REALISTIC SIMULATION OF AN INSECT CHORUS BASED ON COUPLED SONG OSCILLATORS

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Abstract

In several insect species, choruses are formed where many individuals interact acoustically. Particularly interesting are assemblies of males which synchronize (or alternate) their cyclically occurring song elements (chirps) during acoustic interactions. Song synchrony is imperfect, however, since some males (leaders) begin their chirps some tens of milliseconds earlier compared to their counterparts (followers). Leaders are more likely to be chosen by females as mates. We have shown previously, that male-male song interactions in the insect *Mecopoda elongata* (*M. elongata*) could be successfully simulated by coupling two limited-cycle oscillators, which respond to perturbations by a phase shift known from experimentally derived phase response curves (PRCs). Further, the difference between the free-run cycle lengths of two males in a duet mainly determines the establishment of either the leader or follower role. The aim of the current study was to develop a model which allows the simulation of acoustic interactions between many signalers in a large chorus, taking into account an inhomogeneous spacing of individuals and a variability of model parameters observed in nature.

Keywords: Chorusing, coupled oscillators, ecological modeling, multiagent simulation, insect swarm.

Presenting Author's biography

Manfred Hartbauer. I am interested in the acoustic interaction of insects. Our group investigates the fascinating behavior of acoustically synchronizing insects on both, a behavioral as well as neurophysiological level. In order to better understand the mutual interaction resulting in an almost perfect signal synchrony, apparent in some chorusing insect species, I am programming multiagent simulations, which are based on experimentally obtained simulation parameters. In turn, the results of such simulations lead to new hypothesis which we successfully test in the biological system.

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1 Introduction

The synchronization of communication signals in large aggregations of individuals has attracted the interest of many researchers throughout the last century. Synchronized optical signals can be found in the East-Asian fireflies [1,2,3], but also in the acoustic interaction of different insect species (like crickets and bushcrickets) [4,5,6,7].

Synchrony within a population of biological oscillators is achieved by mutual entrainment. Similar mechanisms were found in the pacemaker cells of the heart, circadian pacemakers, the hippocampus, insulin-secreting cells of the pancreas, the menstrual periods of women (for an overview see: [8,9]). Much theoretical work is based on the Peskin model [10] of “integrate and fire” oscillators in which the interaction between two oscillators are either smooth or pulse like [11,12]. As Peskin already conjectured and Mirollo and Strogatz proved, for almost all initial conditions a steady state evolves among a population of homogeneous “all to all” coupled oscillators in which all oscillators fire in synchrony.

In the current work a chorus model was developed which is based on the properties of song oscillators of the chorusing bushcricket species *Mecopoda elongata (M. elongata)*. Males of this species synchronize their chirps in male aggregations in order to attract females. The establishment of a high degree of synchrony in *M. elongata* duets was found to be based on a phase delay and a phase advance mechanism, both acting in the perturbed cycle [5,6]. Together with only small variance in solo chirp period (CP) (< 2%) such properties constitute this type of oscillator to be unique among insect song oscillators. These special properties are of particular interest for developing a model chorus in which agents mutually couple heterogeneous oscillators by acoustic signals. The model would allow to reveal critical parameters influencing the establishment of steady state oscillator coupling.

In contrast to other biological oscillator models, which are based on “integrate and fire” oscillators [12] or inhibitory-resetting oscillators [13], oscillators in the current model show the same behavior in response to a stimulus as males do in playback experiments using a conspecific signal as stimulus. Similar to Ermentrout 1991 [14] this was achieved by modeling a realistic oscillator behavior known from phase response curves (PRCs). This method is principally different from other oscillator studies in which the endogenous oscillator, controlling the rhythmic production of chirps, itself was modeled by assuming several unknown variables like the timecourse of the integrate-and-fire oscillations, firing threshold, oscillator return interval and effector delay [12,13].

Agents in the current model exhibit a natural spacing and a variability of model parameters similar to what was found among real males in a population. Further, the strength of oscillator coupling depends on the distance between two agents. All these properties constitutes this model as more “realistic” compared to model studies in which mutually coupled oscillators become synchronized assuming homogeneous oscillators lacking any spatial structure [8,12]. Whether at all oscillators in the *M. elongata* model will ever show a global stable phase coupling needs to be determined.

Females in some chorusing insect species are known for choosing that male, which initiates his signal first (leader) in a male-male interaction [13,15]. This ultimately results in a chorus in which males compete for the leader role and synchrony is established as a by-product of ongoing male competition [16]. In such a chorus imperfect signal synchrony and a high degree of temporally overlapping signals have to be expected. For a full understanding of *M. elongata* chorusing it is therefore of importance to study those mechanisms that result in the observed variability of male signal properties forming the basis of female choice.

In mutually entrained biological oscillators firing in synchrony those oscillators exhibiting a faster free-run cycle period (CP) were found to be among those firing earlier [12]. A similar result was obtained in duets of *M. elongata* males where the leader was found to exhibit a higher solo chirp rate compared to its competitor [5]. Since chirp rate is a signal character often favored by females [17,18] and associated with higher energetic demands [19], this suggests that females assess the energy reserves of a male by choosing the leader in a chorus. However, as was previously shown [20] no difference was found between the solo CPs of two groups of *M. elongata* males reared on two feeding regimes, differing in the energetic content of their food. This finding does not preclude the possibility that low-nutrition males might show a reduced ability to synchronize to a stimulus presented at a higher rate as their own solo CP.

In different species selective attention allows a male to interact with only one or two males within the acoustic range [21,22,23]. This selective attention mechanism could prevent the establishment of the leader role of a faster signaling male in a chorus situation. The chorusing model allows to investigate the influence of selective attention on male-male interactions and allows to make predictions for females choosing a mate in a chorus situation.

2 Methods

2.1 General assumptions

The species Mecopoda elongata (*M. elongata*) exhibits a solo chirp period (CP) of ~2 s. Individual agents in the chorus model were modeled on the basis of coupled signal oscillators exhibiting the same properties as was found in a population of 11 males of the *M. elongata*. The phase response curves (PRCs) of these individual males were obtained from playback experiments using a conspecific stimulus, which was broadcast at 50, 60 and 70 dB SPL (PRCs were published in [5]). Most simulation parameters like the distribution of individual free-run oscillator cycle lengths, the variability of response phases, chirp intensities, chirp durations and the intensity drop over distance are known from behavioral experiments and were implemented in the model in order to establish a *M. elongata* chorus model as realistic as possible.

In the current model agents couple their oscillators using acoustic signals with an intensity profile similar to conspecific chirps. Such a model allows to study numerous questions dealing with chorus synchrony and it allows to draw inferences for females choosing a male in a chorus. The following model parameters and chorus manipulations were performed in order to investigate their influence on the degree of chorus synchrony: agent density, chorus spacing, free-run cycle length, signal duration, intensity summation, agents joining or leaving a chorus, selective attention to only a subset of agents and a precedence effect.

2.2 Model description

The acoustic interaction between males (agents), which mutually couple their song oscillators on the basis of acoustic signals (chirps), was modeled in the JAVA (Sun Inc.) based multiagent simulation environment Netlogo 3.1 (http://ccl.northwestern.edu/netlogo). Although Netlogo allows to increase the number of agents up to 1000, a simulated chorus always consisted of 15 individuals. This size covers a male aggregation large enough to study principal chorusing effects. Because males do not move while they sing, agents were not allowed to move throughout a simulation run. Each simulation step in the model refers to a 10 ms time period.

2.3 Simulated chirp signals

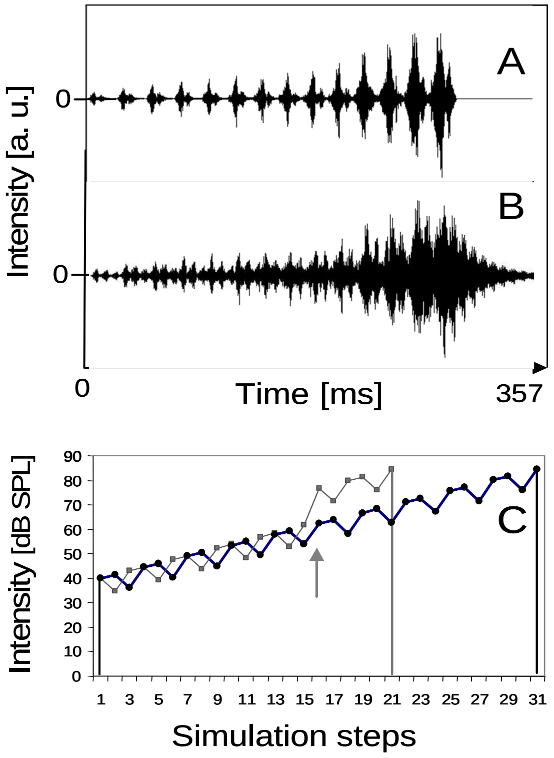
Conspecific chirps of *M. elongata* are characterized by a steady increase of syllable level with brief pauses between subsequent syllables (Fig. 1A). Due to reverberations occurring in the acoustic transmission channel, chirps loose their characteristic temporal pattern (Fig. 1B). Therefore chirps were modeled without silent gaps between adjacent syllables, instead signal level dropped by 7 dB after every third simulation step (Fig. 1C).

Fig. 1
Chirp of a *M. elongata* male.
The oscillogram of a male chirp recorded at a distance of 1 m consists of syllables of increasing intensity (A). B represents the same chirp as shown in A but after echo processing performed in CoolEdit (Syntrillium Inc.) using a delay time of 8 ms and 70% decay. The intensity profile of a simulated chirp is shown in C (black line). In response to the perception of a neighboring chirp (arrow) in the final phase of the oscillator cycle, the chirp was found to be shortened and loud syllables are brought forward in time (grey line).

The average chirp duration of 12 individual males was found to be 273 ms ± 28.6 ms. In the model a longer average chirp duration of 31 ± 2 simulation steps (1 step = 10 ms) was chosen. This compensates for a prolongation of a chirp signal as a result of echoes added to the original signal due to signal transmission (similar to Fig. 1B).
The average chirp level of singing males recorded at a distance of 1 m is about 86 dB_{pe} SPL. This level corresponds to the maximum level of the last syllable of the simulated chirp. In the model the level of subsequent syllables comprising a chirp increased stepwise according to equation 1. This models the increase of signal level of subsequent syllables beginning at 40 dB SPL up to 86 dB SPL as a function of the remaining cycle length (*cl*).

$$s\_level = \frac{(86-40)}{chirp\_dur} * (chirp\_dur - cl) + 40 \tag{1}$$

Chirp_dur denotes the current chirp duration of an agent, which fluctuates on a chirp to chirp basis (31 ± 2 steps). Loud syllables at the end of a male chirp are of about 20 ms in duration corresponding to 2 time steps in the model. Therefore, after every third time step syllable level (s_*level*) was decreased by 7 dB. The resulting intensity profile of a simulated chirp (Fig. 1C) covers the envelope of a transmitted male chirp considering transmission effects which obliterate the characteristic temporal syllable structure of a male chirp.



The average maximum chirp level was on average 86 dB SPL and chirp to chirp level variability was taken from a Gaussian distribution with a SD of 3 dB. This variability accounts for a level fluctuations as a result of signal transmission in a natural habitat.

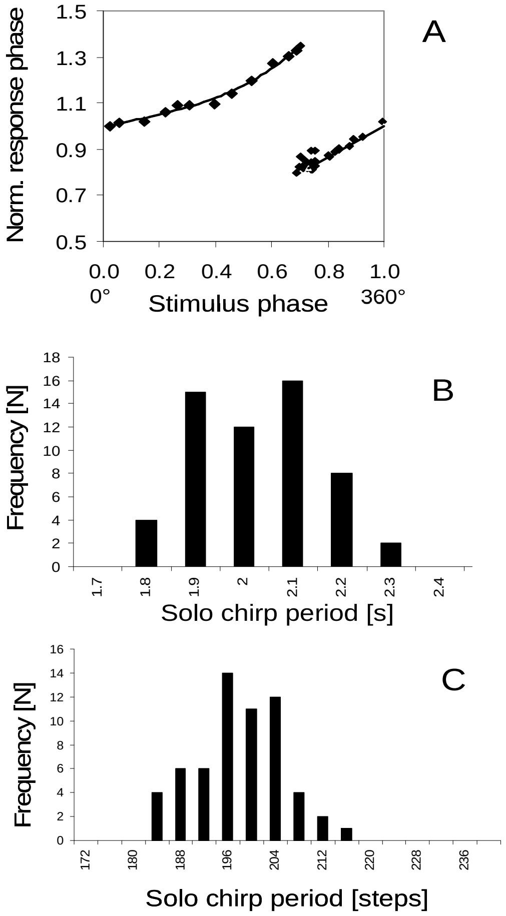


Fig. 2
Phase response curve and distribution of solo chirp periods.
An example of a PRC (male #1) obtained in playback experiments with a conspecific chirp presented at a stimulus level of 70 dB SPL is shown in A. In such a plot the stimulus phase was plotted against the normalized response phase (length of the disturbed cycle / free-run cycle length). These data were fitted with polynomials or linear functions (curves in A). These equations (see appendix) were used to calculate the change in phase following stimulations. B shows the distribution of solo CP (mean: 1.97 s) within a male population. A similar distribution of solo CP of agents was simulated in the model chorus (C). A total of 57 males contributed to the data in B and C.

2.4 Signal oscillators

Oscillators in the model were mutually coupled and after the perception of a stimulus (chirps generated by neighbors) the resulting phase shift was calculated from PRCs obtained in playback experiments of 11 real males. Every agent in the model was randomly assigned to one of these PRCs at the beginning of a simulation run. The degree of phase shift following a perturbation of the signal oscillator depends on stimulus level and on the phase of the stimulus in the oscillator cycle. The relation between stimulus phase (period between the last male signal and the stimulus / free-run cycle length) and the normalized response phase (length of the disturbed cycle / free-run cycle length) are displayed in a PRC.

The left branch in a PRC refers to responses to stimulations (a conspecific chirp) occurring shortly after the focal male's chirp and was modeled using second- or third-order polynomials (see appendix). Stimuli up to a phase of about 0.7 (transition phase) resulted in a prolongation of the perturbed cycle. Linear equations or first-order polynomials were used to model the right branch of PRCs referring to responses to stimulations occurring late in the cycle. The response to stimulations in the second part of the cycle resulted in a shortening of the perturbed cycle length (an example is shown in Fig. 2A). The fitting equations describing the PRCs of all 11 real males are listed in the appendix. Each of these oscillators exhibited an individual transition phase. The data shown in the PRCs of real males were obtained by taking stimulus times and response times at the end of signals.

Each agent in the model exhibits its own free-run period (solo CP), its own PRC and its own transition phase. These properties were assigned to each agent at the start of a simulation run. The PRC and the transition phase was randomly chosen from a total of 11 PRCs. The free-run signal periods (solo CP) of different oscillators (T_0) was taken from a normal distribution with a mean of 2 s (200 simulation steps) and a SD of 70 ms (7 simulation steps). This resulted in a distribution of free-run cycle lengths (Fig. 2C), similar to what was found in a male population (Fig. 2B). A cycle to cycle variability of the free-run cycle length was modeled according to equation 2. This simulates the variability of CPs naturally found in songs in which males synchronized to a conspecific stimulus with a period of 2 s.

$$Tc = \mathrm{int}\left(T_0 + \left(T_0 * \mathrm{rand}(0.02)\right)\right) \qquad (2)$$

"rand" refers to a Gaussian distributed variability with a SD of 0.02 simulation steps. Agents exhibiting a free-run cycle length of 200 steps will therefore exhibit a cycle to cycle variability with a SD of 4 simulation steps.

In every simulation step (corresponding to 10 ms), each agent executes 6 logic queries (Fig. 3). In the first the remaining oscillator cycle length (*cl*) is decremented by one. In the final phase of the signal oscillator cycle (if *cl* <= *chirp_dur*) each agent starts to broadcast a chirp (step 2) which may be detected by neighbors in the active space of the signaler.

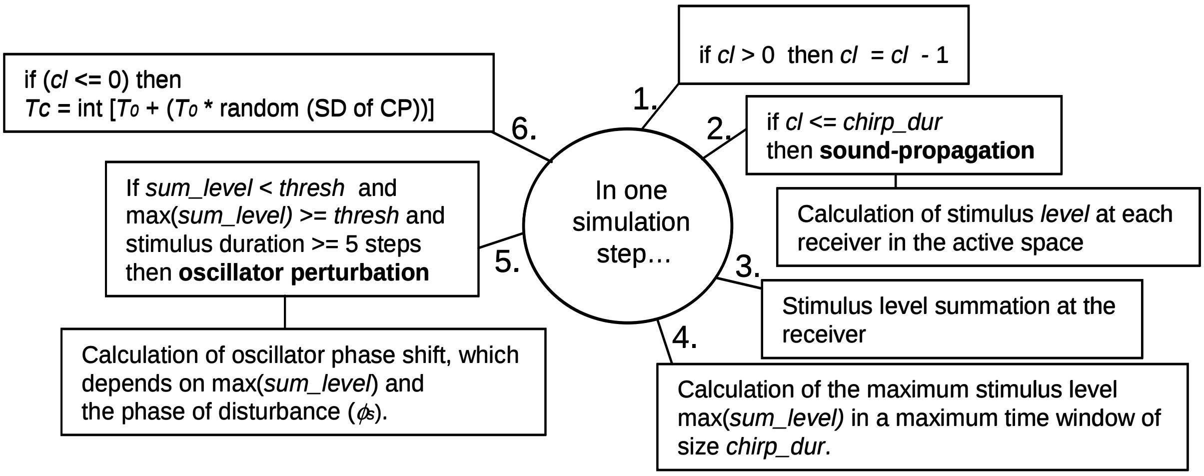


Fig. 3
Logic queries executed by agents in each simulation step.
Every agent executes 6 logic queries independently from each other in every simulation step. For details see methods. *cl* = remaining cycle length, *chip_dur* = chirp duration, *s_level* = stimulus level, sum_level = perceived stimulus level, T_0 = average free-run cycle length, *Tc* = current free-run cycle length

Signals overlapping in time will be summed up at the receiver (steps 3) and the maximum stimulus level detected in a stimulus (steps 4) was used to immediately calculate a perturbation of the oscillator phase of the receiver at the end of a stimulus (step 5). At the end of a cycle a new *Tc* was calculated according to equation 2.

2.5 Signal propagation

The active space in which agents may perceive a signal to be suprathreshold was calculated after equation 3.

$$aspace = \frac{10^{\frac{s\_level - thresh}{20}}}{sf} \qquad (3)$$

Thresh refers to the hearing threshold (48 dB SPL) and *sf* refers to a scale factor allowing the investigation of effects resulting from different inter-agent distances on the establishment of chorus synchrony. In a choruses simulated with the standard parameter set (shown in table 1) almost all agents were found in the active space of each agent.
The level of a signal (*s_level*) attenuates with distance because of spherical spreading and was calculated after equation 4. Access attenuation, which is known from the signal transmission of high-frequency sound signals, was neglected because the frequency spectrum of *M. elongata* chirps is dominated by frequencies below 7 kHz.

$$level = s\_level - [20 * \log_{10}(dist * sf)] \quad (4)$$

The amount of simulation steps corresponding to the delay of a signal traveling from one agent to another was calculated assuming a transmission velocity of sound in air of 340 m/s (equation 5).

$$delay = \mathrm{round}\left(\left(\frac{dist * sf}{340}\right) * 100\right) \qquad (5)$$

Since one simulation step corresponds to 10 ms, the quotient in equation 5 was multiplied with 100 and the product was rounded in order to obtain an integer value. Each agent services a list of delays and the appropriate levels of detected signals (*level$_i$*) and considers these data for signal level summation as explained in the following.

Level addition of temporarily overlapping signals results in an amplification of stimulus level (*sum_level*) at the receiver. Therefore, signals belonging to different sources were summed up in sequence according to equation 6.

$$sum\_level = \sum_{i=1}^{n} 10 * \log_{10}\left(10^{\frac{sum\_level}{10}} + 10^{\frac{leveli}{10}}\right) \quad (6)$$

2.6 Signal perception

As soon as the accumulated signal level (*sum_level*) at a receiver drops below the level of hearing threshold (48dB SPL) and the signal was continuously detectable at least within the last 5 simulation steps, the end of a stimulus was detected. A perturbation of the current oscillator cycle was calculated if the maximum signal level in a stimulus exceeded hearing threshold. This maximum was calculated in a time window of a maximum size which corresponds to the average chirp duration. Temporal overlap of different signals may cause a severe prolongation of signals at a receiver. For practical reasons, signals lasting longer than 35 simulation steps caused a perturbation of the oscillator cycle, even if the end of the stimulus was not reached yet. Different temporarily separated signals could perturb the cycle length several times within a single oscillator cycle. The maximum signal level perceived within the last stimulus was used to calculate the appropriate perturbation of the oscillator cycle.

The phase of perturbation of the oscillator cycle (ϕs) after detection of a suprathreshold stimulus was calculated according to equation 7.

$$\phi s = \left(\frac{Tc - cl}{T_0} \right) \qquad (7)$$

T_0 denotes the average free-run CP and Tc refers to the cycle length of the current cycle. By multiplication of ϕs by 360 the phase of perturbation in degrees can be obtained.

The resulting phase shift following an oscillator perturbation was calculated from individual PRCs, which were originally derived from playback experiments of 11 different males performed at three different stimulus intensities. In order to calculate phase shifts for a broader range than 50, 60 and 70 dB SPL interpolations and extrapolations of the resulting response phases were calculated for the left branch exclusively. The phase shift following a stimulus with a maximum stimulus level between 50 and 60 dB SPL (equation 8) as well as between 60 and 70 dB SPL (equation 9) were linearly interpolated.

$$\phi = \phi_{50} + \frac{(\max(int) - 50) * (\phi_{60} - \phi_{50})}{10} \qquad (8)$$

$$\phi = \phi_{60} + \frac{(\max(int) - 60) * (\phi_{70} - \phi_{60})}{10} \qquad (9)$$

Signals below 50 dB SPL and above 70 dB SPL were linearly extrapolated as a linear function of stimulus level. Because of a simulated variability (see below) of response phases, it was not necessary to interpolate or extrapolate responses for various stimulus levels for the right branch of PRCs.

In order to account for a naturally observed variability of the resulting phase change following a stimulus, Gaussian noise (SD: 3.4 steps for the left branch and SD: 1.8 steps for the right branch) was added to the response phase (ϕ) obtained from PRCs. The size of this response variability was drawn from deviations of response phases from the equations fitting the data displayed as PRCs. All agents in the model exhibited the same degree of response variability.

The resulting response phase (ϕ_r) following an oscillator perturbation was transformed into the length of the perturbed cycle (*Pcycle*) according to equation 10.

$$Pcycle = \mathrm{int}(T_0 * \phi r) \qquad (10)$$

The remaining oscillator cycle length (*cl*) after detection of a stimulus was calculated by subtracting the already passed phase before a stimulus occurred (*Tc - cl*) from the length of the perturbed cycle (equation 11).

$$cl = Pcycle - (Tc - cl) \qquad (11)$$

2.7 Spacing effects

Although the mean inter-male distance for *M. elongata* in the field is unknown and may vary in aggregations of different bushcricket species substantially (e.g. Thiele and Bailey 1980; Römer and Bailey 1986), an inter-male distance of approximately 5 m was frequently observed in male choruses of another *Mecopoda* species [24], and in the synchronizing bushcricket *Neoconocephalus nebrascensis* [25].

Spacing of males observed in nature was found to be more or less clustered. In the model clustering was achieved by a sort of random walk performed by each agent starting in the center of the simulated world. The heading of 15 agents after their sequential creation in Netlogo follows a systematic scheme. Each agent heads towards a direction which is 24 degrees higher compared to the agent which was created before. Agents kept walking by heading towards a randomly chosen direction in the range of 0 - 19 degrees (calculated from the current heading) until there were no other agents in a user defined radius corresponding to a user defined minimum inter-agent distance. A quite realistic spacing of agents was achieved when agents covered a randomly chosen distance in each walking step in the range of 0 – 3 patches. Distances between agents were converted in meters by multiplication of the distance (given in patches) with the scale factor (*sf*). After agents spaced themselves in the simulated world, agents did not move within a simulation run.

2.8 Modeling a precedence effect

Neurophysiological experiments revealed that the representation of two equally loud signals separated in time by some tens of milliseconds resulted in only a weak representation of the follower signal in the CNS of *M. elongata* [15,26]. Such an effect is quite common among vertebrates and invertebrates and was termed precedence effect [27]. Such an effect may have profound consequences on chorus establishment and female choice [15]. In order to appropriately study this effect in the current model, a dynamic hearing threshold replaced the fixed hearing threshold of 48 dB SPL. The dynamic hearing threshold was simulated by integrating the intensity profile of the perceived sound stimulus just 1 dB below its perceived level. The size of the integration window was defined as 1/3 of the mean chirp duration (10 simulation steps). The dynamic threshold was prevented from falling below a hearing threshold of 48 dB SPL (see Fig. 4). As a result silent signals will more likely remain subthreshold if they follow loud ones.

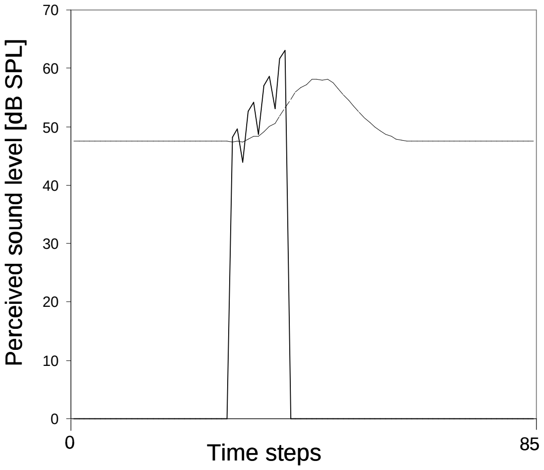


Fig. 4
Dynamic hearing threshold.
An example of the dynamic hearing threshold (dotted line) in response to the perception of a neighbor chirp is shown.

Tab. 1 Standard simulation parameters in the chorus model

Parameter	**Value**	**Unit**
Chorus size	15	N
Hearing threshold	48	dB SPL
Mean chirp intensity	86	dB SPL
SD chirp intensity	3	dB
Mean free-run chirp period	200	steps
SD free-run period	4	steps
Mean chirp duration	30	steps
SD chirp duration	2	steps
SD left branch of the PRC	6	degrees
SD right branch of the PRC	3.2	degrees
Minimum distance between agents	6 or 9	m
Agents start at a random phase in their cycle		yes
Dynamic hearing threshold		no
Selective attention towards local neighbors		no

2.9 Variables left unconsidered in the model

- All agents shared the same average chirp duration and the same average maximum chirp level. Both parameters were found to differ considerably among males in a population.
- Free-run cycle length was left unchanged throughout the simulation. After entrainment of slowly chirping males to a high repetition rate (1.8 s) a gradual return to the free-run cycle length was found within about the next 10 cycles. This behavior suggests a dynamic free-run cycle length adaptation, which was left unconsidered in the current model. In a chorus exhibiting a natural distribution of free-run cycle lengths (Fig. 2B) this effect may be of minor importance and affects only a small number of slowly chirping agents.
- The sound field around a chirping agent was modeled to drop homogeneously over distance. Agents did not face a certain direction: as a result sound propagation and sound perception did not suffer from the current heading of agents. The simulation of a homogenous sound field ignores obstacles present in a habitat and a directional sound output of senders.

2.10 Measurement parameters

Most simulations were performed at least 12 times without changing parameter setting in order to account for the implemented parameter variability. The standard chorus situation refers to simulation runs performed with the parameter set listed in table 1. In each run agents started at a random phase in their oscillator cycle. The degree of synchronously chirping agents in a chorus was calculated on an individual's basis by summing up the number of those agents in the active space of a focal agent that signaled in synchrony. The range of synchronous interactions in the current study is defined from the end of a focal agent's chirp ± the duration of the average chirp length. In each cycle an average of the number of synchronously signaling agents was calculated across all agents. The amount of simulation steps before chorus synchrony was established was divided by the average CP and represents the periods of asynchronous interactions. In the standard chorus model a synchronous chorus refers to a situation in which on average more than 8 agents chirped in synchrony in a focal agents's active space.

In order to quantify chorus synchrony at each time step taking all agents into account a synchronization index was calculated in every simulation step after Goel and Ermentrout 2002 [11].

All statistical calculations were performed with Sigmastat 2.03 (SPSS Inc.). All data were evaluated for normal distribution before applying non-parametric tests.

3 Results

3.1 General behavior of the chorus model

Using the standard parameter set shown in table 1 synchrony among agents was established within only a few signal oscillator cycles. Synchrony turned out to be the only global stable oscillator coupling. At 6 m minimum inter-agent distance about 20% asynchronous choruses were found and about 30% at an inter-agent distance of 9 m. Once synchrony was established the highest chorus synchronization index was found in the last phase of the joint chirp period (~0.6, calculated after Goel and Ermentrout 2002). This index quickly dropped within the first part of the joint CP as a consequence of individual differences in the free-run cycle lengths of oscillators among simulated agents.

Because an adaptation of free-run cycle length to the stimulus period was not possible in the model, agents exhibiting a longer free-run cycle length perceived stimuli in the final part of their oscillator cycle. In contrast, agents exhibiting a shorter free-run cycle perceived slower agents in the first part of their oscillator cycle. Since the response to a stimulus in the first part did not affect cycle length much, slower agents will speed up their CP in a synchronized chorus and faster agents will prolongate their oscillator cycle. This resulted in an average joint CP calculated across all agents which was found to be slightly below the mean free-run CP (200 steps) as soon as synchrony was established. In the model synchrony was maintained on a chirp to chirp basis by propelling signal oscillators forward or backward in their cycle.

Once synchrony was established, 85% - 95% of those agents in close proximity to each other signaled in synchrony (± the average duration of the chirp). In the standard chorus situation (6 m minimum distance between agents) about 50% of all perceived stimuli occurred between 30 degree before and 30 degree after the end of a focal agent’s chirp (± 17 steps of the average CP). The simulation of a small chorus (only 4 agents) resulted in 72% of all stimuli falling within this phase range. In a synchronized standard chorus 2.5 times more stimuli fell within the first phase of the oscillator cycle compared to the final phase. This is a consequence of the global stable oscillator coupling (imperfect synchrony) in which most agents perceived stimuli in the first phase of their cycle where the perturbed cycle length was not affected much.

Interestingly, stimuli perceived in the final phase of the oscillator cycle resulted in a shortening of the chirp (Fig. 1C, grey line). Therefore, the chirp duration in the standard chorus model was found to be on average 22.6 ± 6.4 steps, which is significantly lower compared to the chirp duration of solo chirping agents in the model (31 ± 2.0 steps). This corresponds to a mean chirp shortening of 74 ms. This unexpected result is a direct consequence of the property of the implemented PRCs. A stimulus perceived in the final phase of the oscillator cycle results in a shortening of the cycle because there the remaining oscillator cycle may already be shorter compared to the solo chirp duration.

Among synchronously chirping agents intrinsically faster ones often initiated chirping first and chirping activity spread out across all agents quickly (Fig. 6). Chorus synchrony could be temporarily lost due to the noise added to the oscillator cycle length. Synchrony across agents was therefore not perfect, but agents close to each other were more likely to overlap their signals in time compared to more distant ones.

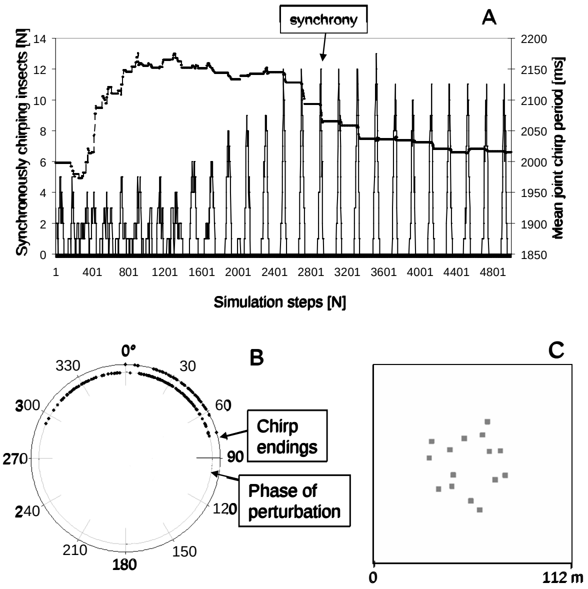


Fig. 5
Development of chorus synchrony.

After about 2600 simulation steps (13 cycles) synchrony was established in the standard chorus model. Then about 12 agents simultaneously contributed to chorus synchrony (lower curve in A exhibiting oscillations). The average joint chirp period (upper line) is increased as long as asynchronous interactions are going on.

B shows a result obtained form a different standard chorus (spacing is shown in C) in which agents signaled in synchrony (minimum inter-agent distance 6 m). The phases of perceived stimuli are shown in a polar plot (inner circle), 0 degree refers to that oscillator phase representing the end of a chirp. Further, the end of chirps were plotted in the outer circle as the phase difference in relation to that agent exhibiting the fastest free-run period (187 steps). The data shown in B were obtained from 4 consecutive chirp interactions.

3.2 Influence of the PRCs on chorus synchrony

In order to investigate the influence of intrinsic properties of individual PRCs on chorusing, simulations of homogeneous choruses were performed in which all agents were assigned to the same PRC (one of the 11 PRCs listed in the appendix) and spacing was maintained constant throughout all simulation runs (9 m minimum inter-agent distance). Among all PRCs two types clustered out: The first type always resulted in the establishment of a chorus in which all members signaled in synchrony, the second type resulted in two alternating choruses. In the latter, two subpopulations of synchronously signaling agents were found at the same time. Each agent belonged to either of two alternating choruses which were about 220° out of phase (interval between joint chirps ~1.3 s) .

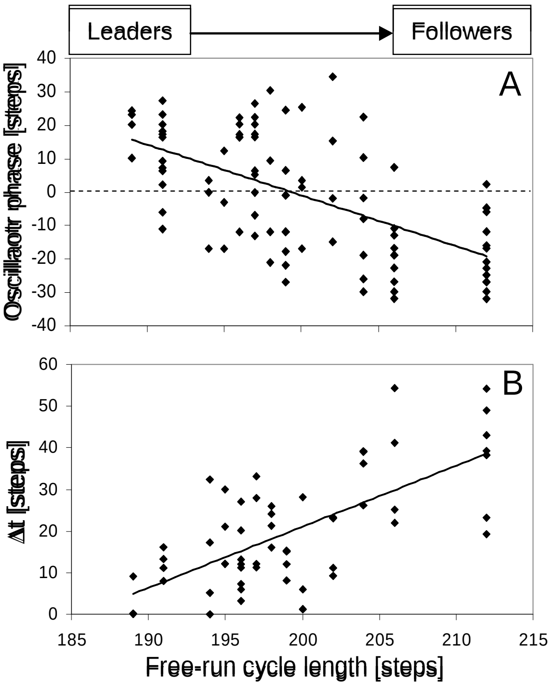


Fig. 6
Faster signaling agents are more likely leaders.
In a synchronous chorus (standard parameter set; minimum inter-agent distance: 6 m) the free-run CP of agents correlated with the oscillator phase (A) and with Δt (B). The free run cycle length of an agent that just terminated his chirp was plotted against the oscillator phase of all other agents present in the active space (A). In this plot the remaining oscillator phase of neighbors is given as a positive number and the beginning oscillator phase as a negative number (simulation steps). The time difference between the relative ends of all chirps (Δt) displayed in four successive synchronous interactions was plotted against free-run cycle length in B. Relative time differences (Δts) were normalized to the first signaler in the chorus.

Synchrony in such alternating choruses is never stable and the average joint chirp period is much longer than the average free-run cycle lengths of individual agents. Interestingly, agents belonging to either of two subpopulations are not necessarily spatially closer to each other. This kind of interacting choruses has been frequently observed in high population density of real insects (personal observations). In the chorus model PRC #5 and #9 resulted in alternating choruses (Fig. 7). This result corroborates simulation results obtained in a male duet both assigned to PRC #5 [5]. This PRC is characterized by a late transition phase and a very steep left branch.

3.3 Influence of inter-agent distance on chorus behavior

The influence of inter-agent distance (chorus density) was investigated in simulations in which agents were assigned to a different PRC and a different free-run chirp period after each run. Only spacing of agents was maintained constant in all simulation runs. At an inter-agent distance in the range of 3 to 9 m synchrony was established after only a few oscillator cycles (Fig. 8) and asynchronous choruses were rarely found. In simulations performed with a larger inter-agent distance (> 9 m) the establishment of synchrony was delayed. At a distance of 15 m only 50% of all simulation runs resulted in the establishment of a synchronous chorus. Further, the number of agents signaling in synchrony significantly dropped at a minimum inter-agent distance of more than 12 m.

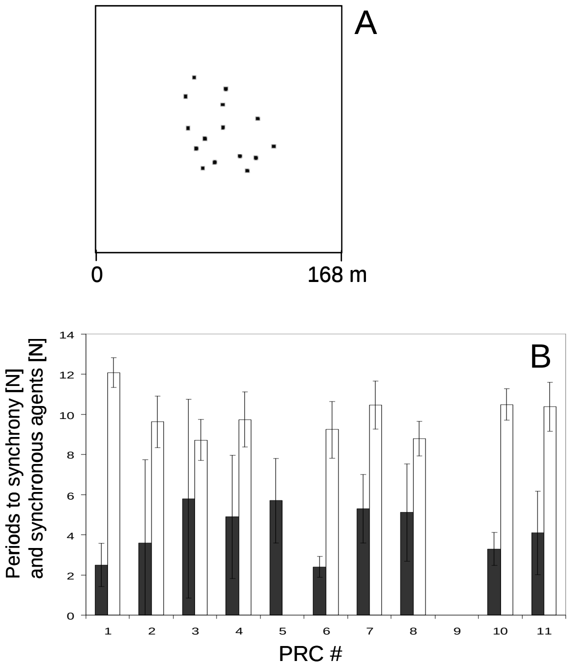


Fig. 7
Homogeneous choruses.
The results of simulations of homogenous choruses (spacing is shown in A) in which all participants were assigned to the same PRC are shown in B. Chorus synchrony was established within 3 – 6 cycles (black bars) with the exception of PRC #5 and #9. These PRCs tend to form choruses in which participants belonged to either of two alternating choruses. Once synchrony was established 9 to 12 agents signaled in synchrony (open bars).

3.4 Influence of spacing on chorus synchrony

In simulation runs in which the spatial arrangement of 15 agents (spacing) changed between each run, but all agents were assigned identical PRCs (#3) 80% synchronous choruses were found at a distance of 6 m and 70% synchronous choruses at a distance of 9 m. In all simulation runs on average ~9 agents contributed to chorus synchronization in each cycle. Since a different spacing goes ahead with altered stimulus levels at receivers, this manipulation was sufficient to affect the outcome of oscillator coupling (either synchronous or asynchronous). This result was reproduced in simulations in which not only the spatial arrangement changed after each simulation run but also agents were assigned to a different randomly chosen PRC.

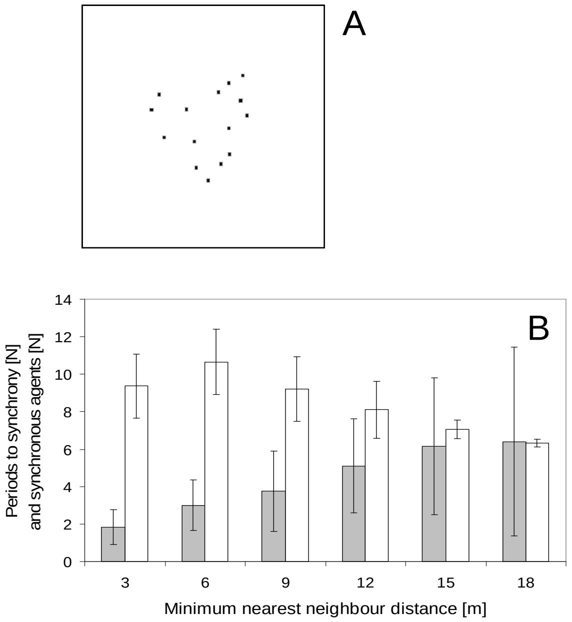


Fig. 8
Influence on agent density on chorus synchrony.
The minimum distance between members in a chorus was constantly increased. The chorus consisted of 15 participants and agent spacing was held constant (A). With increasing inter-agent distance it took a longer simulation period before synchrony was established (filled bars in B). Further, the average amount of synchronously chirping agents present in the active space of a focal agent dropped with increasing inter-agent distance (open bars in B).

The influence of free-run cycle length on the establishment of chorus synchrony was investigated by assigning a new free-run cycle length to each agent after synchrony was established. 10 cycles after re-assigning free-run cycle lengths a similar number of synchronously chirping agents (10.5 ± 2.7) was found compared to the situation before (10.5 ± 2.0 agents). This demonstrates that reassigning a new free-run cycle length alone was insufficient to change global oscillator coupling in the chorusing model (minimum inter-agent distance: 9 m). In this simulation spacing of agents in the chorus and their PRCs were maintained between individual simulation runs.

3.5 The effect of stimulus summation

Since the stimulus level at the receiver increases when several surrounding agents overlap their signals in time, simulation runs were carried out in which this additive affect was either simulated (default in the standard chorus model) or turned off. A significant longer delay before synchrony was established was found in simulation runs performed without stimulus summation compared to simulations considering stimulus level summation (2.2 ± 0.63 periods with stimulus summation; 4.7 ± 3.4 periods without stimulus summation; p < 0.05, Mann Whitney test, n = 15 runs). Further, the average amount of synchronously chorusing agents was slightly but significantly higher in simulation runs considering stimulus summation compared to control (11.1 ± 1.0 agents with summation; 9.8 ± 1.0 without summation; p < 0.05, Mann Whitney test, n = 15 runs). These results were obtained in simulations in which the spacing, PRCs and free-run cycle lengths of agents was maintained between individual simulation runs.

3.6 Chirp duration

Syllable intensity steadily increases in a chirp. Due to geometrical spreading a distant receiver will perceive only the most intense syllables at the end of a chirp. I therefore investigated 3 different chirp durations (25, 27 and 31 steps) for their influence on the establishment of synchrony in a chorus of high agent density (minimum inter-agent distance: 4 m; spacing of agents was maintained between different runs (Fig. 9A). A significantly higher amount of cycles was necessary to establish synchrony in simulations with a mean chirp duration of 250 ms compared to 310 ms (open bars in fig. 9B). Additionally, a significantly higher number of synchronously chirping agents was found in simulations with longer chirps (filled bars in fig. 9B).

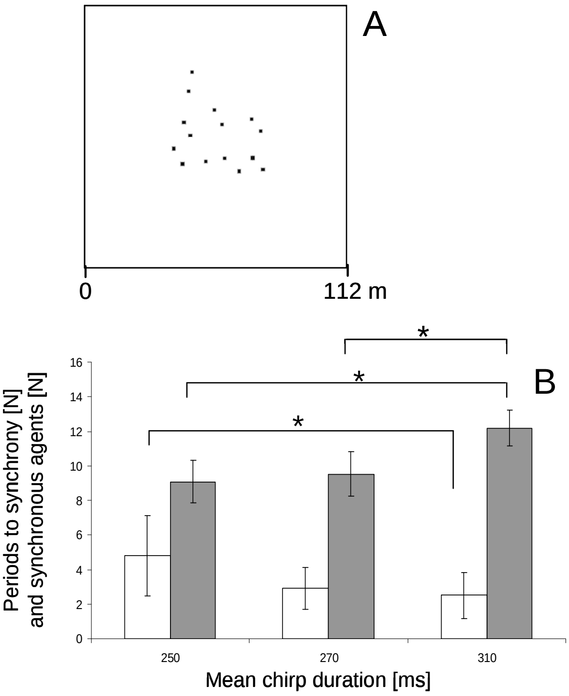


Fig. 9
The effect of chirp duration.
In simulation runs performed at a high chorus density (minimum inter-agent distance: 4 m, spacing shown in A) three different mean chirp durations were

simulated and their influence on chorus synchrony was studied. The amount of oscillator periods which were necessary before synchrony was established (open bars) and the average amount of synchronously chirping agents (filled bars) are shown in B. Bars represent the average of 12 simulation runs. * $p < 0.05$

In simulations with a lower agent density (minimum inter-agent distance: 9 m) it took significantly longer before synchrony was established for an average chirp duration of 270 ms compared to 310 ms (270 ms: 4.8 ± 2.7 periods; 310 ms: 2.7 ± 1.3 periods; $p < 0.05$, Mann Whitney test, n = 12). In a synchronous chorus no significant difference was found in the amount of synchronously chirping agents between simulation runs performed at different chirp durations (270 ms: 9.78 ± 1.3 agents; 310 ms: 9.9 ± 1.4 agents; $p > 0.05$, Mann Whitney test, n = 12).
Because of a phase advance in response to a perturbation occurring in the final oscillator phase, the average chirp duration in a synchronous chorus is much lower (22.6 ± 6.4 steps) compared to the chirp duration of solo signaling agents (31 steps). This effect might have reduced the influence of different solo chirp durations in the model.

3.7 Agents joining or leaving a synchronous chorus

Adding either 2 or 3 agents to a synchronous standard chorus originally consisting of 15 agents significantly reduced the number of agents generating synchronized chirps within the following 10 cycles ($p < 0.001$, Mann Whitney U test, n = 24) (Fig. 10). This indicates a rearrangement of mutual coupling after manipulation of the chorus structure by introducing new agents whose signal oscillators started at a random phase. The observed effect corresponds to a 23% loss of synchronously signaling agents 10 cycles after two or three new agents joint the chorus. A 18% degree loss of synchronization was found after killing a randomly chosen pair of agents in the standard chorus (9 m minimum inter-agent distance). After killing three agents a loss of 20% was observed (30 simulation runs each).

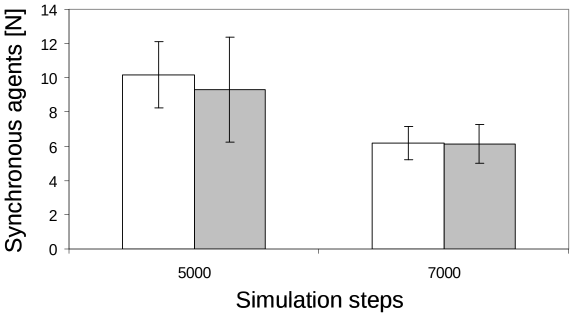


Fig. 10
Increasing the size of a chorus.
After 5000 simulation steps two (open bars) or three (filled bars) new agents joint an already synchronous chorus originally consisting of 15 agents. 10 cycles later (7000 steps) a significantly lower number of synchronously chirping agents were found. Note that new agents started at a random phase in their signal oscillator cycle.

3.8 Precedence effect

Neurophysiological results in which the perception of imperfect synchronized signals in *M. elongata* were investigated revealed that acoustic signals will be less well represented in the sensory system if they immediately follow another signal in time [26]. This precedence effect was simulated in the current model by dynamically shifting the hearing threshold towards higher levels (see methods) according to the currently perceived stimulus level at the receiver (Fig. 4).
Contrary to the expectation, a simulated precedence effect did not influence the amount of time necessary until synchrony was established (about 2.1 ± 1.5 cycles). Further, it did not affect the mean number of agents overlapping their signals in a chorus (without a dynamic threshold: 10.4 ± 0.4; with a dynamic threshold: 9.9 ± 0.5 agents). This result was fully reproduced at a lower chorus density of 9 m minimum inter-agent distance.

3.9 Selective attention to three nearest neighbors

From neurophysiological as well as behavioral studies it is known, that receivers pay attention to the nearest neighbors to a greater extent compared to more distant ones [21,28]. In the current model this could be realized by ignoring all signals except those of nearest neighbors. The number of synchronously chirping agents in a chorus quickly dropped after selective attention to the nearest three agents (arrow at 12000). This effect was reversible because overall synchrony was re-established quickly after switching off the selective response to only three nearest neighbors (arrow at 16000). Throughout this manipulation of receiver attention, synchrony within local neighbors was held quite constant (above line in fig. 11) and waves of synchronous signaling spread throughout the chorus.

Interestingly, the phase difference of song oscillators between agents in a synchronous chorus was found to be the same as in simulations in which agents interacted with only three nearest neighbors (compare lower left plot with lower right plot in Fig. 11). In simulations in which agents selectively attend to only two nearest neighbors it happened quite frequently, that local synchronization dropped below 70%. In “selective attention choruses” a significant correlation of the solo CP of agents with the oscillator phases of local neighbors was restricted to periods in which local synchronization was above 85%.

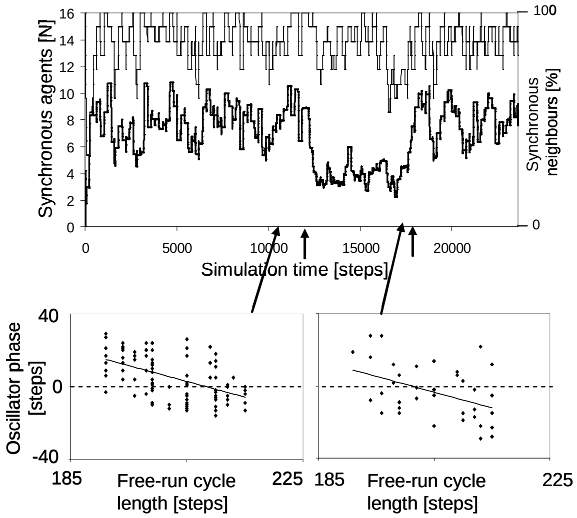


Fig. 11
Selective attention to only three local neighbors.
After synchrony was established in the standard chorus model, selective attention to only three neighbors was turned on (small arrow at 12000 steps). This resulted in a rapid decay of synchronously chirping agents (lower line) without affecting the average synchrony among local agents much (above line). After turning off this kind of selective attention (small arrow at 16000 steps) chorus synchrony was re-established quite fast. In a synchronous chorus a significant correlation was found between the free-run cycle lengths of agents and the phase difference with all other agents present in the active space of an agent (lower left plot). See figure legend 8 for further details. A similar correlation was found when agents interacted with only 3 nearest neighbors in a synchronous chorus (lower right plot).

4 Discussion

4.1 Global stability of chorus synchrony

Interestingly, simulations performed with the standard parameter set (table 1) most likely resulted in a global stable oscillator coupling in which about 11 agents signaled in synchrony. Once synchrony was established, most chorus participants perceived the end of signals in the first phase of their oscillator cycles. There the shape of the PRC (for example: Fig. 2A) is shallow and cycle length will therefore only be affected by noise added to the perturbed cycle length. Synchrony was found to be maintained on a beat to beat basis in which slower agents perceive signals in the final phase of their cycle and respond with a shortening of their cycle. Faster chirping agents perceive signals in the first phase of their oscillator cycle, which does not affect cycle length much. This mechanism leading to synchrony in *M. elongata* is different from other biological oscillators in which an adaptation of the free-run CP to a periodical stimulus was found (*Pteroptyx malaccae*: [29]; electric organ in fish: [30]. In contrast to the snowy tree cricket (*Oecanthus fultoni*) [7], *Neoconocephalus nebrascensis* [4] and *Pteroptyx cribellata* [31] a perturbation always affects the perturbed cycle in *M. elongata* song oscillators without interfering with the subsequent one [5]. Males of the species *Pterophylla camellifolia* show a similar PRC as it was found in *M. elongata* but due to a high transition phase male-male interactions usually result in alternating duets [32].

Alternation in the standard chorus model was possible but appeared to be less stable compared to synchrony. The occurrence of alternating or asynchronous interactions depended on oscillator properties, the spacing and chorus density (inter-agent distance). In alternating choruses the joint chirp period was found to be longer compared to a synchronized chorus. Males interacting in alternation therefore exhibit a longer CP which will reduce the amount of energy spend on signaling.
From the phase in which signals are perceived males in a chorus gain information whether they are interacting in synchrony or alternation. The latter is the case if signals are perceived about 200° in the oscillator cycle. Females may perceive two alternating choruses as one fast chorus with a joint chirp period of only ~ 1.3 s. If females prefer a joint CP that is similar to the solo CPs of individual males (~2 s), sexual selection will force males to synchronize their chirps with that of competitors (similar to *Oecanthus fultoni* [33]). *M. elongata* females selecting between to alternating chirps presented at a period of 1 s were found to spent 2-3 times more time in a phonotactic approach compared to situations in which males imperfectly synchronized their chirps in a duet (CP 2 s) [15]. The reason for this finding may not be found in the disruption of a species specific chirp rhythm but will be more likely the result of an equal neuronal representation of the same signal presented in an alternating fashion. This may delay a decision for either signal [26].

Agents joining or leaving a synchronous chorus strongly affected chorus synchrony which persisted for at least 10 cycles (Fig. 10). Obviously chorusing needed to be re-established after this manipulations. This unexpected result suggests that males joining a synchronous chorus do better in already synchronizing their oscillator cycle before generating their first chirp. This let me investigate the initiation of male songs in response to a conspecific stimulus which was already on for at least a few periods. To my surprise, a synchronous initiation of songs was found in all investigated playback experiments (a total of 11 males were investigated in at least two playback experiments per male). Interestingly, males synchronized from the beginning of their songs to every second chirp if the stimulus period was about 1.3 sec. This result suggests that the way how males were introduced in the current model (starting at a random phase in their cycle) was unrealistic and a loss of synchrony due to males joining a real synchronous chorus need not be expected.

Agents killed in the model chorus were found to disturb synchrony as well. In playback experiments with real males a fade out of chirp intensity within about 5 cycles was observed. Despite of this male behavior a re-establishment of chorus synchrony need to be expected after individual males stop signaling.

4.2 Multi-stimulus response

In the chorusing model a perturbation of the oscillator cycle length was calculated after the end of every suprathreshold stimulus. This may resulted in a phase delay and phase advance both occurring within a single oscillator cycle. Two signals may therefore have opposing effects without changing the perturbed cycle length much. The question arises whether this is a realistic assumption of the model.

A single stimulus alone was not able to result in a similar extended phase shift as it was found after presenting two signals in a single cycle (compare Fig. 12A with 12B). Therefore, both conspecific signals falling within a single oscillator cycle contributed in an additive manner to the perturbation of the oscillator. A second stimulus could cancel out a phase delay, which has to be expected in response to a stimulus that occurred earlier in the cycle. This was the case in the second cycle shown in Fig. 12C. There the resulting cycle length was similar to the free-run cycle length. The immediate calculation of the resulting phase shift after each stimulus therefore constitutes a realistic assumption in the current model and was approved in playback experiments in which males were entrained to a steadily increasing stimulation rate.

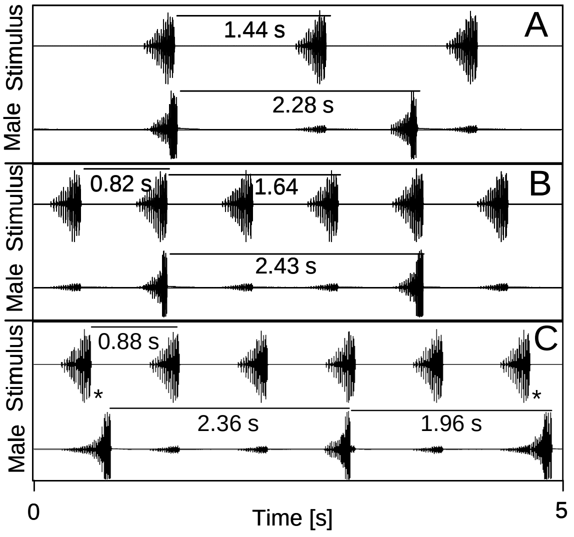


Fig. 12
Multi-stimulus response of the song oscillator of *M. elongata*.

A *M. elongata* male was entrained to a stimulus exhibiting a gradually increasing stimulus rate. Three different episodes of this experiment are shown. The male exhibited a free-run cycle length of 2.0 s and synchronized to every n^th^ stimulus chirp at higher stimulus rates. According to the PRC, signals perceived early or in the middle of the oscillator cycle caused a prolongation of the cycle length. Whereas signals perceived in the final oscillator period (labeled with * in C) resulted in a shortening of the oscillator cycle. The longest perturbed cycle length (2.28 s) was found in response to a single chirp stimulus (A). The playback of two succeeding signals falling into a single oscillator cycle resulted in a strong prolongation of the perturbed cycle (2.43 s in B and 2.36 s in the first cycle in C). If the second stimulus falls into the final phase of the oscillator cycle a follower chirp was immediately produced (* in C). Signals of low amplitude in the oscillogram of the male’s trace represent stimulus artifacts.

4.3 Chirp plasticity

The model resulted in a shortening of chirps if a stimulus was perceived shortly before the end of an agent’s cycle (Fig. 1C, grey line). Interestingly a similar result was found in real males synchronizing to a periodic stimulus which was played back every 2 s. A maximum chirp shortening of 90.0 ± 20.5 ms was found in these experiments, if individuals initiated their chirps as followers. In contrast, the chirp duration of leader chirps was unaffected by a follower stimulus. This interesting behavior will be further investigated in playback experiments.

The degree of chirp shortening observed in different simulations in which the average chirp duration of agents was varied was always found to be similar. In playback experiments with real males chirp shortening was more pronounced when males displayed long lasting solo chirps. This prevents males from falling below a minimum chirp duration of ~200 ms. A shortening of follower chirps and especially the generation of louder syllables earlier in time may be interpreted as an attempt of the follower to mask the leader chirp. This could represent a countermeasure of followers and may explain why followers continue producing chirps despite their unattractive role.

The degree of synchrony in the model chorus was found to depend on the average chirp duration of agents (Fig. 9B). However, chirp duration in the model was not as critical as it might be in real choruses. In the model, a stimulus was detected if the stimulus duration exceeded a certain time period (≥ 5 steps) and the maximum stimulus level became suprathreshold. However, real males entrained to a stimulus of increasing signal rate showed a decreased ability to synchronize to a short signal in comparison to a signal of normal length (personal observations). It seems that a certain signal energy (stimulus duration * level) is responsible for the observed phase shift shown in PRCs. This corroborates to what was found in grasshoppers [34]. Neglecting the stimulus duration in the current model may therefore oversimplify signal perception in a real receiver.

4.4 Distance and spacing effects

The distance between agents had a strong effect on the degree of chorus synchrony (Fig. 7) whereby the likelihood of establishing asynchronous choruses increased dramatically if a critical average inter-agent distance of about 12 m was exceeded. This is a consequence of a shallower slope of the left branch and a higher transition phase of PRCs found at a stimulus level of 50 dB SPL. This favors alternation at higher inter-male distances of more than 5 m in *M. elongata* [6].

In some bushcricket species males space themselves such that a focal male perceives neighbor signals at a level of about 65 dB SPL (an Indian *Mecopoda* species: personal communication with Vivek Nityananda) *Mygalopsis marki* [35] and *Tettigonia viridissima* [21]. Using standard chorus parameters, this sound level corresponds to an inter-agent distance of ~6 m in the chorus model. At this distance synchrony was established quite fast in the standard chorus model and a total of about 11 agents synchronously displayed their signals.

4.5 Leader – follower roles in a chorus

Re-assigning a naturally found distribution of free-run cycle lengths to members of a synchronous chorus did not affect chorus synchrony much. 10 cycles after such a manipulation a similar number of agents synchronized their chirps. However, free-run cycle length nicely correlates with the ability to overtake the leader role in a synchronous chorus (Fig. 8). A similar correlation was obtained in real male duets [5]. Interestingly, such a correlation was absent in asynchronous interactions. Therefore, chorus synchrony was found to be a prerequisite for the establishment of the leader role of faster chirping agents. This result is of high significance in the context of female choice in this synchronizing species. Because this result emphasizes the possibility of females to pick out those males exhibiting a faster free-run CP by selection of the leader in an imperfectly synchronized chorus. In an asynchronous or alternating interaction of competitors such would not be able.

Males and females of the synchronizing bushcricket *N. spiza* only pay attention to one or two nearest neighbors in a chorus [21,28]. The result of the current chorus model suggests that the strategy of some bushcricket females to attend only to a subset of males, and choosing the leader among them, would also be a successful strategy in a chorus in which agents attend to only two or three nearest neighbors (Fig. 11, lower right plot). This assumption holds true as long as males synchronize their signals with the same subset of neighbors as females pay attention to. There is no reason to belief that selective attention mechanisms differ between males and females in a species. Such differences would have been discovered in neurophysiological experiments [15,21].

Selective attention mechanisms reduce the number of simultaneously perceived signals at the receiver and may therefore prevent a confusion of different temporarily overlapping signals in the receiver. On the other hand paying attention to the timing of signals enables males to exploit a receiver bias originally dedicated to the improvement of directional hearing (originally unrelated to sexual selection) [26]. In the synchronous chorus model the ultimate leader will be that male which exhibits the fastest free-run CP in the chorus. In the “selective attention model” the leader will be one of local males signaling in synchrony. In the latter model females will not have to walk a long distance in order to reach the local leader, but arriving there another male among neighbors might then be the leader. It depends on the choosiness of the female which distance she is willing to walk in a male aggregation in order to finally arrive at an attractive male. If she is very choosy she may probably locate the ultimate leader (male with the shortest free-run cycle length in an aggregation) but the path to that male will be much longer in comparison to a situation in which the female heads towards the ultimate leader from the beginning of her phonotactic walk.

Neurophysiological and choice experiments revealed that a time-intensity trade-off exists that enables a follower signal presented at a higher intensity to balance out the preference of the leader [15,36]. Since a male does not know the position of females in a chorus it may payoff for a follower to continue producing follower signals especially if he is closer to a female than the leader. In future studies it will be investigated whether chirp plasticity, as it was found in the current model, suppresses the representation of a leader signal in a receiver. This could be the reason why followers continue to signal at all.

4.6 Precedence effect in a chorus model

The simulation of a dynamical shift of the hearing threshold according to the perceived stimulus did neither change the speed with which synchrony was established, nor did it change the degree of synchronization among agents. This suggests that suppression of a weak follower signal does not influence the establishment of synchronization in a *M. elongata* chorus. Nevertheless, such an effect was found in acoustic neurons of different insect species after presentation of loud and long lasting signals [37,21]. Such a stimulus was accompanied by a hyperpolarization of the membrane potential of acoustic neurons and results in a threshold shift [38]. Another neuronal mechanism is known to suppress a follower signal and was fount to be responsible for the selection of the leader among two conspecific signals presented with a certain time delay from opposite sides [15, 13]. Here a reciprocal inhibition of acoustic neuron was found to suppress the representation of the follower signal [26,15]. The latter mechanism may even have a more pronounced effect regarding the selective attention to a leader signal. Since this mechanism was not implemented in the current model, it can not be excluded that such a mechanism affects the establishment chorus synchrony in *M. elongata* in some way.

4.7 Stimulus summation

In the standard chorusing model the summation of concurrent signals at a focal agent only had a marginal effect on overall chorus synchrony. This is in contrast to the rhythm-preservation hypothesis [33], which suggests chorusing to be a cooperative behavior preserving a species specific rhythm. For a female approaching a male chorus stimulus summation may be of importance since the active space of males synchronizing their signals is larger compared to that of a single male. This results in a “beacon effect” (named after firefly researchers e.g. [31]) which may attract more females, but the ratio of attracted females per male in a chorus may be even worse compared to a single male [39].

In summary, the results obtained from simulations of the chorus model of *M. elongata* resulted in a better understanding of those mechanisms responsible for the establishment of synchrony. Particularly the establishment of synchrony was found to form the basis of female choice in this species. Further, simulation results inspire the investigation of certain oscillator as well as signal properties of *M. elongata* males in future. Additionally choice experiments will be performed in a chorus situation with the aim of proving the relevance for mate choice of the inferences drawn from the current study.

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6 Appendix

The following equations were used to model the change in cycle length after perception of a stimulus at a certain phase (x = phase of perturbation, y = normalized response phase). Polynomials fit the data of PRCs belonging to 11 different males. Equations are grouped in three different stimulus intensities. Each row holds the equations fitting both branches of a PRC belonging to a different male.

Left branch 50 dB SPL	Right branch 50 dB SPL
y = -1.777x3 + 2.0059x2 - 0.4336x + 1.0111	y = 0.5168x + 0.5029
y = 0.213x2 - 0.0712x + 1.0186	y = 1.4287x2 - 1.9928x + 1.5818
y = 0.3299x3 - 0.5729x2 + 0.2973x + 1.0012	y = 2.4401x2 - 3.917x + 2.5135
y = 0.298x3 - 0.1096x2 + 0.1078x + 1.0018	y = 0.5321x + 0.4718
y = 1.3404x3 - 1.1062x2 + 0.2236x + 1.0162	y = -2.3159x2 + 4.4405x - 1.1337
y = 1.9351x3 - 1.8239x2 + 0.5475x + 0.9763	y = 1.6481x2 - 2.5039x + 1.8354
y = 12.281x4 - 16.29x3 + 6.7657x2 - 0.8701x + 1.0257	y = 0.4545x + 0.5455
y = -0.1175x2 + 0.1209x + 0.9997	y = 0.9361x2 - 1.2236x + 1.2932
y = 0.9386x3 - 0.8733x2 + 0.2571x + 0.9929	y = 3.4178x2 - 5.6094x + 3.2278
y = 0.1722x2 - 0.0088x + 0.9962	y = 0.346x + 0.6575
y = -1.5869x3 + 1.5555x2 - 0.2524x + 1.0046	y = 2.3474x2 - 3.6465x + 2.3224

Left branch 60 dB SPL	Right branch 60 dB SPL
y = 2.1121x3 - 2.2858x2 + 1.0388x + 0.9689	y = 0.6253x + 0.3805
y = 0.1145x2 + 0.1471x + 1.0087	y = 0.4797x + 0.5075
y = 1.2052x3 - 0.4901x2 + 0.0828x + 1.0235	y = 0.4187x + 0.5618
y = 0.3454x3 + 0.0571x2 + 0.1366x + 1.0093	y = 0.6314x + 0.3691
y = 1.4612x3 - 0.7697x2 + 0.2132x + 1.0005	y = 0.7732x + 0.2419
y = -0.241x3 + 0.7883x2 - 0.0958x + 1.0222	y = 0.5053x + 0.4752
y = 2.5359x3 - 1.7719x2 + 0.4553x + 0.9995	y = 1.7748x2 - 2.5648x + 1.8084
y = -3.8874x3 + 3.8499x2 - 0.7136x + 1.0222	y = 0.3594x + 0.6177
y = 0.8979x3 - 0.6041x2 + 0.1814x + 0.9956	y = 0.4346x + 0.5569
y = 0.128x2 + 0.2425x + 0.9822	y = 0.6569x + 0.3619
y = 1.7339x3 - 1.0448x2 + 0.3998x + 0.9796	y = 0.5393x + 0.455

Left branch 70 dB SPL	Right branch 70 dB SPL
y = 0.8228x3 - 0.2863x2 + 0.3017x + 0.9953	y = 0.6667x + 0.3333
y = 0.3902x2 + 0.1006x + 1.0301	y = 1.902x2 - 2.6046x + 1.7257
y = -0.5384x3 + 0.9045x2 - 0.043x + 0.9986	y = 2.7953x2 - 4.2665x + 2.4982
y = 1.2387x3 - 0.7263x2 + 0.2923x + 1.0047	y = 0.5756x + 0.4123
y = 2.2969x3 - 1.5169x2 + 0.3072x + 1.0238	y = 0.8284x + 0.188
y = 0.7622x3 - 0.2111x2 + 0.2669x + 0.9777	y = 0.6462x + 0.3491
y = 1.2233x3 - 0.5924x2 + 0.38x + 1.0079	y = 0.5505x + 0.4378
y = 0.3702x2 + 0.0718x + 1.027	y = 0.3372x + 0.6185
y = 0.8343x3 - 0.3668x2 + 0.2113x + 1.0024	y = 0.5132x + 0.4815
y = 0.5481x2 + 0.0871x + 1.0024	y = 0.6333x + 0.3654
y = 1.0759x3 - 0.6753x2 + 0.4408x + 0.9893	y = 0.6318x + 0.3661