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The Functional Role of Stops during Phonotactic Approach in Crickets and Bushcrickets: a Discussion*

Die Funktion von Stopps bei der Phonotaxis von Grillen und Laubheuschrecken: eine Diskussion*

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Summary: Cricket phonotaxis is defined as flying or walking approach towards a sexual partner, guided by acoustic signals of the latter. In crickets, the female approaches the singing male. During this approach, the female (*Gryllus campestris* and *G. bimaculatus*) interrupts its walking by shorter or longer stops. In the past, this stop and go walking mode has been discussed in the context of sensory background noise reduction, since the tympanal organs, located in the forelegs, are disturbed during stepping. A number of investigations addressed the question whether the stops reflect a specific adaptation to avoid these disturbances, with no clear answer so far. The results of these investigations will be discussed, and new experiments added, which indicate that stop and go walking is not restricted to phonotaxis. It seems to be a general property of the walking system in certain insect species.

Keywords: insect, *Gryllus*, *Poecilimon*, phonotaxis, walking system

Zusammenfassung: Die Phonotaxis von Grillen besteht in einer fliegenden oder laufenden Annäherung an den Geschlechtspartner, allein durch dessen Gesang geleitet. Bei Grillen (*Gryllus campestris* und *G. bimaculatus*) läuft das Weibchen auf das singende Männchen zu. Es unterbricht seinen Lauf dabei durch kürzere oder längere Pausen. Dieses Lauf-und-Stopp-Verhalten wird im Kontext einer sensorischen Geräuschminderung diskutiert, da die in den Vorderbeinen liegenden Gehörorgane beim Laufen stark gestört sein können. Eine Reihe von Untersuchungen hat sich mit der Frage beschäftigt, ob die Stopps eine spezifische Adaptation zur Vermeidung der Störgeräusche sind. Bisher fehlt jedoch eine überzeugende Antwort. Die Ergebnisse dieser Untersuchungen werden diskutiert und neue Ergebnisse hinzugefügt. Diese weisen darauf hin, dass das bei der Phonotaxis beschriebene Laufverhalten nicht nur auf die Phonotaxis beschränkt ist, sondern eine allgemeinere Eigenschaft des Laufsystems diverser Insektenarten ist.

Schlüsselwörter: Insekt, *Gryllus, Poecilimon,* Phonotaxis, Laufsystem

1. Introduction

Sexually receptive female crickets walk towards conspecific males which produce a calling song. REGEN (1913) showed in *Gryllus campestris* that this behaviour, called phonotaxis, can be elicited solely by the males' calling song. MURPHEY & ZARETZKY (1972) described the phonotaxis of the east African cricket *Scapsipedus marginatus* quantitatively. The calling song consists of chirps which follow each other by a mean time interval of 1.6 s (ZARETZKY 1972). The phonotactic approach of the female consists of distinct short runs of 395 ms duration, starting 350 ms after the onset of a chirp (Fig. 1). As a result, the female stops long before the male produces the next chirp. Its phonotactic approach is therefore based

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* This article is dedicated to Franz Huber, the pioneer in cricket neuroethology.

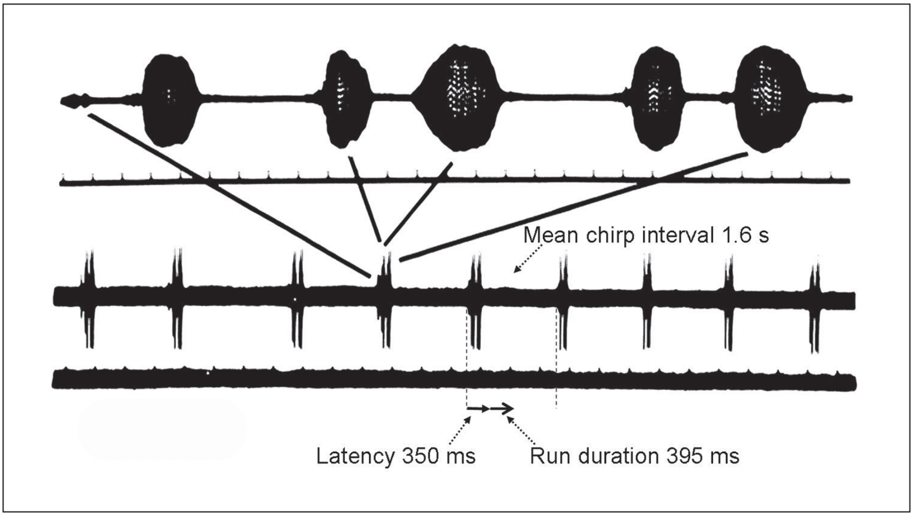

Fig. 1: Oscillographic registration of a natural calling song of *Scapsipedus marginatus* male. Each chirp (third trace from top) consists of several syllables with 5 kHz carrier frequency (top trace). Time marker second trace from top: 10 ms. Time marker bottom trace: 500 ms. After ZARETZKY 1972. Below, the timing of a typical female approach is indicated for one stop-and-go period: mean latency and mean run duration. Since the mean chirp interval amounts to 1.6 s, total stop duration is about 855 ms.
Abb. 1: Oszillogramm des natürlichen Werbegesangs von *Scapsipedus marginatus*. Jeder Vers (3. Spur von oben) besteht aus mehreren Silben mit jeweils 5 kHz Trägerfrequenz (obere Spur). Zeitmarken in der 2. Spur von oben: 10 ms. Zeitmarken in der unteren Spur: 500 ms). Nach ZARETZKY 1972. Unten ist als Beispiel die zeitliche Zuordnung für eine Periode der phonotaktischen Annäherung eines Weibchens dargestellt: mittlere Latenz und mittlere Laufdauer. Da das Versintervall im Mittel 1,6 ms beträgt, stoppt das Weibchen jedes Mal insgesamt etwa 855 ms.

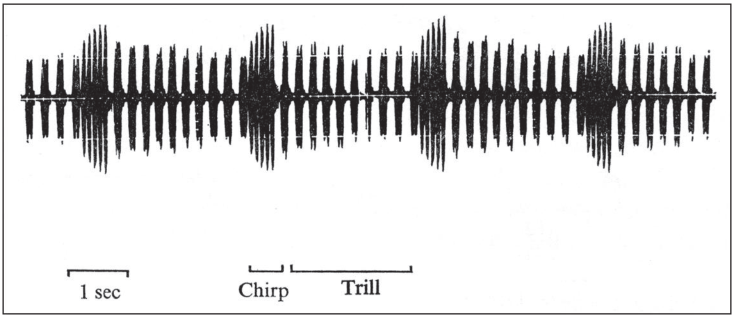

Fig. 2: Natural calling song of *Teleogryllus oceanicus*. Oscillogram of the song used as stimulus. The song is continuous and consists of a phase of a five-pulsed chirp followed by 10 double-pulse trills. Carrier frequency 4.5 kHz. From BAILEY & THOMSON 1977.
Abb. 2: Natürlicher Werbegesang von *Teleogryllus oceanicus*. Oszillogramm einer Bandschleife, die als Reiz benutzt wurde. Der Gesang ist kontinuierlich und besteht aus einem Versanteil mit fünf Pulsen und einem darauf folgenden Triller aus zehn Doppelpulsen. Trägerfrequenz: 4,5 kHz. Nach BAILEY & THOMSON 1977.

on auditory information received only during stops and is not controlled during movement. In contrast to *Scapsipedus marginatus*, *Teleogryllus oceanicus* males produce a continuous song pattern (Fig. 2). In this species, the phonotactic approach of the females consists of pauses in the order of 400 ms and subsequent walking phases with initial turns, followed by a short straight run (Bailey & Thomson 1977). The authors claim, that also the *S. marginatus* females use acoustic signals only during stops and do not orientate while moving, although the signal is available both during stops and the walking sections. Subsequently, the open loop orientation, described in the two cricket species, was regarded as the typical cricket phonotaxis. It has been widely accepted that the functional role of stops in cricket phonotaxis is to listen and determine the target direction. This view is suggestive, since the hearing organs of crickets (Gryllidae) are located in the forelegs and their

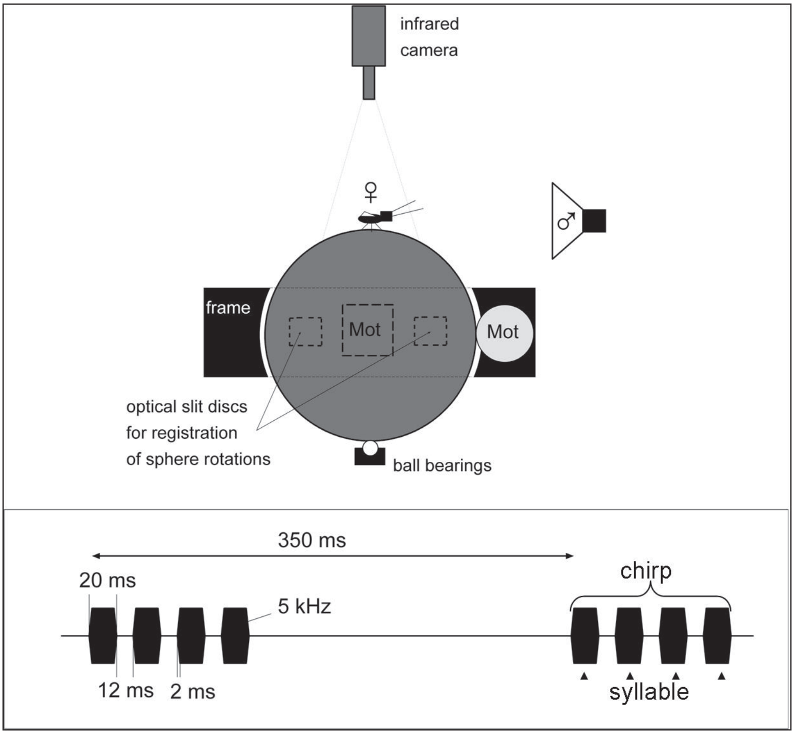

Fig. 3: Locomotion compensator in cross section. Mot = motor. The figure shows the situation for experiments with cricket females. The same apparatus is used in experiments with *Poecilimon affinis*. With *Poecilimon*, the male walks on top of the sphere, and the female's answer is generated by the loudspeaker (see fig. 10 for details of the song). Time delay between the onset of the male's song and the female's answer can be controlled. Lower part: Calling song for *Gryllus bimaculatus*. Carrier frequency of syllables 5 kHz.

Abb. 3: Lokomotionskompensator im Querschnitt. Mot = Motor. Die Skizze zeigt die Anordnung für die Experimente mit Grillenweibchen. Für die Experimente mit *Poecilimon* wurde die gleiche Apparatur verwendet. Dann läuft und singt jedoch das Männchen auf der Kugel, während die Weibchenantwort mit einstellbarer Latenz über den Lautsprecher eingespielt wird. Details zu den *Poecilimon*-Gesängen siehe Abb. 10. Unterer Teil: Werbegesang für *Gryllus bimaculatus*. Trägerfrequenz der Silben: 5 kHz.

function could be heavily impeded by acoustic noise, created by walking movements. It should be noted, however, that no critical tests were performed to determine whether the walking sections are really not influenced by calling songs, e.g. the effect of changing position of loudspeakers during walking phases.

This experiment has been performed with the cricket *G. campestris* (Fig. 3; Wendler et al. 1980, Schmitz et al. 1982). In *G. campestris* and *G. bimaculatus* the male calling song consists of chirps with a time interval of approx. 350 ms. The females interrupt their phonotactic approach by stops. When the position of the loudspeaker, producing a conspecific calling song, is changed by 90 degrees, the females can correct their walking direction accordingly (Fig. 4), and utilise the information about sound direction both during stops and during walking (Weber et al. 1981; Schmitz et al. 1982).

The question whether localisation is more effective during stops than during walking, has been addressed in several investigations (Weber et al. 1981; Schmitz et al. 1982; Schildberger et al. 1988). No final conclusions could be drawn regarding this ques-

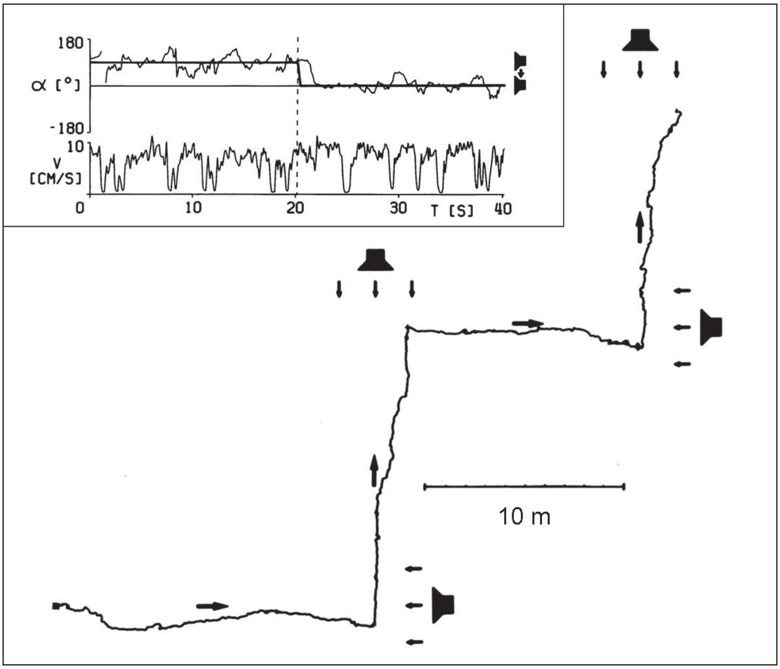

Fig. 4: Orientation towards the loudspeaker producing a conspecific calling song of *Gryllus campestris*. The calling song is switched between loudspeakers in intervals of 5 min. The figure shows the female's tracks and the corresponding loudspeaker positions. Inset: Orientation over time. Thick line: position of the sound generating loudspeaker. The cricket alters its walking direction within 1.5 s without a stop during the run. After Schmitz et al. 1982.

Abb. 4: Orientierung eines Grillenweibchens (*Gryllus campestris*) zum Lautsprecher mit dem Werbegesang des Männchens. Alle 5 min wird der Gesang zwischen den Lautsprechern umgeschaltet. Die Abbildung zeigt die Laufspuren des Weibchens und die dazugehörigen Lautsprecherpositionen. Inset: Orientierung des Weibchens als Funktion der Zeit. Dicke Linie: Position des aktiven Lautsprechers. Das Grillenweibchen ändert seine Laufrichtung innerhalb von 1,5 s ohne Zwischenstopp. Nach Schmitz et al. 1982.

tion. Intracellular recordings from auditory interneurons in the phonotactic situation, however, gave some important insight into the complex situation during walking (SCHILDBERGER et al. 1988). Auditory interneurons respond well to calling songs during stops, even at low sound levels. During stepping movements, however, their activity can be heavily affected or inhibited during certain phases of leg movements. Since the two forelegs move alternatingly, the female could compensate for this if it walks at sufficient low speed. Indeed, walking speed in *G. bimaculatus* is low, just about threshold (about 3 cm/s at 48 dB) and can raise to 8 cm/s at 70 dB (stops excluded) (WENDLER & LÖHE 1993).

To summarise: It is not clear if the stops are really an adaptation for orientation at low sound intensities (SCHILDBERGER et al. 1989). Unfortunately no behavioural test could be performed which compares the hearing threshold for the phonotactic performance in runs with and without stops. It is, however, worthwhile to consider behavioural elements that could support such a specific adaptation.

One would expect, for instance, that either the total stop duration during a run is long at low sound levels and shortens with higher intensities, or that the frequency of stops is high at low levels and reduced at high levels. It turns out that the former expectation has been observed (WENDLER & LÖHE 1993) and the latter has not (SCHMITZ et al. 1982).

Another means to improve phonotactic orientation performance is to adjust the timing of the stops. It is useful to look at the temporal relationship between the song and the walking speed of a female, which is orientated towards the loudspeaker (Fig. 5). The calling song consists of chirps and syllables (see Fig. 3). The syllable repetition rate is about 30 Hz. This frequency is the main parameter the females use for orientation (THORSON et. al. 1982; WENDLER 1990). Since the song pattern is fairly regular in the field and precise in the experiment, the female could ad-

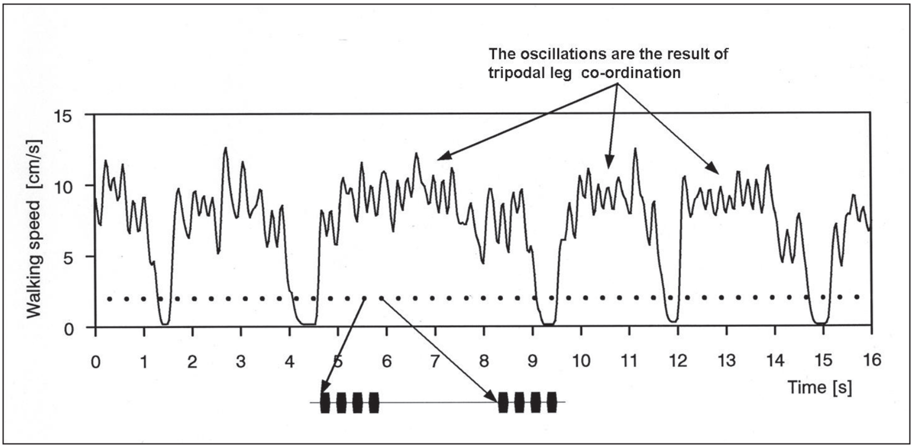

Fig. 5: Time relationship between stops and chirps in a *Gryllus bimaculatus* female. The dots in the dotted line represent the occurrence of chirps in this experiment. The level of the line indicates the speed threshold that has been used for the definition of stops.

Abb. 5: Zeitliche Beziehung zwischen Stopps und Versen bei einem Grillenweibchen (*Gryllus bimaculatus*). Die Punkte der gepunkteten Linie repräsentieren das zeitliche Auftreten der Verse in diesem Experiment. Die Höhe der Linie markiert die Schwelle, die für die Definition der Stopps verwendet wurde.

just the timing of stops in order to receive more syllables per stop. Most of the chirps do not coincide with stops. Only a small number (1-2 in this example, more during longer stops at low sound levels) of chirps coincide with a stop. If the coinciding chirps were the prevailing source for the recognition of the conspecific pattern and orientation, then it would be helpful to stop predominantly at defined times in relation to the song. This possibility was examined experimentally in the following experiments. Further experiments pose the question, whether the stop and go behaviour is restricted only to the context of phonotaxis.

2. Material and Methods

Insects were tested on a locomotion compensator after KRAMER (1975), which has been described in detail by WENDLER & SCHARSTEIN (1986) and WENDLER & VLATTEN (1993). The insect walks on top of a sphere of 50 cm diameter (Fig. 3). Translatory movements of the animal are registered by an infrared camera, the signals of which control two motors which rotate the sphere in such a way that all translatory movements are compensated. The unrestrained insect is thereby held on top of the sphere, while it is able to choose its walking direction. Cricket females maintain their phonotactic approach for a long time, even though the distance to the sound source remains constant (see Fig. 4). The rotation of the sphere, representing the animal's movements, are measured by two optical pulse generators, which produce unit pulses for each 0.5 mm displacement in x, -x, y and -y directions. The pulse trains are transferred online to a computer.

The sound stimulus was provided by a loudspeaker. In the case of *Gryllus bimaculatus*, the artificial calling song consists of chirps and syllables, as described in figure 3, lower part. In the case of *Poecilimon affinis* males, it consists of the female's answer (Fig. 10).

3. Results and Discussion

Phonotactic tests were performed with four sound levels from 50 to 80 dB. Females (*Gryllus campestris*) can orientate already at 50 dB (right side of Fig. 6). At this intensity, ascending interneurons are heavily disturbed by walking movements (SCHILDBERGER et al.1988), and the stops should therefore play a major role in the orientation process. The stops (as defined in Fig. 4) comprise 20% of the whole 15 min walk. How often does a chirp coincide with a stop? At random time relationships between stops and chirps, the number of coincidences should exactly amount to the 20%, the contingent of stops during the run. Any preferred relationship in favour of the stops should however increase this proportion. But the number of coincidences of first and forth syllables matches exactly the 20%. At higher sound levels total stop duration decreases, mainly because single stops are shorter. No preferred time relationship can be seen here, either.

Therefore cricket females seem to stop at random in relation to the calling song. They do not use the timing of stops to improve their orientation. It should also be noted, that stops unnecessarily occur also at high sound levels, as has already been noted earlier (SCHMITZ et al. 1982). These stops (in our conditions 10 to 15% of the total run) would prolong the phonotactic approach and increase the danger of predators.

The current conception has been formulated as follows: „It may well be that the commonly observed stop-orient-and-go strategy of crickets in the field, in an arena, or on the walking compensator reflects an adaptation to orient at low sound intensities..." (SCHILDBERGER et al. 1989: p. 441). This view is still suggestive. However, experimental evidence is not explicit so far.

In such a situation the thought arises, whether the question has been posed partly wrong or too narrow. Are the stops really an adaptation to the phonotactic situation? It

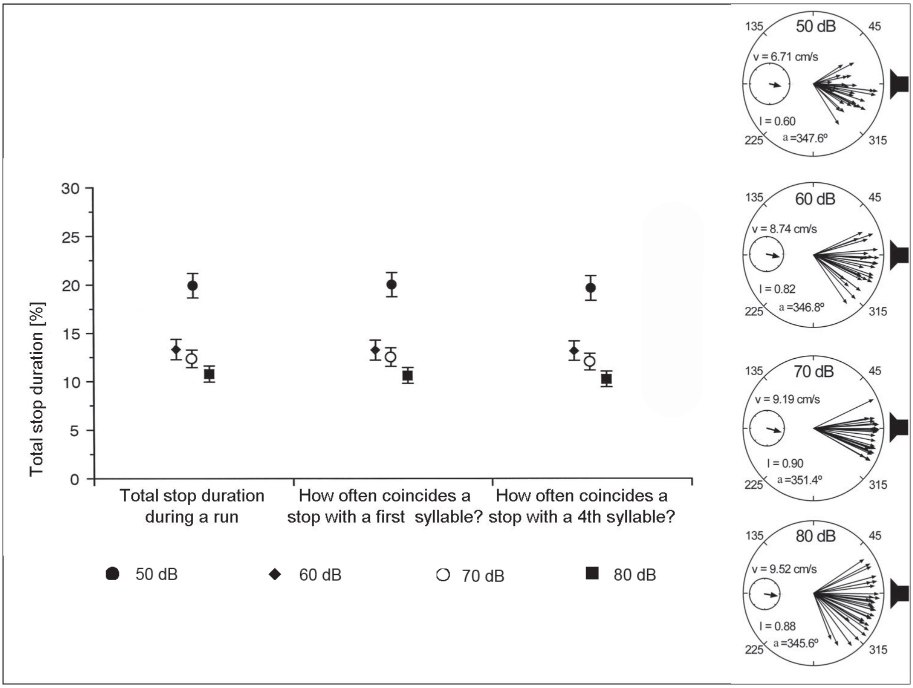

Fig. 6: Test for preferred time relationship between stops and chirps. *Gryllus bimaculatus* females were tested at 50 dB (27 females which performed 6755 stops), 60 dB (n = 26, 5699 stops), 70 dB (n = 25, 5306 stops) and 80 dB (n=30, 6156 stops). Each run is represented by a vector. Its direction is the line connecting the starting point with the endpoint of the 5 min run. The length is calculated as the quotient of the distance (shortest line) between the two points and the actual path length. It serves as a measure of the degree of orientation with values between 0 and 1. a = mean vector direction, l = mean vector length, both shown in the small circle. v = mean walking speed. See text for further explanations.

Abb. 6: Test auf bevorzugte Zeitbeziehungen zwischen Stopps und Versen. Es wurden *Gryllus bimaculatus* Weibchen bei folgenden Schallintensitäten getestet: 50 dB (27 Weibchen mit 6755 Stopps), 60 dB (n = 26, 5306 Stopps), 70 dB (n = 25, 5306 Stopps) und 80 dB (n = 30, 6156 Stopps). Jeder fünfminütige Lauf wird durch einen Vektor repräsentiert, dessen Richtung durch die Verbindungslinie zwischen Start und Laufende bestimmt wird. Seine Länge ist durch den Quotient der Länge dieser Linie durch die tatsächliche Laufstrecke gegeben. Die Vektorlänge dient als Maß für die Genauigkeit der Orientierung, wobei die Werte zwischen 0 und 1 liegen. a = Richtung des mittleren Vektors, l = Länge des mittleren Vektors, beide im kleinen Kreis. v = mittlere Laufgeschwindigkeit. Siehe Text für weitere Erläuterungen.

turns out, and has been known for a long time, that crickets perform stops also in non-phonotactic contexts. Figure 8 gives an example of a *G. bimaculatus* male. This example has been chosen because it shows that slow walking males make stops and can at the same time produce 2- 4-syllable chirps. Females also interrupt their random walk by stops when no calling song is presented (Schmitz et al. 1982). Figure 7 gives an example of this situation.

In the case of crickets one could argue that they stop in order to explore whether a faint calling song of a potential mate or conspecific competitor can be heard. However, other species exhibit the same walking pattern,

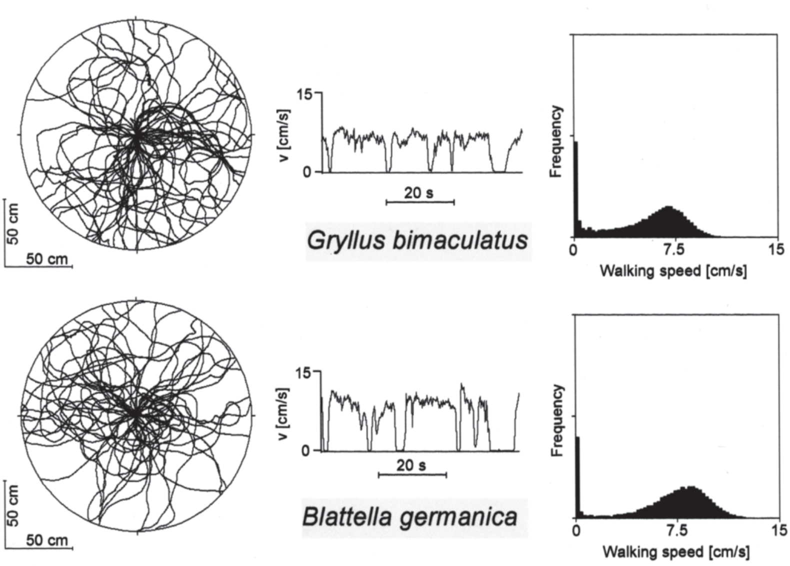

Fig. 7: Examples of single unorientated runs of a female cricket and a cockroach female. The runs on the locomotion compensator were performed in darkness and without sound or other orienting signals. Left: When the animal reaches the distance of 1 m from the starting point, the drawing of the track is being reset to the starting point. Middle: Walking speed over time. Right: Walking speeds are calculated every 0.2 s and shown as relative frequencies. N = 4500. Note the broad distribution of speeds, the complete stops and the transitions between both.

Abb. 7: Beispiel eines unorientierten Laufs eines Grillenweibchens und eines Schabenweibchens auf dem Lokomotionskompensator. Die Läufe erfolgten im Dunkeln und ohne Schall oder andere orientierende Reize. Links: Wenn das Tier 1 m vom Startpunkt entfernt ist, wird die Laufspur auf den Startpunkt zurückgesetzt. Mitte: Laufgeschwindigkeit als Funktion der Zeit. Rechts: Die Laufgeschwindigkeiten werden alle 0,2 s ermittelt und als relative Frequenzen dargestellt. N = 4500. Zu beachten sind die relativ breite Verteilung der Laufgeschwindigkeiten sowie die Stopps in der Null-Klasse und die Übergänge zwischen beiden.

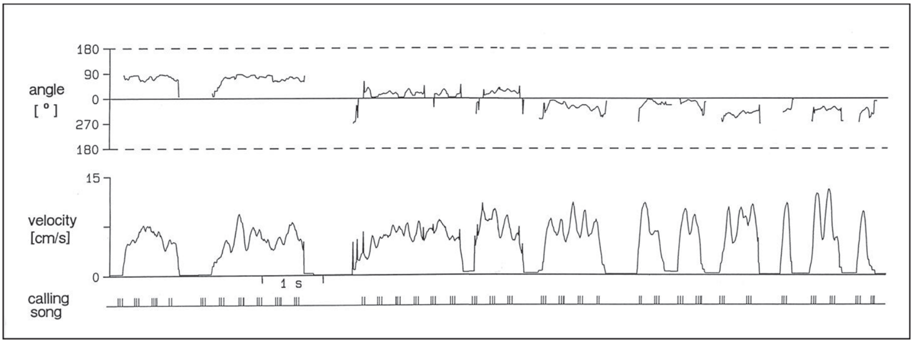

Fig. 8: Stop and go of a *Gryllus bimaculatus* male. This example has been chosen in order to demonstrate that males can produce a calling song during walking. In this example the chirps consist of 2 to 4 syllables. Top trace: walking direction.

Abb. 8: Lauf und Stopp eines *Gryllus bimaculatus* Männchens. Dieses Beispiel wurde gewählt, um zusätzlich zu zeigen, dass ein Männchen auch während des Laufens singen kann. In diesem Beispiel bestehen die Verse aus zwei bis vier Silben. Obere Spur: Laufrichtung.

such as the cockroach female in figure 7. All walking parameters can be so similar that it is not possible to determine the species from the walking behaviour. Some other insect species such as the cricket *Acheta domesticus* or the beetle *Carabus auratus* show similar walking modes (Wendler et al. 1984; Wendler 2003). The reason for the general stop-and-go behaviour in some species is unknown so far.

One other aspect of the walking behaviour is noteworthy. In phonotaxis, females raise their walking speed with increasing sound pressure level (Schmitz et al. 1982; Wendler & Löhe 1993). The proportion of the total time, in which the female is walking and not stopping (relative walking time), also increases (Wendler & Löhe 1993). Both parameters have been described as a function of sound pressure intensity with the idea that they could serve as a measure for increased motivation due to increased sound intensity. Crickets can, however, vary their speed also in a non-phonotactic situation within a wide range. It turns out that the relative walking time in this case also increases with speed (Fig. 9). The same is true for the cockroach *Blattella germanica*, although *B. germanica* reaches the higher values already at lower walking speeds. This correlation may therefore be a general property of the walking system and not restricted to phonotaxis.

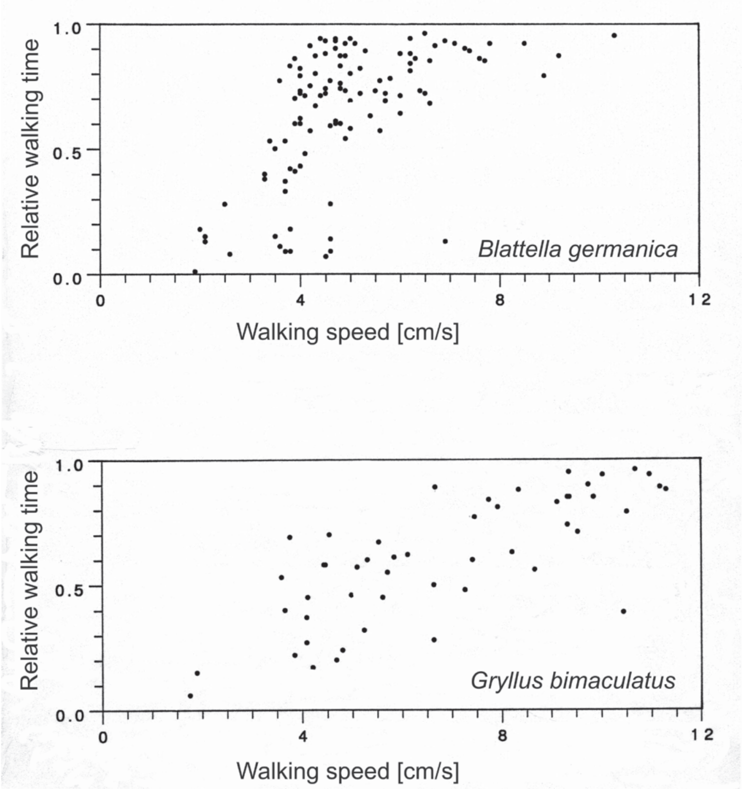

Fig. 9: Relative walking times as a function of walking speed. Relative walking times are calculated as the time the animal is walking divided by the total time of walking plus stopping.

Abb. 9: Relative Laufzeiten als Funktion der Laufgeschwindigkeit. Die relative Laufzeit ergibt sich aus der tatsächlichen Laufzeit im Experiment, geteilt durch die Gesamtzeit des Experiments (Laufzeiten + Stoppzeiten).

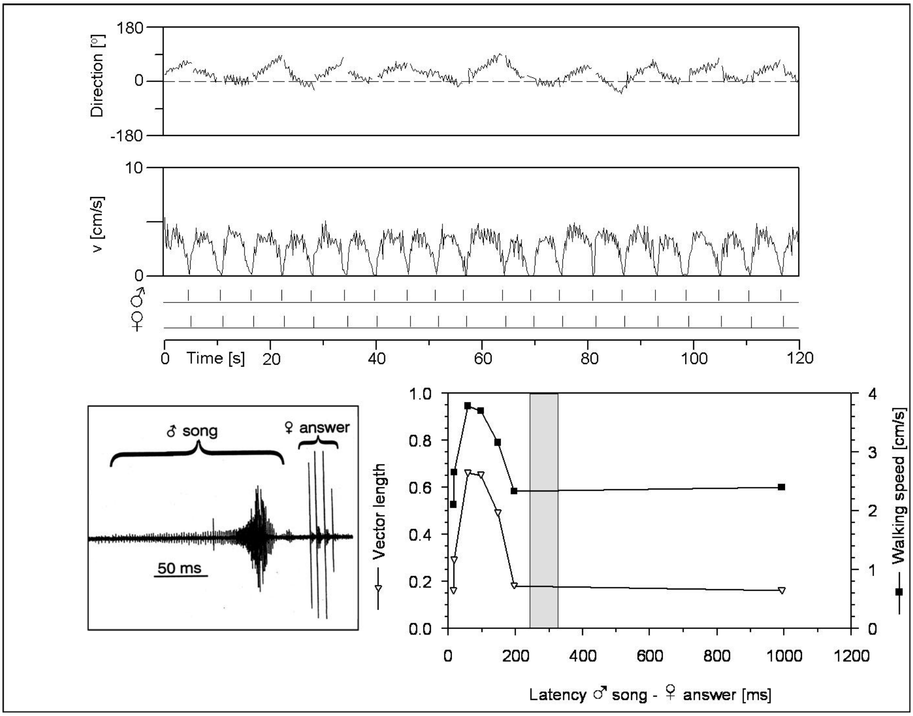

Fig. 10: Phonotaxis of *Poecilimon affinis*. Lower left panel: Oscillogram of a male calling song and female response (latency depends upon distance). To generate the female response signal, the natural female signal was tape-recorded, digitized and stored as a file. The presentation of the female signal was triggered by the male song, which was picked up by a bat detector microphone. Upper graph: Walking speed and direction of a male in a low contrast environment. The female "response" click is given by the loudspeaker at 0 degrees. Latency male song-female response is adjusted to 80 ms. Lower right panel: Walking speed and vector length as a function of latency. Both variables are a measure of male motivation. They increase to a maximum about 80 ms after start of the male song and decrease already before the male starts walking again (shaded area). For further explanations see text. After v. HELVERSEN & WENDLER 2000.

Abb. 10: Phonotaxis von *Poecilimon affinis*. Links unten: Oszillogramm des Gesangs eines Männchens und der Weibchenantwort, deren Latenz zum Männchengesang einstellbar ist. Um die Weibchenantwort zu generieren, wurde die natürliche Weibchenantwort auf Band aufgenommen, digitalisiert und als Datei gespeichert. Die Präsentation der Antwort wurde durch den Männchengesang ausgelöst, der über ein Fledermausmikrofon aufgenommen wurde. Oberes Diagramm: Laufgeschwindigkeit und Richtung eines Männchens in einer Umwelt mit geringen visuellen Kontrasten. Lautsprecherposition bei 0 °. Der Antwortklick des Weibchens wird durch den Lautsprecher übermittelt. Die Latenz zum Beginn des Männchengesangs ist in diesem Lauf auf 80 ms eingestellt. Diagramm unten rechts: Laufgeschwindigkeit des Männchens und Vektorlänge als Funktion der Latenz. Beide Variablen sind ein Maß für die Motivation des Männchens. Ihr Maximum liegt bei etwa 80 ms nach dem Start des Männchengesangs und sinkt wieder auf den Ausgangswert bevor das Männchen erneut startet (schattierter Bereich). Für weitere Erläuterungen siehe Text. Nach v. HELVERSEN & WENDLER 2000.

So it seems that the stop-and-go walking is primarily not an adaptation to cricket phonotaxis. It could serve, however, as a starting feature for the evolution of specific open loop types of phonotaxis, such as in *Scapsipedus marginatus*, or in many phanopterine species (Heller & v. Helversen 1986). In the bushcricket *Poecilimon affinis* (Tettigoniidae), the male walks on a locomotion compensator with a relatively low speed and stops at intervals of 10 to 20 s, calls, and then continues walking (v. Helversen & Wendler 2000). As soon as it receives a female answer, consisting of a few short clicks, it turns to the direction of the female, walks for 10 to 20 s, stops, then calls, subsequently redirects its position and resumes the approach. Stop duration is about 250 to 300 ms. A male responds only if the females response occurs within this time window. As a result, the male approaches selectively only the female which responds to his own calling song. In the case of *P. affinis* (Fig. 10), we observe a highly ritualised phonotaxis with a clear function of stops.

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