Phonotactic walking paths of field crickets in closed-loop conditions and their simulation using a stochastic model

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Summary

Field cricket females localize one of many singing males in the field in closed-loop multi-source conditions. To understand this behaviour, field cricket phonotaxis was investigated in a closed-loop walking phonotaxis paradigm, in response to two simultaneously active speakers playing aphasic calling songs. Female phonotactic paths were oriented towards the louder sound sources, but showed great inter-individual variability. Decisions made in the initial phases were correlated with the overall directions of the paths. Interestingly, the sound pressure levels of stimuli did not greatly influence several features of phonotactic paths such as sinuosity, walking bout lengths and durations. In order to ascertain the extent of our understanding of walking phonotaxis, a stochastic model was used to simulate the behaviour observed in the experiment. The model incorporated data from the experiment and our current understanding of field cricket auditory physiology. This model, based on stochastic turning towards the louder side, successfully recaptured several qualitative and quantitative features of the observed phonotactic paths. The simulation also reproduced the paths observed in a separate outdoor field experiment. Virtual crickets that were unilaterally deafened or had poor ear directionality exhibited walking paths similar to those observed in previous experiments.

Key words: walking phonotaxis, closed loop behaviour, multiple sound sources, simulation, field cricket, *Plebeiogryllus*.

Introduction

Male field crickets produce calling songs in order to attract potential mates from a distance (Alexander, 1967). Each species of cricket produces a calling song with a unique combination of spectral and temporal features (Otte, 1992). Females use these acoustic mate attraction signals to distinguish between conspecific and heterospecific males and also to discriminate between conspecific males (Gerhardt and Huber, 2002). Females also use these songs to localize males in order to mate with them, a behaviour termed phonotaxis (Regen, 1913). Cricket phonotaxis has generated a great deal of research in the areas of acoustic pattern recognition and sound localization (Hedwig, 2006). Recent work has shown that pattern recognition and localization function at different temporal scales and are experimentally separable by virtue of their temporal dynamics (Hedwig and Poulet, 2004; Hedwig and Poulet, 2005; Poulet and Hedwig, 2005).

Field cricket females are believed to solve the complex task of localizing one of multiple calling males by converting it into a simpler problem using their pressure gradient ears (Larsen et al., 1989; Michelsen et al., 1994), selective attention (Pollack, 1988) and contrast enhancement (Horseman and Huber, 1994a; Horseman and Huber, 1994b). The pressure gradient ear of crickets suppresses the representation of sounds from the contralateral hemisphere (Larsen et al., 1989; Michelsen et al., 1994) and the mechanism of selective attention allows the

representation of only the loudest song on each ear, if the songs are sufficiently separated in sound pressure level (SPL) (Pollack, 1988; Römer and Krusch, 2000). If selective attention fails to separate songs on the same side of the animal (i.e. they are similar in SPL), these songs would be perceived as having inappropriate patterns. Songs with inappropriate patterns are ignored or responded to poorly (Hedwig and Poulet, 2005; Stabel et al., 1989). Neural circuitry in the prothoracic ganglion provides contrast enhancement by decreasing the strength of the response on the softer side (Horseman and Huber, 1994a; Horseman and Huber, 1994b). Thus the problem of localizing multiple sources is reduced to a simple choice in turning to one of the two sides, with varying turn magnitude depending on the difference in response (evoked by the SPL difference of songs) between the two ears and the clarity and appropriateness of the temporal pattern. Females are known to turn towards the side with the louder SPL if the song pattern is unmasked and conspecific (Pollack, 1988; Schildberger, 1994; Stabel et al., 1989).

There have been several kinds of studies on field cricket phonotaxis. Many use closed-loop compensated walking phonotaxis paradigms in which crickets exposed to sound stimuli can change their heading angle to face the sound source but cannot approach any closer e.g. Kramer treadmill (Schmitz, 1985; Schmitz et al., 1982; Weber et al., 1981). More recently, an open-loop paradigm (optical trackball system) has been

devised in which the female cricket can change neither her heading angle nor her distance with respect to the sound source (Hedwig and Poulet, 2004). Both open-loop and compensated phonotaxis paradigms are better suited to dissecting the neural mechanisms underlying pattern recognition and sound localization than arena phonotaxis. Female phonotaxis in the field, however, occurs under closed-loop conditions and female locomotor behaviour has direct consequences on the subsequent stimuli perceived. Open-loop and compensated walking paradigms are thus unlikely to be sufficient to understand natural phonotactic walking behaviour. There have been only a few previous studies quantifying the phonotactic trajectories of crickets walking in arenas (Bailey and Thompson, 1977; Murphey and Zaretsky, 1972; Oldfield, 1980; Stout et al., 1983; Stout and McGhee, 1988).

In addition, most studies of phonotaxis have used single sources of calling song (Oldfield, 1980; Schmitz et al., 1982), or multiple sources with only one source active at a given time (Murphey and Zaretsky, 1972; Schmitz et al., 1982). Some studies have used multiple sound sources that produce the same stimuli simultaneously (Hedwig and Poulet, 2005; Schmitz, 1985) or produce calling song with fixed timing relationships between chirps (Hedwig and Poulet, 2005; Stout and McGhee, 1988; Weber et al., 1981). Pollack and Hoy (Pollack and Hoy, 1979; Pollack and Hoy, 1981) used a walking phonotaxis paradigm with two speakers to test female preference for conspecific *versus* heterospecific song and to different components of songs. To our knowledge, a detailed quantification of natural closed-loop walking phonotactic behaviour with systematically varied natural conspecific calling song SPL from multiple, simultaneously active, aphasic, calling song sources has not so far been carried out.

An important approach to integrating and testing our current understanding of field cricket phonotaxis, whether at the behavioural or neurobiological level, has been the creation of quantitative models. The usefulness of models in understanding animal behaviour has been extensively reviewed (Webb, 2000). A strong motivation for such studies is that dynamic quantitative models, whether simulation-based or robotic, make explicit a hypothesis about the mechanisms generating a particular behaviour and can be used to test sufficiency in explaining the target behaviour. Many aspects of phonotaxis behaviour have been recreated using a series of robotic models (Horchler et al., 2004; Reeve et al., 2005; Webb, 1995; Webb, 1998; Webb and Scutt, 2000). A first generation robot of the field cricket used the compensated walking phonotaxis paradigm as its basis and, using neuro-mimetic circuitry, qualitatively reproduced several behaviours displayed by crickets in the closed-loop walking compensator paradigm (Webb and Scutt, 2000). Subsequent robots have been modified not only to better fit known details of field cricket neurophysiology but also to incorporate a walking mechanism and mechanosensory receptors, and they successfully localize single sources of calling song (Horchler et al., 2004; Reeve et al., 2005). These second generation robots have not, however, been tested using multiple sound sources, the natural acoustic conditions encountered by field cricket females (Mhatre and Balakrishnan, 2006). Also, since several sources of data were used, it has not been possible to make direct and quantitative comparisons between the original data of field

cricket behaviour and the data obtained from the robotic approach.

Ideally, it would be best to create a quantitative model of walking phonotaxis with multiple sound sources, using data from a single system. Such a model could then be demonstrated to quantitatively recapture the data used to create it. The behaviour produced by the model should then be tested in situations that were not included in the modeling effort, the outcomes of which are, however, known from behavioural experiments with real crickets.

Plebeiogryllus guttiventris females in the field are known to encounter multiple simultaneously calling males whose calls vary in SPL and are aphasic (Mhatre and Balakrishnan, 2006). The task of sound localization under these situations is expected to be more demanding than the situation studied in conventional phonotaxis experiments. In this study, we first characterized walking phonotactic paths of female field crickets in response to two simultaneously active sound sources playing calling songs, which were identical in quality but aphasic with respect to each other.

Data generated from the experimental phonotaxis trials and current knowledge about the auditory physiology of crickets were then used in combination to simulate walking phonotaxis using a stochastic model. We attempted to recapture in the simulation important and quantifiable features of the original phonotactic paths. We then quantitatively tested the predictions of the simulation against phonotactic paths of females observed in a separate outdoor phonotaxis experiment. We also qualitatively validated this model by replicating two classical experiments in the simulation, i.e. the removal of one ear of the cricket (Kohne et al., 1991) and the reduction of directionality by disrupting the pressure gradient ear (Schmitz, 1985).

(A) PHONOTAXIS EXPERIMENTS
Materials and methods
Animals

Plebeiogryllus guttiventris (Walker) is a common Indian field cricket with a widespread distribution (Chopard, 1969). A laboratory culture of *P. guttiventris* was established in 2002 and is regularly outbred with wild-caught individuals. The culture was maintained in large plastic barrels with a 12 h:12 h light:dark cycle. The animals in the culture were fed with Nutripet CatChow and Sandoz Calcium tablets. Water was provided *ad libitum*.

Adult virgin females were used for phonotaxis trials 3–4 weeks after the final moult. Each female was given an individual code number and a small pin was mounted on her thorax using a 1:1 mixture of beeswax and colophonium. After allowing the female time to get accustomed to the pin, it was used to place the female precisely during the start of the phonotaxis trials. Experiments were carried out in the laboratory between June–August 2004 and June–July 2005.

Stimuli

Phonotaxis trials were carried out at a temperature of 24±2°C. A five-syllable chirp from a *P. guttiventris* song recorded at 24.6°C at a sampling rate of 44.1 kHz, with features appropriate for this temperature (Mhatre and Balakrishnan, 2006), was selected to prepare the stimulus. This chirp was used to

synthesize two songs, each 40 s in length. The period for each chirp in each song was randomly selected from the appropriate chirp period distribution. The synthesized songs were found to be aphasic, similar to songs produced by simultaneously singing *P. guttiventris* males (Mhatre and Balakrishnan, 2006). While the songs did overlap considerably, 25% of the syllables of each song were not overlapped by those of the other. In pilot experiments, two sets of females were presented with songs of equal SPL (at 61 dB and 66 dB, respectively). The positions of the speakers were interchanged to break the association between song and direction. Female orientation responses indicated no preference for either song (χ^2 tests, 61 dB: $P=0.34$, $N=18$; 66 dB: $P=0.69$, $N=28$). The songs were played out using the software Goldwave Shareware Version 3.03 (1996 Chris Craig) *via* a Creative SoundBlaster D/A card and two Philips BA109 loudspeakers (frequency range: 100 Hz–18 kHz).

Arena set-up

The two speakers were placed 60 cm apart on a sheet of high-density acoustic foam with their faces parallel to each other. Sheets of high-density foam were placed around the arena in order to suppress echoes. Females were released midway between the two speakers with both speakers at 90° to the female's midline.

The phonotactic responses in all trials were recorded using an infra-red (IR) sensitive video camera (Sony DCR-TRV17E) with an IR source. The camera was mounted so that the plane of the foam surface was exactly parallel to the lens. The area of the arena that was recorded was limited to a rectangle of 30 cm×20 cm centered upon the female. While *P. guttiventris* females in the field do encounter males at this low spatial separation, the spread of choruses is usually higher (Mhatre and Balakrishnan, 2006) and it would have been ideal to record longer paths. The limitations of our recording equipment, however, forced us to use this high magnification in order to accurately measure the heading angle and centre point of the female in each frame. A 5 cm×5 cm grid was used to scale the video during analysis.

Sound pressure level measurements

The sound pressure level (SPL) of each speaker was measured before each set of trials using a Bruel and Kjaer microphone (Type 4133) and Integrating Sound Level Meter (Type 2231) set at fast RMS with a 500 Hz high pass filter. SPL measurements were made by placing the microphone on the surface of the arena, at the release position of the female, facing each active speaker, with the other muted. The sound field for each playback SPL was also measured by recording the SPL at each grid node in a 5 cm×5 cm grid and then interpolated to a 1 cm×1 cm grid. This matrix is referred to as the SPL profile of a speaker.

Experimental design

We tested the effect of relative SPL (i.e. difference in SPL between the two speakers) and baseline SPL (the SPL of the softer of the two speakers) on the phonotactic walking paths of females. Females were tested at three baseline SPL values, 55 dB, 61 dB and 67 dB, and at four relative SPL values, starting at each of these baselines: 0 dB, 3 dB, 6 dB and 9 dB, in a total of 12 stimulus conditions. Treatments will hereafter be described in the following manner: '55 d3dB', where 55 dB is the baseline SPL and 3 dB is the relative SPL.

Six sets of females were tested. Each female within a set was tested at a single baseline SPL paired with all relative SPL values. To account for possible effects of order of presentation, two sets of females were tested at each baseline SPL, the first with relative SPL values in ascending order and the other in descending order. To control for directional biases, the first set of females was presented with the louder speaker on the left for the relative SPL values d3dB and d9dB and on the right for d6dB and *vice versa* for the second set.

All phonotaxis trials were carried out in complete darkness between 18:30 h and 20:30 h, the normal activity period. The test trial with both speakers active was carried out first. If the female did not move within 3 min of release, the trial was aborted. If the female moved, her response was recorded until she left the arena or 5 min had elapsed since release. After the test trial the female was allowed at least 10 min of rest and then the control trial was carried out with only the baseline SPL speaker active. If the female turned towards the single active speaker within 5 min she was considered responsive. If she did not turn towards the single active speaker or turned away from it, the response to the test trial was discarded. Each female was presented with only one test trial followed by a control trial on a given night.

The female was then tested with the next treatment in the series on the next night. If a female failed to respond to a particular treatment on two subsequent nights, trials were discontinued. Data from females who completed the entire set of trials were used for analysis. Additional data from females who had completed the relative SPL d0dB trial at all baseline SPL values were also used.

Video analysis

Video recordings of the trials were digitized using the ATI All-in-Wonder 128 Pro Video capture card (Sunnyvale, CA, USA). They were converted to image stacks with 5 frames s^{-1} saved as separate serialized bitmap files using Ulead Video Studio (Version 5.0, 2000, Ulead systems Inc., Taipei, Taiwan) and Adobe Premiere Pro (Adobe Systems Inc., San Jose, CA, USA). The position of the female expressed in Cartesian co-ordinates and her heading angle in each frame was measured from the bitmap file using a background subtraction technique implemented in the software ImageJ 1.32j (Wayne Rasband, NIH, USA). These data were then used to reconstruct the path of the female.

Analysis of walking phonotaxis

Path vectors

Path vectors were calculated using standard formulae (Batschelet, 1981). The path vectors were mirrored when necessary and then pooled by stimulus condition. The mean path vector and angular deviation for each condition (Batschelet, 1981) were calculated. Females presented with two songs of the same quality at the same SPL are expected not to make a choice and to have a mean path vector direction of 0°. Similarly females are expected to turn 90° towards the louder speaker in all other trials. Path vectors were tested using a *V*-test (Batschelet, 1981) with 0° as the expectation at d0dB and 90°
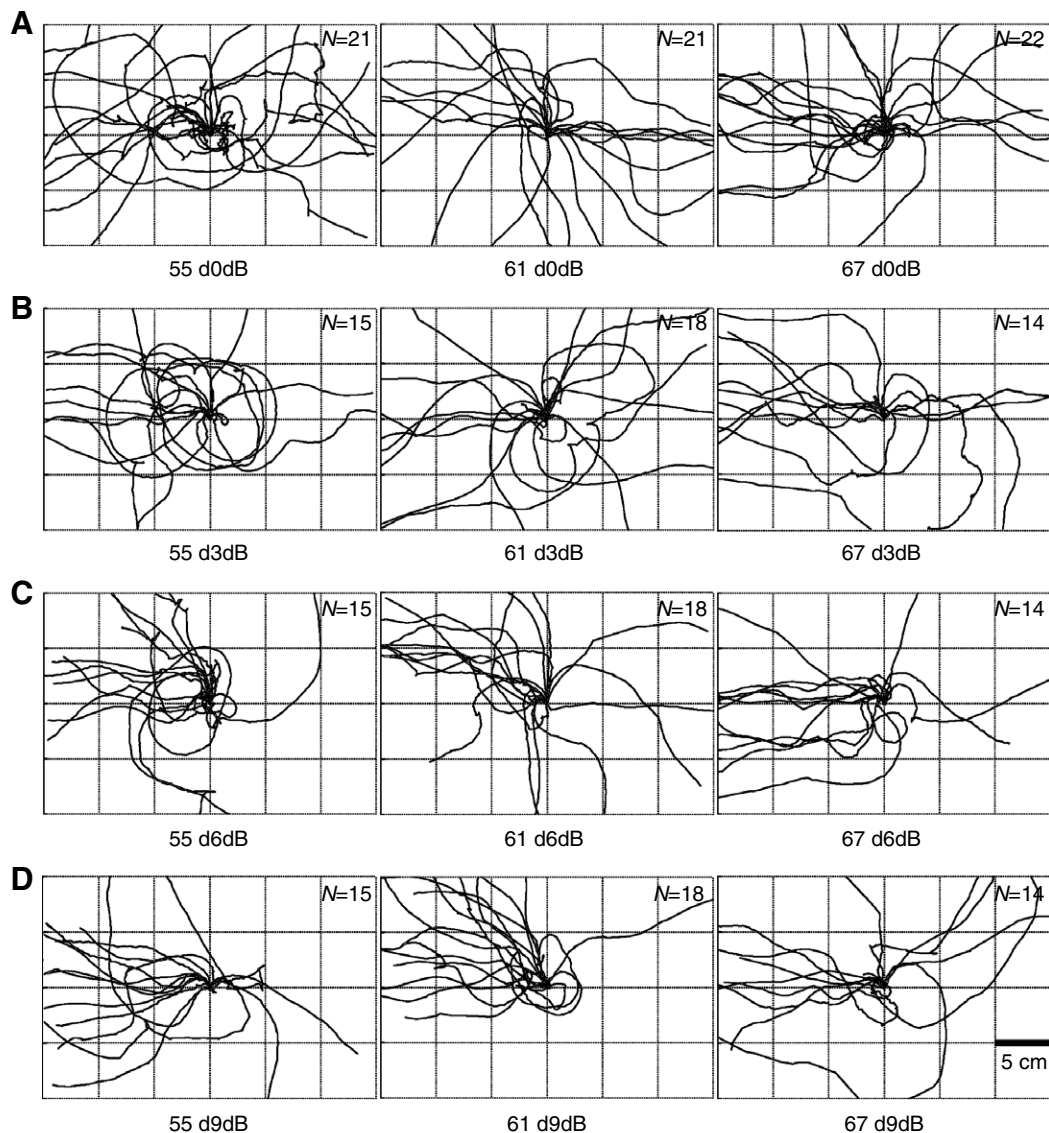
Fig. 1. Phonotactic paths of females presented with songs at different baseline and relative SPL values (A: 0 dB; B, 3 dB; C, 6 dB; D, 9 dB). Paths in which the louder speaker was on the right were mirrored so that the louder speaker is always on the left. Paths were not mirrored at relative SPL d0dB.

as the expectation at all other relative SPL values (α level=0.05). Path vectors, which were not significantly directed towards their hypothetical direction, were tested with a Rayleigh test for a uniform distribution (Batschelet, 1981) (α level=0.05).

Defining pauses and walking bouts

The walking pattern of crickets, like that of many insects, consists of a repeated pause and walk pattern. We defined pauses and walking bouts in order to examine female behaviour within the path. The displacement of the female was calculated between each frame and the next. The first frame in any path was marked as a pause. If the displacement between any of the subsequent frames and the frame preceding it was greater than 0.1 cm, the subsequent frame was marked as a walking frame; if not, it was marked as a pause frame. Multiple pause or walking frames that followed each other were grouped together and marked as pauses and walking bouts.

Baseline and relative SPL perceived at pauses

We inferred the baseline and relative SPL of song perceived by females at each pause using the following three steps.

(i) Attenuation generated by distance and peripheral auditory directionality

For each ear of the female, the SPL of both songs at the female's position was inferred using the SPL profiles of both speakers and the attenuation expected to be generated by the directionality of the cricket ear and the angle subtended by the speaker to the female's midline. The peripheral auditory directionality (PAD) curve of the *Gryllus bimaculatus* ear (Michelsen et al., 1994) was used. The PAD curve of *Gryllus campestris*, which is closer in size to *P. guttiventris*, has also been reported (Larsen et al., 1989). In order to be parsimonious, however, we used the *G. bimaculatus* measurements, as the directionality generated by its pressure gradient ear is lower
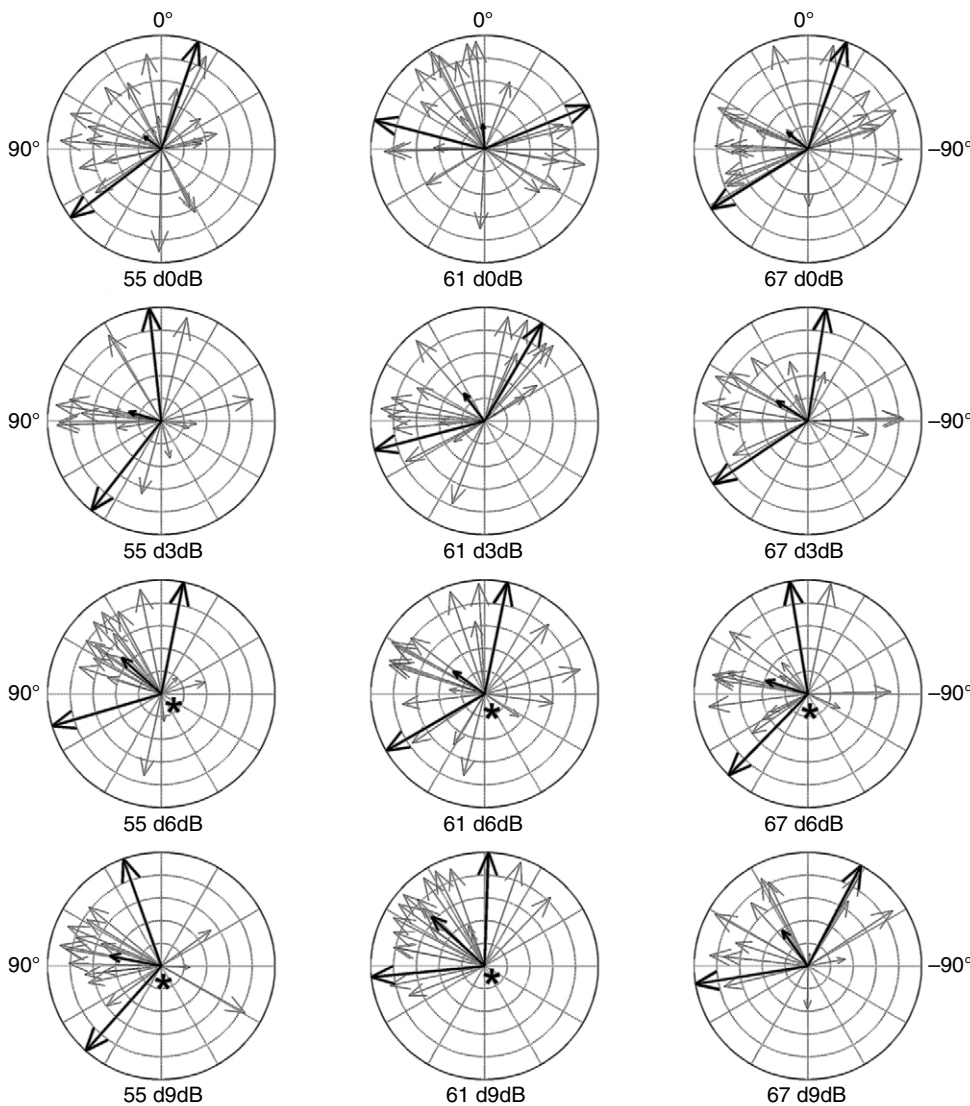
Fig. 2. Path vectors describing phonotactic paths of females presented with calling songs at different baseline and relative SPL values. Path vectors in which the louder speaker was on the right were mirrored so that the louder speaker appears on the left i.e. at 90°. The mean of all path vectors is the central, shorter thick arrow and the two on either side reaching the edge of the polar plot mark the angular deviation around the mean. The polar plots are all uniformly scaled to unit length. Path vectors significantly oriented towards 90° are marked with an asterisk in the polar plot. All other vectors were found to be uniformly distributed.

(15 dB at contralateral position) than that of the *G. campestris* ear (nearly 30 dB at the contralateral position) (Larsen et al., 1989; Michelsen et al., 1994).

(ii) Saturation and threshold

If the SPL of the songs at either ear was greater than 100 dB, it was reset to 100 dB in order to capture the phenomenon of saturation. The calling song of *P. guttiventris* males in the field is on average 75 dB SPL at a distance of 10 cm (Mhatre and Balakrishnan, 2006). Assuming no excess attenuation, the calling song would be 100 dB SPL at about 0.5 cm from a calling male. At such short distances, directional cues from song are probably not important and the response of auditory neurons might saturate with few maladaptive effects. Similarly if the SPL of a song at either ear was found to be below 40 dB, the behavioural threshold for *P. guttiventris* females (Mhatre and Balakrishnan, 2006), it was set as being below phonotactic threshold. This provides a dynamic range of nearly 60 dB, within the range observed in the tympanal nerve of *Teleogryllus oceanicus* (Imaizumi and Pollack, 2001).

(iii) Selective attention and masking

After subtracting all sources of attenuation from the SPL of calling song, we determined which of the speakers was loudest at each ear of the female. Using the principle of selective attention (Pollack, 1986; Pollack, 1988), if the two songs at each ear were at least 3 dB apart in SPL, we considered the stimulus to be unmasked. At the end of this exercise, the SPL and masking status of song at each ear of the female was available and the baseline and relative SPL could be calculated for the female's position during each pause.

Angle changes

During pauses, females usually stood still and the heading angle stayed relatively constant. The change in heading angle occurred gradually during walking bouts, forming curved paths. To estimate total angle change between pauses, the average heading angle of the female at each pause and the change in the average heading angle between consecutive pauses was calculated.

The first angle change was defined as the angle change in longitudinal body axis made during the first walking bout. Mean
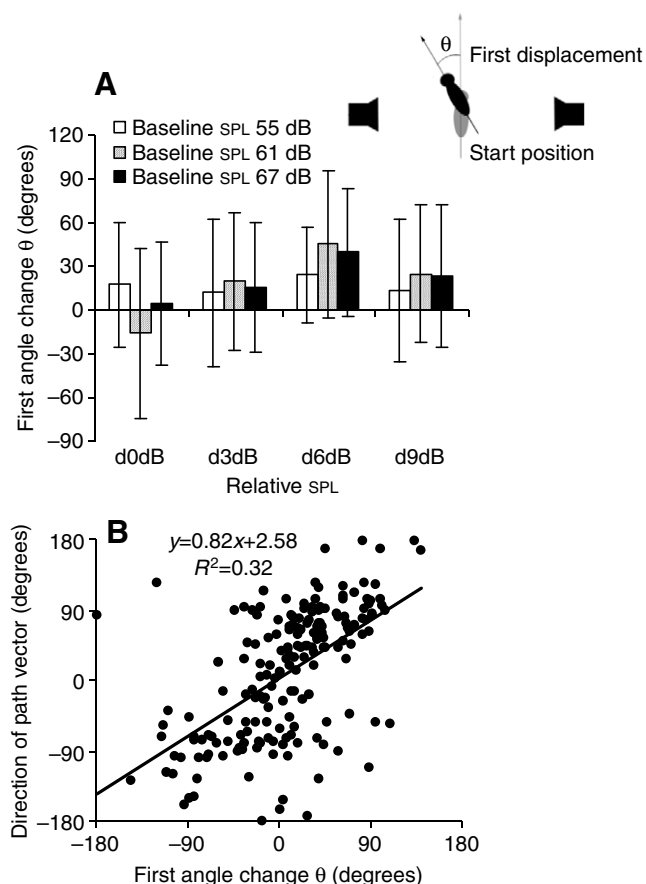
Fig. 3. (A) Mean first angle change θ made by females presented with calling songs at different baseline and relative SPL values. A positive value indicates a turn towards the louder speaker. Error bars indicate the angular deviation around the mean. (B) The first angle change θ made by a female during a phonotaxis trial was significantly positively correlated with the direction of that path vector. Positive values indicate turns to the left and negative values indicate turns to the right. Points represent the responses of all females to all treatments (R^2=0.32, P<0.01; females, N=64; paths, N=205).

first angle changes and the deviation of this angle change were calculated using standard formulae (Batschelet, 1981).

Stimulus angle

We tested the effect of stimulus angle on angle change. The stimulus angle at each pause was defined as the angle of the female's longitudinal body axis to the speaker that she perceived to be louder. If the louder stimulus was masked, the angle of the speaker producing the softer stimulus was used. If both songs were masked and equal in SPL, the stimulus angle of either speaker was picked with equal probability, else the louder stimulus was used. The PAD curve of the cricket ear is symmetric along the front–back axis, i.e. a sound source at 0°, 10°, 20° is indistinguishable from one at 180°, 170° or 160° respectively. We transformed the stimulus angle to account for this property. The angle change after each pause was then regressed against the stimulus angle at that pause.

We then further subdivided the data on the basis of different baseline and relative SPL values to test the relationship between stimulus angle and angle change. Pauses were binned on the basis of baseline SPL at 5 dB intervals, starting from 40 dB SPL. Each set of pauses in a particular baseline SPL bin was then further subdivided using relative SPL bins of 3 dB bin width starting from d1dB. Pauses with relative SPL d0dB to d1dB at all baseline SPL values were treated separately. Regressions of angle change against stimulus angle were calculated and the slopes of these regressions were then plotted in a 3D surface against the centre of each baseline and relative SPL bin.

Statistical tests on features of phonotactic paths

All statistical analyses dealing with linear variables were carried out using Statistica (1999, Statsoft Inc., USA) software. The influence of stimulus conditions on different features of phonotactic paths, i.e. sinuosity, pause number, mean pause duration, mean walking bout duration and length, within a path, were tested using separate two-way repeated-measures ANOVAs with the baseline and relative SPL values as the independent variables and the specific feature as the dependant variable. If the variable in question was non-normally distributed, it was Box–Cox transformed using the statistical toolbox in Matlab (Version 6.5, The Mathworks Inc., Natick, MA, USA), then tested for normality using the Kolmogorov–Smirnov test (pause durations: P=0.20; walking bout duration: P=0.20; walking bout length: P=0.20) before being used for the ANOVA. Only data from females who had completed all trials were used for this analysis.

The displacements between all frames of a walking bout were summed to calculate walking bout length. Sinuosity was calculated using the following formula (Bovet and Benhamou, 1988) where a higher value indicates a more sinuous path, the minimum possible value being zero:

$$S = \sigma / \sqrt{P},$$

where S=sinuosity, σ=standard deviation of angle changes between frames, and P=mean displacement between frames.

Walking behaviour transition

We found that much of the angular change made by a female was achieved in the initial part of the path, over small distances. In the latter part, females walked further with lower changes in heading angle. Data from 151 of 205 paths (73.65%) showed this pattern and were used to find the transition point at which females switched from one type of walking behaviour to another.

To find the transition, a plot of cumulative absolute angle change against distance walked was smoothed using a moving average method with a span of three points. It was then fitted with two lines, the first to all points between the first and the nth pause, the second from the n+1th pause to the last. Multiple such pairs of lines were fitted by varying n from the second to the penultimate pause. The R^2 value was calculated for each line. The average R^2 value for each pair of lines was calculated and the pause n at which this average value was the highest was designated as the transition.
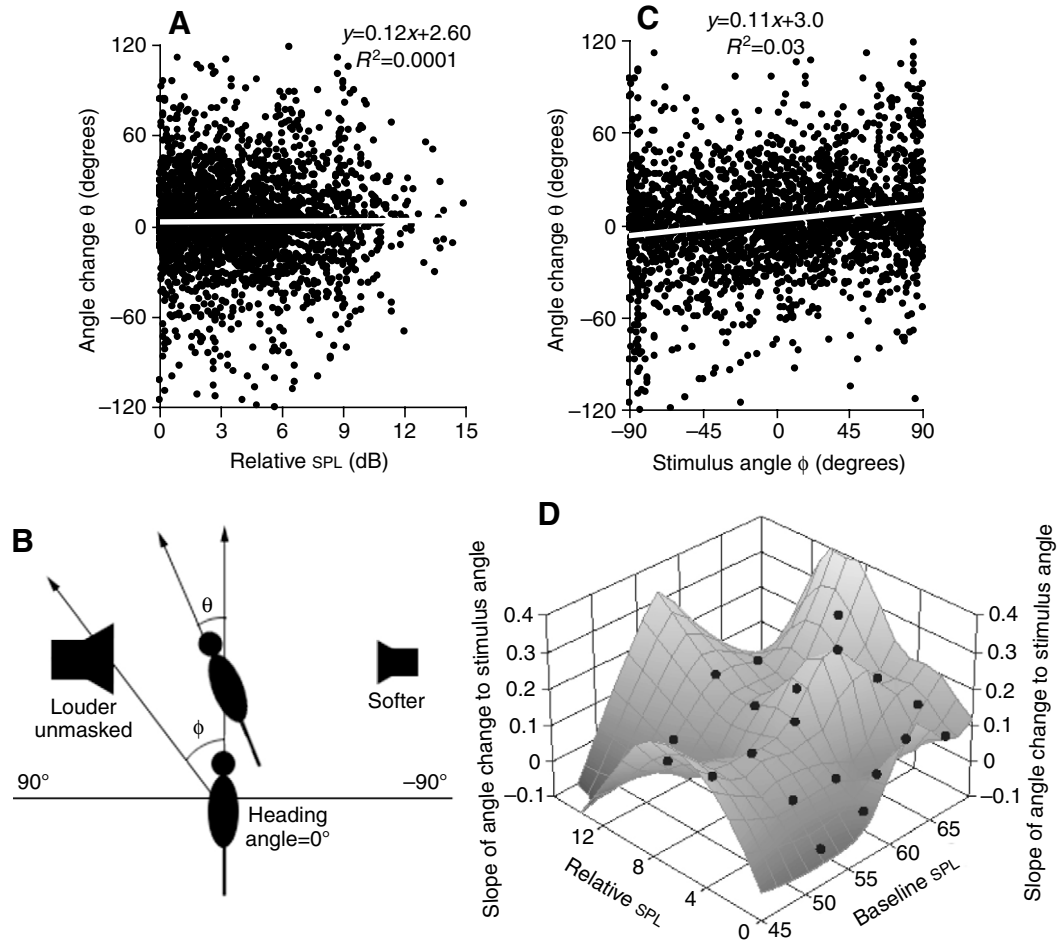
Fig. 4. (A) The angle changes θ made by females during walking bouts plotted against the relative SPL perceived at the pause preceding each walking bout. Positive angle changes indicate a turn towards the louder side. The angle changes made by the females were not correlated with the inferred relative SPL ($P=0.28$; pauses, $N=2493$). (B) A cartoon describing stimulus angle ϕ and the angle change θ made by the female in response. The speaker marked 'louder' is louder at the position of the female. (C) The stimulus angle ϕ at the pause was correlated with the following angle change ($P\ll0.01$; pauses, $N=2493$). A positive angle in this plot indicates left and a negative angle indicates right. (D) The slope of the regression between stimulus angle and subsequent angle change increased with increasing baseline and relative SPL with a decrease at high relative SPL for some baseline SPL values.

Results
Paths

The phonotactic paths of the females in the closed loop walking phonotaxis paradigm (Fig. 1) had several interesting features. In all three instances of relative SPL of d0dB, only a few paths went along the centre of the arena (Fig. 1A). Most females appeared to make a decision between the speakers and then tracked that speaker till the edge of the arena (Fig. 1A). The number of paths that were oriented towards the louder speaker increased with increasing relative SPL (Fig. 1). However, even when the difference between the two speakers was as high as 9 dB (Fig. 1D), a few females approached the softer speaker.

The basic forms of the paths were similar across all treatments. The sinuosity of the phonotactic paths did not change at different baseline and relative SPL values (baseline SPL: $P=0.33$, relative SPL: $P=0.45$, interaction effect: $P=0.99$) and was 14.00±3.34 deg. cm$^{-1/2}$ (mean ± s.d.). Most of the large changes of direction were seen in the initial parts of the paths

and the latter parts were relatively straight. We did not observe marked zig-zag movements during the later tracking phase.

Path vectors

The path vectors were uniformly distributed at the relative SPL d0dB (Fig. 2A), suggesting no marked preference for either of the speakers in the d0dB condition. The path vectors were significantly directed towards the louder speaker, i.e. 90° in five out of nine cases at the other relative SPL values (Fig. 2). The clearest preference for the louder speaker was seen at the relative SPL d6dB (Fig. 2). The angular deviation of the path vectors was high, indicating high inter-individual variability in female response.

First angle change

The first angle changes made by females at all baseline SPL values at d0dB were clustered around 0° (Fig. 3A), suggesting no preference for either speaker. At all other relative SPL values, they
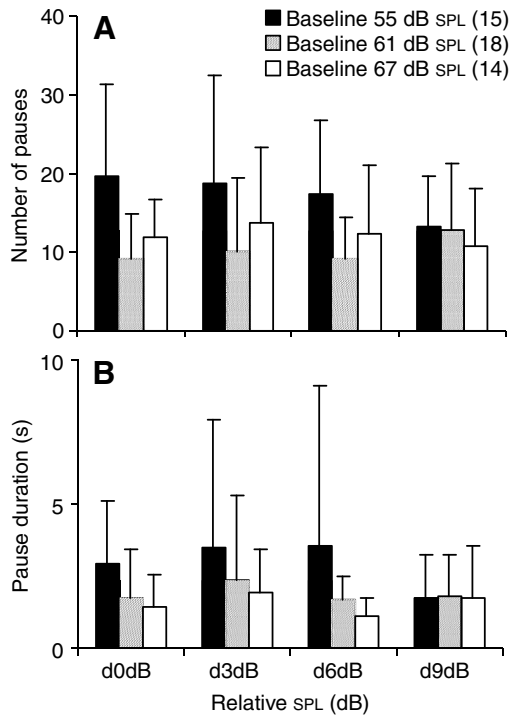
Fig. 5. (A) Mean number and (B) mean duration of pauses within each path made by females when presented with calling songs at different baseline and relative SPL values. Values are means ± s.d. (N values are given in parentheses).
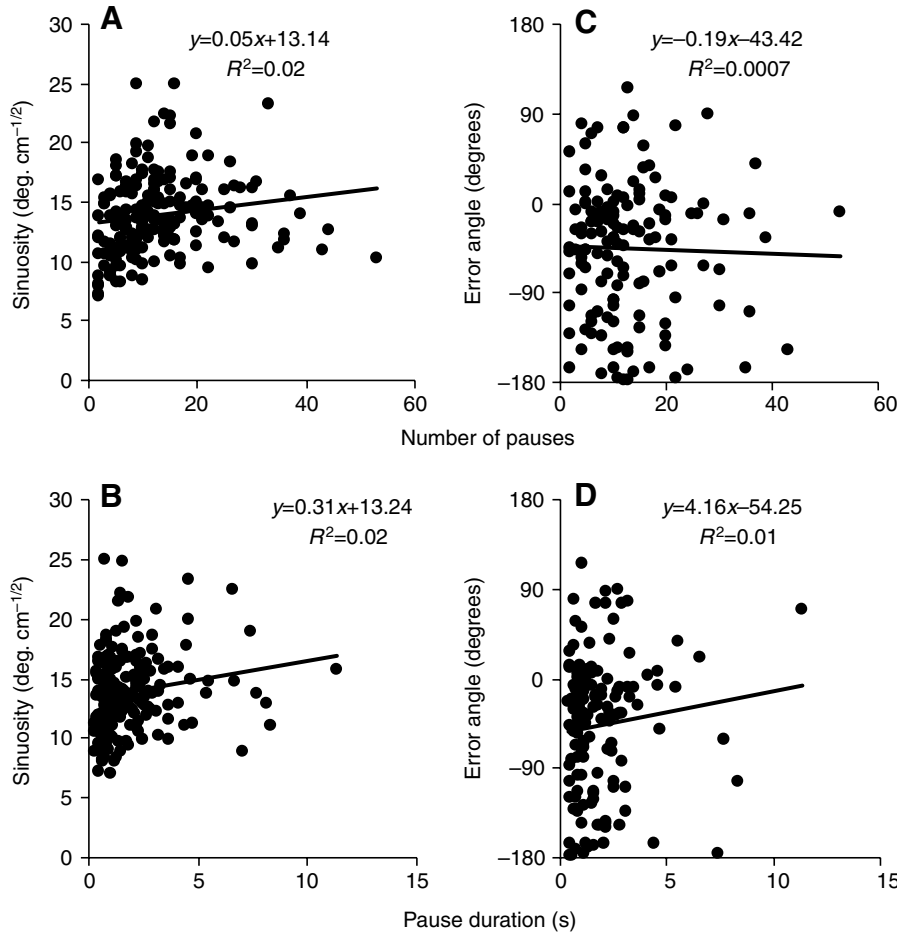
veered towards the louder speaker. The clearest preference for the louder speaker was seen at the relative SPL d6dB, and there was a subsequent dip in the mean first angle change at all baseline SPL values at the relative SPL d9dB (Fig. 3A). The angular deviations around the mean were high in all treatments, suggesting a highly variable response across individuals. The similarities between the patterns seen in path vectors and first angle changes suggested that the initial decisions, i.e. first angle changes made by females, might influence the direction of entire paths. The direction of a female's path was found to be significantly correlated with the first angle change she made (Fig. 3B, R^2=0.32, P<0.01, N=205), suggesting that this was indeed the case.

Stimulus angle

The first angle change made by the female varied with respect to the baseline and relative SPL. However, the starting positions of females were such that the stimulus angle in all these responses was 90° and it was not possible to separate the influence of stimulus angle from that of baseline and relative SPL. A regression of angle change against relative SPL did not show a significant relationship when angle change decisions made after all pauses (in which different stimulus angles were encountered) were included (Fig. 4A, P=0.28, N=2493). However, the regression of angle change versus stimulus angle was significant and heading angle changes were on average directed towards the louder stimulus, which was also unmasked (Fig. 4C, P≪0.01, N=2493). This suggests that the magnitude and direction of turns were not scaled to the perceived difference in SPL alone but also to the direction of the louder, unmasked stimulus. When the data were subdivided on the basis of baseline and relative SPL, we found that the relationship between stimulus angle and angle change, as indicated by the slope, increased with both baseline and relative SPL, and then decreased at high relative SPL values (Fig. 4D).

Pauses

The number of pauses made by females during phonotaxis varied significantly only between the different baseline SPL conditions (Fig. 5A, baseline SPL: P<0.01, relative SPL: P=0.68, interaction effect: P=0.22). More pauses were observed at baseline SPL 55 dB than at 61 dB and 67 dB. The number of pauses was not significantly different between 61 dB and 67 dB baseline SPL values (Tukey's HSD

Fig. 6. (A,B) The number (A) and average duration (B) of pauses made by a female in a path was weakly correlated with its sinuosity. (C,D) The error angle (the difference between the mean direction of the path vector and the angle of the louder speaker at the release position) was uncorrelated with the number of pauses (C) and mean pause duration (D).
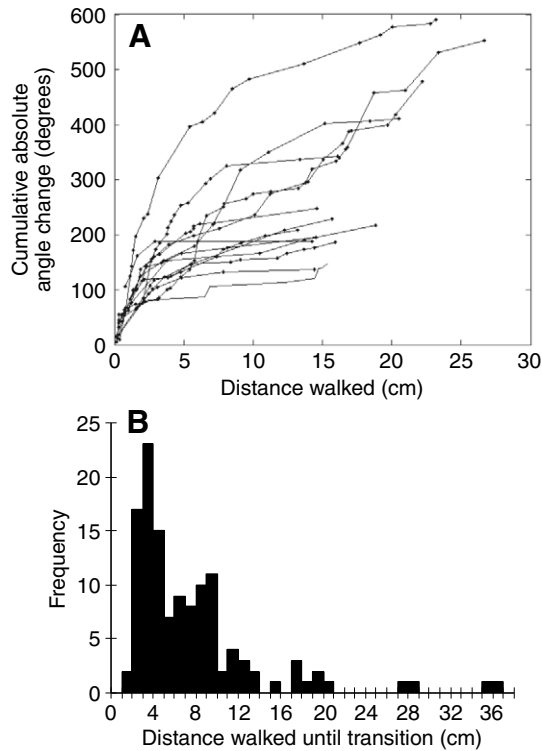
Fig. 7. (A) The cumulative absolute angle change made in a phonotactic path is plotted against the distance walked for all paths in the stimulus treatment 55 d9dB. Each point in the plot represents the pauses made by the female in serial order. Large angle changes occurred in the initial parts of the paths. In the later part, females walked further without greatly changing heading angle. (B) A frequency distribution of the distances at which the transition between the two walking behaviours occurred.

test, 55 dB and 61dB: $P<0.01$; 55 dB and 67 dB: $P=0.04$; 61 dB and 67 dB: $P=0.60$). The duration of the pauses was also affected only by baseline SPL (Fig. 5B, baseline SPL: $P=0.03$, relative SPL: $P=0.47$, interaction effect: $P=0.09$). Pauses at baseline SPL 55 dB were significantly longer than those at 67 dB; however, no difference was observed in other combinations (Tukey's HSD test, 55 dB and 67 dB: $P<0.03$; 55 dB and 61 dB: $P=0.16$; 61 dB and 67 dB: $P=0.67$).

The sinuosity of a path (Fig. 6A) was weakly positively correlated both with the number of pauses made during the path ($R^2=0.02$, $P=0.03$, $N=188$) and the mean pause duration (Fig. 6B, $R^2=0.02$, $P=0.02$, $N=141$). The error angle (see Fig. 6) was, however, not correlated with the number ($R^2=0.00$, $P=0.75$, $N=188$) or mean durations of pauses in the path ($R^2=0.01$, $P=0.23$, $N=139$, Fig. 6C,D).

Walking bouts

Average walking bout durations did not vary with either baseline or relative SPL and showed no interaction effect (baseline SPL: $P=0.66$; relative SPL: $P=0.57$; interaction effect: $P=0.24$). The average walking bout length was similarly unaffected by stimulus conditions (baseline SPL: $P=0.14$; relative SPL: $P=0.74$; interaction effect: $P=0.29$).

A transition between two motor patterns was observed in

several paths, with tighter turns in the initial parts of the path, followed by low angle change with straighter paths in later parts (Fig. 7A). An attempt to find stimulus conditions that co-occurred consistently with this transition failed. The distance at which these transitions occurred was also different in different paths (Fig. 7B). However, the angular and translational velocities of females were different before and after the transition (before transition: $P\ll0.01$, $N=918$; after transition: $P\ll0.01$, $N=752$; Fig. 8).

(B) SIMULATION OF WALKING PHONOTAXIS
General methods

The simulation was carried out using Matlab (Version 6.5, The Mathworks Inc., Natick, MA). Three-dimensional surface fitting was carried out using TableCurve 3D (Version 4, Systat software, San Jose, CA, USA). The simulation was carried out at the same spatial and temporal scales as the experiment. The simulation used a 'pause-measure song SPL-walk' model of female phonotaxis in the following way:

Step (1) Initializing positions. The arena of the simulation was the same size as in the experiment and virtual speakers were placed in the same positions. The path of the virtual female was begun from the same position and in the same orientation as in the experiment.

Step (2) Pause. The pause made by the female was selected from the actual distribution of pause durations observed during the experiment. The position and heading angle of the female were kept constant for the duration of this pause.

Step (3) SPL of calling song and stimulus angle. The SPL perceived by the female at each pause was determined in the same manner as described above in the section '*Baseline and relative SPL perceived at pauses*' and the stimulus angle as described in the section '*Stimulus angle*'.

Step (4) Angle change. The response angle was randomly picked from a normal distribution. The mean ± s.d. of this distribution were determined by the relationship between stimulus angle and angle change at the baseline and relative SPL perceived at each pause. To determine the mean, the slopes of the linear regressions between stimulus angle and angle change at different baseline and relative SPL values were plotted as a 3-D surface (Fig. 4C). A surface was fitted to this plot ($R^2=0.77$). Similarly a 3-D surface was fitted to the intercepts of these regression lines ($R^2=0.59$). The mean of the distribution for a particular baseline and relative SPL was calculated by multiplying stimulus angle with the appropriate slope from the first surface and by adding the intercept from the second surface.

The standard deviation of the normal distribution was similarly determined. The angle changes at the different baseline and relative SPL bins were further subdivided by absolute stimulus angle into 10° bins and the deviation of angles within each bin was measured. These were then regressed against the centre of the absolute stimulus angle bin. The slopes and intercepts of these regressions were fitted to 3-D surfaces (slope of the regression: $R^2=0.87$; intercept of the regression: $R^2=0.84$) and the standard deviation calculated in a manner similar to the mean.

Step (5) Walking bout duration and length. The distance at which the transition between motor programs occurred was randomly picked for each path from the frequency distribution
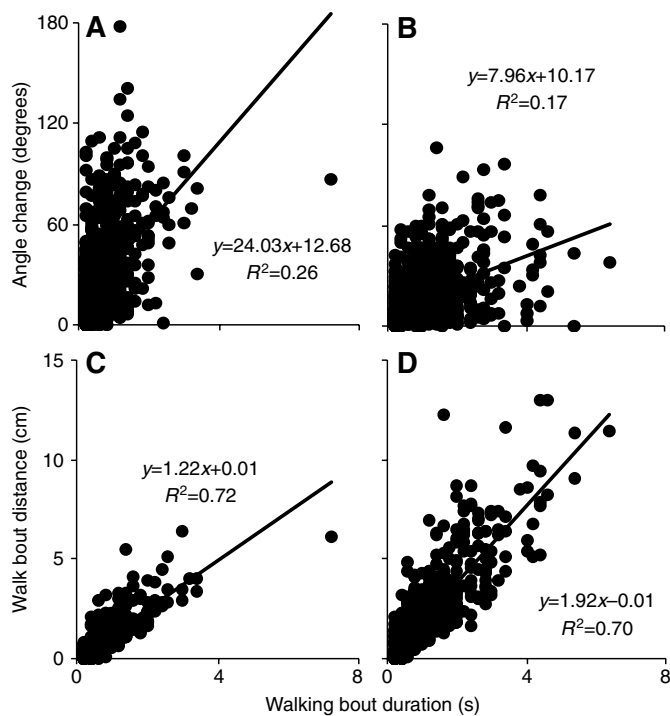
Fig. 8. A regression of the angle change made during a walking bout against the duration of that walking bout had a greater slope before (A) the transition than after (B). The slope of the regression between the distance walked in a walking bout against its duration was lower before the transition (C) than after (D).

in Fig. 7B. At this step of the simulation, when setting the length and duration of a walking bout, we checked if the female had already walked this distance. If not, the walking bout duration was selected based on Fig. 8A and the length on Fig. 8C in a manner that incorporated the variation observed. If the female had already walked the transition distance, the duration and length of the walking bout were selected on the basis of Fig. 8B and D, respectively. The minimum walking bout duration was set at one frame and the minimum distance walked between frames was set at 0.1 cm. The position of the female was updated during the walking bout, one frame at a time. Angle change and distance walked were equally distributed over the entire duration. The direction of translation between frames was determined by using heading angle at each frame.

Step (6) Conditional iteration. If the virtual female was still within the arena, the simulation was iterated, beginning from step 2. If the virtual female had stepped out of the arena, the simulation was ended.

Step (7) Calculating path vector and sinuosity. If the simulation had ended, the path vector and the sinuosity of the paths produced by the simulation were calculated using the same formulae as used for the real paths.

Internal validation of the simulation

To test whether the models of female phonotaxis specified in these simulations captured the major features of the actual paths, we used several different measures of female paths: mean path

vector direction, angular deviation and sinuosity. These measures were found to be uncorrelated with each other in real paths and hence represent independent measures of the success of the simulation (mean direction *vs* angular deviation of heading angles: $P=0.51$, $N=12$; mean heading angle *vs* sinuosity: $P=0.51$, $N=12$; angular deviation of heading angles *vs* sinuosity: $P=0.57$, $N=12$).

Twenty runs of fifteen paths each were carried out at all treatment conditions and the above measures were calculated for each run in order to capture the variation. The mean ± s.d. for each of these measures was calculated. We then determined whether the values measured from the real paths fell within the range described by the mean ± 2 s.d., i.e. 96% of the values of paths derived from the simulation.

We also examined whether the first angle change was correlated with the path vector of the paths produced by the simulation. For this analysis, 16 paths were run at each stimulus condition, eight with the louder speaker on the left and eight on the right.

External validation of the simulation
Phonotaxis in the field

Outdoor phonotaxis was carried out between January and February 2005, at peak activity time. The temperatures ranged from 18°C to 22°C. The stimuli used for the experiment were synthesized in a manner similar to the stimuli used for the indoor experiment with a chirp from a song recorded at 21°C. The temporal pattern features used were appropriate to this temperature.

Two Creative speakers (frequency range 100 Hz to 15 kHz) were placed 62 cm apart with their faces parallel to each other. The female was released in the centre with both speakers at 90° to her midline. The entire phonotactic path of the female was recorded using the same apparatus as the indoor experiment, except with a larger field of view. One of the speakers broadcast the song at 76 dB SPL at source (i.e. 10 cm from the speaker) and the other at 70 dB SPL. Each female was first tested with only the softer speaker active in order to control for motivation, and only females who reached the speaker were further tested. The female was allowed a rest of at least 10 min and then tested with both speakers active. A total of 40 females were tested. Each female was tested only once. In order to control for positional effects, sets of 20 each were tested in two physically separate locations in the field, with the orientations of the setups rotated 180° with respect to each other.

The paths were digitized as before at 5 frames s^{-1}. The acquired paths were scaled using the distance between speakers. We measured only the centroid of the female's position, as it was not possible to measure female heading angle reliably. The path was measured until the background subtraction algorithm could not discern the female. In some cases the measured path ended before the female reached the speaker; however, this could be observed in the video and was separately noted. The angle of each displacement between frames with respect to the speakers was calculated and these angles were used to estimate the path vector as described before.

Simulations were run, mimicking the experiment. A χ^2 test was carried out to test whether the frequency of females reaching the two speakers in the simulation was similar to the
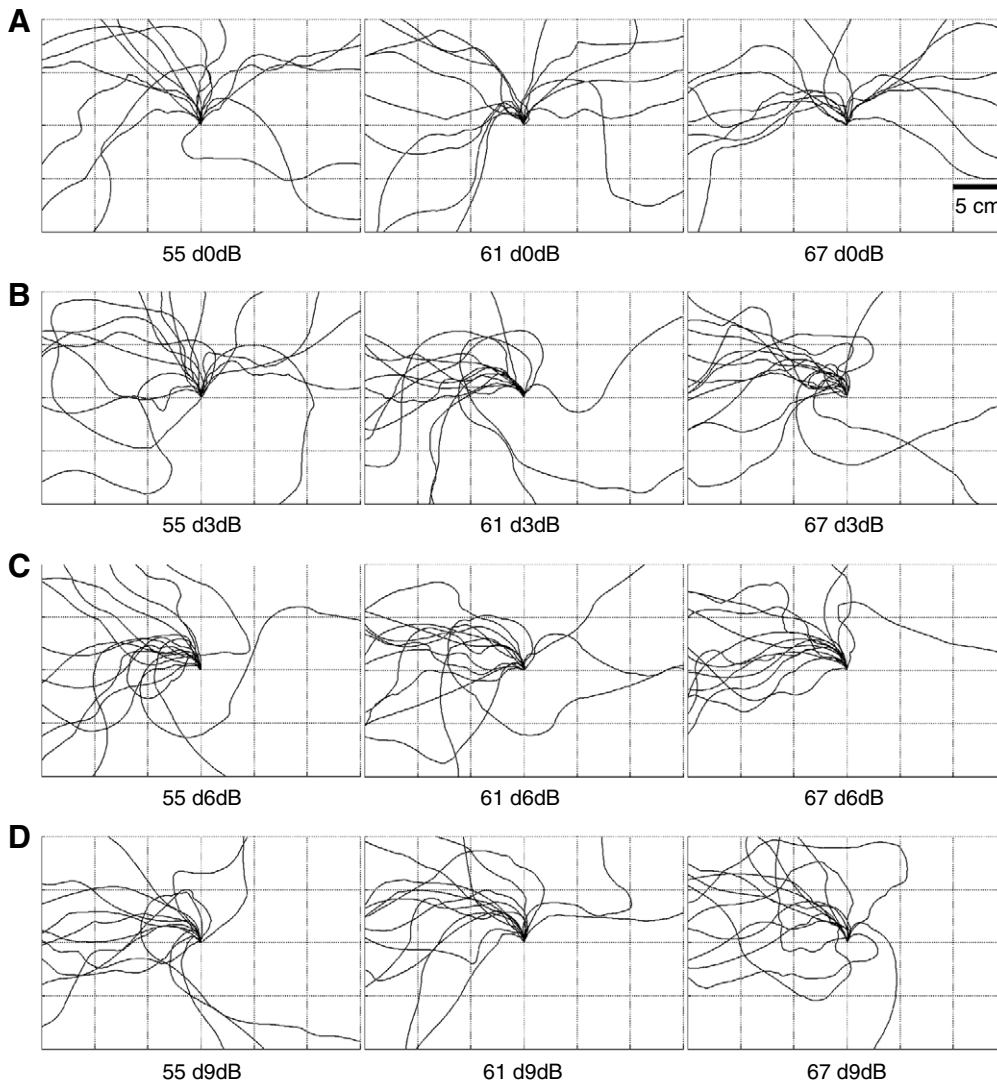
Fig. 9. (A–D) Phonotactic paths (*N*=15) generated by the simulation under the same stimulus conditions of baseline and relative SPL that real females were exposed to (see Fig. 2). The louder speakers are on the left. All plots are uniformly scaled.

real data. To measure the number of females that reached a speaker in the simulation, any path that came within 2 cm of the speaker was considered to have reached it. When comparing path vectors between the simulation and real data, only the directions of the path vectors were used to calculate mean direction and angular deviation.

The simulation used was the same as the one used for the internal validation with only two steps modified. In order to calculate the SPL at the position of the female, we calculated attenuation predicted by spherical spreading of sound and added to this the excess attenuation measured in the field (Mhatre and Balakrishnan, 2006). The excess attenuation at the position of the female was randomly selected from a normal distribution whose mean ± s.d. were derived depending on distance from the source [from data published elsewhere (Mhatre and Balakrishnan, 2006)].

The step involving angle change was also altered. For the outdoor phonotaxis, we did not use the 3-D surface that describes the intercept of the regression of stimulus angle against the subsequent angle change. The intercept describes biases in angle change, which were probably an artifact of the indoor phonotaxis set-up and were ignored for the field experiment. In the outdoor experiment, two set-ups rotated by 180° were used to control for any biases due to non-auditory cues. In the indoor setup, we did not change the physical orientation of the setup and this could have resulted in biases due to non-auditory cues.

One-eared phonotaxis

We tested the simulation with auditory input removed from one ear at a time. The simulation was run to produce five paths at a larger spatial scale than the previous simulation, with the speakers broadcasting at 76 and 70 dB SPL at 10 cm from the speaker using ideal transmission. The louder speaker was on the side of the intact ear. The auditory input from the 'deafened' ear of the virtual female was set just under threshold SPL at all pauses. Since the female will perceive a high relative SPL at all times, the stimulus angle was always set at +90° when the left ear was intact and –90° when the right ear was intact.

Phonotaxis with reduced directionality

The PAD curve of *Gryllus bimaculatus* (Michelsen et al., 1994) used in the simulation was modified for the purpose of this 'experiment'. We maintained the shape of the curve but
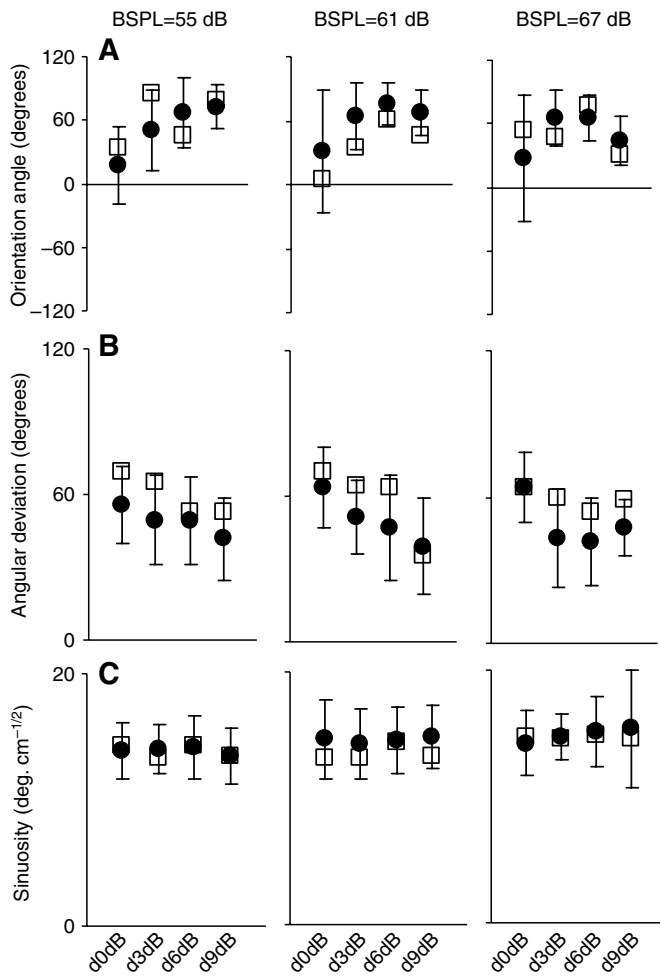
Fig. 10. Mean and ranges of the different path measures produced under different stimulus conditions by the simulation. (A) Mean direction, (B) angular deviation of path vectors, (C) sinuosity. The closed circles indicate the means; error bars indicate ±2 s.d.; open squares indicate the values measured for the real paths. Baseline SPLs (BSPL) are indicated at the top of the figure.
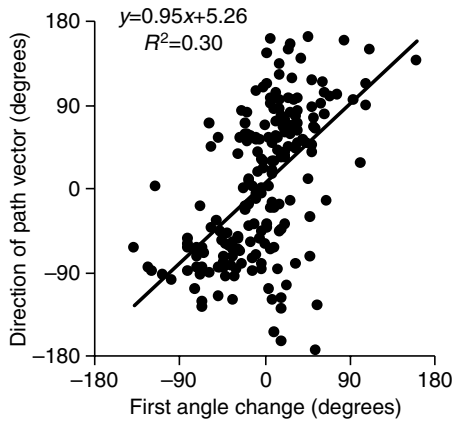

$y=0.95x+5.26$
$R^2=0.30$

Fig. 11. The first angle changes made by virtual females in the simulation were significantly correlated with the direction of their path vectors. The points represent the responses of all females to all treatments ($P \leqslant 0.01$; paths, $N=192$).
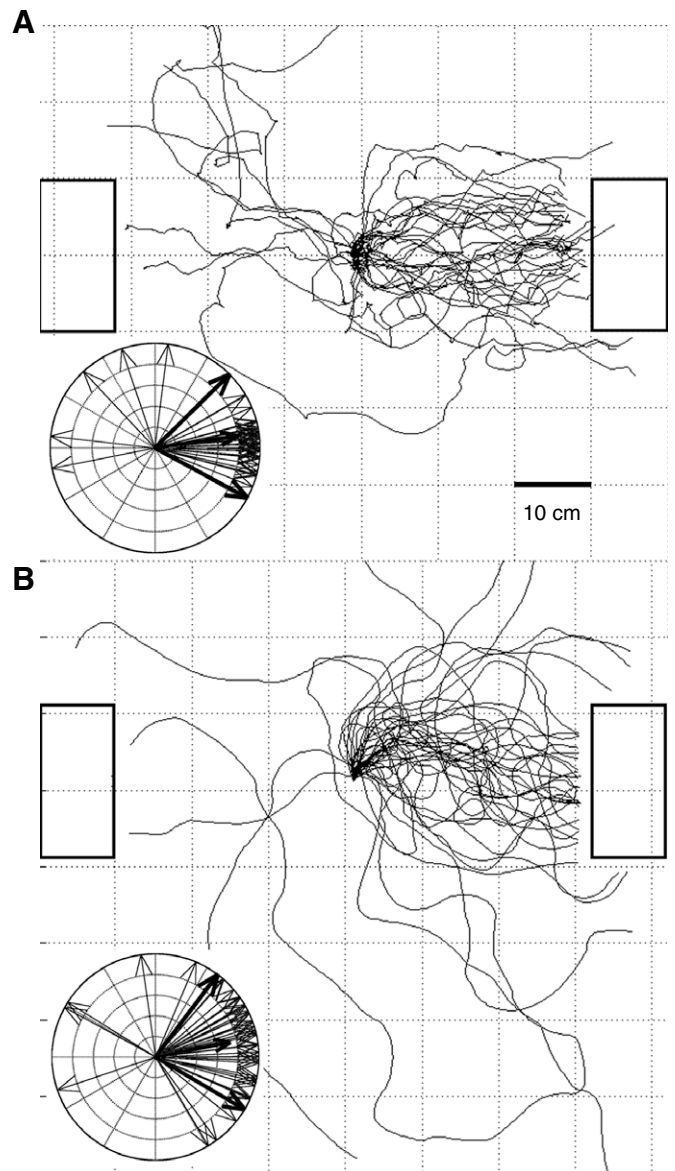

Fig. 12. The phonotactic paths produced by (A) real females ($N=40$) and (B) by the simulation ($N=40$) in the outdoor phonotaxis experiment. The position and approximate size of the speakers are indicated by the rectangles. The directions of path vectors are depicted in the insets; the shorter, thick central arrow indicates the mean direction and two thick arrows on either side the angular deviation.

reduced the dB difference caused by the change in angle of sound incidence. The PAD curve was scaled for maximum directional differences ranging from 1 to 30 dB SPL. The relationship between the stimulus angle and angle change was also reduced when multiplying the slope of the regression by this ratio. These modified ears were then used to simulate 15 paths over 20 runs at the treatment conditions 61d3dB and 61d6dB, louder speaker at left. We calculated the range of the mean heading angles and angular deviations at each of these directionality values and compared them with those obtained with the 'normal' ear.
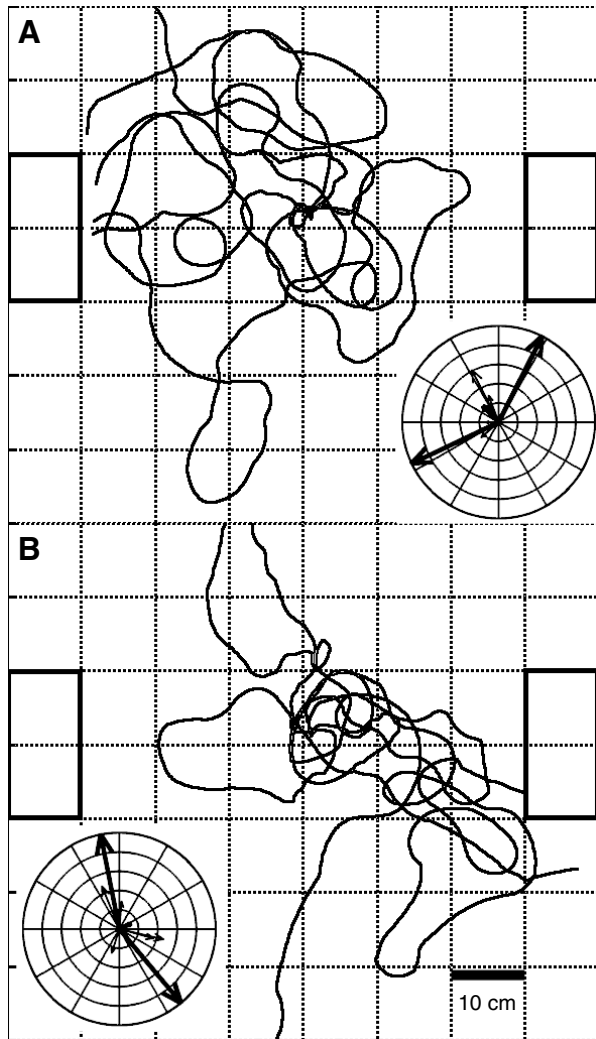
Fig. 13. Paths produced by virtual crickets, deafened in the (A) right ear and (B) left ear. The path vectors are reproduced as insets (*N*=5). For further explanation, see Fig. 12.

Results

Internal validation of the simulation

The paths produced by the simulation captured the essential features of the real phonotactic paths (Fig. 9). The values of mean path vector direction, angular deviation and sinuosity seen in the real paths fell within the range predicted by the simulation (Fig. 10). The simulation predicted the highest range of possible mean directions at the relative SPL of d0dB. It captured the rise in the mean direction from d3dB and a slight dip at the highest relative SPL of d9dB, a feature observed in the real paths (Fig. 10). The simulation also predicted a drop in angular deviation with increasing relative SPL, with a slight rise at the relative SPL of d9dB. The direction of each path vector produced by the simulation was correlated with the first angle change (Fig. 11, R^2=0.30, $P \leqslant 0.01$), as seen in the real paths.

External validation of the simulation
Phonotaxis in the field

The mean direction of the paths observed in the field was 9.73° (towards the louder speaker) and the angular deviation was 39.84° (Fig. 12A). The simulated paths had a similar mean direction of 11.18° and an angular deviation of 41.80° (Fig. 12B). Thirty-one of forty females in the real experiment reached the louder speaker and three reached the softer speaker. Six females walked out of the arena without reaching an active speaker (Fig. 12A). The simulation produced a similar result: 29 females reached the louder speaker, two reached the softer speaker and nine females walked out of the arena (Fig. 12B, χ^2 test: *P*=0.44).

One eared phonotaxis

The paths produced by the deafened 'virtual' female crickets (Fig. 13) had several features similar to those of real deafened crickets (Kohne et al., 1991). The paths showed large meanders with loops on the side of the intact ear suggesting poor localization abilities. There was a large spread of path heading angles and the length of the mean path vector was quite small (right deaf: 0.22; left deaf: 0.13). The angular deviation was also large (right deaf: 71°; left deaf: 75°). However, virtual females in the simulation did not continue making tight circles due to the shift in walking behaviour, which straightens out the later part of the paths.

Phonotaxis with reduced directionality

In the simulation, at both stimulus conditions, reducing the directionality of the ear below 10 dB caused females to localize poorly, as indicated by the lower mean direction (Fig. 14A,B). The variation of heading angles around the mean also increased with reduced directionality of the ear (Fig. 14C,D).

Discussion
The form of closed loop phonotactic paths

The phonotactic paths of females showed low sinuosity and were similar under all conditions of baseline and relative SPL. In closed loop walking conditions, paths did not become straighter or less meandering in response to increasing SPL, unlike in compensated walking phonotaxis (Schmitz et al., 1982). Females made very few abrupt turns and the later parts of their paths, which comprise the directed approach towards one of the speakers, are better described as meanders rather than zig-zags.

The form did, however, vary within each path. Turns were sharper in the initial part and straightened out in the later part of the path, with a relatively clear transition between the two kinds of motor patterns. A stimulus condition that consistently co-occurred with this transition was not possible to find and the transition might occur when a certain amount of 'searching' behaviour has been completed. Previous phonotaxis experiments, particularly those in compensated walking paradigms found relatively uniform angular and translational velocities during walking bouts in the presence of song (Schmitz et al., 1982), suggesting that this may be a feature of closed-loop walking phonotaxis.

We expected other features of walking phonotaxis besides sinuosity to be affected by stimulus conditions. It has been speculated that the decisions to turn towards louder stimuli are made largely during pauses (Bailey and Thomson, 1977; Murphey and Zaretsky, 1972; Weber et al., 1981). The
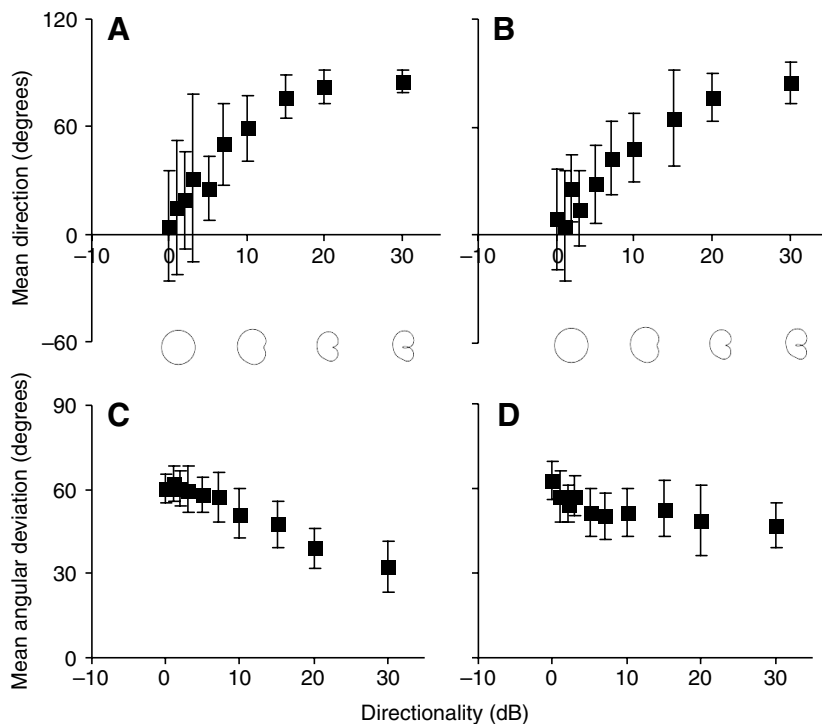
Fig. 14. (A,B) Mean direction of path vectors of 'virtual females' with ears of increasing directionality at (A) 61 d6dB and (B) 61 d3dB. Positive angular values in A and B indicate turning towards the direction of the louder speaker. The inset in the centre shows the changing PAD curve at different values of directionality. (C,D) The mean angular deviations of the paths at the two stimulus conditions.

The decrease in response at high SPL values has been interpreted as search behaviour shown by females as they approach a calling male (Hedwig and Poulet, 2005; Schmitz, 1985; Schmitz et al., 1982). We did not, however, observe the characteristic tight and repeated loops seen during search behaviour even at the highest baseline and relative SPL values. An alternative explanation for this phenomenon might be the saturation of receptors, as observed by Givois and Pollack (Givois and Pollack, 2000). The comparison between the two sides to determine the louder side is made on the basis of the response strength, which saturates sooner at higher SPL values (Pollack, 2003). Hence, a poorly directed response is expected when the calling song is presented at high SPL values (Givois and Pollack, 2000; Pollack, 2003).

The behaviour of females when presented with calling songs with no difference in SPL was different from that previously reported in some paradigms. Bushcricket males responding to female clicks of equal intensity stimuli, presented from two sides of their midline, track a central path in a compensated walking paradigm (von Helversen et al., 2001). Females tracking equally loud calls, in our experiment, rarely walked down the centre of the arena. One of the speakers was chosen and tracked throughout the path. This is similar to the observations made by von Helversen et al. when they recreated the previous experiment under natural walking conditions (von Helversen et al., 2001).

Can the stimulus angle influence female decisions in multi-source conditions?

The relative SPL inferred to be perceived by females during pauses in our analysis would be what females computed over long integration times. This relative SPL did not correlate with the heading angle changes subsequently made by females. We found, however, that stimulus angle was correlated with these heading angle changes. Our current understanding of cricket auditory physiology suggests that females scale their turns to the direction of the stimulus (Pollack and Plourde, 1982). They infer the direction of a stimulus using the perceived relative SPL after the cricket ear has generated the requisite directionality (Boyan, 1979; Boyd and Lewis, 1983; Larsen et al., 1989; Michelsen et al., 1994), at least in the presence of a single source. Hence, the absence of a correlation between angle change and relative SPL is not easily reconciled with a correlation between angle change and stimulus angle.

The processing and perception of a single song in the auditory system of a field cricket, however, is expected to differ from that of multiple songs. If the female simultaneously receives a perfectly synchronous second song, the relative SPL perceived by her will now depend on the relative SPL values of the two sources and their positions with respect to the female. A female should no longer have the ability to determine the stimulus angle of either source based on relative SPL alone.

threshold of the omega neuron 1 is increased during walking, lowering sensitivity to sound, particularly at the lower SPL values (Schildberger et al., 1988). Hence, at lower baseline and relative SPL values, the differences between the two sources will be obscured by neuronal noise. We expected that on average more and longer pauses would be made at lower baseline SPL values in order to increase the integration window and the signal-to-noise ratio. This was seen to be the case at the lowest baseline SPL (55 dB). A larger number of pauses or longer average pause durations during a phonotactic path did not, however, increase the accuracy of orientation of the path towards the speaker or decrease path sinuosity.

Similarly, walking bout lengths and durations were not affected by stimulus SPL. This suggests that behaviour within the walking bouts is largely independent of stimulus intensity. These features of the phonotactic paths may be influenced to a greater degree by other considerations such as motivational factors, energetic costs or predation pressure (Hedrick and Dill, 1993).

Angle change and path vectors

The orientation of female paths was affected by stimulus condition. First angle changes made by females were biased towards the louder speaker. Similarly, the mean direction of the path vectors also suggested orientation towards the louder speaker. Both these measures of female responses, however, showed high inter-individual variability.

If the two songs are alternating or aphasic, however, some syllables of each of the songs will be unobscured by the other song. Earlier experiments (Hedwig and Poulet, 2004) indicate that females are able to estimate the actual stimulus angle over short periods of the order of single syllable durations, suggesting short integration times. Thus, the stimulus angle has the potential to influence the female's turns.

Initial responses might influence long-term behaviour

The direction of the path of the female was correlated with her initial turning decision, at least at the spatial scales of our experiment. In a closed-loop paradigm, a behavioural decision made by the female changes the stimulus perceived by the female. A turn towards a source will reinforce the representation of that source at the expense of others which might bias her path in that direction. Due to the stochastic nature of the turning angle decision, an initial turn will occasionally be in the direction of the softer source. An initial erroneous decision has the potential to propagate throughout the entire path. Maintenance of initial stochasticity through error propagation might explain the higher angular deviations seen under closed loop conditions compared to those observed in compensated walking and open-loop paradigms (Hedwig and Poulet, 2005; Schmitz, 1985; Schmitz et al., 1982).

Simulated phonotaxis

The simulation was sufficient to explain multiple independent features of the real phonotactic paths. It produced paths with a range of possible values of mean direction, angular deviation and sinuosity, within which the observed values lay. It also captured another feature of the real paths, the influence of first angle change on the heading angle of the path vector. The model is principally based on the '*turn towards the side which is more stimulated*' rule (Schildberger, 1994). In the same review, Schildberger suggests an alternative '*turn towards the side increasingly stimulated*' algorithm that incorporates history, which he believed might better explain some features of phonotactic behaviour (Schildberger, 1994). We found, however, that the first rule is sufficient to explain the observed behaviour. Historical effects were also not apparent in the phonotactic behaviour of females in open-loop paradigms (Hedwig and Poulet, 2004; Hedwig and Poulet, 2005).

We unsuccessfully attempted several other approaches to recreate paths that were qualitatively and quantitatively similar to those produced by the females. In particular, we used an approach in which the direction and magnitude of turns were dependent only on the baseline and relative SPL perceived by the female. We incorporated the concept of history, the idea that previous behaviour influences later decisions. Yet another model made different responses depending on the number of males heard at a time, presuming that a female could distinguish between a single male and two aphasic males. None of these models satisfactorily captured all of the qualitative and quantitative features of real phonotactic paths (N.M. and R.B., unpublished observations). The presented model was the only one that produced a satisfactory fit.

The simulation also successfully recaptured the orientation ability of females in a field experiment and predicted outcomes accurately. A unilaterally deafened 'virtual female', like real crickets, produced paths that looped, and could not orient accurately (Kohne et al., 1991). 'Virtual females' with 'damaged ears', which produce poor directionality cues, also showed similarly poor orientation (Schmitz, 1985).

Implications for female phonotaxis in the field

Plebeiogryllus guttiventris females show variable phonotactic behaviour in response to two simultaneously active speakers playing aphasic song in the laboratory. The two-speaker situation is a simplified version of the real field conditions in terms of both attenuation and number of sound sources (Mhatre and Balakrishnan, 2006). The number of sound sources encountered by the female in a real chorus will be higher (Mhatre and Balakrishnan, 2006), decreasing the ability of the pressure gradient ear and selective attention to separate calls that are similar in SPL and adding to response variability. As the acoustic conditions within a chorus in the field become more complex we expect that the responses of females will become more variable. Females in dense multi-male choruses are thus unlikely to consistently locate the loudest male based on passive sound localization.

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