J Comp Physiol (1983) 153:393–401

Journal
of Comparative
Physiology · A

Song recognition and song pattern in a shorthorned grasshopper

O. Skovmand[1] and S. Boel Pedersen[2]
[1] The Danish Pest Infestation Laboratory, Skovbrynet 14, and,
[2] The Acoustics Laboratory, Technical University of Denmark DK-2800 Lyngby, Denmark

Accepted June 10, 1983

Summary. 1. Computer generated, artificial songs (Fig. 1) were played to grasshoppers of the gomphocerine species *Omocestus viridulus* L. in a temperature-regulated, echo-reduced chamber (Fig. 2). The animals often responded by singing their response song, and the occurrence of response songs was used to indicate the animals' preference for the artificial songs. At various temperatures, the chirp duration and impulse rate preferred by the animals were determined and compared with the magnitudes of these parameters in the response songs.

2. The duration of the response songs decreases with temperature (Fig. 5), and so does the chirp duration (Fig. 3). The chirp rate (which in this species is the reciprocal of the chirp duration) decreases during a response song (Fig. 6).

3. In the first experiments the chirp duration was varied in the artificial songs, while the ratio chirp rate to impulse rate was kept constant (as in the natural songs). The preferred chirp duration changes more with temperature than does the chirp duration of the response songs (Fig. 3). At all temperatures, songs with chirp durations half or double of the preferred one could also release a response song. The animals even responded to chirp durations outside the natural range (Fig. 3).

4. In the second experiments, the chirp rate (C) and impulse rate (I) at 28 °C (C_{28} and I_{28}) and 38 °C were combined into four different songs: $C_{28}I_{28}$, $C_{38}I_{38}$, $C_{28}I_{38}$ and $C_{38}I_{28}$. The former two songs correspond to the natural songs at 28° and 38 °C, whereas the latter ones are artificial. The temperature of the listening animals was also varied. The choices made by femal grasshoppers showed that the chirp rate is the major parameter and the impulse rate the minor parameter in determining the acceptance of a song.

5. Four different criteria for measuring the female song discrimination were compared: (a) the behavioural threshold (i.e. the sound level of an artificial song which is just sufficient for response songs to be released in the females), (b) response or no response, (c) the number of response songs in a response, and (d) whether the response was given to the 1st, 2nd or 3rd song presentation. (a) was more sensitive than (b), and both gave rather similar results. In (c) and (d) the responses appeared to be independent of the type of songs presented.

6. The behavioural threshold increased before and decreased after egg deposition (Fig. 7).

Introduction

The mechanisms responsible for song generation and song recognition in orthopterans are normally well adjusted to each other (review: Elsner and Popov 1978). In crickets, cross-breeding experiments led to the idea that the neuronal template responsible for the song generation may also function as part of the song recognition system (Bentley and Hoy 1974). In contrast, in gomphocerine grasshoppers (Acrididae) there is no strict genetic or physiological coupling between the two mechanisms (Helversen and Helversen 1975b).

The gomphocerine grasshoppers are a group of shorthorned grasshoppers with a complicated song repertoire. These grasshoppers are able to distinguish between the conspecific songs and the songs of other species, and they are also able to distinguish between different song types of their own. Both males and females may respond to

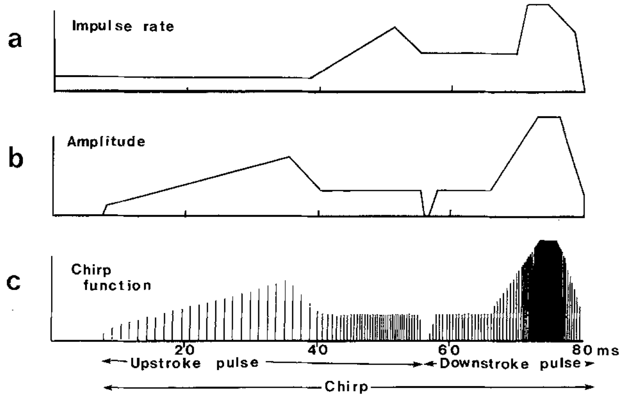

Fig. 1a–c. Synthesis of an artificial song. The impulse rate (**a**) and the amplitude (**b**) are used for the synthesis of the chirp function (**c**). In the final synthesis, each vertical line is replaced by an impulse isolated from a male calling song (not shown)

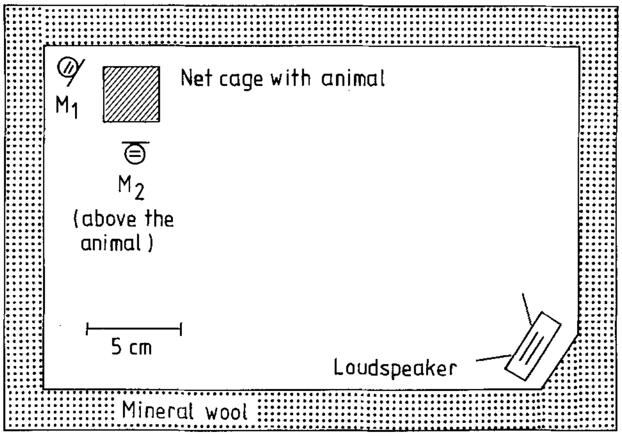

Fig. 2. Schematic diagram of the experimental set-up. The mineral wool is lining a temperature-regulated chamber. M_1 and M_2, microphones

songs by singing response songs. The songs are produced by stridulation, a process in which a row of teeth on a file passes over a scraper. Each impact of a tooth against the scraper produces a short 'click': the *impulse*. A train of impulses is named a *pulse*, and the pulses produced by a whole up-and-down movement of the leg constitute a *chirp* (Fig. 1c).

In grasshoppers producing discontinuous songs, i.e. with pauses between the pulses or chirps, the repetition rate of the chirps (the *chirp rate*) and the *pulse duration* are known to be the main sound parameters carrying behavioural information (von Helversen 1972). In contrast, in the grasshoppers producing songs without pauses between pulses or chirps, the chirp rate (which is here reciprocal to the chirp duration) is a main parameter. At least for these grasshoppers, behavioural information may also be carried by the impulse repetition rate, the *impulse rate* (Skovmand and Pedersen 1978). The impulse rate appears to be perceived as changes in the frequency spectrum of the songs, as proposed by Michelsen (in Elsner 1974).

In our earlier experiments we used artificial songs with a chirp rate corresponding to that of the natural song at 28 °C combined with an impulse rate corresponding to 28 °C or to one half of the 28 °C impulse rate. Receptive females tested with these songs at 28 °C seemed to prefer the normal combination of chirp rate and impulse rate.

We now report experiments, in which the preference of the animals for some of these parameters is investigated by means of a battery of artificial songs. In some of these songs, the combination of chirp rate and impulse rate corresponds to that of the natural song at a certain temperature, whereas in other songs unnatural combinations are used. The results elucidate the mechanism of song recognition and its relationship to the mechanism of song production.

Methods and materials

Males and females of the gomphocerine grasshopper *Omocestus viridulus* L. (Gomphocerinae, Uvarov) were collected as nymphs during summer or raised during winter. The two sexes were separated from the final nymph stage. The animals were kept in boxes (20 × 30 × 15 cm) with sand and grass. About a week after the final moult the females became receptive and responded to male calling song by singing their response song. The males started singing just a few days after the final moult.

The set-up was similar to that used by von Helversen and von Helversen (1975b). The test animal was placed in a small mosquito net box (5 × 5 × 5 cm) with fresh food. A climate cabinet (Heräus, type 360) was used as test room (Fig. 2). The walls of the cabinet were covered with 5 cm mineral wool to reduce echoes. A 10 cm thick layer of mineral wool was placed behind the loudspeaker. Because of the mineral wool and the arrangement of the loudspeaker and net box, the echo was about 20 dB below the signal (in the range 5–40 kHz). The inner diameter of the lined, cylindrical cabinet was 30 cm. The distance between the loudspeaker and the grasshopper was 15–20 cm.

During the sound recordings a microphone (M 2 in Fig. 2) was placed 15 cm above the animal. This microphone was removed during the song discrimination experiments to avoid echo and heating from the pre-amplifier of the microphone (B & K, 4133). The signals were band-pass filtered, 5 to 20 kHz and recorded on tape. During the song discrimination experiments another microphone (M 1 in Fig. 2) was placed close to the net box. The pre-amplifier of this microphone does not heat the surroundings (B & K, 2642). The cabinet was lighted by a lucid rod; a blue glass filter reduced light heating of the animals. Measurements with a calibrated thermistor (U23UD, ITT, diameter 0.5 mm) in the cabinet and in 3 live, non-singing female grasshoppers showed that the temperature in the cabinet and in the grasshoppers fluctuated less than 0.5 °C during each experiment.

All experiments were controlled by a computer (PDP 8/I). The test signals recorded on different channels on the tape recorder were chosen by a random choice programme in which the 6 or 4 channels were used one after the other in a random sequence. The number of sequences could be varied.

Analysis of response songs. The chirp rate and impulse rate in the response songs of the males were measured at various temperatures. The response song is identical with the male calling song (Skovmand and Pedersen, in preparation). The chirp rate was monitored continuously during the song. The actual RMS-value of the song was determined using an integration time of 1 ms (Skovmand and Pedersen 1978). A spectrum analysis of the RMS-signal performed every 1.3 s then indicated the chirp rate with an uncertainty of ± 0.1 Hz.

The impulse rate was determined by means of a computer programme made by P. Schiolten (Institute of Biology, Odense University) on short series of chirps taken from recorded songs.

Generation of artificial songs. Two groups of artificial songs were generated on the computer by repeating a natural impulse at proper rates and amplitude modulations (Fig. 1). The signals were low-pass filtered at 40 kHz and recorded on a multichannel tape recorder (Philips Analog 7) from which they were replayed to the grasshoppers through a condenser loudspeaker designed for this study (see Skovmand and Pedersen 1978).

In the songs made for the first experiments the chirp rate and impulse rate varied, but the ratio of the rates was constant (as in a natural song). The chirp durations of the songs were: 166, 128, 102, 83, 64, 51, 42, and 32 ms. Only six songs were used in each experiments, and either the two longest or the two shortest chirp durations were omitted.

In the songs made for the second experiments the chirp rate and impulse rate varied independently. The four songs in these experiments can shortly be described by indices refering to temperature: $C_{28}I_{28}$, $C_{28}I_{38}$, $C_{38}I_{28}$, $C_{38}I_{38}$. C_{28} is the chirp rate of a natural song at 28 °C, etc. Of these four songs the first and the last song correspond to natural songs, whereas the two middle songs present unnatural combinations of the two parameters.

Test procedure. The song presentation in the experiments designed for testing the two groups of songs was slightly different. In the first experiments a grasshopper was presented to six songs in a random order. Each song was presented four times. All songs were presented at the same sound level. When the grasshopper responded to a test song, the computer recorded the type of test song eliciting the response, and how many times the test song had been presented (1–4). Furthermore, different parameters of the response song(s) were measured: the duration of the song(s), the number of songs, the temporal distribution of songs within the first 2 min after the first response song, and the chirp rate during each song. Each grasshopper was presented to 10–20 sequences of artificial songs, the more songs the less eager a grasshopper was to respond. The results from grasshoppers, which did not respond to at least 8 sequences of songs, were discarded. During these experiments the grasshopper was placed in a small net box in a temperature-regulated cabinet at temperatures of 24, 28, 31, 38, or 41 °C in experiments with females. The results are based on 33 males used in 88 experiments and 12 females used in 14 experiments.

In the second experiments, each grasshopper was presented to a random combination of four songs presented at various sound levels. The first presentation of each song was done at the same sound level for all song types. Thereafter, the sound level was increased in steps of 3 dB until the grasshopper responded (but not more than 15 dB). Each sound level of a song was tested three times.

When the grasshopper responded the computer recorded the type of test song, the sound level at which it was presented, and the presentation number (1–3). The following parameters of the response song(s) were measured: the number of songs, their temporal distribution within a period of 10 min after the first response song, their intensity, and the temporal variation within each song.

Young females with no prior male contact were used in these experiments. The females were tested at 28 °C or 38 °C. The chirp duration of the test songs corresponded to that of the males' response songs (or calling songs) at these temperatures. Several females were tested at both temperaturs on the same day or on succeeding days. Many grasshoppers responded only to the pilot presentation or to the first signal presentation. The results obtained from these animals and from animals which habituated during the first sequence of 4 signals were discarded. Several grasshoppers were tested in up to 20 random sequences of the 4 signals.

A total of 115 females were pre-tested, 48 of which responded and met the criteria mentioned above. They were used in 71 experiments. The thresholds were measured in dB (rel. $2 \cdot 10^{-5}$ N/m^2) as measured on a sound level meter (B & K, 2606, meter function 'fast'; microphone type 4133).

The significance of the song discrimination is calculated by a Friedmann two-way variance analysis (Siegel 1956), and the significance of the order of preference is calculated by a Tukey-test (Meyers and Grossen 1974).

Results

Effect of temperature on songs and song preference

The male and female grasshoppers responded to artificial songs by singing their response songs. In the first experiments we could compare the chirp duration in the preferred test song to that of the animals' response song at various temperatures. The chirp duration of the *response song* in both males and females can be described as an exponential function of the ambient temperature, which was almost identical to the animals' interval temperature:

$$y = 195 \exp(-t/75) \quad r^2 = 0.94, \quad P < 0.001$$

where y = chirp duration in ms, t = temperature in °C between 24 and 41 °C, and r = correlation coefficient.

The data for males are presented in Fig. 3. A slightly better approximation can be obtained by a hyperbolic function, but this will not allow us to compare our data with those of other authors.

The chirp duration of the *preferred songs* can also be described as an exponential function of the temperature, but this function is different from that of the response songs:

$$y = 396 \exp(-t/40) \quad r^2 = 0.96, \quad P < 0.001.$$

Around 28 °C, the preferred chirp duration was identical to the mean chirp duration of the animals' own response song, whereas this was not true at other temperatures. The grasshoppers may even

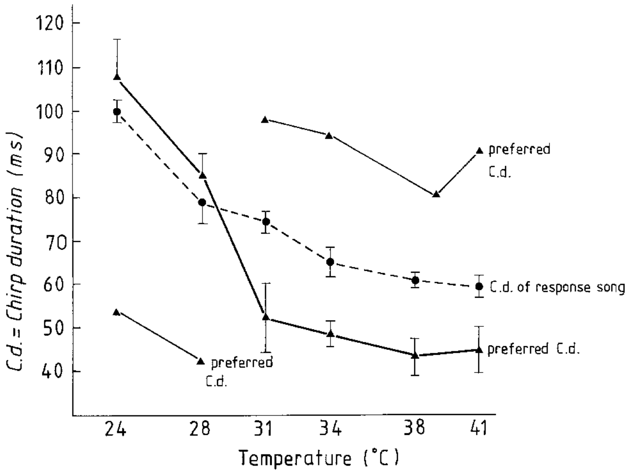

Fig. 3. The chirp durations of preferred songs (▲) and produced songs (●) decrease at increasing temperatures, although not to the same degree. The grasshoppers also show preference for artificial songs with half or double the normally preferred chirp duration. Data from males

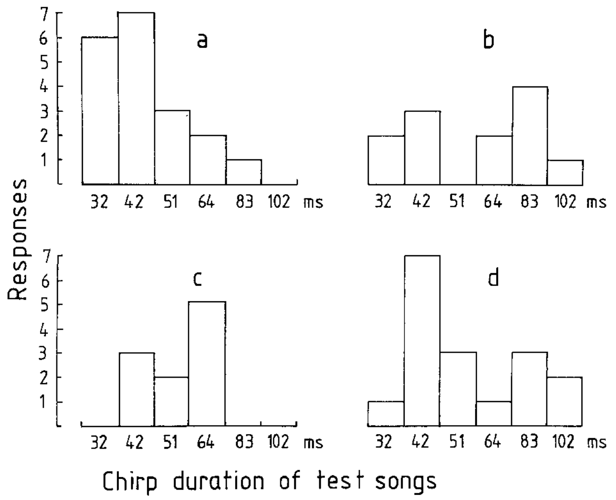

Fig. 4a–d. Two types of preference are observed when males are presented with test songs of various chirp durations (c.d.). About two third of the males (here **a** and **c**) show one-peak response histograms, and about one third two-peak histograms (here **b** and **d**). Six test songs (with c.d. from 32 to 102 ms) were played to the males in a random order, and this procedure was repeated 20 times for each male. The temperature was 38 °C in **a** and **b**, and 34 °C in **c** and **d**

prefer songs which they cannot produce themselves at any temperature (Fig. 3).

For each grasshopper the preferred chirp duration at a certain temperature was calculated by drawing a histogram showing how many times each type of test song elicited a response (Fig. 4). The histograms show that the grasshoppers had either one or two preferred chirp durations at a certain temperature. The *preferred chirp duration* of a one-peaked histogram is defined here as the median value of the columns contributing to the peak (Fig. 4a and c). In two-peaked histograms (Fig. 4b, d), the intervening columns are divided into two groups by eye. The median for each group is then calculated as above. In these histograms one of the preferred chirp durations corresponds to the preferred chirp duration of the grasshoppers with one-peaked response patterns, and the other preferred chirp duration is either about the double or one half of this duration. The exponential function given above refers to one-peaked histograms and to the corresponding peak in two-peaked histograms.

Some grasshoppers showed a one-peaked response histogram at one temperature and a double-peaked histogram at another temperature, but no clear relationship was found between the occurrence of double-peaked and one-peaked histograms and temperature. Double-peaked histograms tend to be more narrowly tuned to their peaks than the one-peaked histograms. About one third of the males produced double-peaked histograms. The experiments were repeated with a small number of receptive females. The females showed the same preferences as the males. Generally, the females responded more often and more vigorously than the males. $^{2}/_{3}$ of the females had double-peaked histograms.

In the second experiments the chirp rate (C) and the impulse rate (I) were combined in natural and unnatural ways in the test songs. These were $C_{28}I_{28}$, $C_{28}I_{38}$, $C_{38}I_{28}$, and $C_{38}I_{38}$, where the indices refer to the temperature at which these rates occur in the natural response song (as described in 'Methods'). Female grasshoppers were presented to these songs in random order at either 28 °C or 38 °C.

32 females were tested successfully at 28 °C, but many other females did not respond, or they ceased to respond after one or two responses. The responsive females preferred the signals in the following order:

$$C_{28}I_{28} > C_{28}I_{38} \quad \text{or} \quad C_{38}I_{38} > C_{38}I_{28}.$$

In this array > means that the signal to the left is preferred to that/those to the right ($P < 0.01$). 'Or' means that the two songs were equally effective (here the two middle songs).

At 38 °C 22 females were tested successfully for 5–12 h each. The order of preference was:

$$C_{38}I_{38} > C_{38}I_{28} \quad \text{or} \quad C_{28}I_{28} \quad \text{or} \quad C_{28}I_{38}$$

with the same definition as above: $C_{38}I_{38}$ was significantly better than the other signals ($P < 0.01$), whereas the order of the other three songs was not significantly different.

Most of the females (17 of 32 females at 28 °C and 18 of 22 females at 38 °C) responded for many hours. The results from these females were analysed closer in order to compare four different criteria for estimating the recognition of the songs. The animals' preference for the test songs may be estimated by comparing:

a) the minimum sound levels at which they responded to the different songs. This is the procedure used above where the sound levels necessary for eliciting a response were averaged over four presentations of each song. The accuracy of the estimation does not increase significantly, when more than four presentations are used for calculating the average sound level.

b) the number of responses to a song divided by the number of presentations. The results are the same as above, but the influence of the impulse rate (I) is not significant.

c) the number of response songs to each test song. No preference for certain types of songs could be found, when this criterion was used.

d) the number of test song presentations necessary for evoking a response. No preference could be established with this criterion (see Discussion).

Temporal variation of response songs

The duration of the response songs of individual males varied slightly at a certain temperature (the standard deviation was between 8 and 15% of the mean). The variation was much larger for the response songs of all the males (Fig. 5). The duration of the response song decreased from about 35 s at 24 °C to about 15 s at 41 °C (Figs. 5 and 6).

During the male response songs the chirp rate decreased by 10 to 20% (Fig. 6). The decrease was most prominent during the first seconds. The mean chirp rate of a song is used above to calculate the relationships between chirp duration (the reciprocal of the chirp rate) and temperature.

Except for the first, almost silent chirps of each song, the impulse rate is directly proportional to the chirp rate at all temperatures.

The female response songs were always rather short, and large differences were found between the individual females. The response songs of the females can be divided into two groups. In some songs, the chirp rate varied irregularly up and down. These songs were very short (a few s). Other songs were of longer duration (about $^1/_3$–$^1/_2$ of the male songs), and here the chirp rate decreased more regularly during each song (the decrease was similar to that observed in male songs). Only this song type is used in the calculations presented here. Females may produce both song types during a test, but usually most females made just one type.

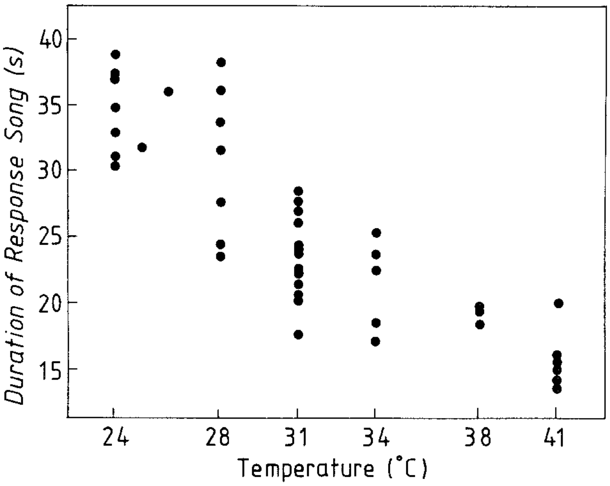

Fig. 5. The duration of the response song decreases with temperature. Each (●) represents the mean duration of male response song at a certain temperature. Data from 30 males and 43 experiments

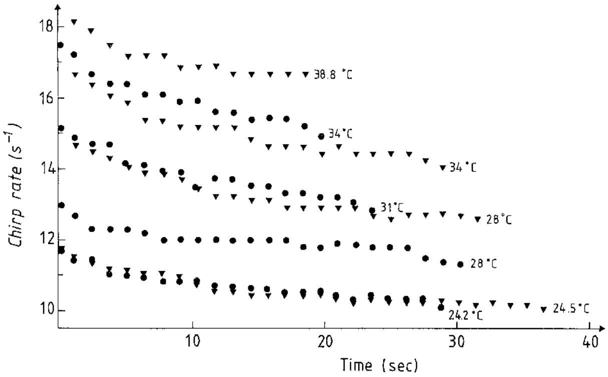

Fig. 6. Chirp rate of two males (● and ▲) measured at 4 different temperatures. Chirp rate decreases during the song, and duration of the songs decreases with temperature. There is, however, a considerable variation between the individuals

Effect of temperature on behavioural thresholds

The ambient temperature seems to have a general effect on the arousal response activity of the females. In the pre-test situation about 60% of the females responded at 38 °C compared to about 30% at 28 °C. A few females, which did not respond to the test series at 28 °C, responded afterwards for several hours at 38 °C. Further, more females habituated during the first test series at 28 °C than at 38 °C, and 50% of the females

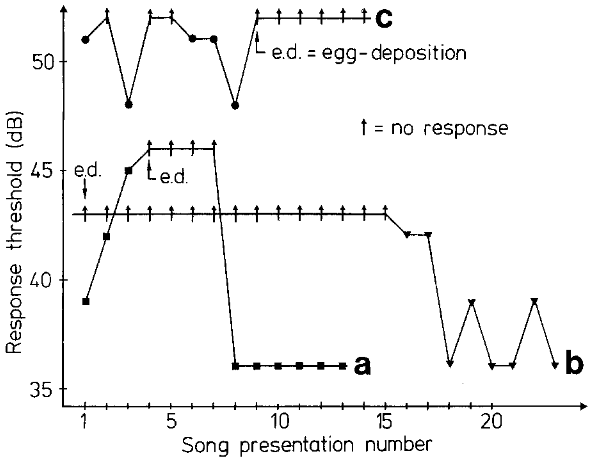

Fig. 7. Behavioural response thresholds of 3 females to artificial songs around the time of egg deposition. The songs were presented with time intervals of about 30 s. Threshold was measured in steps of 3 dB

adapted slowly during all test series at 28 °C, as compared to just 10% at 38 °C.

The average behavioural threshold to all test signals was 44.6 ± 5.8 dB at 28 °C and 39.8 ± 5.6 dB at 38 °C. The data are obtained from females tested at both temperatures. The difference is significant ($P < 0.001$, $N = 130$). A few females were tested at both temperatures on the same day. Their behavioural thresholds changed with temperature as described above.

Influence of egg deposition on the behavioural threshold

3 females deposited eggs during the behavioural threshold tests, one at 28 °C and two at 38 °C. One female deposited eggs in the middle of a behavioural threshold test. During the egg deposition the behavioural threshold of this female increased until she ceased to respond for about one hour. After this, the behavioural threshold declined quickly and the female responded to the lowest sound level presented (Fig. 7a). A second female deposited her eggs at the beginning of the test after having responded in the pre-test. 2 h later, the female started responding again, and the behavioural threshold decreased to a steady level (Fig. 7b). A third female deposited her eggs at the end of the test. The behavioural threshold of this female increased steadily and she finally ceased responding (Fig. 7c). During the experiments designed to investigate the discrimination of chirp duration, 2 females deposited eggs at 28 °C. The experiments took several hours, and the females responded more and more selectively to the test songs and at increasing sound levels, until they ceased responding just before egg-laying.

Discussion

Omocestus viridulus is a gomphocerine grasshopper. The male produces calling songs, response songs, and courtship songs with chirps without intervening pauses, i.e. a continuous song. (For this song type the chirp duration is the reciprocal of the chirp rate.) The female response songs were shorter and often more irregular than the male response songs. Like other activities of insects, the songs are influenced by temperature: the chirp rate and impulse rate (Fig. 1) decrease with temperature. Two experiments were designed to measure the influence of temperature on the response songs and on the animals' behavioural song preference.

The results showed that the chirp duration of the response song and the preferred chirp duration are affected in different ways by temperature (Fig. 3). Furthermore, the grasshoppers may not only prefer one chirp duration at a certain temperature, but they may also prefer chirps with the double or half duration.

The chirp rate (chirp duration) is the major parameter carrying behavioural information in these animals. This is evident both from the first experiments on the preferred chirp duration and from the second experiments, where chirp rates and impulse rates were combined in natural and unnatural ways. The second experiments also demonstrate the importance of the impulse rate as a carrier of information. In these experiments the animals preferred the natural combination to the unnatural ones. This finding suggests that the impulse rate is not evaluated per se, but in relation to the chirp rate. The coupling between these parameters may not be simple, however, and this problem deserves further study.

It has been shown (Skovmand and Pedersen 1978) that the impulse rate determines the main spectral components of the songs, as originally proposed by Michelsen (in Elsner 1974). Independent manipulations of this parameter revealed behavioural information carried by the impulse rate.

It has been proposed that the neuronal network determining the chirp rate of a cricket song may share neurons with the song recognition template (Bentley and Hoy 1974). This theory was supported by crossbreeding experiments. However, experiments on gomphocerine grasshoppers (Helversen and Helversen 1975a,b) showed that here there was no strict coupling. The F_1 hybrid females (and males) produced songs intermediately between the parents' songs, but preferred the songs of their parents to the songs of their hybrid brothers. Similar results have been obtained on fruit flies by Ewing and Bennet-Clark (Bennet-Clark 1975).

Our results support the latter view, since the temperature affects the song recognition and the song productions of *O. viridulus* in different ways (Fig. 3).

In the songs of *Omocestus viridulus* the *ratio* between the chirp rate and the impulse rate is independent of temperature (Skovmand and Pedersen, unpublished). The reason is mechanical: the legs are simply moved faster during the stridulation at higher temperatures, and the same parts of the files are used at different temperatures.

The decrease in chirp duration with increasing temperature can be described by an exponential function. The chirp duration does not decrease from 38 °C to 41 °C, even though the internal temperature of the grasshopper follows ambient temperature – at least in non-singing females. Below 24 °C, it was very difficult to elicit response songs. The function relating chirp duration to temperature is very different from that found in *Chorthippus biguttulus* by von Helversen (1972), and the chirp duration of *O. viridulus* is less influenced by the temperature.

The *preferred* chirp duration also decreases with temperature, but the temperature dependency is not the same as for the chirp duration in the songs (Fig. 3). About $^1/_3$ of the males and $^2/_3$ of the females had response histograms with two peaks. One of the peaks corresponded to that found in the histograms of animals with only one peak. The other peak was found at either one half or the double of this value (Figs. 3, 4).

Neurons detecting the chirp rate in locusts and crickets have been described by several authors (Kalmring and Rheinlaender 1974; Kalmring 1975a, b; Stout and Huber 1972). The broad, single-peak histograms found in this study demonstrate that the chirp rate discriminating system of shorthorned grasshoppers is not a narrowly tuned system. Also, the discrimination between a preferred rate and its multiplum is not good.

Chirp rate decoding cells responding in a special, regular way to conspecific song, have been resported by Kalmring (1975b). It would be interesting to know whether the discrimination of these cells depends on the temperature.

Discrimination of chirp rate and impulse rate

In these experiments, receptive females were presented with 4 different combinations of chirp rate and impulse rate. The test procedure allowed us to record, whether the female responded, how she responded, and the lowest sound level at which she responded to each type of song.

At 28 °C, $C_{28}I_{28}$ was preferred to all other songs, i.e. the 'natural' song was the best. More interestingly, $C_{38}I_{38}$ is preferred to $C_{38}I_{28}$, i.e. the natural combination of chirp duration and impulse rate at 38 °C is preferred to the unnatural one, even though the latter has the correct impulse rate at 28 °C (the temperature at which the grasshopper was tested).

For mechanical reasons, the chirp rate and impulse rate are locked to each other. That the grasshopper prefers $C_{38}I_{38}$ to $C_{38}I_{28}$ (at 28 °C) means that it is preferring a natural *ratio* between chirp rate and impulse rate to an unnatural one. This supports the conclusion reached by D. von Helversen (1972) and O. von Helversen (1979) that grasshoppers mainly use parameters for communication which are not influenced by temperature. At 38 °C the results are not so clear. $C_{38}I_{38}$ was preferred to all other songs, but the grasshoppers discriminate badly between the 3 other songs. A possible explanation may be that at 38 °C the grasshoppers prefer a chirp duration around 40 to 50 ms or the double (80 ms $= C_{28}$), but produce chirps with a duration of about 65 ms (C_{38}) (Fig. 5).

Four criteria were used to determine the discrimination between the test songs. Two of these criteria gave similar results, although with slightly different sensivity, whereas no preference could be established with two other criteria. This demonstrates the importance of testing several criteria in such studies.

Influence of temperature on the behavioural threshold

The mean behavioural threshold of the females was 45 dB at 28 °C and 39 dB at 38 °C. Accordingly, at higher internal temperatures the females should be able to detect a male at longer distances. This may be one of the advantages that the females obtain from their sun-exposing behaviour. Perhaps this may partly compensate for the loss of sound energy expected from an upward refraction of the sound waves on sunny days (Michelsen 1978).

In previous experiments carried out in an anechoic chamber at 27 ± 1 °C, the behavioural threshold of receptive females to replayed male calling song was 42 ± 2.2 dB (SD) (Skovmand and Pedersen 1978). In these experiments the receptive behaviour observed was either a response song or a jump towards the loudspeaker from a platform in the middle of the room. The more open set-up and the possibility of displaying both types of respective behaviour, may explain the slightly lower behavioural thresholds in these experiments.

The nature of the temperature-sensitive processes is unkown. A decrease in the jumping threshold of a locust to light stimuli with increasing temperature was reported by Heitler et al. (1977), who were able to identify the neuronal mechanism as a temperature-dependent spike threshold of the fast extensor tibia motoneuron. It would be interesting to learn whether the effect of temperature on the response song threshold is due to the efferent part – as in the study of Heitler et al. – or to the central or afferent parts of the nervous system.

Influence of egg deposition on behavioural threshold

The females cease to respond to the test signals during egg deposition. The behavioural threshold increased immediately before the egg deposition and decreased quickly afterwards. In *C. biguttulus*, von Helversen (1972) observed a similar cessation of response during egg deposition.

At least a part of this change must be contributed to motivational (internal and non-physical) factors, since the threshold increases and decreases steadily before and after the egg deposition. The decrease in threshold after the egg-laying may partly be explaind by the physical influence of the ripe eggs and the fluid of the accessory glands on the hearing threshold. Michelsen (1971) and Miller (1977) have shown that the hearing threshold increases with increasing amounts of fat and ovaries in the abdomen. But the influence on the behavioural threshold observed here is partly a central phenomenon. Several studies have dealt with the influence of various hormonal and mechanical (i.e. the presence of a spermatophore in the spermatek) factors on the receptiveness of the female grasshoppers (review: Barth and Lester 1973). The effect of the different factors seems to depend on the species.

Criteria for behavioural threshold

In these experiments, each female was presented with a test signal 1 to 3 times at a certain sound pressure level. If the female responded, this sound level was defined as her 'behavioural threshold'. It may be argued that some of the non-responding females at a certain sound level might have responded, if the signal had been repeated more than 3 times.

Independent of the kinds of test song and sound level, 60% of the responses of the females were given to the first presentation, 60% of the rest (=24%) responded to the second presentation and about 16% to the third (and last) presentation (the actual data were compared in a chi square analysis and were found not to deviate from the distribution: 60%–24%–16% ($P>0.50$). If we present the songs n times we obtain distribution of the responses according to a series expansion of $(1-k)^n$: 60%–24%–9.6%–3.8%–1.6%, etc. Accordingly, the first three presentations will reveal 94% of the responses we may obtain, and the remaining ones can be ignored.

Acknowledgements. The first part of this study was carried out in the laboratory of D. and O. von Helversen, Biologisches Institut, Universität Freiburg, whom we thank for their help and for valuable discussions. Der Deutsche Akademische Austauschdienst granted the stay in Germany. The authors are indebted to A. Michelsen, University of Odense, for valuable criticism of the manuscript and to B. Høyer and J. Ramussen, the Technical University, Lyngby, for assistance with the electronics.

References

Barth RH, Lester LJ (1973) Neurohormonal control of sexual behaviour in insects. Annu Rev Entomol 18:442–472

Bennet-Clark HC (1975) Acoustics and the behaviour of *Drosophila.* Verh Dtsch Zool Ges 68:18–28

Bentley DR, Hoy R (1974) The neurobiology of cricket song. Sci Am 23:34–44

Elsner N (1974) Neuroethology of sound production in gomphocerine grasshoppers (Orthoptera:Acrididae). J Comp Physiol 88:67–102

Elsner N, Popov AV (1978) Neuroethology of acoustic communicaton. Adv Insect Physiol 13:229–335

Heitler WJ, Goldman CS, Rowell CHF (1977) The effects of temperature on threshold of identified neurons in the locust. J Comp Physiol 117:163–182

Helversen D von (1972) Gesang des Männchens und Lautschema des Weibchens bei der Feldheuschrecke *Chorthippus biguttulus* (Orthoptera:Acrididae) J Comp Physiol 81:381–422

Helversen D von, Helversen O von (1975a) Verhaltensgenetische Untersuchungen am akustischen Kommunikationssystem der Feldheuschrecken (Orthoptera:Acrididae). I. Der Gesang von Artbastarden zwischen *Chorthippus biguttulus* und *Ch. mollis.* J Comp Physiol 104:273–299

Helversen D von, Helversen O von (1975b) Verhaltensgenetische Untersuchungen am akustischen Kommunikationssystem der Feldheuschrecken (Orthoptera:Acrididae) II. Das Lautschema von Artbastarden zwischen *Chorthippus biguttulus* und *Ch. mollis.* J Comp Physiol 104:301–323

Helversen O von (1979) Angeborenes Erkennen akustischer Schlüsselreize. Verh Dtsch Zool Ges:42–59

Huber F (1977) Lautäusserungen und Lauterkennen von Insekten (Grillen). Rhein Westf Akad Wiss, Vorträge 265, Westdeutscher Verlag, Opladen

Kalmring K (1975a) The afferent auditory pathway in the ventral cord of *Locusta migratoria* (Acrididae). I. Synaptic connectivity and information processing among the auditory neurons of the ventral cord. J Comp Physiol 104:103–141

Kalmring K (1975b) The afferent auditory pathway in the ventral cord of *Locusta migratoria* (Acrididae). II: Response of the auditory ventral neurons to natural sounds. J Comp Physiol 104:143–159

Kalmring K, Rheinlaender J (1974) The afferent auditory system in the CNS of Katydids and Locustids. In: Schwartzkopff J (ed) Rhein Westf Akad Wiss, Abh Band 53, Symp Mechanoreception. Westdeutscher Verlag, Opladen

Meyers LS, Grossen NE (1974) Behavioral research. Freeman and Co, San Francisco

Michelsen A (1971) The physiology of the locust ear, III: Acoustical properties of the intact ear. Z Vergl Physiol 71:102–128

Michelsen A (1978) Sound reception in different environments. In: Ali MA (ed) Sensory Ecology: Review and Perspectives. Plenum, New York, London, pp 345–374

Miller L (1977) Directional hearing in the locust *Schistocerca gregaria* Forskål (Acrididae, Orthoptera). J Comp Physiol 119:85–98

Siegel S (1956) Nonparametric statistics. McGraw-Hill, New York, San Francisco

Skovmand O, Pedersen SB (1978) Tooth impact rate in the song of a shorthorned grasshoppper: A parameter carrying specific behavioral information. J Comp Physiol 124:27–36

Stout JF, Huber F (1972) Response of central auditory neurons of female crickets (*Gryllus campestris* L.) to the calling song of the male. Z Vergl Physiol 76:302–313