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Rhythm interaction in animal groups: selective attention in communication networks

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Animals communicating interactively with conspecifics often time their broadcasts to avoid overlapping interference, to emit leading, as opposed to following, signals or to synchronize their signalling rhythms. Each of these adjustments becomes more difficult as the number of interactants increases beyond a pair. Among acoustic species, insects and anurans generally deal with the problem of group signalling by means of 'selective attention' in which they focus on several close or conspicuous neighbours and ignore the rest. In these animals, where signalling and receiving are often dictated by sex, the process of selective attention in signallers may have a parallel counterpart in receivers, which also focus on close neighbours. In birds and mammals, local groups tend to be extended families or clans, and group signalling may entail complex timing mechanisms that allow for attention to all individuals. In general, the mechanisms that allow animals to communicate in groups appear to be fully interwoven with the basic process of rhythmic signalling.

This article is part of the theme issue 'Synchrony and rhythm interaction: from the brain to behavioural ecology'.

1. Introduction

When animals advertise in the company of conspecifics, a distinctive timing of their collective signalling is often observed [1]. Collective timing patterns are particularly evident in those species that keep a regular (isochronous) rhythm when signalling in solo. After a neighbour joins, the two rhythms are often 'phase-locked' in that they maintain a given angular relationship with each other. The most striking of these phase-locking relationships are synchrony, in which two or more individuals align their broadcasts with an approximately 0° phase angle, and alternation (i.e. anti-synchrony), in which two individuals maintain an approximately 180° phase angle (figure 1). Synchrony and alternation are best known from acoustic animals, but the phenomena can arise in any signalling modality where signal transmission through the medium—air, water or a solid substrate or the water surface—is rapid and signals consist of discrete units with sudden onsets and endings. Thus, conspicuous phase-locking displays appear in fireflies and ostracods (bioluminescence), fiddler crabs (reflected light) and ghost crabs, stem-inhabiting homopterans and

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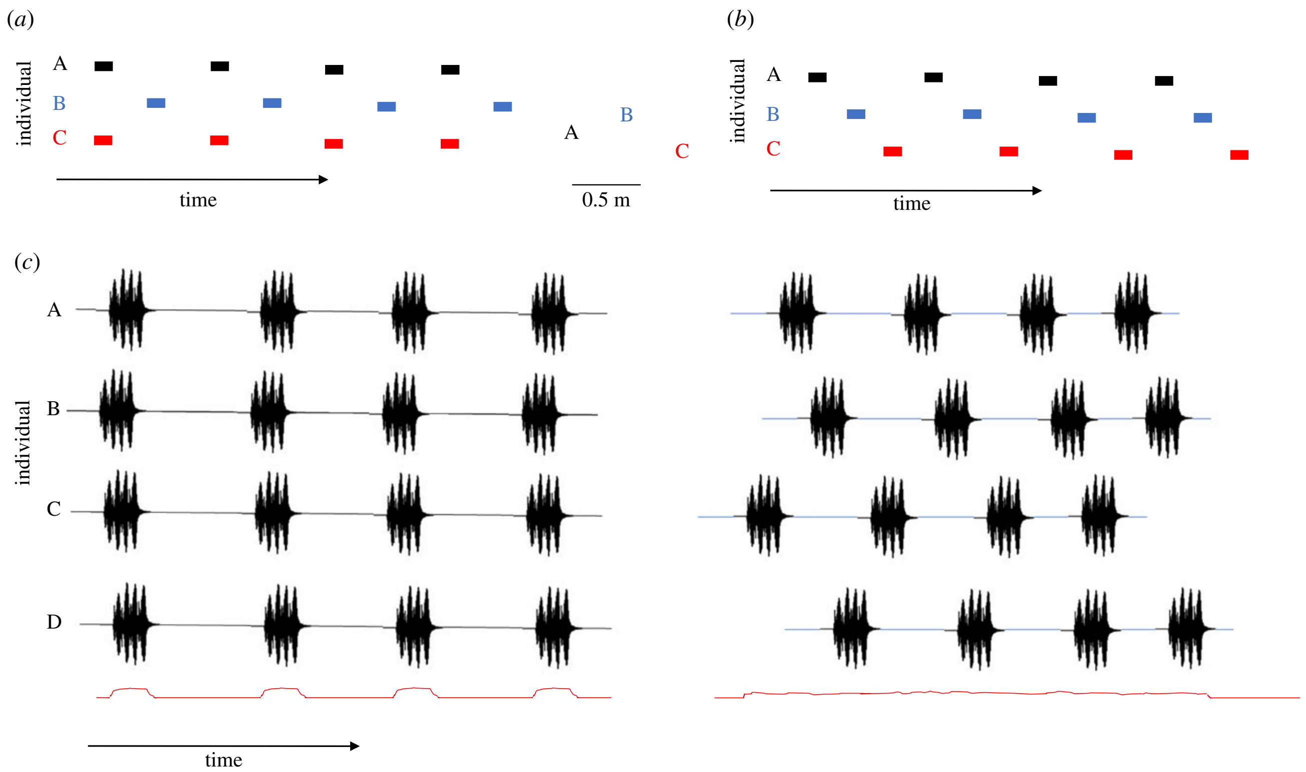

Figure 1. Phase relationships in rhythm interactions among animal groups. (*a*) Traces show timelines of signals of three individuals, each represented by coloured horizontal bars and referenced to absolute time; A and C each alternate with their nearest neighbour, B, and synchronize, by default, with each other [2]. (*b*) Traces show timelines of signals of three individuals exhibiting *n*-way alternation, each phase-locked at 120° (=360°/*n*) with a different neighbour (B with A, C with B, A with C) [2]. (*c*) Black traces show timelines of signals of four individuals when synchronized (left traces) and when signalling randomly in time (right traces). Red trace at bottom shows collective signal intensity of group. Synchrony retains characteristic signal 'envelope', general intensity profile of an individual's oscillogram, and elevates the group's peak intensity [3].

ground-dwelling beetles (substrate vibration). But precisely timed displays are unlikely to involve olfactory signals: owing to diffusion, any pulses of odour would coalesce over time and distance from the source [4]. Synchrony and alternation are also typically studied in paired individuals, or in individuals interacting with a synthetic stimulus: rhythm interactions are much easier to record, analyse and interpret in the simple setting of an isolated dyad. But observation of the natural world tells us that strict dyads are the exception, not the rule. Outside of aggressive and territorial tournaments, courtship, conjugal situations and other pair bonds within social groups, most rhythm interactions involve more than two, and sometimes many more than two, individuals. Thus, our challenge in reporting the natural world with accuracy is one of scaling up from a duet to a chorus, elucidating the mechanisms that choreograph the multitude, and understanding the evolution of interactive displays.

2. Processes and features of signalling in groups

Here, we present our current knowledge of rhythm interaction in animal group displays that extend beyond the pair, the dyad and the duet. In some cases, only slight differences arise in the multitude. For example, in species that exhibit near-perfect synchrony and are distributed in high-density clusters, e.g. some fireflies, a signaller may simply be influenced by a neighbour's signal coming from any direction within the cluster and gradually align with it. Over time, all local individuals converge on a single rhythm, and no phase angles appreciably different from 0° remain between the signallers (box 1). This process [7] may work similarly whether there is one neighbour or 50, although the time to convergence could be commensurate with the number of neighbours. However, once individuals are distributed heterogeneously in the landscape, complications arise. The influence that a neighbour exerts on phase-locking likely reflects his distance, and hence perceived signal intensity, although other behavioural and habitat factors might play a role. This outsized effect of close individuals can establish a pattern of local neighbourhoods, each characterized by consistent phase-locking and separated from other neighbourhoods with their own phase-locking—as referenced to absolute time. In our review, we treat these patterns under the rubric of 'selective attention'.

Where the typical phase-locking between neighbours differs greatly from a 0° phase angle, as in 180° alternation, the transition from two to three individuals immediately generates a prominent group effect: when the third individual initiates its first signal, it is unable to alternate with both individuals that have already started signalling. Consequently, it may (1) remain 'mute', (2) abandon the phase-locking 'rules' of the dyad and signal regardless of what its neighbours are doing, (3) selectively attend to one neighbour and alternate with it (figure 1*a*), or (4) shift to 120° alternation with one neighbour and 'hope' that the first and second individuals follow suit (figure 1*b*). The third 'option' can lead to an expanding spatial pattern of nearest-neighbour alternators where each signaller then synchronizes by default with its second nearest-neighbour. The fourth option, while conceivable and, in fact, observed in some species [2,8], will eventually break down as more individuals join. That is, there is likely a limit to the number n of signallers that can be packed into a 360° cycle, each one phase-locked at $(360/n)°$ with a given neighbour.

Box 1. Phase-oscillator differential models.

(a) Basic coupled-oscillator model including the classical Kuramoto model [5]:

$$\frac{\mathrm{d}\theta_n}{\mathrm{d}t} = \omega_n + \sum_{m \neq n} \Gamma_{nm}(\theta_m - \theta_n),$$

where θ is phase of an oscillator, ω is its natural or free-running frequency measured in radians, m and n represent two different oscillators, and Γ_{nm} is the interaction function linking the oscillators. When we assume a simple sinusoidal function, a positive coupling yields synchrony, whereas a negative coupling yields alternation. Results hold for multiple (greater than or equal to 3) oscillators [5,6].

(b)

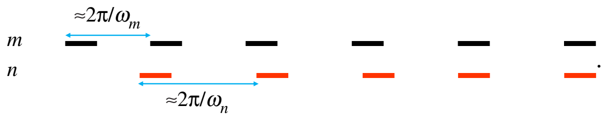

Figure 2. Schematic timelines show signals of two oscillators, each referenced to absolute time, as generated by a phase-oscillator model with the interaction function Γ_{nm} $(\theta_m - \theta_n) = K \cdot \sin$ $(\theta_m - \theta_n)$. If m and n have similar natural frequencies, i.e. $(\omega_m - \omega_n)$ is sufficiently smaller than the coupling strength K, synchrony is attained after multiple cycles.

(c)

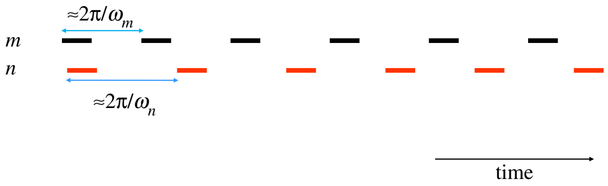

Figure 3. Schematic timelines show signals of two oscillators, each referenced to absolute time, as generated by a phase-oscillator model with the interaction function Γ_{nm} $(\theta_m - \theta_n) = -K \cdot \sin$ $(\theta_m - \theta_n)$. If m and n have similar natural frequencies, alternation is attained after multiple cycles.

The neighbourhoods of synchronizers and of alternators interdigitated with synchronizers described in the above paragraphs suggest that ‘social networks’—assemblages of individuals that interact more strongly with each other than with ‘outsiders’ [9]—may occur in group displays and be responsible for some of the complexity. Of course, a network may just represent a local group wherein mutual perceived signal intensities are higher at a given time and thus elicit stronger and more consistent rhythm interaction during that period. Alternatively, behavioural and genetic similarity might characterize the members of a network, and such affiliations may not coincide perfectly with microgeography and perceptual distance. But a ‘self-sorting’ of behaviourally similar individuals during settlement might occur and ultimately enhance the connectedness of the network by linking spatial distribution and features of rhythm interaction.

The movement of signallers within group displays can introduce an additional, spatio-temporal layer of complexity. A relative movement of signallers is common in bioluminescent species that signal in flight [10] or while swimming [11], and it can generate temporary, high-density clusters within which rhythm interaction, e.g. synchrony, is particularly strong. Nodes of high density, with concomitant strong rhythm interaction, may move across the landscape and give the impression of waves of synchrony. Moving nodes may form as individuals newly arrive in close contiguity while those that had formed a tight cluster a short time ago in the node’s trajectory have since separated.

Sound and vibration, as opposed to optical signals, present relativistic problems owing to their slower transmission velocities. Where a group of signallers is distributed over a wide area, temporal relationships between individuals depend on the position of the receiver perceiving the several signals. As an illustration, consider two nearby acoustic signallers, A and B, separated by 5 m and a more distant signaller, C, 50 m away. A, B and C are all synchronized with reference to absolute time, but a receiver near A and B will perceive them as relatively advanced with respect to C, while a receiver near C will perceive A and B as delayed (145 msec). These differences can have major consequences should relative timing be a critical factor when receivers assess and respond to their neighbours (box 2, figure 5) [15].

Evaluating any of the group effects presented here requires a thorough understanding of the fitness costs and benefits accrued from the alternatives. We use acoustic synchrony as an illustration. Synchronizing with neighbours may afford a cluster of advertising males preservation of its collective ‘call envelopes’, a species-specific feature that females must hear before moving toward the cluster and mating with any male within (figure 1*c*). That is, in the absence of synchrony, a rather continuous intensity of sound would emanate from the cluster, and single calls would be obscured and difficult to discern. But at an individual level, a male that broadcasts longer calls or at an elevated rhythm—and thereby disrupts the cluster’s synchrony and collective call envelopes—may be more attractive to a female that has already entered the cluster and is choosing

Box 2. Phase-delay difference models.

(a)

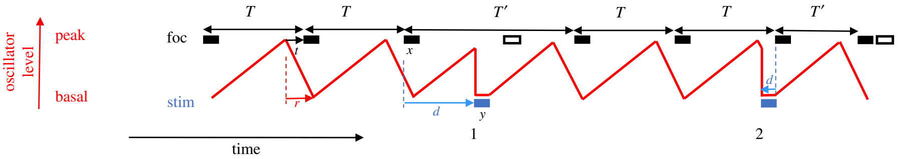

Figure 4. Sawtooth oscillator. Upper trace of horizontal black bars represents timeline of a focal animal (foc) broadcasting periodic signals of length x. Lower trace of horizontal blue bars indicates timeline of a stimulus (stim) or neighbour's signal of length y. The focal animal's central oscillator, sawtooth red line, ascends to its peak level and triggers a signal that is broadcast after a brief effector delay t. The oscillator returns to its basal level over an interval r; it is immediately reset to its basal level when a stimulus is perceived, and it remains inhibited at basal level until the stimulus ends. Ascent following inhibition is faster than during solo signalling. The focal animal's free-running period is T; a stimulus perceived during oscillator ascent (positive d, event 1) lengthens the concurrent period (T'), a temporary phase delay, while a stimulus during oscillator return (negative d, event 2) shortens the next period, a temporary phase advance. Once triggered by the oscillator, a signal is invariably broadcast. Open black bars indicate when the focal animal would have signalled were the stimulus absent. Timelines are all referenced to absolute time. Model developed from tests with fireflies [12,13] and acoustic insects [14].

(b)

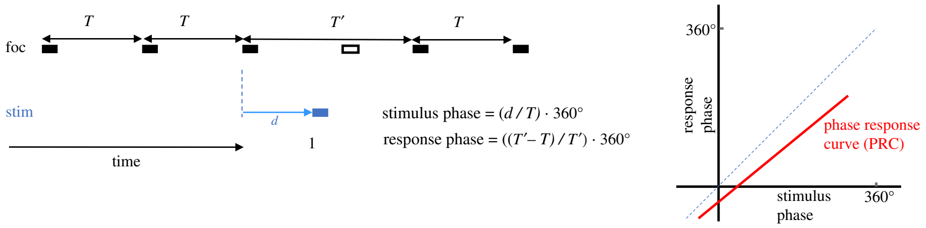

Figure 5. Phase response curve. Determination of stimulus phase, response phase and the phase response curve (PRC), which is regression of stimulus phase over response phase. Observed PRCs typically have a slope (s) between 0.4 and 0.95 and pass below the origin [15]; in some species PRCs are not linear [16,17].

(c) Linear model. Simple expression of modified period:

$$T' = s \cdot d + (T + \varepsilon),$$

where ε is a stochastic element. Full expression:

$$T' = s\left[\left(d + \frac{l}{v}\right) - (r - t)\right] + (T + \varepsilon) + (y - x),$$

where l is the distance between the focal animal and a neighbour and v is the velocity of signal transmission [15]. Here, it is assumed that the focal animal can perceive its neighbour during its own signals. l/v accounts for signal transmission time between animals, and $r - t$ accounts for a 'relativity correction', i.e. 'overcompensation', that the focal animal makes in its rebound from inhibition such that it may be perceived as a leader, relative to its neighbour, by distant receivers; e.g. receivers situated adjacent to the neighbour. The relativity correction is expressed in part b by the PRC passing below the origin. Monte Carlo simulation shows that males achieve synchrony when $s \geq \approx 0.7$ and alternation when $s \leq \approx 0.7$ [15]. Results hold for multiple males ($n \geq 3$); alternation is expressed as alternation interdigitated with synchrony (figure 1*a*).

between adjacent neighbours. The resolution of this dilemma may depend on the relative weights of group and individual effects. In other cases, a group-level phenomenon, i.e. synchrony or alternation, may simply emerge from basic neighbour–neighbour interactions and have no immediate influence *per se* on female choice or on the fitness of the calling males [18]. Nonetheless, influences can materialize indirectly. While the group phenomenon may only be an emergent property, it is the acoustic environment in which individuals call, listen and make decisions [19]. This environment has the potential to favour some simple neighbour–neighbour interactions and select against others. Thus, feedback loops may accentuate group effects and add to the rich diversity of rhythm interactions found in the natural world.

3. Oscillators and coupled oscillators: building blocks of rhythm interactions

The mechanisms controlling signal timing in animal groups are related to mechanisms in simple pairs, which in turn originate in rhythms in solo individuals. Several lines of evidence from diverse arthropod and vertebrate species indicate that the isochronous rhythms that interest us are controlled by central (nervous system) pattern generators [20]: first, a signaller may continue its rhythm in the absence of any external stimulus or when it cannot perceive its own signals. Second, it may even miss broadcasting a signal or two for some unknown reason, possibly spontaneous, but then resume on schedule two or three cycles later [12,21]. The central pattern generator is typically modelled as an oscillator that ascends to its peak level—at which point a signal is triggered—falls rapidly to its basal level and then begins its re-ascent for a subsequent cycle (box 2a, figure 4). Actual signal onset always occurs following a brief 'effector delay', measured from the triggering point [22].

When two contiguous oscillators interact repeatedly and in a consistent fashion, they are said to be coupled. Coupled oscillators may achieve synchrony by incremental changes in rhythm: the oscillator that is relatively behind accelerates ever so slightly while the other one decelerates, both continuing their respective adjustments until they converge after multiple cycles [5,7,23]. Alternation may also be achieved in this way [2] (box 1). Other cases of oscillator coupling entail somewhat different responses. In a protocol found in many arthropod species, one oscillator makes a major change in its phase with respect to its neighbour during a given cycle and then returns immediately to its previous, intrinsic (i.e. free-running) rhythm [12,13,24] (box 2). The resumption may be constrained by energy limitations that preclude sustaining a faster rhythm, at least not without shortening the signals. When performed repeatedly and mutually, these sudden phase changes may also yield either synchrony or alternation [20], but the interactions are generally much less perfect than those achieved via a lengthy series of incremental rhythm changes. A more aligned synchrony or regular alternation tends to occur where the two oscillators have similar intrinsic rhythms. In yet another procedure, also known among arthropods, one oscillator is inhibited from initiating a signal during a given time interval measured from the end of the other's signal [3]. This simple rule—mutual respect of inhibition intervals—ensures a rather stable synchrony, notably in species with high duty cycles (i.e. song length/cycle length).

Two of the coupled oscillator types presented above have been modelled formally. Synchrony achieved by incremental rhythm changes can be simulated accurately by 'phase-oscillator' differential models including the classical 'Kuramoto model' [5] (box 1), which are derived from a general class of coupled oscillators. Changing the coupling coefficient in the Kuramoto model from a positive to a negative value shifts the prediction from synchrony to alternation [2,6]. Recent progress in a statistical approach allows researchers to determine the interaction term from empirical data and thus quantify the strength of interaction between oscillators [25]. Coupled oscillators that incorporate sudden phase changes are better simulated by 'phase-delay' difference models (box 2). Here, one oscillator is reset to its basal level upon perceiving the other's signal. Following resetting, the oscillator resumes by ascending to its trigger level, but this ascent, or rebound, can be much faster than during solo function. The degree to which the rebound speeds up depends on the point in the focal oscillator's cycle during which resetting occurred and the oscillator's phase response curve (PRC; box 2b, figure 5) [15]: rebound is faster when resetting occurs late during the oscillator's cycle and when its PRC has a shallower slope (s). Ultimately, the PRC slope predicts the nature of oscillator coupling: steep slopes ($s > \approx 0.7$), which imply that the oscillator's rebound is similar to its ascent when in solo, yield synchrony, whereas shallower slopes ($s < \approx 0.7$), implying that rebound is much faster than solo ascent, yield alternation. A variant of the phase-delay model occurs where signals are long, and the reset oscillator remains inhibited at its basal level for the duration of the other oscillator's signal (inhibitory resetting; box 2a, figure 4) [15]. Another variant includes a fundamental shift in rhythm that persists for many cycles following a sudden phase change [16], a combined process also known from human behaviour [26,27]. Phase-oscillator and phase-delay models are not mutually exclusive, and some species show characteristics of both in their signalling interactions [17,28]. Relevant to our interest in group behaviour, both phase-oscillator differential and phase-delay difference models have been adapted to assemblages of three or more signallers [2,6,15,25,29]. The simulated assemblages exhibit synchrony comparable to that arising in pairs, and alternation in the formats depicted in figure 1.

Because rhythm interaction generated by phase oscillation tends to be stable and nearly perfect in timing [25,30], it is likely found where the synchrony or alternation per se is favoured by selection. Examples include cases where synchrony retains a critical signal envelope, where it affords protection against natural enemies via 'confusion' or 'dilution', and where it increases the peak signal intensity broadcast by a cluster, the so-called 'beacon effect' [24,28]. Similarly, alternation may enhance an individual's ability to monitor its neighbour—and to be monitored itself [8,19]. This factor can be particularly strong for sound signals, which spread spherically from the source and tend to 'mask' one another when two individuals call at the same time. But where synchrony and alternation are merely emergent properties, phase oscillation may not be particularly favoured. Synchrony and alternation emerge by default where females prefer a male signaller that leads his neighbour by a brief time interval [18]. Such preferences can select for a coupled oscillator with which a male reduces his incidence of following signals, and phase delay is an ideal mechanism for accomplishing that.

4. Evidence from the field and laboratory

Whereas studying communication in animal groups is admittedly difficult, its value is duly recognized, and some researchers have provided key observations as well as experimental analyses of the signal interactions. Their investigations fall into three areas. (1) In arthropods and anurans, studies have focused on phase-locking interactions of acoustic and visual signals. The rhythms are somewhat isochronous and rapid, with periods ranging from 0.2 to 10 s. Mostly, the signals are long-range male advertisements. (2) In birds and mammals, by contrast, studies concentrated on social groups wherein signalling occurs in various contexts in addition to mating. Notable investigations in mammals have been made in bats, elephants, meerkats, primates and whales and dolphins. The signalling studied here is largely acoustic, and it encompasses both isochronous and non-isochronous rhythms. (3) At a much longer time scale, the circadian rhythm of signalling and its collective display are studied in the 'dawn chorus' of songbirds [31] and in analogous 'evening choruses' of arthropods [32,33]. Other studies have probed intermediate scale rhythms in the 'unison bout calling' of acoustic insects and anurans [34], events wherein individuals signal collectively for 5–30 min, fall silent, and repeat the cycle multiple times during the daily activity period.

Some of the ability to study communication in animal groups has depended on technological advances or applications enabling scientists to track individuals that form tight clusters in the field [35], and in the laboratory, with accuracy and attribute recorded signals to specific individuals. Technical innovations have been particularly critical for frogs [2,6,36], which are generally nocturnal and sensitive to the activity of human observers, fireflies [37], where many species signal while in flight, and marine mammals, notably cetaceans.

(a) Acoustic insects and anurans: focusing on a select few

Local choruses of several species of Orthoptera have been recorded in the field using multiple directional microphones fitted with shields to reduce crosstalk. Reliable recordings were feasible because singing males in the grasshopper (Acrididae) and bushcricket (Tettigoniidae) species chosen for study are rather immobile during the daily activity period. The species included those that typically alternate when singing in a pair and that synchronize imperfectly. In all species, a given male mostly paid attention to only a few nearby neighbours despite having the physiological capacity to hear the weaker intensity of more distant ones [38]. Here, attention was assessed by using the timing rule normally exhibited in pairwise interactions, e.g. a male does not initiate a song during a given interval measured from the onset of his partner's song, and determining whether it is applied to each member of the chorus. Moreover, males paid attention to as many as three of their chorus neighbours in species that exhibited imperfect synchrony, but to only 1 or 2 neighbours in species where pairs of males alternated. Thus, choruses in alternating species displayed the predicted pattern in which males alternate with their nearest neighbours while at the same time synchronizing with slightly more distant ones. However, in other species, e.g. the synchronising bushcricket *Mecopoda* 'Chirper' [39], males largely deal with the problem of signal interference by spacing themselves at relatively long distances from neighbours. Population density, the acoustic environment and acoustic features such as song intensity probably influence the methods with which animals reduce interference. In a model of katydid synchrony [29], restricting attention to three neighbours kept local synchrony but disrupted group synchrony by generating waves of synchrony spreading through the chorus. Thus, selective attention might influence the dynamics of synchrony as well as its degree and occurrence.

Similar tests of chorusing in anuran species have yielded comparable findings. Male anurans typically alternate during simple pairwise interactions, and in larger choruses ($n > 3$) they tend to 'insert' their calls within silent gaps when they appear. But these gaps become less and less frequent as more males join, and analyses of chorus recordings show that males tend to focus on several nearby neighbours and ignore the rest [2,6,36,40–43]. Thus, lengthy and regular gaps—essentially, time intervals during which the sound pressure level (SPL) of conspecific calling is below the peak level of the chorus as generated by the nearby neighbours—are present, and a male continues signalling by placing his songs in these intervals. This process is found in species whose chorusing is generated by phase oscillation as well as in those where it is generated by phase delay. But a different approach to the group problem is found in *Hyla versicolor* [44], a treefrog with long calls that make some overlap in groups inevitable. Here, males actually lengthen their calls while reducing the pulse rate within calls, signal characters that increase the frequency of unmasked pulses that have escaped overlapping interference. A laboratory study of *H. versicolor* did not find selective attention to close neighbours in choruses comprised of up to eight frogs [45]. One feature observed occasionally in anuran choruses, but not reported in acoustic insects, is where n males, each one phase-locked at $(360/n)°$ with another, call in 'n-way alternation' (figure 1*b*) [2,8]. Shallow PRC slopes—which are associated with rapid rebound from inhibition—characterizing the phase-delay mechanisms in some anurans [15] may be responsible for this solution to the group signalling problem.

Several laboratory investigations of acoustic insect and anuran species have probed selective attention in choruses further. In a highly variable, alternating bushcricket species (*Ephippiger diurnus*) [46], playback of male calls from multiple loudspeakers that was adjusted to represent nearby and more distant neighbours showed that test males paid attention to fewer neighbours in populations where choruses typically had infrequent and brief silent gaps; gap frequency and length were largely determined by male call length and call repetition rate in the population [47]. As in many other acoustic insects and anurans, *E. diurnus* females prefer males that broadcast leading calls, and males adjust their relative call timing such that they avoid following a neighbour. But not singing immediately after neighbours needs to be regulated, since attention—avoidance in this context—to all could lead to complete silence. Presumably, this regulation would be more severe, with attention to only one or two neighbours, in populations whose choruses include few gaps; these lulls are opportunities to sing without concern for following anyone. This explanation may be equally applicable to the differential attention in synchronizing versus alternating species described above. Indeed, in the synchronizing bushcricket species *Mecopoda*, 'Chirper' males adjusted their calls to both louder and softer simultaneous calls [39], a response range consistent with reduced selective attention in synchronizers.

The general findings on selective attention in choruses led to studies of the mechanisms regulating that attention. In the Tungara frog, *Engystomops pustulosus*, whose male call alternation and female preference for leading calls resemble behaviour in the bushcricket *E. diurnus*, the protocol of multiple loudspeaker playback showed that the basic mechanism was a 'sliding threshold': a calling male pays attention to his loudest neighbour and to others whose perceived calls were within X dB SPL of the loudest. In *E. pustulosus*, the sliding threshold was 6–8 dB below the peak level [41]. But additional factors undoubtedly modify the sliding threshold. The number of attended neighbours above the sliding threshold in *E. pustulosus* is limited by a 'fixed number rule', generally 2 or 3. Moreover, when many neighbours were found above the sliding threshold, the 2 or 3 attended ones may be determined by spectral and temporal features of their calls and their relative positions. This complex twist invites work in cognition and neuroethology.

Physiologically, sliding thresholds that regulate attention in choruses are most likely neuronal adaptation to the SPL of conspecific calling. When the SPL is high, as where a focal male is surrounded by several nearby neighbours, the behavioural threshold is elevated, whereas if the SPL is much lower, the threshold is lowered commensurately and responses to other males above this threshold can occur [48,49]. This interpretation begs the question of whether female attention to calling males in the chorus is regulated by the same process. If yes, male attention and the resulting spatio-temporal structure of the chorus would ultimately be derived from female choice: a male does not pay attention to his relatively distant neighbours, i.e. he may call immediately following them, because local females assessing that male do not pay attention to these neighbours either. But in both males and females, the origin of neural adaptation itself may be in the sharpened focus it affords on neighbours, with whom one inevitably interacts. Perhaps such focus is what allows males in the bushcricket *Mecopoda elongata* to synchronize under high environmental noise, even when the signal-to-noise ratio is −1 dB [50]. More neuroethological data for both sexes would help address this conundrum.

Analogous factors may be at play in female attention to leading calls, an equally fundamental element of the synchronous and alternating choruses in various acoustic insects [14] and anurans [41]. It is speculated that responses to leading stimuli are a general means of improving stimulus localization, and that weak leading responses occur in both males and females in many animal species [3,18]. Over evolutionary time male signalling features that happen to ‘exploit’ perceptual biases for leading stimuli, e.g. phase-delay rhythm adjustments, may arise, and they can be favoured by selection. Moreover, males distinguished by characteristics such as faster calling may be more adept at rhythm adjustments, and coevolution between male signalling and female response may then ensue and lead to pronounced female preferences for leading calls.

Cicadas are the other major group of acoustic insects with distinct rhythm interaction. Cicada chorusing may be best known in the North American periodical species of the genus *Magicicada*, where local ‘broods’ emerge and sing in massive numbers every 13 (southern populations) or 17 years (northern populations) [51]. In addition to such multi-year synchrony, males in one species, *Magicicada cassini*, align their songs, 1 s ‘buzzes’ with a repetition rate $\approx 0.2\ \mathrm{s}^{-1}$, with high precision. Simultaneous recordings at multiple locations in a chorus extending over many hectares showed that synchronous alignment, termed ‘phase coherence’, of the male songs was highest for pairs of locations separated by short distances and fell off as inter-location distance increased [52]. The fall-off with distance was much greater than what would be expected from delays simply reflecting the time for sound transmission, ≈1 s over a 343 m distance. Rather, the restriction of synchrony to males within an ≈60 m radius of a recording location most probably results from neural adaptation to the SPL of local conspecific calls: synchrony becomes increasingly imperfect and ultimately disappears as distance to a neighbouring recording location increases and its perceived SPL falls below the threshold level set by local calling.

Local phase coherence is also reported in bushcrickets, where laboratory recordings of *Mecopoda* sp. S showed that neighbours synchronize their calls with high precision when close but switch to alternation if separated by greater distances [53]. Correspondingly, the male bushcrickets exhibit a shallower PRC (box 2b, figure 5)—which would yield alternation—in response to lowering the intensity of call stimuli in playback tests [16,17]. These adjustments suggest that in the field, clusters of synchronizing males could alternate with neighbouring clusters. Would males in a cluster achieve more precise synchrony in this way? If females are influenced by a cluster’s peak intensity via the beacon effect, would the alternation allow a given cluster to exhibit its peak intensity more reliably?

(b) Reflected light and bioluminescence

Prominent cases of rhythm interaction that occur entirely within the visual modality include fiddler crabs (*Uca* spp.) and fireflies (Lampyridae). Males in several species of fiddler crabs synchronize waving of an enlarged foreleg when courting females [54,55]. The critical signal is the moving, visual display, as confirmed by tests with synthetic stimuli represented by robotic crabs [56]. These tests showed that females prefer leading waves, as in many acoustic species, and local males surrounding a receptive female compete via rhythm or phase adjustment to lead. As in some bushcricket species, competing males appear to synchronize by default. A modelling study predicted that synchrony would be most likely in species with females, as opposed to males, searching and in complex visual environments where the line of sight between females and males may be partly obscured [57]. Another modelling study [58] suggested that signaling male fiddler crabs likely attend only to their neighbours while ignoring more distant males, which agrees with observations that males surrounding a female generally wave in synchrony but do not align their signals with males outside of the entourage [59].

Synchronous fireflies are known from both Southeast Asia and eastern North America, but it is the former group that perform more regularly, with higher precision, and in larger assemblages [10]. In many of the southeast Asian species males flash in synchrony while perched on vegetation, often on the banks of waterways, whereas the North American species display while roving in flight. Synchrony in one SE Asian species, *Pteroptyx cribellata*, matches the predictions of a phase-delay difference model [12], but in other species having faster flash rhythms and more precise synchrony, e.g. *P. malaccae*, a phase-oscillator differential model may offer a better description [10]. In the North American species consistent synchrony appears mostly in locations and times of the year when density is high; e.g. *Photinus carolinus* in the Great Smoky Mountains [60]. Otherwise, synchrony may be restricted to temporary nodes in the landscape where the trajectories of numerous males happen to intersect. An experimental study of *P. carolinus* deploying synthetic flashing males demonstrated that synchrony preserves a male cluster’s collective ‘flash envelope’, a feature that females need to see before responding to anyone in the cluster [61]; cf. figure 1*c*. The role of selective attention in rhythm interactions of fireflies has not been investigated.

(c) Birds and mammals: communication in social groups

Rhythm and rhythm interaction in birds and mammals differ from arthropods and anurans in several general aspects. First, many rhythms in birds and mammals are not isochronous; nonetheless, pronounced interactions between rhythms—periodic and non-periodic—are widespread. Second, the participants in these interactions are often members of a structured social group, i.e. an extended family, an assemblage of inter-related families, a ‘clan’, etc., rather than individuals that merely congregated at a given vicinity. While such structure could strongly influence the nature of rhythm interaction in the group at large, relatively few studies have probed how three or more individuals coordinate their rhythms and continue to communicate effectively. Investigations have mostly analysed acoustic interchanges in dyads, in duets and in pairs of duets, and while acknowledging that the pairs are part of a larger assemblage, rhythm coordination by that assemblage was seldom determined.

Breaking ranks, a recent investigation of South African meerkats, *Suricata suricatta*, a highly social mongoose species with diverse vocalizations, specifically addressed rhythm coordination [62]. The study examined brief 'sunning' calls, a presumably cooperative signal made during basking. Meerkats alternate their sunning calls, an interaction termed 'turn-taking' as in many other mammals. The alternated timing pattern of turn-taking in sunning calls would enhance clarity of both transmitted and received signals. For comparison, turn-taking—which implies a mutual 'agreement'—is not used to describe the choruses in arthropods and anurans [63]. In those species alternation can emerge competitively when two males, signalling with similar intrinsic call repetition rates, avoid calling immediately after one another because females tend to ignore following calls. When the males have markedly unequal rates, the faster one does not slow and 'accommodate' the other but simply dominates the interaction [8]. Competitive alternation in arthropods and anurans may also arise when two males conduct an 'acoustic duel' and the one that cannot match the other's rhythm evaluates himself as 'inferior' and departs [64].

Observing and testing 13 meerkat groups comprising from 7 to 34 individuals showed that alternate calling, with little or no overlap, persisted in larger assemblages and resulted from two simple mechanisms. A short-term inhibitory process kept a meerkat from calling for 0.2 s measured from the onset of another individual's sunning call, while a long-term excitatory process raised the meerkat's propensity to call during the subsequent 3–5 s [62]. The precise moment when the call is released might be determined stochastically. Selective attention to a subset of neighbours, as in arthropods and anurans, was not reported. Perhaps this absence reflects the structured relationships within the assemblage and the importance of evaluating and interacting with everyone. At present, the occurrence of this method of rhythm coordination among other non-human mammals is unknown. The general problem has been studied extensively in humans, however, where 'conversation analysis' [65] reveals a variety of more complex rules for avoiding 'jamming' in groups: policing or supervision; a previously determined hierarchical sequence; a current speaker selects the subsequent one; and 'segmentation', in which a designated speaker addresses another who replies specifically to the former, e.g. air traffic control.

Rhythm interaction comparable to the coordination reported in meerkat groups may occur in some colonial-nesting birds. An extensive study of the European starling *Sturnus vulgaris*, a species whose songs and calls are variable and influenced by the social context and local density, provides some valuable information on signalling in groups [66]. Males in colonies produce more discontinuous, short calls, than solo individuals or those in a conjugal pair. In larger colonies, calls are shortened further and separated by longer inter-call intervals, adjustments that appear to reduce the amount of call overlap greatly. The ability to adjust call length and timing is learned, as birds raised in isolation are unable to avoid overlapping their neighbours. More specific timing rules might enhance overlap avoidance, but these remain unidentified. A comparative study of starlings showed that the pattern described above for *S. vulgaris* was more pronounced in species with a simple, colonial social structure that did not include extended family units. Elsewhere, similar timing adjustments are observed in the bottlenose dolphin, *Tursiops truncatus*, where individuals reduce the rate at which they emit 'signature whistles' as group size increases [67].

In both arthropods and vertebrates, interacting and communicating in groups of conspecifics is the norm and a fundamental aspect of evolutionary history. Thus, it is unlikely that the specialized mechanisms for rhythmic signalling in groups presented here were recent additions, somehow 'appended' onto dyadic exchange to accommodate crowd situations. Rather, adjustments such as selective attention appear to be intertwined with the basic processes of signalling and perception. This perspective may ultimately allow for a more complete understanding of rhythmic signalling in animal communication. Succumbing to the trap of treating the group mechanisms as fully distinct elements might best be avoided.

5. Group coordination: self-organization and multiple levels of selection

Rhythm coordination in animal groups raises the question of who is doing the coordinating. Thus far, there are no reports of a 'conductor' or a small elite group that ensures phase-locking or other rhythm interactions generating overall synchrony, alternation interdigitated with synchrony, or minimum signal overlap. Instead, rhythm coordination appears to be 'self-organized' in that it results from all group members following the timing rules [68]. In this respect, the timing of group displays resembles the coordination of animal movement in fish schools, bird flocks and many social insect colonies.

That group displays are self-organized leads to reflections on the level at which selection acts. Individuals are clearly the key units, and the timing rules that they follow must have been favoured by selection acting on individual fitness. Nonetheless, the display that individuals generate collectively could also be subject to selection via simple 'by-product mutualism' wherein the entire group would immediately suffer if any participant abandons the protocol of signal coordination; e.g. synchrony. Here, complexity arises if selection at individual and group levels favours different traits. This dilemma can arise, for example, when the survival or overall attractiveness of a cluster of signalling males relies on individual timing rules that differ from the rules that would maximize an individual male's attractiveness to nearby females. The species' exposure to predation and its demography might influence the relative strengths of these several selection pressures and consequently the group display observed.

Group displays that simply emerge from individual timing rules and are not favoured by selection per se can present murkier situations [18,46,69]. Synchronous and alternating choruses and analogous displays in other modalities can arise by default where females prefer leading male signals and male timing rules have coevolved with the preferences. But emergent choruses represent the social and signalling environments for the males and females [19], and we have described how choruses with few lulls may favour restrictive selective attention, perhaps to a single neighbour, in male signallers. Conversely, a high incidence of lulls appears to allow a more indiscriminate attention to neighbours. Because restrictive attention in signallers may engender choruses with even fewer lulls, the possibility exists for a positive feedback loop with steadily decreasing lulls and more and more restrictive attention. Similarly, indiscriminate attention in signallers may yield choruses with yet more silence and a feedback loop with steadily increasing lulls and more and more indiscriminate attention. Understanding these potentially runaway phenomena will demand formal modelling and considerably more information on what males and females perceive in group displays and how they behave therein. More broadly, these considerations underscore how group signalling events afford superb opportunities for studying the complexity of selection in natural populations.

6. Conclusion

Our review of group signalling in animal species suggests several promising directions for future study. A broader understanding of rhythm interaction could be achieved by adapting lines of inquiry already being taken in the study of communication networks: Can some interactions be explained by 'audience effects'? How does perception at a given time and place in the field influence who interacts with whom and how? Do social relationships with neighbours determine the nature of interactions? And conversely, consideration of rhythm interaction in communication network research may bring that field to a finer level of analysis, potentially revealing hitherto unrecognized connections.

Data accessibility. No data are included in this paper.

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References

1. Schwartz JJ, Freeberg TM. 2008 Acoustic interaction in animal groups: signaling in noisy and social contexts. *J. Comp. Psychol.* **122**, 231–234. (doi:10.1037/0735-7036.122.3.231)
2. Aihara I, Takeda R, Mizumoto T, Otsuka T, Takahashi T, Okuno HG, Aihara K. 2011 Complex and transitive synchronization in a frustrated system of calling frogs. *Phys. Rev. E* **83**, 031913. (doi:10.1103/PhysRevE.83.031913)
3. Greenfield MD, Marin-Cudraz T, Party V. 2017 Evolution of synchronies in insect choruses. *Biol. J. Linn. Soc.* **122**, 487–504. (doi:10.1093/biolinnean/blx096)
4. Greenfield MD. 2002 *Signalers and receivers: mechanisms and evolution of arthropod communication*. Oxford, UK: Oxford University Press.
5. Kuramoto Y. 1984 *Chemical oscillations, waves and turbulence*. Berlin, Germany: Springer.
6. Aihara I, Mizumoto T, Otsuka T, Awano H, Nagira K, Okuno HG, Aihara K. 2014 Spatio-temporal dynamics in collective frog choruses examined by mathematical modeling and field observations. *Sci. Rep.* **4**, 3891. (doi:10.1038/srep03891)
7. Strogatz S. 2003 *Sync: How order emerges from chaos in the universe, nature, and daily life*. New York, NY: Hyperion.
8. Greenfield MD. 2005 Mechanisms and evolution of communal sexual displays in arthropods and anurans. *Adv. Study Behav.* **35**, 1–62. (doi:10.1016/S0065-3454(05)35001-7)
9. Croft DP, James R, Krause J. 2008 *Exploring animal social networks*. Princeton, NJ: Princeton University Press.
10. Buck J. 1988 Synchronous rhythmic flashing in fireflies. II. *Quart. Rev. Biol.* **63**, 265–289. (doi:10.1086/415929)
11. Morin JG. 1986 Firefleas of the sea: luminescent signaling in marine ostracode crustaceans. *Fla Entomol.* **69**, 105–121. (doi:10.2307/3494749)
12. Buck J, Buck E, Case JF, Hanson FE. 1981 Control of flashing in fireflies. V. Pacemaker synchronization in *Pteroptyx cribellata*. *J. Comp. Physiol. A* **144**, 287–298. (doi:10.1007/BF00612560)
13. Hanson FE, Case JF, Buck E, Buck J. 1971 Synchrony and flash entrainment in a New Guinea firefly. *Science* **174**, 161–164. (doi:10.1126/science.174.4005.161)
14. Greenfield MD, Roizen I. 1993 Katydid synchronous chorusing is an evolutionarily stable outcome of female choice. *Nature* **364**, 618–620. (doi:10.1038/364618a0)
15. Greenfield MD, Tourtellot MK, Snedden WA. 1997 Precedence effects and the evolution of chorusing. *Proc. R. Soc. Lond. B* **264**, 1355–1361. (doi:10.1098/rspb.1997.0188)
16. Nityananda V, Balakrishnan R. 2007 Synchrony during acoustic interactions in the bushcricket *Mecopoda* 'Chirper' (Tettigoniidae: Orthoptera) is generated by a combination of chirp-by-chirp resetting and change in intrinsic chirp rate. *J. Comp. Physiol. A* **193**, 51–65. (doi:10.1007/s00359-006-0170-1)
17. Hartbauer M, Kratzer S, Steiner K, Römer H. 2005 Mechanisms for synchrony and alternation in song interactions of the bushcricket *Mecopoda elongata* (Tettigoniidae: Orthoptera). *J. Comp. Physiol. A* **191**, 175–188. (doi:10.1007/s00359-004-0586-4)
18. Greenfield MD, Schul J. 2008 Mechanisms and evolution of synchronous chorusing: emergent properties and adaptive functions in *Neoconocephalus* katydids (Orthoptera: Tettigoniidae). *J. Comp. Psychol.* **122**, 289–297. (doi:10.1037/0735-7036.122.3.289)
19. Greenfield MD. 2015 Signal interactions and interference in insect choruses: singing and listening in the social environment. *J. Comp. Physiol. A* **201**, 143–154. (doi:10.1007/s00359-014-0938-7)
20. Greenfield MD. 1994 Cooperation and conflict in the evolution of signal interactions. *Annu. Rev. Ecol. Syst.* **25**, 97–126. (doi:10.1146/annurev.es.25.110194.000525)
21. Case JF, Buck J. 1963 Control of flashing in fireflies. II. Role of central nervous system. *Biol. Bull.* **125**, 234–250. (doi:10.2307/1539400)
22. Walker TJ. 1969 Acoustic synchrony: two mechanisms in the Snowy Tree Cricket. *Science* **166**, 891–894. (doi:10.1126/science.166.3907.891)
23. Murphy MA, Thompson NL, Schul J. 2016 Keeping up with the neighbor: a novel method of call synchrony in *Neoconocephalus ensiger* katydids. *J. Comp. Physiol. A* **202**, 225–234. (doi:10.1007/s00359-016-1068-1)
24. Buck J, Buck E. 1978 Toward a functional interpretation of synchronous flashing by fireflies. *Am. Nat.* **112**, 471–492. (doi:10.1086/283291)
25. Ota K, Aihara I, Aoyagi T. 2020 Interaction mechanisms quantified from dynamical features of frog choruses. *R. Soc. Open Sci.* **7**, 191693. (doi:10.1098/rsos.191693)
26. Wolf T, Vesper C, Sebanz N, Keller PE, Knoblich G. 2019 Combining phase advancement and period correction explains rushing during joint rhythmic activities. *Sci. Rep.* **9**, 9350. (doi:10.1038/s41598-019-45601-5)
27. Merker B, Madison G, Eckerdal P. 2009 On the role and origin of isochrony in human rhythmic entrainment. *Cortex* **45**, 4–17. (doi:10.1016/j.cortex.2008.06.011)

28. Nityananda V, Balakrishnan R. 2009 Modeling the role of competition and cooperation in the evolution of katydid acoustic synchrony. *Behav. Ecol.* **20**, 484–489. (doi:10.1093/beheco/arp022)
29. Hartbauer M. 2008 Chorus model of the synchronizing bushcricket species *Mecopoda elongata*. *Ecol. Model.* **213**, 105–118. (doi:10.1016/j.ecolmodel.2007.11.010)
30. Hartbauer M, Römer H. 2016 Rhythm generation and rhythm perception in insects: the evolution of synchronous choruses. *Front. Neurosci.* **10**, 223. (doi:10.3389/fnins.2016.00223)
31. Gil D, Llusia D. 2020 The bird dawn chorus revisited. In *Coding strategies in vertebrate acoustic communication, animal signals and communication 7* (eds T Aubin, N Mathevon), pp. 45–90. Cham, Switzerland: Springer. (doi:10.1007/978-3-030-39200-0_3)
32. Walker TJ. 1983 Diel patterns of calling in nocturnal Orthoptera. In *Orthopteran mating systems: sexual competition in a diverse group of insects* (eds DT Gwynne, GK Morris), pp. 45–72. Boulder, CO: Westview Press.
33. Greenfield MD. 1992 The evening chorus of the desert clicker, *Ligurotettix coquilletti* (Orthoptera: Acrididae): mating investment with delayed returns. *Ethology* **91**, 265–278. (doi:10.1111/j.1439-0310.1992.tb00868.x)
34. Schwartz JJ. 1991 Why stop calling? A study of unison bout singing in a Neotropical treefrog. *Anim. Behav.* **42**, 565–577. (doi:10.1016/S0003-3472(05)80240-4)
35. Rhinehart TA, Chronister LM, Devlin T, Kitzes J. 2020 Acoustic localization of terrestrial wildlife: current practices and future opportunities. *Ecol. Evol.* **10**, 6794–6818. (doi:10.1002/ece3.6216)
36. Jones DL, Jones RL, Ratnam R. 2014 Calling dynamics and call synchronization in a local group of unison bout callers. *J. Comp. Physiol. A* **200**, 93–107. (doi:10.1007/s00359-013-0867-x)
37. Sarfati R, Hayes JC, Sarfati E, Peleg O. 2020 Spatio-temporal reconstruction of emergent flash synchronization in firefly swarms via stereoscopic 360-degree cameras. *J. R. Soc. Interface* **17**, 20200179. (doi:10.1098/rsif.2020.0179)
38. Greenfield MD, Snedden WA. 2003 Selective attention and the spatio-temporal structure of orthopteran choruses. *Behaviour* **140**, 1–26. (doi:10.1163/156853903763999863)
39. Nityananda V, Stradner J, Balakrishnan R, Römer H. 2007 Selective attention in a synchronizing bushcricket: physiology, behaviour and ecology. *J. Comp. Physiol. A* **193**, 983–991. (doi:10.1007/s00359-007-0251-9)
40. Brush JS, Narins PM. 1989 Chorus dynamics of a neotropical amphibian assemblage: comparison of computer simulation and natural behaviour. *Anim. Behav.* **37**, 33–44. (doi:10.1016/0003-3472(89)90004-3)
41. Greenfield MD, Rand AS. 2000 Frogs have rules: selective attention algorithms regulate chorusing in *Physalaemus pustulosus* (Leptodactylidae). *Ethology* **106**, 331–347. (doi:10.1046/j.1439-0310.2000.00525.x)
42. Boatright-Horowitz SL, Horowitz SS, Simmons AM. 2001 Patterns of vocal interactions in a bullfrog (*Rana catesbiana*) chorus: preferentially responding to far neighbors. *Ethology* **106**, 701–712. (doi:10.1046/j.1439-0310.2000.00580.x)
43. Grafe TU. 2005 Animal choruses as communication networks. In *Animal communication networks* (ed. PK McGregor), pp. 277–299. Cambridge, UK: Cambridge University Press.
44. Schwartz JJ, Brown R, Turner S, Dushaj K, Castano M. 2008 Interference risk and the function of dynamic shifts in calling in the gray treefrog (*Hyla versicolor*). *J. Comp. Psychol.* **122**, 283–288. (doi:10.1037/0735-7036.122.3.283)
45. Schwartz JJ, Buchanan BW, Gerhardt HC. 2002 Acoustic interactions among male gray treefrogs, *Hyla versicolor*, in a chorus setting. *Behav. Ecol. Sociobiol.* **53**, 9–19. (doi:10.1007/s00265-002-0542-7)
46. Greenfield MD, Esquer-Garrigos Y, Streiff R, Party V. 2016 Animal choruses emerge from receiver psychology. *Sci. Rep.* **6**, 34369. (doi:10.1038/srep34369)
47. Marin-Cudraz T, Greenfield MD. 2016 Finely tuned choruses: bushcrickets adjust attention to neighboring singers in relation to the acoustic environment they create. *Behav. Ecol. Sociobiol.* **70**, 1581–1589. (doi:10.1007/s00265-016-2166-3)
48. Pollack G. 1988 Selective attention in an insect auditory neuron. *J. Neurosci.* **8**, 2635–2639. (doi:10.1523/JNEUROSCI.08-07-02635.1988)
49. Römer H, Krusch M. 2000 A gain-control mechanism for processing of chorus sounds in the afferent auditory pathway of the bushcricket *Tettigonia viridissima* (Orthoptera; Tettigoniidae). *J. Comp. Physiol. A* **186**, 181–191. (doi:10.1007/s003590050018)
50. Hartbauer M, Siegert ME, Fertschai I, Römer H. 2012 Acoustic signal perception in a noisy habitat: lessons from synchronizing insects. *J. Comp. Physiol. A* **198**, 397–409. (doi:10.1007/s00359-012-0718-1)
51. Ito H, Kakishima S, Uehara T, Morita S, Koyama T, Sota T, Cooley JR, Yoshimura J. 2015 Evolution of periodicity in periodical cicadas. *Sci. Rep.* **5**, 14094. (doi:10.1038/srep14094)
52. Sheppard LW, Mechtley B, Walter JA, Reuman DC. 2020 Self-organizing cicada choruses respond to the local sound and light environment. *Ecol. Evol.* **10**, 4471–4482. (doi:10.1002/ece3.6213)
53. Sismondo E. 1990 Synchronous, alternating, and phase-locked stridulation by a tropical katydid. *Science* **249**, 55–58. (doi:10.1126/science.249.4964.55)
54. Backwell P, Jennions M, Passmore N, Christy J. 1998 Synchronized courtship in fiddler crabs. *Nature* **391**, 31–32. (doi:10.1038/34076)
55. Pope D. 2005 Waving in a crowd: fiddler crabs signal in networks. In *Animal communication networks* (ed. PK McGregor), pp. 252–276. Cambridge, UK: Cambridge University Press.
56. Reaney LT, Sims RA, Sims SWM, Jennions MD, Backwell PRY. 2008 Experiments with robots explain synchronized courtship in fiddler crabs. *Curr. Biol.* **18**, R62–R63. (doi:10.1016/j.cub.2007.11.047)
57. Perez DM, Crisigiovanni EL, Pie MR, Rorato AC, Lopes SR, Araujo SB. 2019 Ecology and signal structure drive the evolution of synchronous displays. *Evolution* **74**, 434–446. (doi:10.1111/evo.13841)
58. Araujo SBL, Rorato AC, Perez DM, Pie MR. 2013 A spatially explicit model of synchronization in fiddler crab waving displays. *PLoS ONE* **8**, e57362. (doi:10.1371/journal.pone.0057362)
59. Backwell PRY, Jennions MD, Christy JH, Passmore NI. 1999 Female choice in the synchronously waving fiddler crab *Uca annulipes*. *Ethology* **105**, 415–421. (doi:10.1046/j.1439-0310.1999.00387.x)
60. Copeland J, Moiseff A. 1995 The occurrence of synchrony in the North American firefly *Photinus carolinus* (Coleoptera: Lampyridae). *J. Insect Behav.* **8**, 381–394. (doi:10.1007/BF01989366)
61. Moiseff A, Copeland J. 2010 Firefly synchrony: a behavioral strategy to minimize visual clutter. *Science* **329**, 181. (doi:10.1126/science.1190421)
62. Demartsev V, Strandburg-Peshkin A, Ruffner M, Manser M. 2018 Vocal turn-taking in meerkat group calling sessions. *Curr. Biol.* **28**, 3661–3666. (doi:10.1016/j.cub.2018.09.065)
63. Ravignani A, Verga L, Greenfield MD. 2019 Interactive rhythms across species: the evolutionary biology of animal chorusing and turn-taking. *Ann. NY Acad. Sci.* **1453**, 12–21. (doi:10.1111/nyas.14230)
64. Greenfield MD, Minckley RL. 1993 Acoustic dueling in tarbush grasshoppers: settlement of territorial contests via alternation of reliable signals. *Ethology* **95**, 309–326. (doi:10.1111/j.1439-0310.1993.tb00480.x)
65. Schlegoff EA. 2007 *Sequence organization in interaction. Volume 1. A primer in conversation analysis*. Cambridge, UK: Cambridge University Press.
66. Henry L, Craig AJFK, Lemasson A, Hausberger M. 2015 Social coordination in animal vocal interactions. Is there any evidence of turn-taking? The starling as an animal model. *Front. Psychol.* **6**, 1416. (doi:10.3389/fpsyg.2015.01416)
67. Quick NJ, Janik VM. 2008 Whistle rates of wild bottlenose dolphins (*Tursiops truncatus*): influences of group size and behavior. *J. Comp. Psychol.* **122**, 305–311. (doi:10.1037/0735-7036.122.3.305)
68. Camazine S, Deneubourg J-L, Franks NR, Sneyd J, Theraulaz G, Bonabeau E. 2001 *Self-organization in biological systems*. Princeton, NJ: Princeton University Press.
69. Party V, Streiff R, Marin-Cudraz T, Greenfield MD. 2015 Group synchrony and alternation as an emergent property: elaborate chorus structure in a bushcricket is an incidental by-product of female preference for leading calls. *Behav. Ecol. Sociobiol.* **69**, 1957–1973. (doi:10.1007/s00265-015-2008-8)