive values, when the SPL of leader and follower signal is the same. With an increasing intensity advantage of the follower, *v* becomes more negative. The trading function is less steep at higher playback levels.
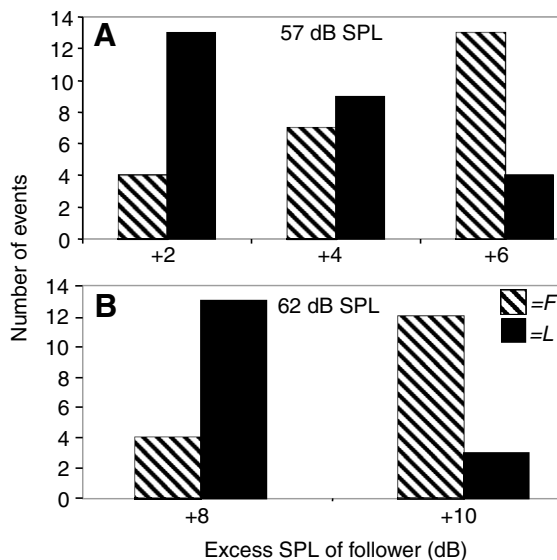

Fig. 2. Time–intensity trading of female preference at intensities of 57 dB SPL (A) and 62 dB SPL (B) for the leader signal. The preference for the leader signal is reversed by an additional 6 dB and 10 dB for the follower, respectively, depending on the absolute playback level. *L*, leader; *F*, follower.

compensated. The results of a typical time–intensity-trading experiment are shown in Fig. 3A. With a temporal advantage of 140 ms for the leader signal, its representation in the omega-neuron of the leader side is much stronger compared to the follower, when both signals are broadcast at the same SPL. This asymmetrical representation can be traded by an additional loudness of the follower signal, so that with an excess of 8 dB there is almost equal representation, and another 2 or 4 dB resulted in an asymmetrical representation in favour of the follower. Fig. 3B,C summarize the results obtained at four different intensities of 57, 62, 67 and 72 dB SPL. As a control experiment, the representation of both signals was studied, when there was no time delay between them, and the intensity of one signal was varied by either increasing or decreasing its SPL by up to 15 dB (Fig. 3B). Ideally, when both signals are identical and are presented at the same time and loudness from opposite sides of a symmetrical hearing system, they should result in an identical representation in the respective omega-neurons on both sides, yielding a parameter v=0.0. This is indeed the case for SPLs of 10 and 15 dB above threshold, whereas there is a slight deviation from an ideal symmetrical representation for 57 and 72 dB SPL. However, if one signal (here called the 'follower', although there is no time delay) is increased or decreased by only 3 dB, the representation of both signals becomes asymmetrical, with the louder signal yielding the stronger response. However, the sensitivity for such changes in intensity differences is greater for absolute SPLs close to the threshold (57 and 62 dB SPL), whereas the steepness of the curves decreases at 67 and 72 dB SPL.

With an additional temporal advantage of 140 ms for the leader signal, v is shifted to positive values, i.e. the leader signal is represented more strongly in the respective omega-neuron (Fig. 3C). The advantage of the leader signal is compensated or even reversed to v<0.0 by increasing the SPL of the follower signal. For an equal representation (v=0.0) an additional 5 dB was needed at 72 dB SPL, but only 2 dB at 57 dB SPL. In addition, even higher SPLs of the follower signal result in more negative values of v with lower SPLs, so that the steepness of the trading function decreases with increasing SPL. This is also evident when comparing values of v with a 15 dB advantage of the follower signal, where the asymmetry in the neuronal representation ranges from v=–0.5 at 72 dB SPL to v=–1.5 at 57 dB SPL, respectively.
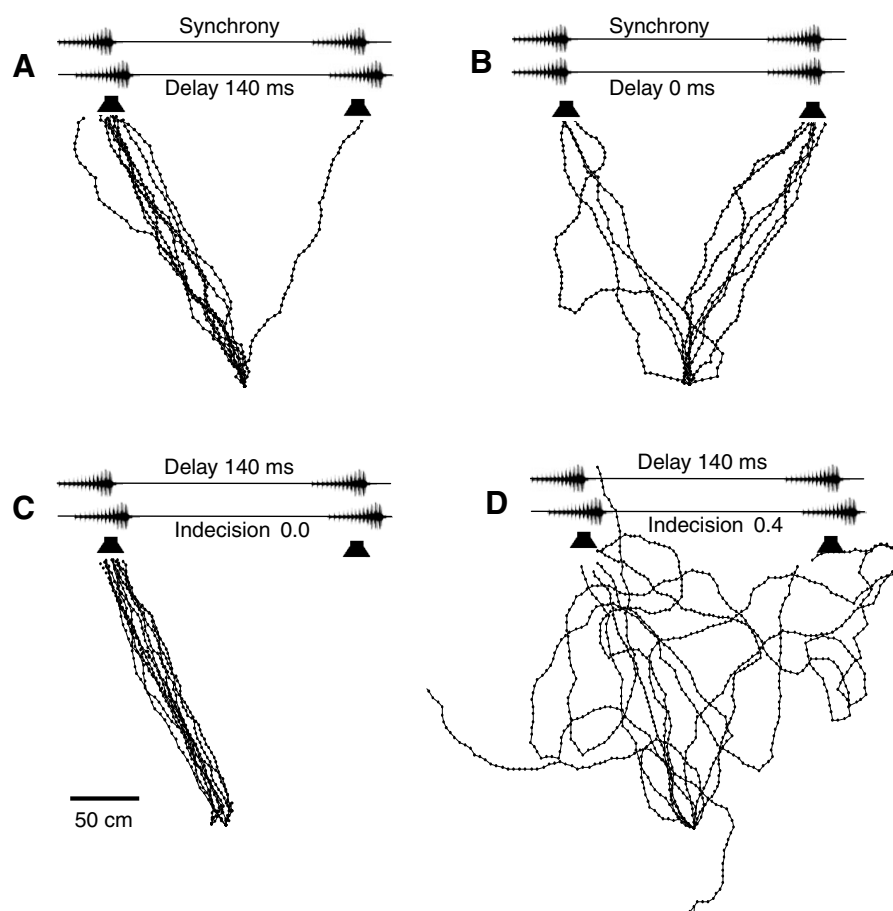

Fig. 4. Simulated phonotactic movements of agents towards synchronized signals in a virtual arena, with a time delay of 140 ms (A), and with no time delay (B). In both cases, the variable indecision was set to 1.5. If the time delay was 140 ms and indecision was set to 0.0 (C), all agents moved to the follower signal, but the phonotactic path was rather straight, which was never observed with real females in the arena (compare with Fig. 1A). By contrast, when indecision was set to 0.45 (D), most agents moved randomly in the virtual arena.

Simulation of female preferences

The simulation results of movements of agents towards synchronized signals in a virtual arena are shown in Fig. 4. When the two synchronized signals are simulated as leader and follower of identical SPL and with a time delay of 140 ms, nine of ten agents moved to the leader, similar to real females in an arena, although the actual phonotactic paths of females had a stronger meandering pattern (Fig. 4A; compare with Fig. 1). By contrast, when the two signals are synchronized with no time delay, agents moved with equal probability to one or the other virtual speaker (Fig. 4B).

The effect of varying the variable *indecision* for the phonotactic path of simulated agents is shown in Fig. 4C,D. Only when the variable is set to values of ±0.1–0.2 do the agents exhibit movements towards the leader signal similar to real females in the arena (Fig. 4A; compare with Fig. 1). This value corresponds to a deviation of the neuronal discharges by more than 10–20% of the mean. With an indecision of 0.0 all agents move to the leader signal as well, but the phonotactic

Table 1. *Result of a time-intensity-trading simulation with ten different agents in a virtual arena, performing phonotactic movements towards leader and follower signals (delay 140 ms) from a total of 53 different starting positions, each repeated 100 times*

Excess SPL of follower (dB)	Agents to leader	Agents to follower	No preference	Number of agents	% agents to follower
0	3483	1487	330	5300	28,1
5	2112	2803	385	5300	52,9
8	1588	3581	131	5300	67,6
10	1355	3885	60	5300	73,3

With an intensity advantage of 5 dB, the follower signal attracted more agents than the leader, and with a 10 dB advantage 73% of all started agents went to the follower. For further explanation see text.

path is unrealistically straight (Fig. 4C). By contrast, if only deviations of more than 30% of the mean cause a directed movement (indecision value > ±0.30), about 50% of the agents do not orient to either the leader or follower, but rather move into a random direction (Fig. 4D).

The simulation tool was also used to examine the success of leader and follower signals under conditions that include variable distances of agents to leaders and followers, and thus more variable time–intensity relationships. Two males were positioned 10 m apart from each other in the centre of a virtual arena broadcasting leader and follower signals, and the 10 different agents – starting 10 times from 53 different starting positions – simulated phonotactically responding females. Again, each patch was defined by its specific time–intensity relationship of the two sound signals and agents moved towards one or the other source based on their implemented neuronal rules.

When the leader male had a temporal advantage of 140 ms over the follower and the SPL of both signals was the same (85 dB SPL at a distance of 1 m), the leader male attracted more than twice the number of agents than the follower (Table 1; 3483 compared to 1487). This is due to the fact that the area (the number of patches) where the signal of the leader produces a net neuronal advantage is much larger (about 66%) compared to the area where the follower dominates; the remaining area is assigned to the neutral zone with no clear advantage of either signal. In order to simulate, how an increased intensity of the follower signal affects its success in the attraction of females, the follower intensity was increased in a further simulation with 5, 8 and 10 dB relative to the SPL of the leader signal. As expected, an increase of the intensity of the follower signal gradually increased its success in attracting more and more females (Table 1). Equal success for both signals was recorded when the follower SPL was increased by 5 dB, and with still higher SPL of the follower the advantage was shifted towards the follower.

Discussion

The aim of this study was to examine the underlying neuronal basis for a preference of female bushcrickets *Mecopoda elongata* to male songs, which seemingly does not favour follower males. Males that sing in synchrony with another male, but with a delay of 140 ms, are significantly less approached by receptive females in a choice situation. Since the intrinsic chirp period largely determines the leader and follower role for interacting males – those with the shorter period are leaders most of the time (Hartbauer et al., 2005) – the result should be strong selection for faster chirping males.

We have argued previously (Römer et al., 2002; Hartbauer et al., 2005) that various factors in the natural settings of a chorus may nevertheless contribute to a significant ultimate success of followers, despite the preference of females for leaders. The argument was based on the assumption that a time–intensity trading, similar to what was investigated here, also happens in nature. We do not know if male *M. elongata* are able to increase the SPL of their calls depending on the presence of other singing males or the amount of environmental background noise, as has been shown, e.g. for songbirds (Brumm and Todt, 2002). However, various environmental factors can produce considerable variation in the relative SPL of leader and follower signals at the position of a receiving female. Such factors include distance and geometric spreading of sound, excess attenuation, the height and broadcast directivity pattern of the signaller in more or less dense vegetation, and different ambient noise levels at different receiver sites (reviewed by Römer, 1998). Frogs and insects can improve the broadcast range of their signal by choosing calling locations which guarantee best broadcast conditions and less excess attenuation (Wells and Schwartz, 1982; Arak and Eiriksson, 1992; Römer and Lewald, 1992). Thus, a male *M. elongata* could compensate his disadvantage in a synchronous interaction with a leader male by singing from an elevated position within the vegetation, so that the increased loudness of his signal at the position of the listening female would compensate the negative effects of the time delay. It should be pointed out, however, that this option may be associated with other costs, so that there is a trade-off between the advantage of the increased detection range of the signal and the costs of singing at higher, exposed elevations because of exposure to potential predators. As a result, insects may establish positions that are less than ideal for maximal sound transmission (Arak and Eiriksson, 1992).

We have examined the time–intensity trading aspect in

synchronous interactions in more detail, both in behaviour and neurophysiology. One important finding was the non-linear dynamics of this trading phenomenon. At lower sound pressure levels of 57 dB SPL an additional 6 dB for the follower signal significantly reversed the preference, whereas 10 dB are necessary for this reversal at 62 dB SPL. However, even a 10 dB advantage was not enough for the leadership compensation at 72 dB SPL. Thus, if a female is further distant from synchronously interacting males, the temporal advantage of a leader can easier be compensated by an increased loudness of the follower than if she is at close range. An interesting conclusion from this finding would be a difference in the fitness outcome of synchronous calling for followers in choruses that vary in density. At higher densities, where the SPL of all members of the chorus at any possible position relative to a female is high, the chance to compensate the leader advantage is low for a follower, because the additional SPL necessary for the follower chirp is higher (Fig. 2 and Table 1). A time–intensity trading has also been reported in synchronously calling frogs (Dyson and Passmore, 1988; Klump and Gerhardt, 1992) and another bushcricket (*N. spiza*) (Snedden and Greenfield, 1998). Consistent with our own observations, in *N. spiza* a higher intensity was necessary for compensation of the leader signal at higher playback levels.

The basic neuroethological concept of the present paper is the assumption, that the proximate mechanism for the preference of females for leading calls is their asymmetry in the representation of both signals in the afferent auditory pathway. Römer et al. suggested that contralateral inhibition, a mechanism that most probably evolved for sound localisation, is responsible for this female preference (Römer et al., 2002) [for an interesting case of a negative sensory bias as a result of inhibition in the auditory system of frogs see Gerhardt and Höbel (Gerhardt and Höbel, 2005)]. When synchronizing males are separated in time and space, leader and follower signals will impinge on the female from different directions, and direction-selective neurons such as the pair of omega-neurons receive excitatory inputs from the ipsilateral side but strong inhibition from the contralateral side (reviewed by Pollack, 1998). Here we have confirmed that mutually inhibitory connections between these omega-neurons create strong asymmetries in favour of the leading signal. However, if this proximate interpretation for the female preference is correct, we must assume that the properties of the time–intensity-trading phenomenon, as observed in phonotactic behaviour, is also reflected in the responses of the pairs of omega-neurons. This is indeed the case: the asymmetry in favour of the leader signal is reversed with increased loudness of the follower. More importantly, however, the trading functions exhibit similar non-linear properties as the behaviour, most obvious in the steepness of the trading curves at different playback levels (Fig. 3B,C). One would therefore predict that at higher sound pressure levels of 72 dB SPL the additional intensity required to compensate the advantage of the leader has to be higher than at lower SPLs, which has been found in behaviour (Fig. 2).

At the neuronal level, the non-linear relationship can probably best be explained by the ramp-like nature of the chirp, which increases in amplitude with each successive sound pulse within the chirp. At lower SPLs, only the most intense final pulses elicit a short excitatory response on the ipsilateral side, which, due to the reciprocal nature of connectivity between the two neurons, elicits an inhibition in its contralateral counterpart. This inhibition is short and weak and can be compensated by a relatively small increase in intensity of the follower signal. However, at higher SPL also the initial, low intensity sound pulses in the chirp result in an excitatory ipsilateral response with a duration lasting for the whole chirp, which thus translates into a strong, long lasting inhibition of the mirror-image omega-cell. Therefore, there is more sound pressure needed to compensate for the temporal advantage of the leader.

Another hint for a causal relationship between the discharge of a reciprocal inhibitory network and female preference in *Mecopoda* is the steepness of the behavioural switch from a preference from leader to follower with increasing follower SPL (Fig. 2). For example, at 62 dB SPL, with an 8 dB advantage of the follower signal, females still preferred the leader, at a ratio of *L:F*=13:4, but with an additional 2 dB in the follower signal there was a switch in preference to the follower at a ratio of *L:F*=3:12. Thus, the underlying neuronal network responsible for the preference appears not to respond in a linear fashion to intensity differences of the two auditory sides, but rather exhibits a critical intensity value, where one side dominates the other significantly. The enhancement of small differences is a characteristic feature of reciprocal inhibitory networks, and in the auditory system of Orthoptera this has been documented in the context of directional hearing, with interneurons receiving excitatory synaptic input from one side, and inhibitory input from the other (for a review, see Pollack, 1998). A second feature of such networks is their asymmetrical discharge with symmetrical stimulation; even when both sides receive the same excitatory input, noise within the system will produce small asymmetries which are again enhanced by reciprocal inhibition, thus favouring a strong response of one side over the other, the leading role switching randomly between both. The behaviour of females in response to synchronous signals with no time delay at all and both of the same SPL, randomly preferring one or the other speaker in the arena (see Fig. 1C), is compatible with the properties of such inhibitory reciprocal networks. The same must be the case at the point of compensation of a temporal advantage of the leader by an increased SPL of the follower.

We must emphasize, however, that the correlation between neuronal and behavioural data is not perfect. For example, at a playback level of 72 dB SPL an additional 10 dB for the follower is necessary to compensate the temporal advantage of the leader in behavioural arena experiments, whereas equal representation of both signals in the pair of omega-neurons occurs when the follower is increased by only 6 dB. Here we have to consider that in the arena, these different SPLs exist only at the starting position, and they change with the

phonotactic approach towards one of the speakers, whereas in the neurophysiological experiments the SPLs of the two signals remain constant. For a better correlation it would thus be necessary to perform behavioural experiments on a walking compensator such as the Kramer treatmill, where the distance between female and speakers does not change so that the orienting animal receives a constant SPL despite its movement.

An interesting result was obtained in behavioural experiments when females were subject to a choice towards alternating, rather than synchronized, signals (Fig. 1B). As expected, when both signals were identical and presented in a strictly alternating fashion at an interval of one second, female preference was random. In terms of representation on both signals in the CNS of the females this result makes sense, since there is no advantage of one side over the other due to contralateral inhibition, and each signal is represented equally well on both sides (Römer et al., 2002). However, the time needed for the phonotactic approach was three times longer than the same signals presented in a synchronous fashion. We interpret this result as a response to the ongoing ambivalence of the afferent information in this particular stimulus configuration, because with alternating signals the female receives unambiguous information that the conspecific signal is on one side, and then, changing every second, the same information is on the opposite side. By contrast, the imperfect synchrony produces a dominance in the representation of the leader signal for most of the time, which gives the female consistent information over time that the 'stronger', most effective stimulus is on one side. From an ultimate point of view, the finding that females take three times longer in their phonotactic approach towards alternating compared to synchronized signals strongly supports the view (Dawkins and Guilford, 1996) about the adaptiveness of female choice, if based on a sensory bias. Given that a prolonged approach to males may represent a possible cost of female choice due to increased conspicuousness with ongoing movement, in the presence of potential visually hunting predators, females may indeed benefit from being exploited, even if the preferred leader male does not provide good genes or direct benefits at all.

In addition to examining the preferences of females and relating these to the asymmetry of representation within a receiver, we also used simulation tools, in which neurophysiological results had been incorporated in agents. These simulated agents had implemented rules such as 'move to the side most strongly activated', which appear to be also used in real orthopteran insects when approaching a sound source. Since these agents moved in a virtual acoustic space where each spot was characterized by a defined sound field of leader/follower loudness and time relationships, we were able to compare such simulated choice with real female behaviour. A related methodological approach has been taken (Webb, 1995; Webb and Scutt, 2000) by implementing a simple hypothesis regarding localization and recognition of acoustic signals in crickets into a small network of four neurons, and testing it on a robot base. The robots 'behaved' like crickets, and both recognition and localization was robust under a variety of conditions. Our approach was somewhat different, since we implemented the results of neurophysiological experiments, rather than a model circuit, into the agents. This approach turned out to be a valid tool for several reasons. First, the high correlation between the preference of real females and that of agents moving towards virtual males is a further hint for the correctness of the underlying hypothesis, that the asymmetrical representation of leader and follower signals is the internal cue of the CNS guiding females to their target. It is important to note that each individual result of a neurophysiological preparation was implemented into an agent separately, and because there was some variation in the responses of the pair of omega-neurons (Fig. 5), each agent varied, to some extent, when presented to a leader/follower sound field. This variation can be seen for example in the result that one out of ten agents still moved to the follower when both signals were presented with equal SPL (Fig. 4A). This is despite the fact that under these conditions, on average, there is significant positive value of v (i.e. a representation in favour of the leader signal). Interestingly, a similar kind of variation was also found in the behaviour of females: under the same conditions as mentioned above, three out of 18 females moved to the follower, although on average there was a significant preference for the leader (Fig. 1A). It is tempting to speculate that in both the behaviour and simulation the underlying proximate mechanism for the variation is the same, by assuming that in some females deviations from auditory symmetry cause such deviations in behaviour. An ongoing study with a comparison of individual female behaviour, the neural representation of synchronous signals in the same individual, and the implementation of such results into agents will better be able to draw such conclusions.

The simulation tool is particularly useful when it comes to the question of why followers should call at all, if their call is less attractive for females, or why they do not adopt a strategy that improves their call timing, as in *N. spiza* (Greenfield and Roizen, 1993). It is surprising to see individual males fixed in
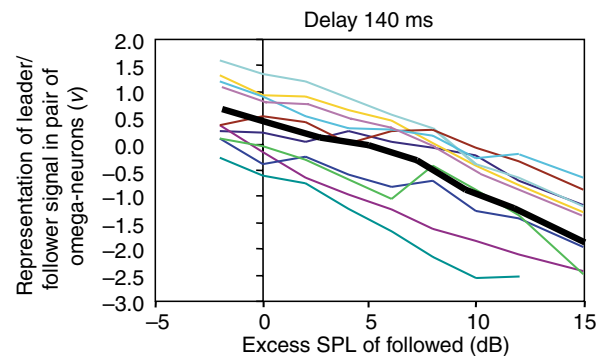

Fig. 5. Representation of leader and follower signals in the pair of omega-neurons of ten different individuals (coloured lines; playback levels of 67 dB SPL, time delay 140 ms). Note that although the representation in each individual follows the mean trend (black thick line) there is considerable variation in the degree of neuronal asymmetry at any point in the trading function.

their calling strategies as followers throughout their lifetime, as a result of their individual endogenous slower call rate, if they are confronted with a faster chirping male. Moreover, over the lifetime of a male the call rate decreases, and thus the likelihood of being the follower in an interaction increases (Kratzer, 2000). So far no active mechanisms are known that would enable followers to compensate their disadvantage relative to leaders. We have argued that part of the answer to this question is the ecological setting under which synchronous calling and hearing by females takes place. If we assume females being randomly spaced in a population of calling males, there exist numerous time–intensity relationships of competing signals that could lead a female to a particular signal. It is almost impossible to incorporate all these signal conditions in either behavioural and/or neurophysiological experiments, in order to find out which of the signals would be favoured by female choice. In contrast, once the virtual sound field has been calculated, many agents can be placed at any position within this sound field and results about differential attraction can be obtained within a short time. One such simulation, although in a simplified situation with only two males calling, revealed that the success of the follower in attracting females was about 30%. This contrasts with the result of the arena experiment with a success of only 10% for the follower. The difference is due to the fact that in the simulated field situation female agents are regularly spaced in the virtual arena, so that different distances of agents to the leader and follower experience much higher signal amplitude from the follower compared to the leader, thus resulting in a trading of the temporal advantage. Although it is true that, on average, females in a population will be as likely to be closer to leaders and followers when they start phonotaxis, from the viewpoint of the success of followers, only those cases are important when females are closer to their position, because followers will loose anyway, even when females are equidistant to both leaders and followers. If we further consider that a constant temporal advantage of 140 ms for one male is the exception rather than the rule in signal interactions between males (Hartbauer et al., 2005), the representation of the follower signal in receivers, and thus the attraction rate, would be even higher.

For a better understanding of a chorus situation in the field it would certainly be valuable to know the actual spacing of males, and whether males change their positions relative to each other over the singing period of one night. For a closely related synchronizing species of *Mecopoda* from India with about four times the singing rate as in *M. elongata,* field data indicate intermale distances of about 5-10 m (V. Nityananda and R. Balakrishnan, personal communication), and little male movement. Future simulations will include more natural and complex parameter settings, in particular the interaction of more than two males, as it normally happens in an insect chorus. But preliminary behavioural and simulation results would suggest that call timing within larger groups of males would be principally similar to that described by Hartbauer et al. (Hartbauer et al., 2005) and in the present paper, and thus does not require other explanations.

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