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ORIGINAL PAPER

Selective attention in a synchronising bushcricket: physiology, behaviour and ecology

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Abstract Synchronising bushcricket males achieve synchrony by delaying their chirps in response to calling neighbours. In multi-male choruses, males that delay chirps in response to all their neighbours would remain silent most of the time and be unable to attract mates. This problem could be overcome if the afferent auditory system exhibited selective attention, and thus a male interacted only with a subset of neighbours. We investigated whether individuals of the bushcricket genus *Mecopoda* restricted their attention to louder chirps neurophysiologically, behaviourally and through spacing. We found that louder leading chirps were preferentially represented in the omega neuron but the representation of softer following chirps was not completely abolished. Following chirps that were 20 dB louder than leading chirps were better represented than leading chirps. During acoustic interactions, males synchronised with leading chirps even when the following chirps were 20 dB louder. Males did not restrict their attention to louder chirps during interactions but were affected by all chirps above a particular threshold. In the field, we found that males on average had only one or two neighbours whose calls were above this threshold. Selective attention is thus achieved in this bushcricket through spacing rather than neurophysiological filtering of softer signals.

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Introduction

Adult male crickets and bushcrickets call to attract potential mates over long distances (Alexander 1967). In some species, males call in aggregates called choruses and display synchrony, i.e., their chirps are timed to overlap with those of their neighbours (reviewed in Greenfield 1994). Males achieve this synchrony by delaying their chirps if they hear external chirps during certain times in the chirp period, i.e., they are reset by their neighbours' chirps (Greenfield and Roizen 1993; Greenfield et al. 1997; Hartbauer et al. 2005; Nityananda and Balakrishnan 2007). Males calling in the field, however, often have multiple neighbours (Römer and Bailey 1986). If a male heard multiple neighbours and repeatedly delayed his chirps in response to all neighbours' chirps, it is possible that he would never manage to produce chirps and so be unable to attract a female. We would therefore expect a male to restrict his attention to a subset of his neighbours, i.e., the male would display selective attention (Greenfield et al. 1997). Greenfield et al. (1997) used computer simulations to argue that selective attention is necessary for synchrony to be an evolutionarily stable strategy in chorusing bushcrickets.

Selective attention can be achieved at different levels: neurophysiological, behavioural and ecological. At the neurophysiological level, it is possible for the nervous system to filter out softer chirps so that the male perceives only the loudest neighbour. This has been observed in both crickets (Pollack 1988) and bushcrickets (Römer and Krusch 2000): the omega neuron (an auditory neuron that receives inputs from the majority of auditory receptor neurons: Römer

et al. 1988) preferentially represents the louder of two signals received from the same side. In the species studied, this is due to a long-lasting inhibition (hyperpolarisation) caused by the louder signal, which the excitation in response to a softer signal cannot overcome. Hence, for as long as the inhibition lasts, the representation of the softer signal in the nervous system of the cricket will be reduced. The extent to which it is reduced depends on the relative intensity of the two signals and the duration of the signal that causes the inhibition (the louder one; Pollack 1988).

The implications of selective attention at the physiological level have usually been considered in the context of how it helps to reduce the complexity of the acoustic environment of the receiver (Pollack 1988; Römer and Krusch 2000). A few studies have examined how selective attention or the lack of it affects acoustic interactions between signalling males (Greenfield and Snedden 2003; Snedden et al. 1998). These studies have not, however, investigated how behavioural selective attention relates to selective attention at the neurophysiological level. On the one hand, even if the louder of two chirps is preferentially represented in the omega neuron, it is not necessary that the difference in representation between the louder and softer chirps is sufficient for only the louder chirp to be perceived. On the other hand, even if louder and softer chirps are equally represented in the afferent auditory system, it is not obvious that a male would perceive or be reset by all of them. It is possible that there are other mechanisms that enable behavioural selective attention despite all neighbours being heard. Ultimately, this can only be determined through behavioural experiments involving male acoustic interactions. A few such studies have been carried out using both playback experiments (Snedden et al. 1998) and recordings of natural choruses in the field (Greenfield and Snedden 2003). Snedden et al. (1998), using field playback experiments, found evidence for selective attention at a behavioural level in two grasshopper species (*Ligurotettix coquilletti* and *Ligurotettix planum*) that show call alternation. Greenfield and Snedden (2003) found evidence for selective attention in the alternating grasshopper species *L. planum* and the alternating bushcricket species *Ephippiger ephippiger*. In the synchronising bushcricket species *Neoconocephalus spiza*, however, they found only weak selective attention during playback experiments: 40% of all males showed no selective attention while calling in the field. They suggested that selective attention is less necessary for synchronising species as the simultaneous calling of multiple neighbours ensures that a male does not hear most of them and is therefore unlikely to be reset by them. To validate such a pattern it is important to carry out comparative studies on other synchronising and alternating species.

Finally, another means of overcoming the problem of being reset by multiple neighbours is to choose appropriate calling positions: if a male spaces himself in the field such that he hears only one neighbour, then the problem of being silenced by multiple neighbours would be solved. Studies in the field have investigated the effect of spacing on the number of neighbours a male might hear (Bailey et al. 1993; Brenowitz et al. 1984; Römer and Bailey 1986). While Brenowitz et al. (1984) suggested that males of the frog *Hyla crucifer* called from outside the acoustic ranges of their partners, Römer and Bailey (1986) found that the spacing of males of the bushcricket species *Mygalopsis marki* in the field was such that they could hear their nearest neighbours. If there were, however, a behavioural threshold which was different from the hearing threshold, then despite hearing multiple males they would each have only one "relevant" neighbour. Determining the number of neighbours the male is interacting with (the relevant neighbours) would require knowledge of the behavioural threshold of the animals, which these studies have not investigated.

To the best of our knowledge, no study so far has combined neurophysiology, behaviour and ecology to examine how selective attention might operate at different levels and its effect on acoustic interactions amongst males in a field chorus. In this paper we investigated selective attention in the bushcricket *Mecopoda* at all three levels. First, we investigated whether there exists a neurophysiological inhibition in the omega neuron in response to chirps of the bushcricket species *Mecopoda* "Chirper" that is strong enough to prevent representation of softer chirps. We then conducted behavioural experiments to investigate whether males preferentially synchronised with louder chirps. Finally, we investigated whether males space themselves in the field in such a way that they can hear only one relevant neighbour.

Materials and methods

Neurophysiological basis of selective attention

Electrophysiological experiments were conducted on *Mecopoda elongata*, a synchronising species, which is morphologically indistinguishable from *Mecopoda* "Chirper" and has a similar call structure (Hartbauer et al. 2005; Nityananda and Balakrishnan 2006). Eight individuals were anaesthetised with CO_2 and mounted on a stand using wax after removal of the wings, mid- and hind legs. The prothoracic legs were fixed at an angle of 90° to the body axis. The gut was removed and replaced with a piece of cotton. The prothoracic ganglion was exposed and extracellular spike activity was recorded after inserting an electrolytically sharpened insulated tungsten electrode into the anterior part of the ganglion. The omega neuron ipsilateral to the sound stimulus was identified by its response to acoustic

stimuli. The response of the neuron was amplified and recorded using a PowerLab AD converter and the software Chart5 (AD Instruments Limited, Oxfordshire, UK). The number of spikes generated in response to sound stimuli was counted using custom-built programs in Spike2 (Version 4.01, Cambridge Electronic Design Limited, Cambridge, England)

Animals were stimulated with chirps broadcast from two speakers (DynAudio D21/2; frequency range 2–40 kHz) on the same side of the animal. The sound was broadcast at a sampling rate of 96 kHz using the software Cool Edit Pro and a D/A converter in conjunction with a TDT (Tucker Davis Technology) amplifier. A single chirp of the species *Mecopoda* "Chirper" was played out in a loop repeating every 490 ms, corresponding to the period of the species (Nityananda and Balakrishnan 2006). The chirp had previously been recorded using a Bruel and Kjaer Sound Level Meter 2231 with a ¼″ microphone (4939, frequency range 4 Hz–70 kHz) and acquired at a sampling rate of 200 kHz using a NI-DAQ AT-MIO-16E-2 card and the software Labview 6.0. It was then down sampled to 96 kHz and played back in a loop during experiments.

The chirps from the two speakers were broadcast such that the chirps of one speaker led the chirps of the other by a specific time delay. Three sets of stimuli were used. In the first set, unfiltered leading chirps were played out so that the SPL at the preparation was 10 dB above the threshold of the omega neuron. In the second set, the leading chirps were filtered with a low pass 20 kHz filter and the SPL at the preparation was 10 dB above the threshold of the omega neuron. Low-pass filtering was performed in order to mimic a stimulus which had been transmitted over some distance and thus had lost higher frequencies through excess attenuation (Römer and Lewald 1992). The following chirps were not filtered. In the third set, unfiltered leading chirps were played out so that the SPL at the preparation was 20 dB above the threshold of the omega neuron.

For each of these three treatments, the follower chirp was played out at time delays of 140, 170, 200 and 250 ms with respect to the onset of the leading chirps. For a given delay, the SPL of the following chirp was varied from 0 to 25 dB above the threshold of the omega neuron in steps of 5 dB. Approximately 20 chirps (and the corresponding leading chirps) were played out at each of these sound pressure levels. At the start of every experiment, a set of chirps was also broadcast from a single speaker at each of these sound pressure levels. These served as the control so that the neural response to these could be compared to the neural response to the chirps following leading chirps. All SPL measurements for the sound stimulation were made using a RION Sound Level Meter, and are given as RMS (fast) reading (re 20 μPa).

Statistical analysis

Since the analysis involved responses from the same individuals to different sets of stimuli, we performed repeated measures ANOVAs to investigate the influence of different factors (Frank and Althoen 1994). Two-way repeated measures ANOVAs were performed across intensities and delays for each of the treatments to check for the effect of intensity and delay on the mean spike number. Two-way repeated measures ANOVAs were also performed across intensities and treatments for each of the delays to check for the effect of intensity and treatment on the mean spike number across treatments. Post-hoc unpaired t tests (significance level $\alpha = 0.05$) were performed to compare the number of spikes generated in response to following chirps with the number of spikes in response to chirps of the same SPL when presented alone, i.e., without the leading chirps played from the second speaker. All statistical analyses were performed using the software STATISTICA (1999, Statsoft, Oklahoma, USA).

Selective attention during acoustic interactions

A series of 100 chirps were broadcast at an output rate of 200 kHz from two Tucker Davis Technology ES1 speakers placed side by side (frequency range 2–110 kHz) using a NI-DAQ AT-MIO-16E-2 card and a Tucker Davis Technology ED1 electrostatic speaker driver. The chirps were broadcast at a period of 490 ms to an individual male placed in a nylon mesh cage in an anechoic room (approximate dimensions: 2.4 × 2.2 × 2.4 m). The SPL of the chirps was initially at 67 dB SPL and was gradually increased. The SPL at which the male started synchronizing his chirps with the broadcast chirps (the behavioural threshold) was noted.

Four sets of stimuli were presented to the animal in the following sequence:

1. *Softstim*: A series of 100 chirps was broadcast from a single speaker at the behavioural threshold, which varied for different individuals and was between 69 and 78 dB SPL at the position of the male.
2. *Equalstim*: The series of 100 chirps was broadcast at the same SPL from two speakers placed on the same side of the male. The chirps had a delay of 140 ms from one speaker relative to the other.
3. *Diffstim*: Stimuli were presented as described in the *equalstim* case but the following chirps were 20 dB louder than the leading chirps.
4. *Loudstim*: A series of 100 chirps were broadcast from a single speaker at SPL 20 dB louder than that at which the leading chirps had been played out.

A gap of at least a minute was left between the presentations of different sets of stimuli. Both the loudspeaker

outputs and the response of the male were recorded using tie-pin microphones and custom made amplifiers. The output of the microphones was digitised using a Measurement Computing DAS 16/330 card at a sampling rate of 16 kHz. The times of offsets of the chirps were determined using a custom built MATLAB program (Chandra Sekhar, ECE, IISc). The times of the chirp offsets were used by custom built MATLAB programs to calculate the phase of the male's chirps relative to the chirps played out from the speaker. For the two-speaker presentations, phase was calculated relative to the speaker producing the leading chirps. A mean phase vector was calculated for each set of stimuli presented to the male according to Batschelet (1981). The length of this phase vector, which ranges from 0 to 1, is an indication of the spread of phase angles. A length of 1 indicates that all the chirps are exactly at a particular phase. A length close to zero indicates that the phase angles are distributed uniformly. The mean number of chirps analysed to calculate the mean phase vector was 93.9 (±13.3) and ranged from 124 to 56 chirps.

All SPL (peak) measurements were made using a CEL 414 Precision Impulse Sound Level Meter measured with a Larson Davis 2540 microphone (frequency range 32 Hz–40 kHz). This was calibrated against a Bruel and Kjaer Sound Level Meter 2231 with a ¼″ microphone (4939, frequency range 4 Hz–70 kHz). All SPL values measured (including those in the next section) were corrected using this calibration.

Selective attention due to spacing and intensity in the field

Eight choruses of calling males of the species *Mecopoda* "Chirper" were located in the field. The SPL (peak) of males was measured at 30 cm from the male using a CEL 414 Precision Impulse Sound Level Meter with a Larson Davis 2540 microphone (frequency range 32 Hz–40 kHz). One of the males in the chorus was chosen as the focal male. The SPL of the neighbours at the focal male's position was calculated by measuring the attenuation from their positions to the focal male's position on the following day and deducting the attenuation from the source SPL. The attenuation was measured by either broadcasting chirps of an individual of the same species from the position of the relevant male at the SPL at which the male had been calling, or by placing another calling male at that position and measuring the difference between the SPL 30 cm from the source and the SPL at the focal male's position. Chirps were broadcast at an output rate of 200 kHz from a laptop computer (IBM Type 1830) in conjunction with a NI DAQ 6715 card, and an Avisoft amplifier and Ultrasonic Scanspeak speaker (frequency range 1–120 kHz). The chirps had previously been recorded using a Bruel and Kjaer Sound Level Meter 2231 with a ¼″ microphone (4939, frequency range 4–70 kHz) and digitised at a sampling rate of 200 kHz using a NI-DAQ AT-MIO-16E-2 card and the software Labview 6.0.

Results

Neurophysiological basis of selective attention

If a leading chirp presented on the ipsilateral side causes a subsequent hyperpolarisation in the omega neuron, then we expect the representation (number of spikes per chirp) of a following chirp to be less than in response to a control with no leading chirp. The two-way repeated measures ANOVA indicated that there was a significant effect of both delays and intensities for all three treatments ($P < 0.001$ in all cases). The second two-way repeated measures ANOVA indicated that there was a significant effect of both treatment and intensity for all four delays ($P < 0.001$ in all cases). The number of spikes per chirp in response to the following chirps was significantly lower than the number of spikes in response to chirps of the same SPL when presented alone in most of the combinations of delays and relative sound pressure levels (529 of the 574 pairwise comparisons). This indicates that the leading chirp causes an inhibition that suppresses the response to the following chirp. Figure 1 shows a representative example of recordings taken in response to a single chirp and to a combination of a leader and follower chirp.

The response to following chirps at all delays was similar (Fig. 2) and there was not much inter-individual variation. The following chirp on average had to be approximately 10 dB louder than the leading chirp in order to elicit the same response that a chirp presented alone did (Fig. 2). In many cases, the difference between responses to following chirps and chirps presented alone was significant even when the following chirp was up to 20 dB louder than the initial, leading chirp and when the following chirp lagged the leading one by up to 250 ms (Fig. 2). Thus, the inhibition was strong and long lasting.

In most cases (138 of the 192 pairwise comparisons), louder leading stimuli (20 dB above threshold) had a significantly greater inhibitory effect than softer leading stimuli (10 dB above threshold) (Fig. 3a–d). Even the louder leading stimuli, however, did not completely abolish the representation of softer following stimuli that were as much as 20 dB softer (Figs. 3a–d). Filtered stimuli had a significantly greater inhibitory effect than unfiltered stimuli of the same SPL (Figs. 3a–d) for most combinations of delays and relative SPLs (128 of 168).

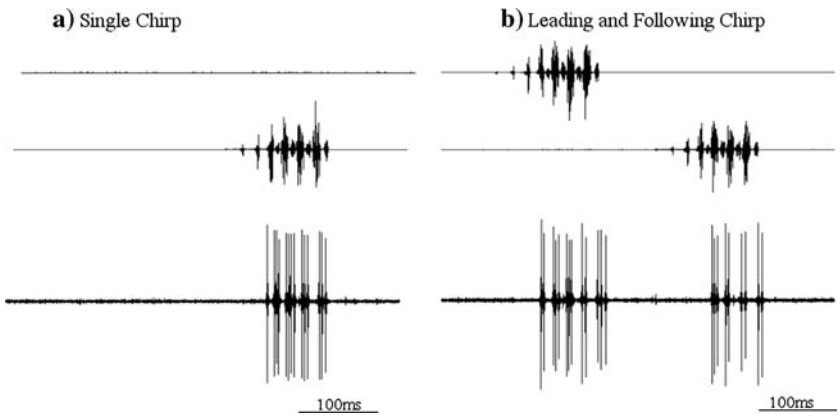

Fig. 1 Oscillograms of chirp stimuli and responses of the omega neuron to (**a**) a solo chirp and (**b**) a combination of a leading and following chirp (delay 140 ms) of *Mecopoda* "Chirper". The response to the following chirp is reduced compared to the solo chirp

Selective attention during acoustic interactions

If the difference in representation of leading and following chirps of equal intensity in the nervous system was enough for the male to perceive only the leading chirp, then we would expect the following chirp not to affect the calling male, who should synchronise only with the leading chirp. This would be equivalent to the case in which a single chirp is broadcast to the male and the phase relationship between the male's chirps and the chirps played back should be similar to that observed in such a case. When, however, we broadcast the following chirp at a sufficiently greater SPL than the leading chirp, this chirp should also be represented in the nervous system, as the increase in SPL would cause enough excitation to overcome the inhibition caused by the leading chirp. Playing back the following chirp at a sufficiently high SPL should elicit a greater response than the leading chirp. In such a case, we would expect a shift in synchrony, with the male's chirps being at a phase that is closer to synchrony with the following chirp.

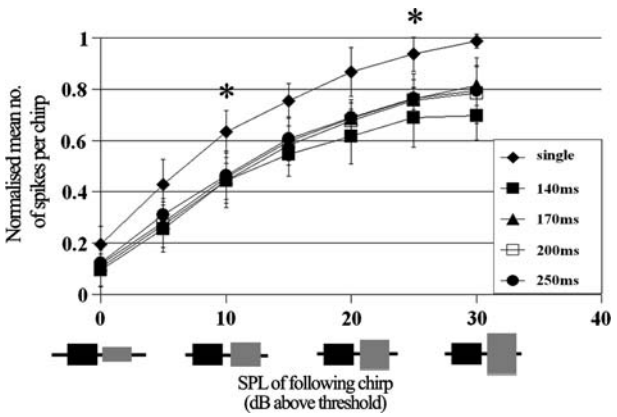

Fig. 2 Electrophysiological response of the omega neuron to follower chirps across all preparations in response to chirps of different intensities following a "leading" chirp with different delays. The number of spikes produced by the omega neuron was normalised by dividing by the maximum number of spikes in response to the stimuli. The leading chirp was presented unfiltered at 10 dB above the threshold of the omega neuron. The series labelled "single" denotes the presentation of the chirp alone without a leading chirp. Each of the other series corresponds to a particular delay. *Asterisks* indicate a significant difference between the value for a single chirp and the values for all the other sets of presentations. *Black* and *grey* rectangles below the *X*-axis represent leader and follower chirps respectively. The relative heights of the rectangles represent the relative intensities of the leader and follower chirps corresponding to each value on the *X*-axis (not to scale)

The mean behavioural threshold for synchrony across all eight males was 73 (±3 SD) dB SPL (Fig. 4). Since the phase vectors were calculated with respect to the leading chirps, we would expect an animal that synchronised perfectly with the leading chirps to have a mean phase vector with a mean phase angle of 0° (or 360°). An angle less than 81° or more than 279° would imply overlap of chirps, i.e, the outer bound for synchrony (assuming the duration of the chirp = 110 ms; Nityananda and Balakrishnan 2006). The following chirp was broadcast at a delay of 140 ms. This corresponds to a phase angle of 103° as the chirps had a period of 490 ms. Hence, a male that synchronised perfectly with the following chirps would have a mean phase vector with a phase angle of 103°.

The mean phase vector for the *equalstim* presentation was at an angle within the bounds for synchrony for seven of the eight animals, with angles less than 62.6° or greater than 316.4°. The phase angle corresponded to a later time of onset than that for the *softstim* presentation (Fig. 4a–g) for seven of the animals. This indicated that though males synchronise with the leading chirp in the *equalstim* presentation, the presence of a second stimulus shifts the timings of onsets of the calling male towards a later time, i.e, closer to the following chirp. The difference in response strength of leading and following chirps at equal SPL was therefore not sufficient for the male to perceive only the leading male.

The mean phase vector for the *diffstim* presentation was at an angle corresponding to a later time of onset than that for the *equalstim* presentation for five of the eight animals (Fig. 4a–e). The angles of the phase vectors were however not close to 103°. Only one male shifted from synchrony

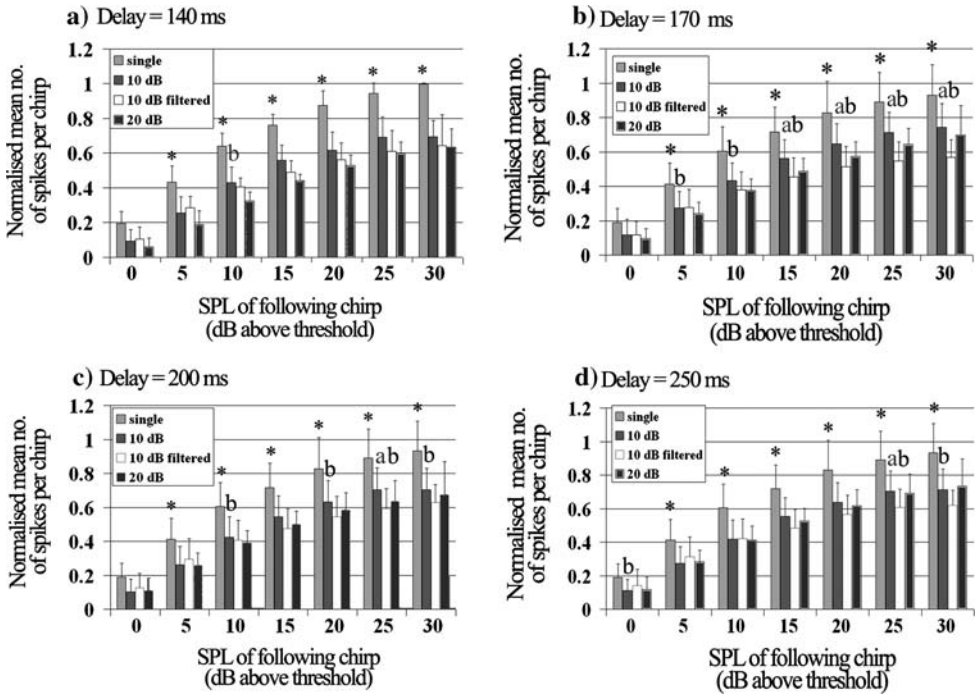

Fig. 3 Mean number of spikes per chirp across all preparations in response to chirps of different intensities following a "leading" chirp with a delay of (**a**) 140 ms, (**b**) 170 ms, (**c**) 200 ms and (**d**) 250 ms. The number of spikes produced by the omega neuron was normalised by dividing by the maximum number of spikes in response to the stimuli. The leading chirp was presented unfiltered at either 10 or 20 dB above the threshold of the omega neuron or filtered at 10 dB above the threshold of the omega neuron. The series labelled "*single*" denotes the presentation of the chirp alone without a leading chirp. *Asterisks* indicate a significant difference between the value for a single chirp and the values for all the other sets of presentations. Lettering indicates a significant difference in all animals between the mean number of spikes for a following chirp in the first presentation (unfiltered leading chirp at 10 dB) and those for a chirp following either a filtered leading chirp at 10 dB (difference indicated by "*a*") or an unfiltered leading chirp at 20 dB (difference indicated by "*b*")

with the leading chirp to synchrony with the following chirp (Fig. 4d). In most cases, synchrony was further shifted towards a following chirp when the following chirp was louder than the leading chirp but the calling male still synchronised his chirps with the leading chirp and not the following one.

The angle of the mean phase vector for the *loudstim* presentation was either similar to that for the *softstim* presentation or corresponded to a later time of onset of the calling male's chirps. Two of the animals (Fig. 4g, h) showed a lack of synchrony in either the *equalstim* or the *diffstim* case and so comparison between the two was not possible.

Selective attention due to spacing and intensity in the field

Choruses consisted of three to four animals. The mean SPL of males 30 cm from source was 92.5 (±5.6) dB (Table 1). The mean SPL of males at the position of the focal male was 71.6 (±8.1) dB. Using the results of the behavioural experiments, we can specify different criteria in order to judge how many relevant neighbours a male can hear. If we take one standard deviation (3 dB) from the mean behavioural threshold of 73 dB, i.e., 70 dB as the cut off SPL for judging whether or not a neighbour is relevant, then a male has only one or two relevant neighbours with the mean number being 1.2 (±0.7 SD). If we take two standard deviations from the mean behavioural threshold, i.e., 67 dB as the cut off SPL, then a male has one to three relevant neighbours with the mean number being 1.9 (±0.6 SD). Thus, spacing typically reduces the number of relevant neighbours to one or two.

Discussion

Neurophysiological basis of selective attention

Our results suggest that, similar to the findings of Pollack (1988) and Römer and Krusch (2000), the chirps of *Mecopoda* "Chirper" do produce a hyperpolarisation in the omega neuron as evidenced by the decrease in response after a leading stimulus. Pollack (1988) found, in the field cricket *Teleogryllus oceanicus*, that this hyperpolarisation lasted 5 s or more depending on the intensity of the stimulus and that the representation of the less intense stimulus was abolished with a relative intensity of 20 dB. Römer and Krusch (2000) similarly found in the bushcricket *Tettigonia viridissima* that a difference of 15 dB was sufficient for the

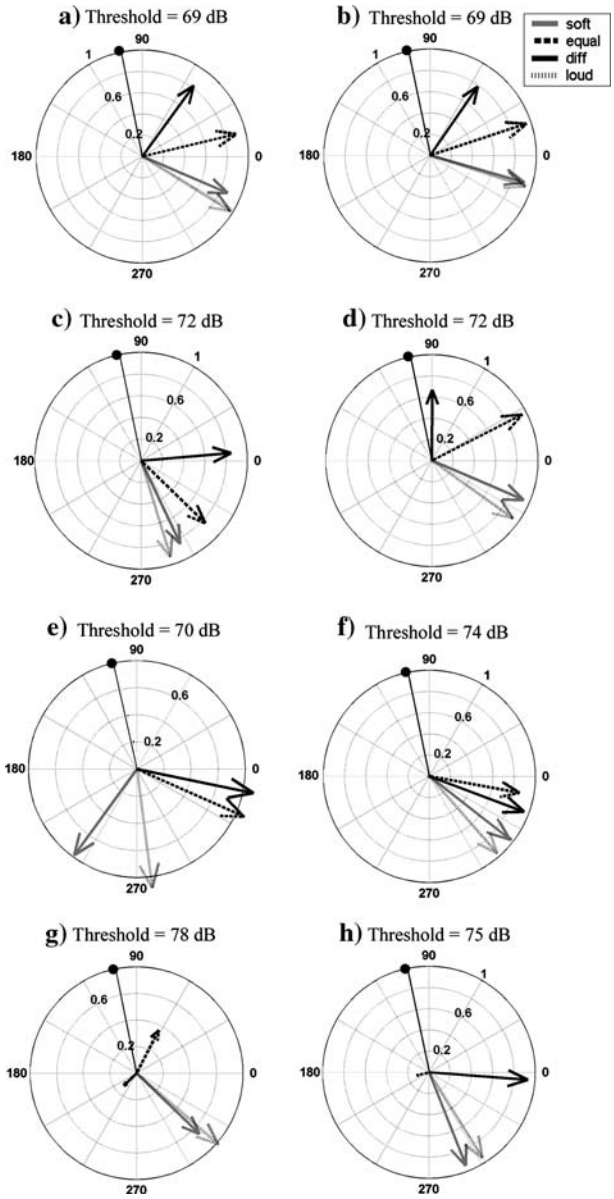

Fig. 4 Mean phase vectors for each of the four presentations in the behavioural selective attention experiment. The *line* with the *dot* at the end represents the phase angle of 103°, the angle corresponding to the onset of the following chirp in the *equalstim* and *diffstim* presentations. All phase values were calculated with respect to the leading chirps in these two presentations. Each figure corresponds to results from one individual

omega neuron to represent only the louder stimulus and that a difference of only 2 dB was enough for the neuron to have a preferential representation of the louder stimulus. The hyperpolarisation in this system also lasted for 5–10 s.

In *Mecopoda*, we found preferential representation of louder leading signals with a 5 dB differential between the two stimuli. We found, however, that even when the leading chirp was as much as 20 dB louder, the representation of the softer following stimulus was not completely abolished (Fig. 3). The incomplete suppression of spike activity is possibly due to the low duration of the stimulus (110 ms, Nityananda and Balakrishnan 2006) and relatively low duty cycle. In both the previous studies, the hyperpolarisation was shown to be duration dependent, with stimuli of longer duration causing a greater hyperpolarisation than those of shorter duration.

The greater reduction in activity induced by filtered stimuli (with mainly low frequency components) is interesting in the context of males calling in the field. The filtered stimuli would be equivalent to males that are calling further away, as frequency filtering due to factors such as scattering by vegetation would cause only the low frequency component of the call to be available to the receiver (Römer 1998; Römer and Lewald 1992). Unfiltered stimuli would be equivalent to closer males. Our data suggest that if males calling from further away manage to be louder than nearby males, their calls would cause a greater inhibition than loud males calling nearer to the receiver. Our study did not determine how long the suppression of activity by the leading chirp lasted. However, our data show that it lasts for at least 250 ms, which is high relative to the chirp period of the animal, i.e., 490 ms (Nityananda and Balakrishnan 2006).

Selective attention during acoustic interactions

The implications of the electrophysiological experiments for synchronising males were tested in the behavioural experiment. The results indicate that a calling male can potentially perceive both of two chirps that are as much as 20 dB apart in SPL. Despite preferential representation of following chirps that are 20 dB louder than the leading chirps in the omega neuron (Fig. 2), we find that males synchronise with leading chirps rather than with these louder chirps. Therefore, despite the presence of a neurophysiological representation that could enable it, selective attention to louder following chirps does not manifest behaviourally during acoustic interactions in this species. In contrast, Greenfield and Snedden (2003) and Minckley et al. (1995) found high levels of selective attention during chorusing interactions in alternating species of katydids and grasshoppers. In the one synchronising bushcricket species they investigated, however, they found poor selective attention during acoustic interactions. Since *Mecopoda* "Chirper" also shows synchrony during acoustic interactions (Nityananda and Balakrishnan 2007), our results further support their suggestion that selective attention would be expected to be weaker in choruses of synchronising species as compared to alternating species.

Apart from this general conclusion, our results from the behavioural experiments also show interesting patterns and variations across both presentations and animals. In the *softstim* presentation, the mean phase vector angle was

Table 1 Neighbours of focal males in choruses of calling males in the field

Neighbour number	Chorus number	SPL 30 cm from source (dB)	SPL at focal male's position (dB)	Distance to focal male (m)	Number of relevant neighbours (behavioural threshold: 70 dB)	Number of relevant neighbours (behavioural threshold: 67 dB)
1	1	90.6	68.5	5.2	1	3
2	1	89.6	67.6	4.9		
3	1	96.3	72.9	10.0		
1	2	92.9	65.8	6.5	1	1
2	2	90.9	63.3	9.1		
3	2	89.0	71.6	3.6		
1	3	112.0	96.9	1.5	2	2
2	3	95.0	76.8	2.8		
1	4	92.1	82.0	1.1	2	2
2	4	93.7	79.9	3.2		
3	4	85.1	57.9	4.5		
1	5	97.0	74.8	3.4	1	1
2	5	91.3	65.8	13.4		
1	6	89.7	71.8	5.2	1	2
2	6	91.5	67.9	12.0		
1	7	88.6	73.6	3.1	2	2
2	7	88.5	70.1	8.6		
1	8	94.2	68.1	10.9	1	3
2	8	95.1	67.7	10.8		
3	8	86.1	69.6	3.9		

greater than 279° and below 360° in all but one of the males (Fig. 4e), indicating that the males led the stimulus broadcast. The difference in their periods relative to the stimulus could explain the variation in angle across males. Along with variation in the shape of the phase response curve (PRC), this could be one of the reasons for the variation in the mean phase vector angle for the other presentations (Nityananda and Balakrishnan 2007). The difference in chirp period would not, however, explain the lack of synchrony in the *equalstim* presentation for two of the males (Fig. 4g, h). This could perhaps be explained by an unusual shape of the PRC for these two animals or a change in perceived intensity levels due to the movement of the animal.

The results of the different presentations can be interpreted in light of the underlying mechanisms governing synchrony. The difference between the results of the *softstim* and *equalstim* presentations indicates that the male is reset by both chirps in the *equalstim* presentation. The shift in mean phase vector angle between the two presentations is explained by the additional delay caused due to the following chirp resetting the calling male. Thus, the presence of a following chirp affects the actual amount of time by which the male's chirps lead or lag the leading chirps. Furthermore, the difference between the results of the *equalstim* and the *diffstim* presentations indicates that a louder following chirp often causes a greater delay. This could be due to the change in the shape of the PRC with increase in intensity. It has been seen in both *Mecopoda* species that stimuli of greater SPLs generate PRCs with steeper slopes (Hartbauer et al. 2005; Nityananda and Balakrishnan 2007). This means that louder chirps cause a greater delay of the next chirp of the calling male. It is interesting, however, to note that for both the *softstim* and *loudstim* presentations, the mean phase vector angle was almost the same in all but one of the males (Fig. 4e). This indicates that both the stimuli were able to reset the male to a similar extent if presented alone, but louder chirps cause a greater delay if presented soon after another chirp (as in the *diffstim* presentation).

Since leading chirps are attractive to females of many species (Greenfield and Roizen 1993; Römer et al. 2002; Fertschai et al. 2007) including *Mecopoda* "Chirper" (Nityananda V., unpublished results), the shift in phase due to a second chirp might have implications for female choice. The effect appears especially important when we consider that the preference for leading chirps is restricted to a window of lead (Greenfield and Roizen 1993; Römer et al. 2002) and so if the following chirp shifts the lead out of this window, the male might no longer be attractive to females.

Selective attention due to spacing and intensity in the field

Though males appear to be responding to both louder and softer calls, ultimately it is the spacing of males and the intensities at which they are perceived by their neighbours

in the field that would determine whether males interacted with multiple partners. While some studies on frogs (Brenowitz et al. 1984) suggest that males space themselves in the field such that they are out of the hearing range of other males, other studies (Brenowitz 1989; Gerhardt et al. 1989) as well as studies on katydids (Bailey et al. 1993; Römer and Bailey 1986) indicate that males do hear their neighbours. In our study, we found that a male hears only one or two relevant neighbours in the field. He can potentially be reset by a maximum of three males. In the cases where the male can hear two relevant neighbours, our laboratory experiments suggest that he will manage to synchronise with one of them (the one whose chirps arrive earlier) and not be constantly reset and remain silent. In the species *Mecopoda* "Chirper" selective attention appears to be achieved by spacing in the field rather than by neurophysiological filtering of softer signals.

Greenfield et al. (1997) argue that selective attention is necessary for synchrony or alternation to evolve as an evolutionarily stable strategy. In species that produce chirps of short duration and have a low duty cycle one would, however, expect that there is a poor neurophysiological basis for selective attention. In such a situation, any mechanism that generated alternation rather than synchrony would not be able to persist in the population. Mechanisms that led to synchrony, however, might persist with low levels of selective attention due to a lack of constant resetting (as discussed in Greenfield and Snedden 2003). Another alternative is that selective attention is achieved in these species through spacing, in which case, both synchrony and alternation could evolve. In *Mecopoda* "Chirper", we find both the alternatives, i.e., selective attention achieved through spacing as well as synchrony. It would be interesting to examine whether other acoustically interacting species with low duty cycles synchronise rather than alternate and also whether acoustically interacting species with low duty cycles are more spatially dispersed than species with high duty cycles.

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