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# TEMPERATURE COUPLING AND 'TRADE-OFF' PHENOMENA IN THE ACOUSTIC COMMUNICATION SYSTEM OF THE CRICKET, *GRYLLUS BIMACULATUS* DE GEER (GRYLLIDAE)

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SUMMARY

The effects of ambient temperature on stridulation (calling song) in males, and phonotaxis in females, were studied in the chirping cricket, *Gryllus bimaculatus*. In the male, temperature had the greatest effect on the syllable and chirp repetition rates. Both increased linearly with increasing temperature between 15 and 24°C; there was no effect of temperature on these temporal properties at higher temperatures (24–33°C). Syllable duration, number of syllables per chirp and dominant frequency remained relatively unaffected by changes in temperature. Stridulation and phonotaxis were temperature coupled because the female at 15, 22 and 30°C responded best to synthetic songs with syllable and chirp repetition rates that matched these temporal properties of the male's calling song at the same temperature. The phonotactic behaviour of the female indicates that certain combinations of temporal properties in the male's calling song improve the female's response at different temperatures, suggesting the presence of 'trade-off' phenomena in phonotaxis and pattern recognition in *G. bimaculatus*.

## INTRODUCTION

Acoustic communication among conspecifics requires that signal production in the sender be matched with signal recognition in the receiver. This matching between sender and receiver is complicated in poikilothermic animals that signal and respond over a range of ambient temperatures (e.g. Walker, 1962*a*,*b*, 1975; Schneider, 1977; Gerhardt, 1978, 1982, 1983). In some poikilotherms which produce signals that change with temperature, this problem has been solved by 'temperature coupling' (Gerhardt, 1978). This means that a change in temperature causes parallel shifts in signal generation and signal recognition, so that sender and receiver remain matched over the entire range of temperatures in which communication occurs. Temperature coupling is best expressed in communication systems that employ temporal signals and has been described in acoustic communication in crickets, grasshoppers and treefrogs, and in visual communication in

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fireflies (e.g. Walker, 1957; Helversen & Helversen, 1981; Gerhardt, 1978, 1982, 1983; Carlson, Copeland, Raderman & Bulloch, 1976).

Temperature coupling is not the only solution to the problem of maintaining effective communication at different temperatures. In some species of acridid grasshoppers, for example, the receiver evaluates properties of the signal (i.e. ratios between syllable durations and pause durations) that are independent of temperature (see Helversen, 1972; Helversen, 1979; Helversen & Helversen, 1981; Skovmand & Pedersen, 1983).

The study of temperature coupling phenomena can provide new insights into the interrelationships of the physiological mechanisms that underlie pattern generation and pattern recognition. Studies of interspecific hybridization in crickets and treefrogs have provided indirect evidence that pattern generation and pattern recognition have common neural elements (see Hoy, 1978; Hoy, Hahn & Paul, 1977; Doherty & Gerhardt, 1983, 1984). This idea has been termed the 'genetic coupling' hypothesis, and the phenomenon of temperature coupling supports this hypothesis (Hoy, 1974).

In this paper, I report on how the cricket, *Gryllus bimaculatus*, changes signalling and phonotaxis at different temperatures and establishes sender-receiver matching. I provide new evidence for temperature coupling in a chirping cricket and discuss the interactions of temporal properties and 'trade-off' phenomena that underlie calling song recognition and the elicitation of phonotaxis behaviour at different temperatures. This paper is an extension of Walker's pioneering study on the effects of temperature on acoustic communication in trilling tree crickets (Walker, 1957). The calling song of *G. bimaculatus* differs from that in tree crickets, as it is composed of discrete chirps that contain three to five sound pulses (syllables). These chirps are repeated in a continuous though variable temporal sequence, whereas the pulse (syllable) repetition rate within individual chirps is more stereotyped. As in tree crickets, the calling song of *G. bimaculatus* and other Gryllids attracts conspecific females for mating. Furthermore, these crickets commonly sing over a broad temperature range between 15 and 35 °C (Alexander, 1957; Alexander & Meral, 1967; Walker, 1962*a*,*b*). Finally, the recognition process in the female can be elucidated indirectly by studying phonotaxis behaviour on a walking compensator to playbacks of synthetic models of the calling song (see Wendler, Dambach, Schmitz & Scharstein, 1980; Weber, Thorson & Huber, 1981; Thorson, Weber & Huber, 1982; Schmitz, Scharstein & Wendler, 1982).

## MATERIALS AND METHODS

### *Male stridulation*

The calling songs of single males of *G. bimaculatus* from laboratory cultures were recorded 2–10 weeks after the final moult. Singing males were isolated in glass jars and recorded in the dark in a temperature-controlled incubator (Memmert RO-8), after being acclimated to the incubator temperature for a period of 2 h to several days. Acclimation times had no systematic effects on the physical properties of calling song. Songs were recorded on an Akai 280D-SS tape recorder ($9{\cdot}5\ \mathrm{cm\ s^{-1}}$), and the recording microphone (AKG) was suspended above the glass

jar within 10 cm of the male. Usually, spontaneous singing was recorded, although sometimes stridulation was initiated by playing back synthetic calling songs that had physical properties that were characteristic of the natural calling song. Air temperature was measured by a thermister that was suspended within 5 cm of the singing male. Due to the small body sizes of these crickets, it was assumed that the temperature of the surrounding air was the same as the body temperature of the singing male (see Prestwich & Walker, 1981). All temperatures reported in this paper were ±1 °C.

The temporal and spectral properties of the calling song were analysed by using either a digital oscilloscope or a PDP 11/40 (DEC) computer. Syllable periods (SP), chirp periods (CP) and the number of syllables per chirp (SN) were digitized and analysed by the computer (see Figs 2, 3 for definitions of temporal properties). The temporal properties of chirps with 3–5 syllables were pooled. The syllable duration (SD) of the third, fourth or fifth syllables of chirps was measured directly from the oscilloscope (±2 ms). The sinusoidal nature of calling songs enabled the direct measurement of dominant frequency by taking the reciprocal of the time between successive zero crossings of the expanded wave form on the digital oscilloscope (±10 Hz).

In some males, calling songs were recorded several times at the same temperature. The data from these recordings were pooled in individuals because there were no differences in the songs that were recorded at different times at the same temperature. The calling songs of some males were recorded while other males were singing at the same time in the incubator. These data were pooled also because there were no systematic differences in the calling songs of individuals which sang either in acoustic isolation or with other singing males.

### *Female phonotaxis*

Adult virgin females from laboratory cultures were studied 2–12 weeks after the final moult. Within a week after the last moult, they were kept in isolation until the experiments, and did not hear songs during this isolation period. Phonotactic tracking was studied by using a feedback-controlled walking compensator (Kramer spherical treadmill) in an anechoic chamber (for details, see Weber *et al.* 1981; Thorson *et al.* 1982). Briefly, the female walked on top of a sphere and the change in the female's position was detected by a pulsed-infrared scanning system. This system drove compensatory motors that moved the sphere in the direction opposite to the direction of the female's movement. The compensatory movement kept the female on top of the sphere, enabling study of a freely walking female in an unchanging but controllable sound field. By analysing instantaneous velocity and direction profiles of the female's movement (see Fig. 1), the tracking performance to an acoustic stimulus could be quantified by calculating the percentage of the stimulus presentation time that the female clearly 'tracked' the stimulus (Weber *et al.* 1981; Thorson *et al.* 1982). A stimulus that was not tracked by a female was deemed unattractive, whereas a stimulus that was clearly tracked was considered attractive. In this paper, clear tracking was defined as: (i) corrective meandering about the angular direction of the speaker (usually less than ±60°); (ii) female following of switches of the song between two loudspeakers with an angular

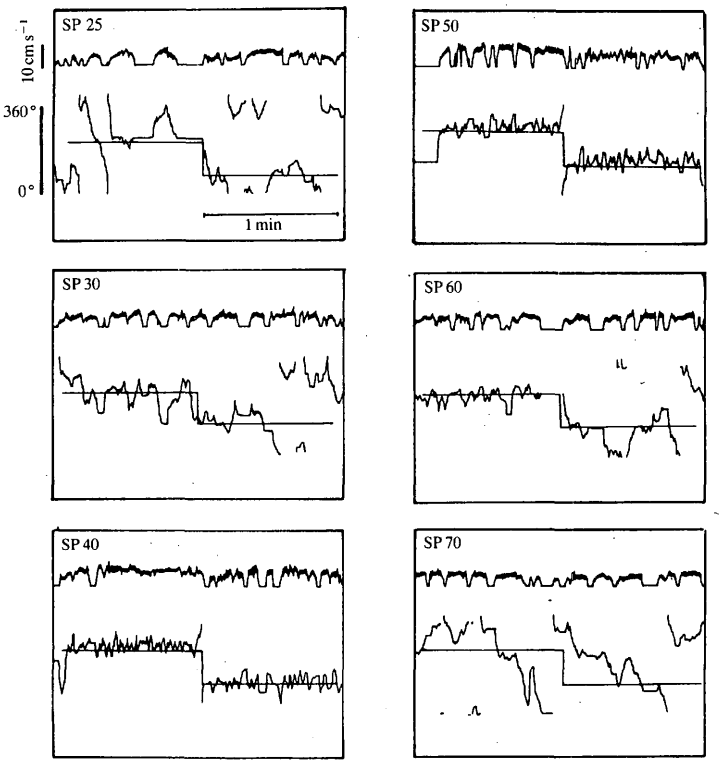


Fig. 1. Instantaneous velocity and direction profiles for one female that tracked equal-duty-cycle stimuli (see Fig. 9) at 22°C. Horizontal lines show active speaker positions (angular separation of 135°). Chirp period was 500 ms and the sound pressure level (SPL) was 80 dB. SP, syllable period.

separation of 135°; (iii) continuous walking or walking in a start-stop pattern characteristic of the individual. Stops longer than 5 s were not included in measurements of tracking time.

The anechoic chamber in which the locomotion compensator was situated was heated to 30°C by a heater, and cooled to 15°C by opening the windows to the laboratory during the winter months. Air temperature was measured by a thermister that was suspended within 5 cm of the female at the top of the sphere. Females were acclimated to experimental temperatures for at least 12 h before experiments were begun and all experiments were run in the dark.

### *Presentation of synthetic stimuli*

Acoustic stimuli were electronically synthesized; temporal properties (SP, SN, CP) were controlled by a microcomputer (built by J. Sagunsky, Seewiesen). All syllables had 2 ms linear rise and fall times. The carrier frequency of all synthetic songs was 4·8 kHz, which was characteristic of the carrier in natural calling song. Sound intensities in dB (rms) were measured at the top of the sphere where the cricket ran and referred to the maximum of the carrier envelope. Stimuli were played back (usually at 80 dB) from one of two speakers that had an angular separation of 135° (see Weber *et al.* 1981).

Two series of synthetic stimuli were played back to females (Fig. 9): the equal-duty-cycle series (=DC) and the unequal-duty-cycle series (≠DC, DC = SD/SP). In the =DC stimuli, all chirps had duty cycles of 50 % (SDs: 10–40 ms) and SN and SP covaried to maintain constant chirp durations of about 220 ms, so the =DC stimuli had approximately equal sound powers (Fig. 9). The ≠DC stimuli consisted of chirps with unequal duty cycles (range: 25–80 %), equal SNs (4), equal SDs (20 ms, except when the SP was 20 ms, in which case the SD was 16 ms), and different SPs that caused the chirp duration to range from 76 to 260 ms (Fig. 9).

The =DC and ≠DC stimuli were played back to each female at 15, 22 and 30 °C, and had three different chirp periods of 700, 500 and 350 ms, which were characteristic of the CPs of male calling song at these temperatures (see Fig. 3). Each stimulus was played back to the female for 2 min (1 min from each speaker) and was followed by a 15–30 s silent period before the next stimulus was presented. The order of playback of stimuli with different SPs was 50, 40, 60, 70, 25, 80, 20 ms at 15 °C, and 40, 50, 30, 60, 25, 70, 20, 80 ms at 22 and 30 °C. To check for female responsiveness to calling song, each stimulus series was directly preceded and followed by a standard stimulus, which elicited optimal phonotactic tracking. A silent period of 15–30 s separated the playback of the standard stimulus from the stimulus series being tested. This standard stimulus had SDs of 20 ms and 4 syllables per chirp. Syllable and chirp periods were 60 ms and 700 ms at 15 °C, 45 ms and 500 ms at 22 °C, and 40 ms and 350 ms at 30 °C. At each temperature, all stimuli were played back to each female within a period of 2–3 h. A silent period of at least 3 min separated the series of stimuli with different chirp periods.

Experiments were run to ascertain the range of CPs tracked by females at 15 and 30 °C. Here, the synthetic songs had optimal SPs (60 ms at 15 °C and 40 ms at 30 °C), 4 syllables per chirp and equal syllable durations (20 ms). The songs with different CPs were presented sequentially (no silent periods between successive stimuli) in the following 'to-and-fro' order: 500 ms to 200 ms, 200 ms to 1000 ms (or even 4000 ms), 1000 ms to 500 ms (see Fig. 8).

## RESULTS

### *Effect of temperature on male stridulation*

Most males produced calling songs between 15 and 33 °C; one male called at 36 °C and two males called between 10 and 12 °C. Syllable period (SP) and chirp period

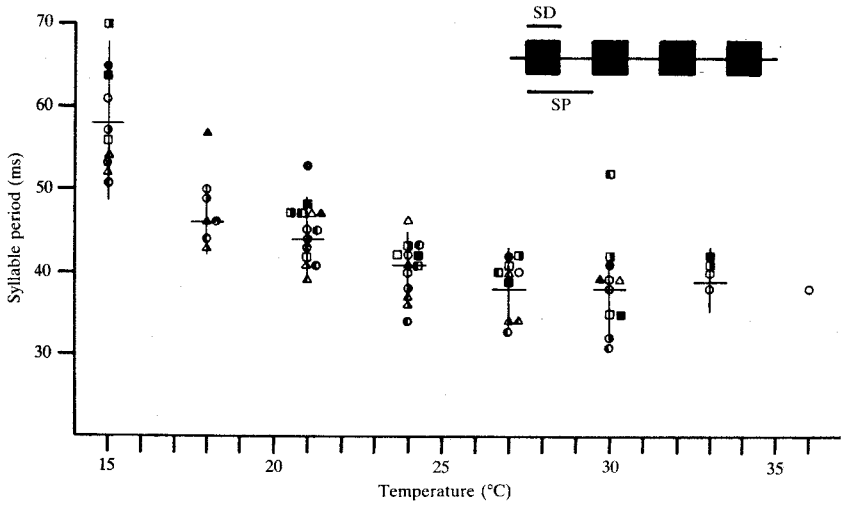


Fig. 2. The effect of temperature on syllable period (SP) in the calling song. Symbols indicate means of individuals (same individuals as in Figs 3, 5, 6). Horizontal and vertical lines indicate population means (pooled data from all individuals) and standard deviations. The number of syllable periods measured per individual ranged between 473 and 9100. SD, syllable duration.

(CP) in the songs of individual males decreased with increasing temperature (Figs 2, 3). At 15°C, the mean SP was about 60 ms, at 22°C about 45 ms, and at 30°C about 40 ms. Mean SPs in the calling songs of the two males which stridulated from 10–12°C were between 65 and 70 ms. The CP had a mean of 660 ms at 15°C, 470 ms at 21°C and 340 ms at 30°C; between 10 and 12°C (two males) it increased to 800 ms. Between 15 and 25°C, the $Q_{10}$ was 1·6 for CP and 1·4 for SP; there were little or no effects of temperature on CP and SP above 24°C. There was no effect of temperature on the variances of SP and CP within individuals; mean coefficients of variation (standard deviation/mean) were 9% for SP and 19% for CP.

To facilitate comparison with the results of similar studies of other cricket species (see Discussion), the effects of temperature on syllable and chirp repetition rates (the reciprocals of SP and CP) are shown for *G. bimaculatus* in Fig. 4. Both syllable and chirp repetition rates increased linearly with increasing temperature between 15

Fig. 3. The effect of temperature on chirp period (CP) in the calling song. See Fig. 2 legend for description of symbols. The number of chirp periods measured per individual ranged between 160 and 3182. CD, chirp duration.

Fig. 4. The effects of temperature on syllable repetition rate and chirp repetition rate in calling songs. Closed circles indicate mean syllable repetition rates, calculated by summing the reciprocals of mean syllable periods of individual males (from Fig. 2). Open circles indicate mean chirp repetition rates, calculated in the same manner as syllable rate (from Fig. 3). Vertical lines are standard deviations. Lines are linear regressions of chirp and syllable rates on temperature (method of least squares).

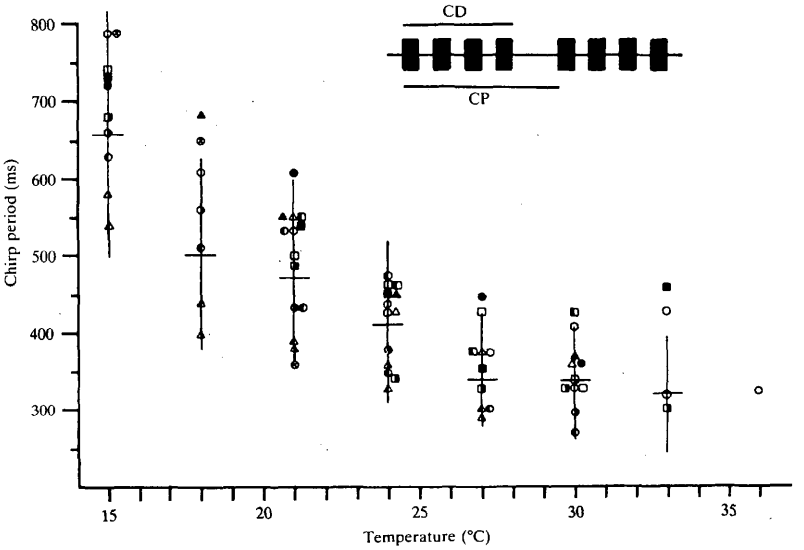
CD
CP
800
700
600
500
400
300
Chirp period (ms)
15
20
25
30
35
Temperature (°C)

Fig. 3

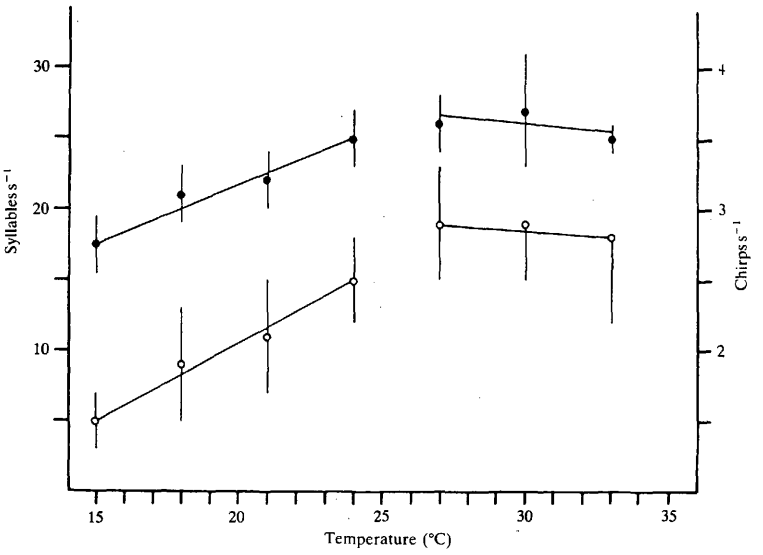
30
20
10
Syllables s$^{-1}$
4
3
2
Chirps s$^{-1}$
15
20
25
30
35
Temperature (°C)

Fig. 4

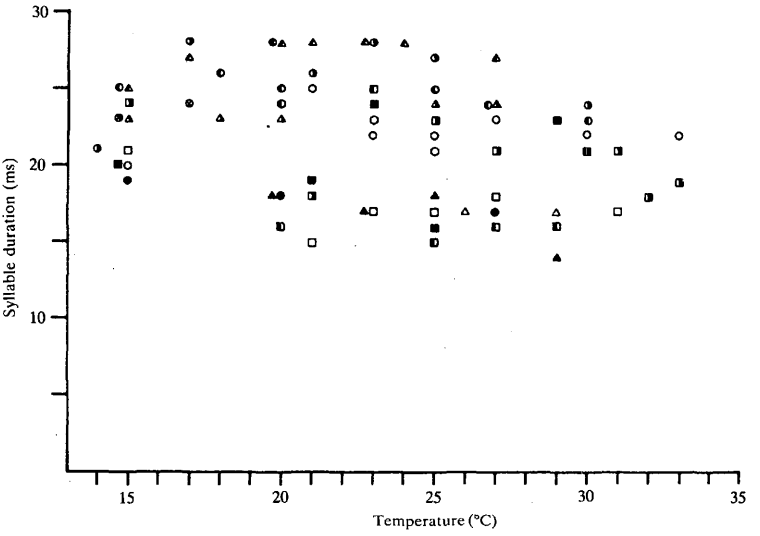
30
20
10
Syllable duration (ms)
15
20
25
30
35
Temperature (°C)

Fig. 5

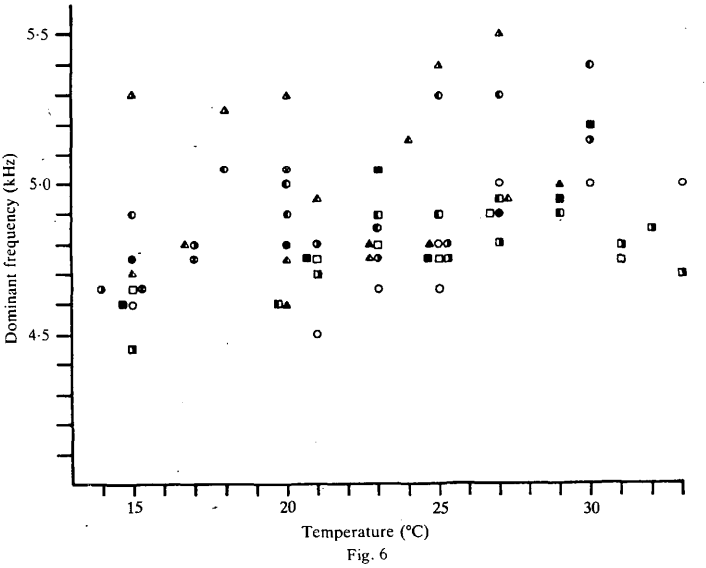
5·5
5·0
4·5
Dominant frequency (kHz)
15
20
25
30
Temperature (°C)

Fig. 6

and 24°C; at higher temperatures, these temporal properties did not change with temperature.

Compared with SP and CP, there were little or no effects of temperature on syllable duration, dominant frequency and the number of syllables per chirp. Mean syllable durations of individuals ranged between 14 and 28 ms (Fig. 5) and mean dominant frequencies of most individuals ranged between 4·6 and 5·0 kHz (Fig. 6). At 15, 22 and 30°C, the majority of chirps (about 70 %) contained 4 syllables. The percentage of 3-syllable chirps increased with increasing temperature from 10 % at 15°C to 25 % at 30°C, whereas the percentage of 5-syllable chirps decreased from 20 % at 15°C to 5 % at 30°C, indicating a tendency of the male to shorten chirp duration by reducing the number of syllables per chirp.

### *Effect of temperature on female phonotaxis*

If temperature coupling occurs in *G. bimaculatus*, then the effect of temperature on the tracking behaviour of females should parallel that on the calling song of males. That is, the SPs and CPs that elicit optimal tracking by females should shift from longer to shorter values with increasing temperature to match the effect of temperature on these temporal properties in the calling song. This appeared to occur in *G. bimaculatus* and the results are summarized in Fig. 7 (individual data are presented in Figs 8, 9). At 15°C, females tracked synthetic calling songs with SPs that ranged from 40 to 80 ms and some even tracked songs with 90 ms SPs; tracking was best when the SP was between 50 and 70 ms. This range of best tracking corresponded with the range of SPs in calling song at the same temperature (means of individual males at 15°C ranged from 50 to 70 ms). At 22°C, females tracked songs with SPs that ranged from 30 to 60 ms, and the best tracking occurred when the SP was 40–50 ms, which was similar to the range of SPs in calling songs of males at the same temperature (means of individual males ranged from 40 to 55 ms at 21°C). The range of SPs that elicited tracking in females shifted further downward at 30°C. At this high temperature, females tracked songs with SPs that ranged from 30 to 50 ms and the best tracking occurred when the SP was 40 ms. The majority of males at 30°C produced calling songs with mean SPs that ranged from 36 to 42 ms.

Temperature also affected the range of CPs tracked by females (Fig. 8). Synthetic songs with CPs greater than 700 ms were tracked better at 15°C than at 30°C; some females even tracked songs with CPs as long as 4 s. Among individual females, tracking performance at 15°C was least variable to songs with CPs that ranged from about 400 to 900 ms. This 'optimal' range of CPs overlapped the range of CPs in calling song at the same temperature (see Fig. 3 and bar in Fig. 8). At 30°C, no females tracked songs with CPs greater than 900 ms; the majority failed to

Fig. 5. The effect of temperature on syllable duration in the calling song. Symbols are means of individuals (same individuals as in Figs 2, 3, 6). Sixteen syllables were measured per individual, and the standard deviations of individuals ranged between 0·3 and 3·8 ms.

Fig. 6. The effect of temperature on dominant (carrier) frequency of the calling song. Symbols are means of individuals (same individuals as in Figs 2, 3, 5). Eight measurements were averaged per individual, and the standard deviations of individual means ranged between 10 and 400 Hz.

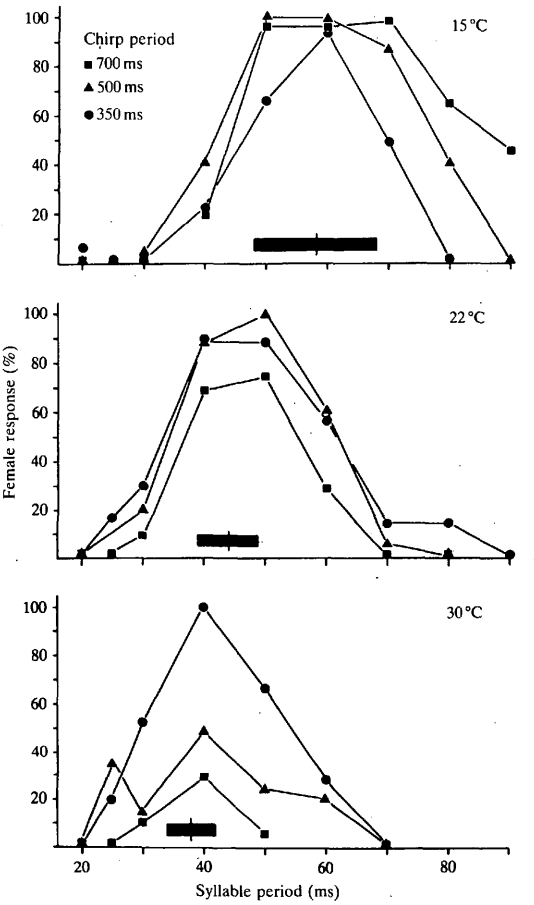


Fig. 7. The effect of temperature on female tracking performance to synthetic stimuli (unequal-duty-cycle-series, ≠DC, see Fig. 9) that had different syllable periods and chirp periods. Symbols indicate means, calculated by summing the tracking percentages of individual females (for individual data, see Fig. 9). Ordinate is the percentage of the stimulus time that females tracked the stimulus (see Materials and Methods). Vertical lines and horizontal bars at the bottom of the graphs indicate population means and standard deviations of syllable periods in the calling song (from Fig. 2).

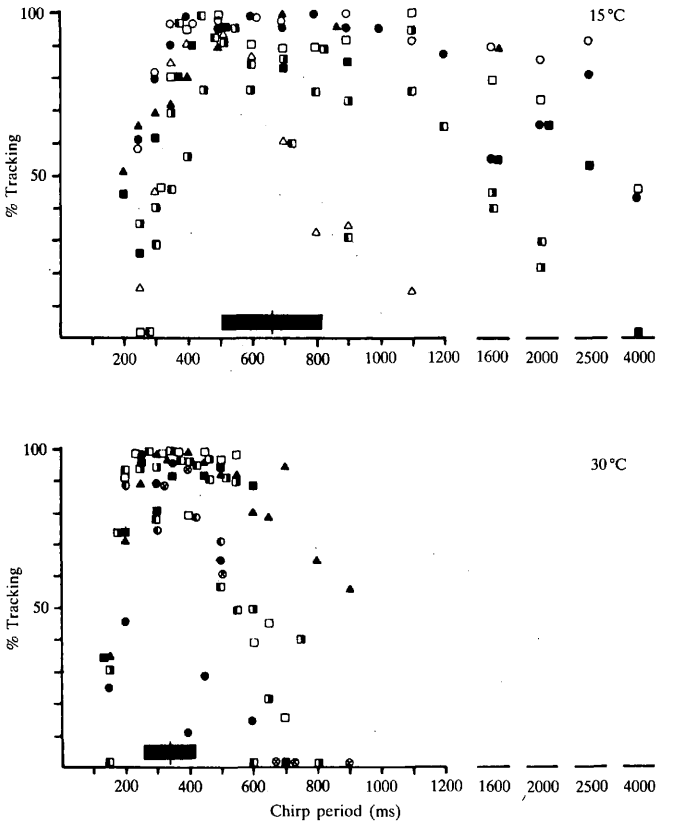


Fig. 8. The effect of temperature on female tracking performance to synthetic stimuli with different chirp periods. Symbols indicate tracking performances (percentage of stimulus time the stimulus was tracked) of individual females at 15 and 30 °C. All stimuli had 4 syllable chirps and 20 ms syllable durations. Syllable period was 60 ms at 15 °C and 40 ms at 30 °C, so the chirp durations at these two temperatures were different (200 ms at 15 °C and 140 ms at 30 °C). Vertical lines and horizontal bars at the bottoms of the graphs indicate population means and standard deviations of chirp periods in the calling song (from Fig. 3).

track songs with CPs greater than 500–600 ms. The variability of tracking performance among females at 30 °C was minimal to songs with CPs that ranged between 250 and 450 ms. This range was comparable to the range of CPs in calling songs at 30 °C (see Fig. 3 and bar in Fig. 8).

In summary, there was a good match between the range of SPs of synthetic

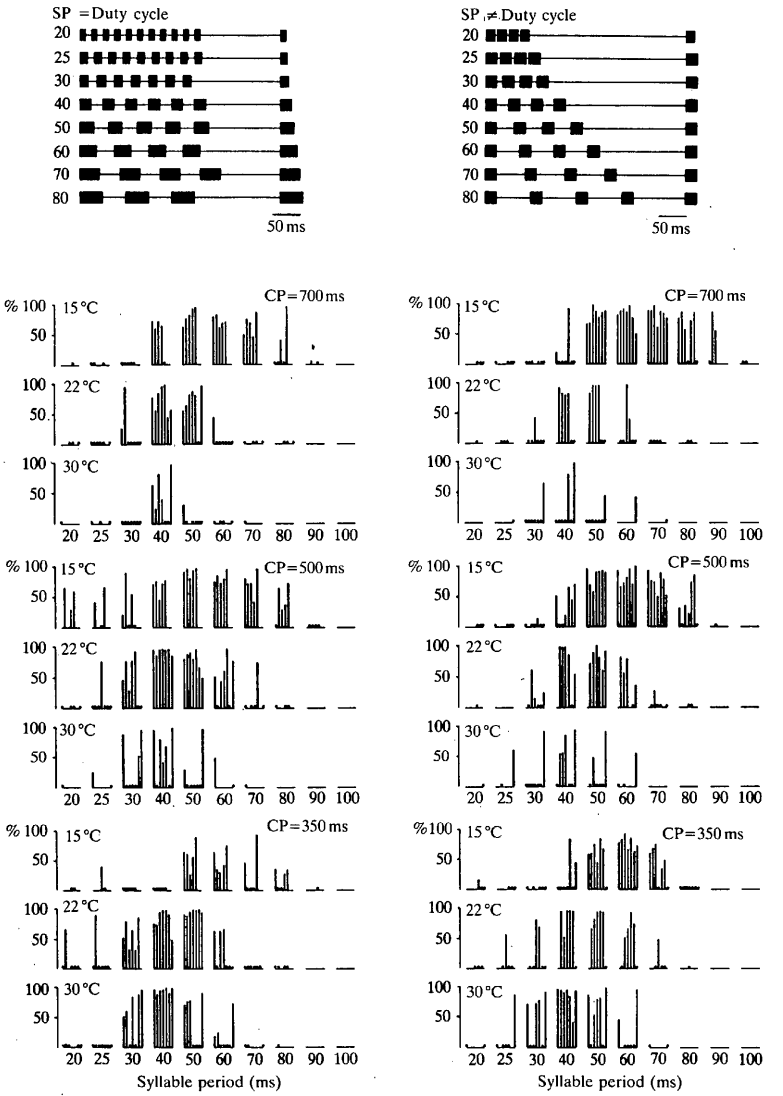
SP =Duty cycle
20
25
30
40
50
60
70
80
50 ms
SP ≠Duty cycle
20
25
30
40
50
60
70
80
50 ms
% 100
50
15 °C
CP=700 ms
100
50
22 °C
100
50
30 °C
20 25 30 40 50 60 70 80 90 100
% 100
50
15 °C
CP=500 ms
100
50
22 °C
100
50
30 °C
20 25 30 40 50 60 70 80 90 100
% 100
50
15 °C
CP=350 ms
100
50
22 °C
100
50
30 °C
20 25 30 40 50 60 70 80 90 100
Syllable period (ms)
% 100
50
15 °C
CP=700 ms
100
50
22 °C
100
50
30 °C
20 25 30 40 50 60 70 80 90 100
% 100
50
15 °C
CP=500 ms
100
50
22 °C
100
50
30 °C
20 25 30 40 50 60 70 80 90 100
% 100
50
15 °C
CP=350 ms
100
50
22 °C
100
50
30 °C
20 25 30 40 50 60 70 80 90 100
Syllable period (ms)

Fig. 9

calling song that elicited optimal phonotaxis by females and the range of SPs in natural calling songs emitted by males at the same temperature (Figs 7, 9). This match between sender and receiver was less evident for CP, although at high temperatures, songs with long CPs were not tracked well compared to songs with shorter CPs (Figs 7, 8, 9). Females appeared to track songs with short CPs equally well at 15 and 30°C, but one must realize that the songs at these two temperatures had optimal SPs (SPs adjusted to these temperatures, see Materials and Methods). Differences in tracking performances to songs with different CPs may have been more apparent at the margins of the SP-range; that is, if only 'marginally-attractive' syllable periods were used (i.e. at 40 ms SP at 15°C).

### *Female phonotaxis and the interaction of calling song properties*

#### *Interaction of chirp period and syllable period*

Chirp period affected the range of syllable periods that females tracked at different temperatures (Fig. 7). In general, the range of SPs tracked by females was broad if the CP was within the range of CPs of calling song at this temperature, and narrower when the CP was at the margins or even outside this natural range. CP had little effect on the tracking of songs with SPs in the centre of the female's response range, whereas this effect was most evident at the margins of the SP range. This is seen best when one compares female tracking at 15 and 30°C (Fig. 9). At 15°C, the range of SPs tracked by females was broad (40–80 ms) when songs had longer CPs of 500 and 700 ms. This range contracted to 50–60 ms (=DC stimuli) and to 50–70 ms (≠DC stimuli) when the CP was shortened to 350 ms. At 30°C, the range of SPs tracked by females was broad (30–50 ms) when stimuli had a short CP of 350 ms (characteristic of calling song at 30°C) and was narrower (40 ms) when stimuli had longer CPs of 500 and 700 ms. At both temperatures, the tracking performances of most females to songs with optimal SPs remained unchanged, regardless of what CP was used. In some females, however, there was a clear reduction in the tracking performance to songs with optimal SPs when CPs were short (15°C) and long (30°C) (see Fig. 9).

#### *Interaction of syllable period and chirp duration*

Female tracking performance to songs with different SPs also appeared to be dependent upon chirp duration (or the number of syllables per chirp, but see J. A. Doherty, in preparation). As for CP, the interaction between SP and chirp duration

Fig. 9. The effect of temperature on tracking performances of seven females to synthetic stimuli with different syllable periods (SP) and chirp periods (CP). The graphs on the left summarize the responses of individuals to equal-duty-cycle stimuli (top left) and the graphs on the right summarize the responses to unequal-duty-cycle stimuli (top right). The timing relationship for a CP of 350 ms is shown in the diagrams of the synthetic stimuli. The ordinates of the graphs indicate the percentages of the stimulus times that females tracked the stimulus (see Methods). Bars indicate the tracking scores of individual females, and the responses of individuals can be followed over different SPs, CPs and stimulus paradigms. For example, the responses of female number 3 can be followed by looking at the third bar from the left for each stimulus. Closed circles indicate a 0% tracking score. No bars or points indicate that the female was not tested with the stimulus. Playback levels of stimuli were 80 dB SPL, except for the following females: 4 (70 dB at 22 and 30°C), 5 (85 dB), 6 (85 dB at 15 and 22°C), 7 (85 dB).

(CD) was most evident at the margins of the SP range; CD had little effect on tracking performance to songs with SPs in the middle of this range. The interaction between SP and CD (or SN) is seen best when the results from the =DC and ≠DC experiments are compared (Fig. 9). At 15 °C and with a CP of 700 ms, most females tracked songs with SPs ranging from 40 to 70 ms in the = DC experiment, and from 50 to 80 ms in the ≠DC experiment. The differences in these results were in the tracking of stimuli with 40 ms and 80 ms SPs. The differences in the tracking performance to stimuli with 80 ms SPs may have been due to different syllable numbers (3 *versus* 4) and different syllable durations (40 ms *versus* 20 ms) in the stimuli (Fig. 9). Stimuli with 40 ms SPs in the =DC and ≠DC experiments differed only in the number of syllables per chirp (6 *versus* 4 syllables, see stimuli in Fig. 9), so females apparently tracked longer duration chirps (or chirps with greater SNs) better than shorter duration chirps at 15 °C. Furthermore, when one compares tracking performances to songs with shorter SPs in the = DC and ≠DC experiments (15 °C, CP 500 ms, SPs 20–30 ms), some females tracked longer duration chirps better than shorter duration chirps that had the same SP.

Further comparisons of =DC and ≠DC experiments at 22 °C reveal that chirps with longer durations elicited better tracking than shorter duration chirps (Fig. 9). When the CP was 500 ms or 350 ms and the SP was 30 ms, females tracked longer duration chirps (7 syllables, =DC stimulus) better than shorter duration chirps (4 syllables, ≠DC stimulus). This improved tracking performance was probably not due to differences in total sound energy because the sound energy per chirp was greater in the shorter duration chirp (≠DC stimulus, 67 % duty cycle) compared to that in the longer duration chirp (=DC stimulus, 50 % duty cycle).

## DISCUSSION

### *The effect of temperature on calling song*

#### *Syllable and chirp repetition rates*

Temperature affected syllable (pulse) repetition rate (PR) and chirp repetition rate (CR) in the calling song of *G. bimaculatus* only below 24 °C (Fig. 4). The effect of temperature on PR was small compared to what has been reported in trilling species of crickets (Walker, 1962*a*,*b*, 1963). The PR in the calling song of trilling crickets rose linearly between 15 and 35 °C, and PRs of individual species ranged between 25 and 100 pulses $s^{-1}$ (see Walker, 1962*b*). In *G. bimaculatus*, mean PRs of individuals were considerably lower than those of trilling crickets at comparable temperatures and ranged from 14 to 33 pulses $s^{-1}$ (Fig. 4). Similar ranges of PRs have been reported in other chirping species of *Gryllus*, including *G. pennsylvanicus* (Alexander, 1957) and *G. campestris* (Kutsch, 1969; Kriechbaum, 1983). These findings agree with those of Walker (1962*b*), which showed that the effect of temperature on pulse rate was greater in species that had higher PRs at a given temperature.

The effect of temperature on chirp repetition rate in the calling song of *G. bimaculatus* was comparable to that on CR in other chirping crickets. In *G. bimaculatus*, mean CRs of individuals ranged from 1·2 to 3·9 chirps $s^{-1}$ between 15 and 33 °C (Fig. 4). This range of CRs was similar to that in the chirping tree cricket,

*Oecanthus fultoni*; CRs of individuals ranged from about 1·8 to 3·8 chirps $s^{-1}$ between 15 and 32°C (Walker, 1962*a*,*b*). In the field cricket, *G. campestris*, CRs ranged from about 2·5 to 4·1 chirps $s^{-1}$ between 20 and 30°C (Kutsch, 1969).

The PR and CR in the calling songs of many species of crickets and katydids increase linearly with increasing temperature over the entire temperature range experienced by these animals (Walker, 1962*a*,*b*, 1963, 1975). In *G. bimaculatus*, the effects of temperature on PR and CR were also linear, although this linearity was not observed over the entire temperature range. Instead, the linear effects of temperature on PR and CR were evident only between 15 and 24°C and these temporal properties reached a maximum and did not change with temperature above 24°C (Fig. 4). Similar results have been reported in other chirping species of *Gryllus*, such as *G. pennsylvanicus* and *G. campestris* (Alexander, 1957; Kutsch, 1969; Kriechbaum, 1983), although temperature-independence of calling song temporal properties at high temperatures is not universal in chirping crickets. In the chirping tree cricket, *O. fultoni*, for example, the effects of temperature on PR and CR were linear between 18 and 32°C (Walker, 1962*a*). Indeed, the linear correlation of CR with temperature is so good that this cricket has been called the 'thermometer cricket' because one can determine the air temperature by counting the chirps in a specified time (see Walker, 1962*a*, for earlier references).

The mechanisms underlying temperature-dependence in trilling and chirping tree crickets and temperature-independence in *G. bimaculatus* and other chirping species of *Gryllus* at high temperatures remain unclear. At high temperatures, sources for rate saturation (i.e. no further increase in PR and CR) in the calling songs of chirping *Gryllus* may include mechanical as well as physiological constraints on song pattern generation. More insights into this problem await the results of studies on the mechanisms underlying stridulation at different temperatures.

*Syllable duration and dominant frequency*

Temperature had little or no effect on syllable duration in the calling song of *G. bimaculatus* (Fig. 5). Comparable results have been reported in trilling species of tree crickets (*Anurogryllus* and *Oecanthus* sp., Prestwich & Walker, 1981) and in the chirping species, *G. campestris* (Kutsch, 1969). These results indicate that the wing closing phase during stridulation is little affected by changes in temperature and that the increase of PR results primarily from shortening the silent, opening phase of the wings. This interpretation is supported by the results of studies on wing movements and electromyogram activity during stridulation at different temperatures (Kutsch, 1969; Volleth, 1981).

Compared with other temporal properties (PR, CR), there was little or no effect of temperature on dominant frequency in the calling song of *G. bimaculatus* (Fig. 6). This result may be due to dominant frequency being determined by mechanical resonance of the wings, which is also relatively unaffected by temperature (Koch, 1980; C. J. H. Elliott and U. T. Koch, in preparation). Variable effects of temperature on dominant frequency have been described in several subfamilies of crickets (see Walker, 1962*b*; Volleth, 1981; Prestwich & Walker, 1981). In *G. rubens* and *A. arboreus*, this effect was slight and comparable to that in *G.*

*bimaculatus*. Stronger influences of temperature on dominant frequency occurred in some species of *Oecanthus* and *Nemobius*, but in other species, the dominant frequency reached a plateau at high temperatures (Walker, 1962*b*).

### *The effect of temperature on phonotaxis*

The effect of temperature on female phonotaxis paralleled the effect of temperature on male stridulation in *G. bimaculatus*. As far as syllable repetition rate and chirp repetition rate were concerned, the female's response was matched to the male's signal at temperatures between 15 and 30°C. This matching of sender and receiver at different temperature has been termed 'temperature coupling' (Gerhardt, 1978), and these results agree with those in studies of other temperature-coupled communication systems. Temperature coupling has been demonstrated in acoustic communication in tree crickets, grasshoppers and treefrogs (e.g. Walker, 1957; Helversen, 1972; Helversen & Helversen, 1981; Skovmand & Pedersen, 1983; Gerhardt, 1978, 1982, 1983; H. C. Gerhardt and J. A. Doherty, in preparation), and in visual communication in fireflies (e.g. Carlson *et al.* 1976). In all of these studies, the effects of temperature on signal generation in the sender are paralleled by similar effects of temperature on signal recognition in the receiver. Temperature coupling usually occurs over the entire temperature range, although in some cases, coupling appears to break down at higher temperature (see Gerhardt, 1978; Skovmand & Pedersen, 1983).

### *Signal production and recognition systems*

The existence of temperature coupling is consistent with the predictions of the genetic coupling hypothesis (Hoy, 1974). This hypothesis states that there are neural elements (individual neurones or networks of neurones) common to both pattern generation and pattern recognition. These common elements would be specified by the same genes and may exist in the form of neural filters or sensorymotor templates (Hoy, 1978). Besides temperature coupling phenomena, indirect evidence for genetic coupling also comes from studies of interspecific hybridization in crickets and treefrogs (Hoy *et al.* 1977; Doherty & Gerhardt, 1983, 1984). Evidence against genetic coupling comes primarily from studies of interspecific hybridization in acridid grasshoppers (Helversen & Helversen, 1975*a*,*b*; for a review see Elsner & Popov, 1978).

At present, neither the results of hybridization studies nor the temperature coupling phenomena observed in behaving animals provides conclusive evidence for or against the existence of common neural elements in sender and receiver (see Doherty & Gerhardt, 1984). More direct morphological and physiological analyses are needed of the neural elements involved with pattern generation and pattern recognition. Studies of the neural correlates of temperature coupling phenomena may provide new insights. As expressed by Gerhardt (1978), temperature coupling could result either from temperature having a single effect on the neural network common to both pattern generation and pattern recognition, or from temperature affecting completely different neural networks in the same way. Considering the accuracy of sender-receiver matching at different temperatures in several diverse

communication systems, the common network idea is the most parsimonious in explaining temperature coupling phenomena. Obviously, the falsification of either one of these possibilities will require new investigations into how and where in the animal's nervous system temperature is affecting pattern generation and pattern recognition.

### *Simplicity* versus *complexity in calling song recognition*

A male cricket can convey individual and species information to the female *via* several temporal and spectral properties of its calling song. The results of behavioural studies make it clear that some properties of the calling song are more important than others in triggering recognition and eliciting phonotaxis in female crickets (e.g. Zaretky, 1972; Hill, 1974*a*,*b*; Popov & Shuvalov, 1977; Pollack & Hoy, 1979, 1981; Weber *et al.* 1981; Thorson *et al.* 1982; Stout, DeHaan & McGhee, 1983). Furthermore, within the auditory pathway, neurones have been recorded and partly identified that encode spectral and temporal properties of the calling song (for reviews see Elsner & Popov, 1978; Huber, 1983; Boyan, 1984), although elements involved in the recognition process have not been identified until recently (Schildberger, 1984).

Recent results obtained by studying females of *G. campestris* on a walking compensator show that the syllable repetition rate of around 30 Hz is the 'chief – and in some cases both necessary and sufficient – property' of the calling song that triggers recognition and phonotaxis in females (Thorson *et al.* 1982). Thorson *et al.* formulated the '30-Hz hypothesis' for calling song recognition, which states that the 30-Hz syllable modulation is the only feature required for recognition, as long as the carrier frequency is audible. This hypothesis reflects 'simplicity' in calling song recognition in chirping crickets because it implies that as long as the 30-Hz modulation is present other temporal properties, such as chirp duration and chirp repetition rate, are not essential in the recognition process.

In *G. bimaculatus*, calling song recognition appears to be more complex (see also Popov, Shuvalov, Svetlogorskaya & Markovich, 1974; Stout *et al.* 1983). The attractiveness of the calling song, as expressed by the tracking performance of the female on a locomotion compensator, was dependent upon the evaluation of several temporal properties. That is, female tracking of stimuli with 'unattractive' syllable periods (i.e. at the margins of the effective range for tracking) was turned on or off by changing the values of supposedly 'non-essential' temporal properties, such as chirp period and chirp duration (Figs 7, 9). The influence of different temporal properties on the attractiveness of the calling song in *G. bimaculatus* reflects what could be called a 'trade-off', which expresses the relative weightings of combined parameters of the calling song in the recognition process. Hints for such trade-off phenomena in the recognition process in *G. bimaculatus* are evident at all temperatures (Figs 7, 9; see also J. A. Doherty, in preparation). If one temporal property is 'unattractive', the attractiveness of the entire stimulus can be maintained by raising the attractiveness of other temporal properties. Trade-off effects in females may well serve to 'buffer' the recognition process against differences in the calling song that may result from males singing at different temperatures, singing at different chirp repetition rates, or from different amounts of environmental degra-

dation of the physical properties of the calling song during signal transmission between sender and receiver.

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