A relationship between wing beating rate in flight and during sound emission in some species of Ensifera (Insecta, Orthoptera)

P.V. Ozerski*, E.E. Shchekanov**

Соотношение между частотой биения крыльев при полете и при звукоизлучении у некоторых видов Ensifera (Insecta, Orthoptera)

П.В. Озерский*, Е.Е. Щеканов**

*A.I. Herzen State Pedagogical University of Russia, St. Petersburg, 191186, Russia (Российский Государственный Педагогический университет им. А.И. Герцена, С.-Петербург, 191186, Россия); e-mail: ozerski@list.ru
** I.M. Sechenov Institute of Evolutionary Physiology and Biochemistry, Russian Academy of Science, St. Petersburg, 194223, Russia (институт эволюционной физиологии и биохимии им. И.М. Сеченова РАН, С.-Петербург, 194223, Россия); e-mail: shchek@insect.ief.spb.su

Abstract. Comparative analysis of wing beating rate in 8 species of katydids and crickets during stridulation and in flight has demonstrated that their rhythms during sound emission and in flight do not coincide. Possible causes of this discrepancy and ways of the evolution of sound emission are discussed.
Key words. Ensifera, Gryllidae, Tettigoniidae, flight, sound emission.

Резюме. Сравнительный анализ частоты биения крыльев при стрекотании и в полете у 8 видов кузнечиков и сверчков показал, что свойственные им ритмы при звукоизлучении и в полете не совпадают. Обсуждаются возможные причины этого несоответствия и пути эволюции звукоизлучения.
Ключевые слова. Ensifera, Gryllidae, Tettigoniidae, полет, звукоизлучение.

Introduction

Insects produce sounds in various ways (Zhantiev, 1981; Popov, 1985). One of these manners is stridulation during which sounds are produced by rhythmic frictions of forewings against each other (in crickets and katydids) or legs over forewings (in acridid grasshoppers). Sounds produced during this type of sound emission are arranged in a rhythmic sequence of short pulses (syllables) which may be grouped in chirps. Pulse and chirp rates are defined by a neural activity pattern and controlled by the central nervous system.

Presence of the elytral (forewing) stridulatory apparatus is typical for sound-producing crickets and katydids (Ensifera). According to Gorochov (1995), this sound-producing organ was present already in a Mesozoic Orthoptera family, Hagloedischiidae, which is considered to be the ancestral group for all recent Ensiferan insects. It seems very likely that also the whole acoustic communication system in most recent crickets and katydids was inherited from the common ancestors. Therefore, one may suppose that the principles of its formation and further evolution can be defined by common physiological mechanisms.

According to current concepts, rhythmic locomotor activity in insects, including the forewings movements in stridulation, is controlled by rhythm generators which consist of cells or cell groups (Sviderskii, 1999). Apparently, different kinds of locomotor activity originated at different times during

evolution. It is evident that stridulation emerged well after walking or flight and by the time of stridulation origin insects already possessed a set of rhythm generators. Thus, a new generator for stridulation could either originate independently or as a derivative of one of the already existing generators. Due to the fact that in crickets the neuromuscular apparatus involved in flight and stridulation is essentially the same (Huber, 1962), one may suppose, that most probably, the central flight rhythm generator would be used for stridulation coordination.

Huber (1962) demonstrated that in the field cricket, *Gryllus campestris* L., approximately the same forewings vibration rate (20–30 Hz) occurs under conditions of tethered flight (induced by stimulation of the insect head with an air stream provided that a contact between the legs and substrate was lost) and during stridulation. On the basis of community of the neuromuscular apparatus subserving flight and stridulation and also on the basis of experiments with different kinds of central nervous system and conduction tracts dissections, Huber came to a conclusion that in crickets stridulation movements are closely related to wing movements in flight. He concluded also that control of both kinds of movements provided by central nervous system is organized to function in the similar manner. The main difference between these two kinds of movements is that in flight wings are moving continuously while during stridulation their movements are more or less rhythmically interrupted.

Kutsch (1969) investigated in detail electrical activity of wing muscles during stridulation or induced flight in some cricket's species. In *G. campestris* wing muscle potentials followed with the same frequency (~ 30 Hz) both in flight and in stridulation. On the basis of this data he postulated the existence of two rhythm generators (oscillators) in the cricket's central nervous system. According to Kutsch the faster oscillator (~ 30 Hz) defines wing beating rate in flight and pulse sequence rhythm in stridulation. The slower oscillator (3–4 Hz) defines grouping of the calling song pulses in chirps. However, in the same work Kutsch found that in another cricket species, *Acheta domesticus* (L.), the rhythms of wing beating in flight and during stridulation did not agree so well.

Elsner & Popov in their review (1977) considered the problem of the origin of stridulatory rhythm generator and, referring to Huber's and Kutsch's data, also supposed that stridulation pattern appeared on the basis of pre-exisiting motor patterns, like flight pattern, with a possible subsequent modification of the temporal structure of acoustic signal due to inclusion of additional oscillators.

Hennig (1989, 1990a, b) investigated neuronal and muscular electrical activity during stridulation and in flight in the Australian cricket, *Teleogryllus commodus* (Walk.). Hennig compared the electrical activity of the meso- and metathoracic ganglion neurons during stridulation and flight, induced by electrical stimulation of the brain structures and by stimulating cerci with air puffs, correspondingly. The characteristic features of neuron reactions during both kinds of muscular activity brought Hennig to a conclusion that flight and stridulation in *T. commodus* are served by different pools of mesothoracic ganglion interneurons. Like most *Teleogryllus* Chop. species, *T. commodus* has two-component acoustic signals, and each component of these signals is characterized by its own duration of the pulse repetition period. Hennig raised a question about the number of oscillators involved in calling song generation in this species, but the question remained open.

According to current concepts, the neuronal part of the sound generating system in Orthoptera consists of a central neuron (or neurons) located in the brain and a group of interneurons located in the mesothoracic ganglion and connected to motoneurons controlling the wing muscles movements (Hedwig, 1996, 2000). The command neurons were identified (Hedwig, 2000). It was demonstrated that stridulation start and termination depend on their activity level (spike frequency) which, however, was not locked to the pulse period in the calling song. The latter parameter which is fundamentally important for calling song recognition by females is defined by the characteristics of mesothoracic ganglion interneurons not identified yet. The neuronal structure of the flight central rhythm generator in crickets and katydids is also yet not identified. In the Acridoidea (Orthoptera: Caelifera) grasshoppers posessing a different type of stridulatory apparatus, it was demonstrated that their flight wings movement generator is located, most probably, in the mesothoracic ganglion (Wolf, Pearson. 1987).

Despite the attractiveness of the hypothesis postulating a common central rhythm generator for flight and stridulation, direct experimental data confirming it were obtained for only one cricket species, *G. campestris* (which is unable to fly under natural conditions!). Therefore, we considered it desirable to investigate the problem of relation between the stridulation and flight rhythms in a broader set of

Ensiferan species. We assumed that in case of existence of a common rhythm generator involved both in stridulation and flight similar rhythms of wing movement during both processes should be observed whereas in case of two independent generators these rhythms might be different. The present paper provides data on these rhythms in different species of katydids (Tettigonioidea) and crickets (Grylloidea).

Materials and methods

The following taxa of Ensifera were investigated: katydids of the subfamily Tettigoniinae (super-family Tettigonioidea, family Tettigoniidae) from the tribes Tettigoniini [(1) *Tettigonia cantans* (Fuessly) – 1 male from St. Petersburg environs; (2) *T. viridissima* (L.) – 1 male raised from a larva originated from Astrakhan environs], Decticini [(3) *Decticus verrucivorus* (L.) – 3 males from St. Petersburg], Platycleidini [(4) *Platycleis grisea* (Fabr.) – 2 males raised from larvae originated from Astrakhan environs; (5) *Bicolorana roeselii* (Hag.), f. macroptera – 1 male from Novgorod Region]; crickets of the subfamily Gryllinae (superfamily Grylloidea, family Gryllidae) from the tribe Gryllini [(6) *Gryllus bimaculatus* (De Geer) – 1 male from a laboratory culture of Sechenov Institute of Evolutionary Physiology and Biochemistry; (7) *Gryllus* sp. of the American origin – 2 males from a laboratory culture of the same institute; (8) *Acheta domesticus* (L.) – 9 males from a laboratory culture of the same institute].

Acoustic signals (calling songs, CS) were recorded under air temperatures between 19 and 28 $^{\circ}$C using analogous tape recorders Panasonic RQ-L349. Recorded signals were loaded into personal IBM-compatible computer and pulse periods were measured with help of the specially developed software. Periods of wings beating in tethered flight were determined with an original set-up based on an optical registering device developed by us earlier (Ozerski, Shchekanov, 2005). Wing movements in tethered flight were recorded under the same temperature conditions as the calling song recording for these individuals. Oscillations of the envelope of the output signal were analyzed in the same way as the calling songs. A diagram to illustrate measuring the repetition periods of acoustic pulses and wing beatings in flight is presented in Fig. 1.
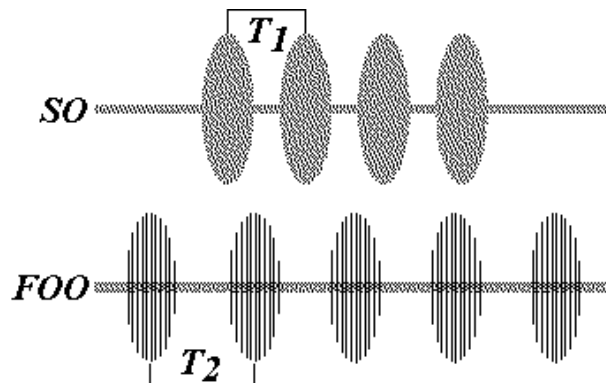

Fig. 1. Schematic diagram of rhythms measurements. SO – sound oscillogram; FOO – flight optical oscillogram; T1 – pulse repetition period during stridulation; T2 – wing beating period during flight.

A degree of the accordance of wings movement rhythms during sound emission and in flight was determined using the Spearman rank correlation coefficient. In case when the calling song contained two rhythmical components (*T. viridissima*, *D. verrucivorus*) pulse repetition periods for each component and for their sum were analyzed separately.
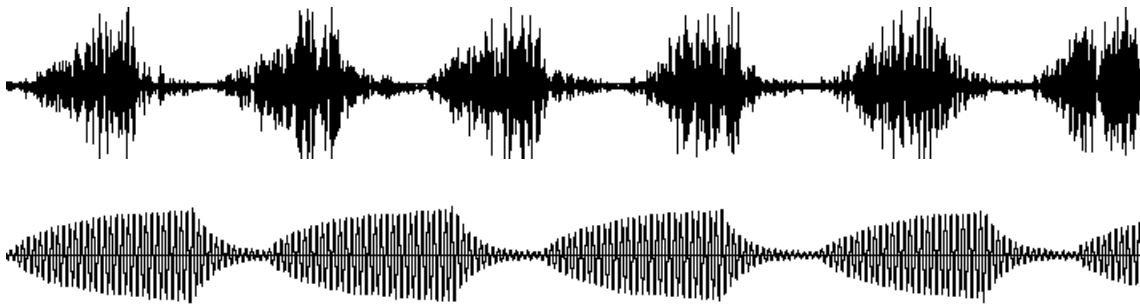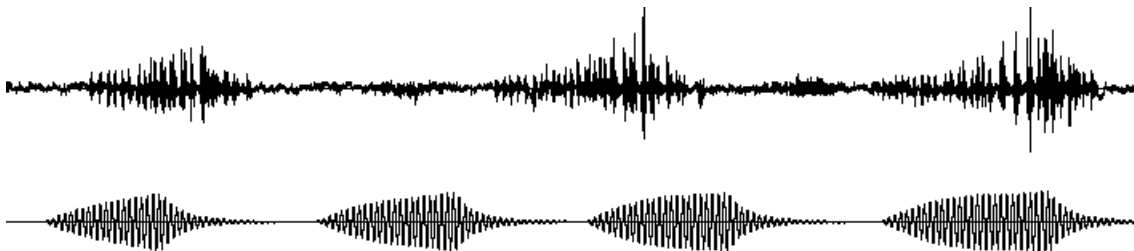
a. Tettigonia cantans
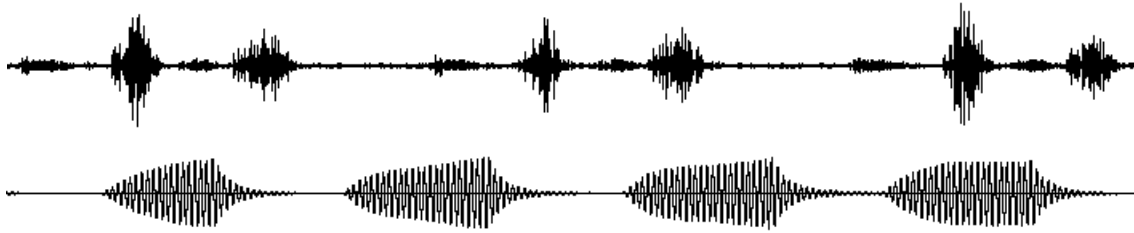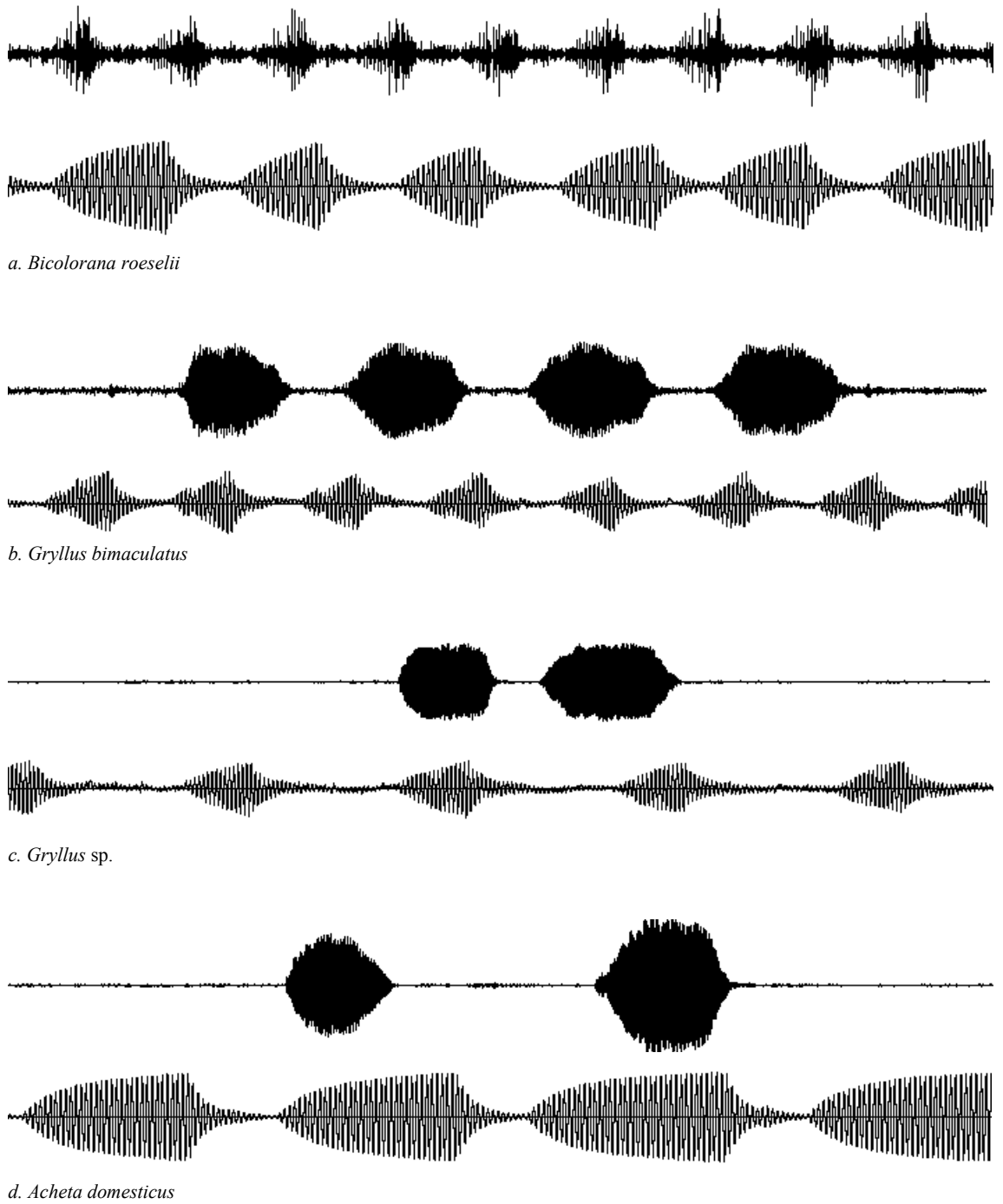

b. Tettigonia viridissima
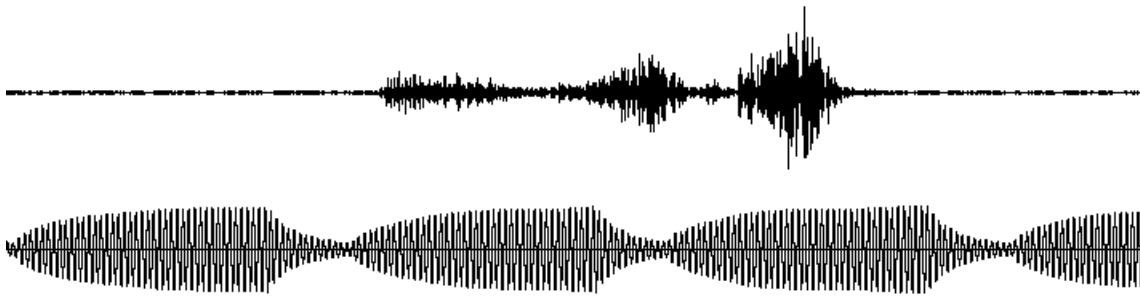
c. Decticus verrucivorus

d. Platycleis grisea

Fig. 2. Each pair of recordings shows oscillograms of the katydids calling songs (top) and the wing beatings recorded in flight (bottom) in the investigated Ensifera species. Duration of all records is 200 ms.

a. Bicolorana roeselii

b. Gryllus bimaculatus

c. Gryllus sp.

d. Acheta domesticus

Fig. 3. Each pair of recordings shows oscillograms of the katydids and crickets calling songs (top) and the wing beatings recorded in flight (bottom) in the investigated Ensifera species. Duration of all records is 200 ms.

Results

Katydids (Tettigonioidea)

All katydids studied, except *B. roeselii*, under natural conditions use a short gliding flight in combination with jumping in dangerous situations. Under tethered flight conditions they can demonstrate a stable flight lasting up to several dozens of seconds.

T. cantans (Fig. 2, a). The calling song is a long trill (from several seconds to dozens of minutes).

T. viridissima (Fig. 2, b). The calling song is a long trill consisting of pairs of pulses.

D. verrucivorus (Fig. 2, c). The calling song is a sequence of chirps consisting basically of three pulses with different durations strongly modulated in amplitude.

P. grisea (Fig. 2, d). The calling song is a sequence of chirps consisting of several similar pulses weakly modulated in amplitude.

B. roeselii (Fig. 3, a). Most specimens under natural conditions are unable to fly due a partial wing reduction. Occasionally founded macropterous specimens as a rule also do not show flight activity under natural conditions, only few specimens used gliding flight in danger. Under tethred flight conditions macropterous specimens can demonstrate a stable flight with duration up to several dozens of seconds. The calling song is a long trill (from several seconds to dozens of minutes).

Crickets (Grylloidea)

All cricket species studied under tethered flight conditions can demonstrate a stable flight with duration up to several dozens of seconds.

G. bimaculatus (Fig. 3, b). These crickets fly actively under natural conditions, they use flight for dispersal and settling. The calling song of this cricket is a sequence of chirps basically consisting of 3–5 pulses similar in their duration and weakly modulated in amplitude.

Gryllus sp. (Fig. 3, c). The ability of this species to fly in nature is unknown for us. The calling song of this cricket is a sequence of chirps basically consisting of two pulses similar in their duration and weakly modulated in amplitude.

A. domesticus (Fig. 3, d). In nature young specimens of this species use active flight for settling but subsequently loss their flying ability (Chudakova, Bocharova-Messner, 1965). The calling song of this cricket is a sequence of chirps basically consisting of two pulses similar in their duration and weakly modulated in amplitude.

Comparison of rhythms (the periods of acoustic pulses and wing beatings in flight) based on data from 16 specimens belonging to 8 species, 6 genera, 4 tribes and 2 superfamilies showed an absence of statistically significant correlation between these rhythms ($r^2 < 0.03$, $p > 0.05$) (Fig. 4).

Discussion

Our data clearly demonstrate an extremely low correlation between the wing beating rhythms in flight and during stridulation. These results allowed us to make a conclusion about either full independence of neuronal regulation of these rhythms or, at least, about strong differences in the modulation of the activity of the central rhythm generator in two different behaviors – stridulation and flight. Therefore one can suppose that the similarity between these rhythms described earlier for forewings movements during sound emission and in flight is true only for the species *G. campestris* and is, obviously, the unique feature of this species.

In addition, our conclusion about independence of the mechanisms of generation of wing beating rhythm during sound emission and in flight for Ensifera corresponds well to data on other species. Some
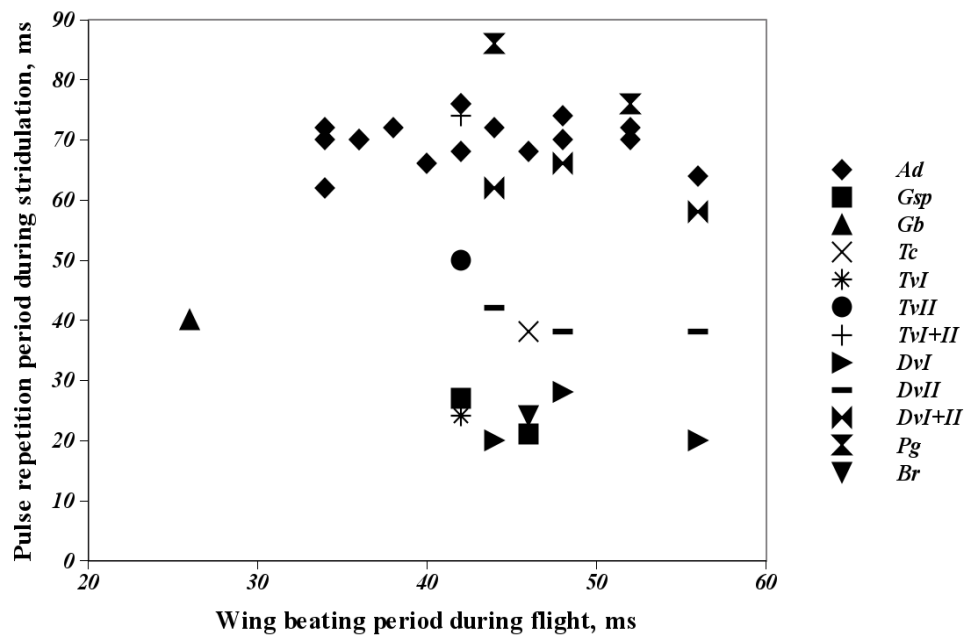
Fig. 4. Relation between the rhythm of wing movements in flight and during sound emission. Abbreviations: *Ad* – *A. domestica, Gsp* – *Gryllus sp., Gb* – *G. bimaculatus, Br* – *B. roeselii, Dv* – *D. verrucivorus, Pg* – *P. grisea, Tc* – *T. cantans, Tv* – *T. visidissima*. Each specimen is represented by one or three marks, according to the signal structure (one or two rhythms). Roman numbers correspond to different signal components.

cricket species posess signals with a regularly changing pulse rhythm during sound emission. The most typical from this point is the genus *Teleogryllus* Chop., where species have calling songs consisting typically of two components with different and even not multiple pulse repetition periods (Otte, Alexander, 1983; Otte, Cade, 1983; Hennig, 1989). This type of song, in our opinion, practically excludes the possibility to use only one common rhythm generator both for flight and stridulation.

The existence of separate central rhythm generators for wings movement in flight and in stridulation does not exclude a possibility of their phylogenetic community. If, following Huber (1962) and Kutsch (1969), we would suppose that stridulation developed on the basis of flight, then, most probably, originally both kinds of wing movement activity were served by the same central rhythm generator. On this stage of evolution stridulation, apparently, had two important features: first, the range of possible forewing movement rates was restricted by values suitable also for flight, second, this rhythm could be unstable and depend, for instance, on signals coming from wind-sensitive receptors as it happens in flight (Hedwig, Pearson, 1984). Such features of acoustic communication could not provide stability of species-specific signal characteristics and, thus, could not be effective for tuning away from signals of different species and for formation of different acoustic niches. But on the early stages of acoustic communication the problem of the identification of conspecific signals in the complex acoustic environment was not urgent for the ancestors of Ensifera because other singing species were absent. At the same time the natural selection must favour to louder male acoustic signals because it should increase their effectiveness in attracting females. Thus, already on this evolution stage preconditions existed for emergence and improvement of the wing stridulation apparatus as a specialized morphological structure. Afterwards, when multi-species communities of the singing insects appeared and the pulse repetition period in the calling song became a critical species-specific feature providing recognition of specimens of the own species, then separate, specialized rhythm generators for stridulation could arise, particularly for the independence from the variable flight rhythm and for attaining high own rhythm stability necessary for interspecific isolation.

Acknowledgements

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