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Parallel processing in auditory pattern recognition and directional analysis by the grasshopper *Chorthippus biguttulus* L. (Acrididae)

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Summary. In behavioral experiments on females of the acridid grasshopper species *Chorthippus biguttulus* the relationships between pattern recognition and directional hearing were examined.

1. The grasshoppers displayed no capacity for direction-specific pattern recognition. That is, when two effective sound patterns were presented from different directions, superimposed in time so as to form an ineffective pattern, neither signal elicited a singing response no matter how different the directions were (Fig. 1).

2. The behavior of unilaterally deafened grasshoppers was used to study the attenuation of contralaterally incident sound (and to obtain a directional characteristic). With pulsed noise signals (bandwidth 3–40 kHz), the threshold curve for contralateral presentation was shifted by ca. 8 dB as compared with ipsilateral presentation (Figs. 2 and 3).

3. The grasshoppers responded to two ineffective patterns superimposed to form an effective pattern, even when each tympanal organ was receiving only one of the ineffective patterns (Figs. 5 and 7). Therefore the pattern of excitation that corresponds to an effective sound pattern could only be produced in neurons above the receptor level, presumably in the metathoracic ganglion. Evidently the input functions of the two tympanal organs are added (or processed in a manner equivalent to addition), before they enter the process of pattern-recognition.

Introduction

Auditory communication among grasshoppers requires two major forms of auditory-system function: the conspecific signals must be *recognized* – that is, detected as distinct from many other environmental acoustic events, some of them very similar, and responded to in a selective manner – and the partner emitting the signals must be *located*, at least to the extent that its direction is determined. In acridid grasshoppers of the genus *Chorthippus*, the female bears most of the responsibility for the first task, recognition of the conspecific song. That is, when the female is ready to mate, she responds (by singing) only to the calling song of males of her own species. The male, on the other hand, is chiefly responsible for determining the location of a responding female and going to her.

That acridid grasshoppers, both male and female, have a fairly elaborate system for analyzing the direction of sound stimuli has already been demonstrated by a number of excellent neurophysiological studies. For example, the directional characteristic of the tympanal organs is quite well known (Autrum et al. 1961; Römer 1976; Adam 1977; Miller 1977), as are the basic features of directional analysis at the level of thoracic interneurons (Rheinlaender and Mörchen 1979; Römer et al. 1981); the latter work has examined the influence of latency as well as that of differences in spike frequency. In fact, a beginning has been made in the study of the central nervous representation of sound directions (Adam 1977). Adam found central neurons with specific, narrow directional sensitivity, which could not be explained from the directional characteristics of the tympanal organs simply by amplification or inhibition. It seems possible, then, that the grasshoppers might be capable of relatively complex behavioral achievements such as direction-specific pattern recognition.

The behavioral experiments described here were designed to explore the extent to which these two processes, pattern analysis and determination of direction, are coupled, and to reveal whether in various instances they operate in parallel. Are the grasshoppers capable of direction-specific pattern recognition? That is, can they distinguish from one another the signals emitted simultaneously from several sound sources? Are the input functions from the two ears conducted independently to a pattern-analyzing system, or are they first processed to give a single function which is then input to a pattern detector?

Material and methods

Animals. All experiments employed virgin female *Chorthippus biguttulus*, which had been caught as subadult larvae in the field (southern Germany) or raised from eggs in the laboratory.

Apparatus. Most of the experiments were done in a sound-attenuating room heated to 28°–30° C. Two piezoelectric loudspeakers (L1 and L2) were mounted about 1.2 m above the floor, 2 m apart from one another. A third speaker (L3) was attached to a movable arm so that it could be rotated about the midpoint of the line connecting L1 and L2. (In some of the experiments condenser loudspeakers were used.) In the center of this arrangement was the experimental animal, entirely free to move on a small disk of foam rubber. The socket bearing this disk could be shifted so that if the animal walked or turned so as to change its position with respect to the loudspeakers, it could be gently brought back to the standard position. A marker suspended from the ceiling served as a reference, by which the grasshopper could be positioned in the center of the sound field to within a few millimeters. A red lamp in the otherwise dark room warmed the central position, which gave the animal an incentive to stay there.

The female grasshoppers are very easily disturbed by vibration, drafts and the like, in which case they cease to sing in response to male song (sometimes for long periods). The room was darkened so that the animals would not be excessively disturbed by the movements of the experimenter.

The artificial songs presented to the females were noise pulses (syllables) with an approximately flat spectrum (±6 dB) in the range of about 3–40 kHz. In order to present patterns via the two loudspeakers that were in a precisely defined phase relation to one another (see Results), the onset of one pulse triggered a delay element, the output of which in turn triggered a timed modulator that determined the duration of the delayed pulse. The original pattern (noise syllables of 80 or 40 ms, separated by pauses of 20 or 60 ms, respectively) was sent to loudspeaker L1 by way of a power amplifier, and the delayed pattern, amplified by a second power amplifier, could be switched between loudspeakers L2 and L3. The gain of the power amplifiers could be reduced in 1-dB steps. The intensity of the two patterns could be changed simultaneously in fixed steps by means of an attenuator at the output of the noise generator.

The output voltage of the power amplifier (frequently tested with a digital voltmeter) was used as the measure of sound intensity. Calibration was done with a B&K precision sound level meter in dB SPL (Brüel & Kjaer, measuring amplifier 2606 with microphone 4133, using 22.4-Hz filter).

In general, the same noise source was used to produce both patterns. In the experiments in which two effective patterns were superimposed to form an ineffective one – that is, coherent noise signals from two directions were superimposed – interference phenomena at the site of the animal were to be expected. Therefore the experiments were controlled with an arrangement in which noise signals independent of one another were produced by two sources of identical spectral composition. (This was accomplished by recording the output of the noise generator on two channels of a tape recorder (Racal 4D) in two separate operations, and using the two recorded channels as noise sources.) This modification of the experiment produced no difference in the behavioral results. The problem of interference does not arise in the experiments in which two ineffective patterns were superimposed to produce an effective one, because in this case the patterns were shifted in time such that the two speakers were never active simultaneously.

Experimental procedure. An individually identified female in responsive condition was carefully placed on the foam-rubber disk and brought into the correct position with respect to the speakers by adjusting this substrate. Then the (5 s long) stimuli were presented, separated by an interval of about 30 s or more so as to allow the influence, if any, of the preceding stimulus to die out, and to minimize fatigue. The sequence of stimulus situations was continually altered, so as to average out short-term changes in responsiveness.

For the measurements of threshold curves the traditional procedure, in which all the intensities to be tested are presented equally often and the response is expressed as the percentage of stimuli that were effective, was rejected because the very long time required to complete a curve would make it essentially impossible to compare several threshold curves (for various stimulus conditions or directions). Therefore, because differences in threshold were of the greatest interest, the following abbreviated procedure was used.

Beginning with low intensities, an artificial male song 5 s duration was presented every 30 s, at intensities progressively adjusted as follows: if the female responded at a certain intensity, the next stimulus was reduced in intensity by one step; if a stimulus elicited no response, the intensity of the next stimulus was increased by one step. With this procedure the stimuli are always at near-threshold intensities, so that the female does not become fatigued by too-frequent exposure to high-intensity stimuli. A quiescent female could be presented with about 10 to 30 stimuli in succession – often always responding at the same intensity – before it moved, at which time the series was terminated and the animal was repositioned.

A plot of these data that could be compared with traditional threshold curves was obtained as follows. First a list was made of all the intensities at which the animal responded for the first time (when intensity was being increased) or the last time (decreasing intensity), and the frequencies of occurrence of these transitional intensities were determined. This distribution was plotted as a cumulative function (% of the total number of all transitions – i.e., 'first' or 'last' responses – observed). This cumulative function coincides with the threshold curve (R-logI-curve) found by the more elaborate method mentioned above when the animals are highly motivated and respond persistently. (When they are less responsive, the cumulative functions may rise somewhat more steeply than the associated R-logI-curves.) Because the plot is based on the number of transitions between answering and not answering that actually occurred, all the curves reach the 100% level, even those for which the stimulus was a relatively ineffective pattern, which in an effectiveness test would not elicit 100% responses (cf. threshold curve d in Fig. 7 and the effectiveness of patterns in which the 2nd half of the syllable was reduced by 6–9 dB, Fig. 6).

Surgical operations. Some of the female grasshoppers were deafened on one side by cutting a window in the cuticle of the thoracic sternum through which the tympanal nerve was cut near its entry into the metathoracic ganglion; then the window was replaced and fixed in position with wax-colophonium. In an earlier series of experiments several animals had been deafened by destruction of the receptor organ itself, with a very fine-tipped hot soldering needle inserted through the tympanal membrane in the vicinity of the receptor cells. In both cases some of the animals soon began to respond again, so that they could be tested by the usual procedures. The results of the surgery were confirmed by post-mortem examination.

Results

Is there direction-specific pattern recognition?

The experiment designed to answer this question was as follows: Synthetic sounds representing modifications of the conspecific song were presented to a female grasshopper simultaneously by two loudspeakers. In one case each of the two stimuli was a pattern effective in eliciting a singing response, but superposition of the two stimuli in a single source produced an ineffective pattern. In the second the reverse was true: two stimuli ineffective in themselves formed an effective pattern when superimposed in a single source. When the two loudspeakers are side by side, one would expect the grasshopper to give no response in the first case and to respond in the second case (superposition to give an effective pattern). If the angle between the two loudspeakers is increased step by step, with one speaker kept in position and the other moved over an arc about the female, her behavior must reveal whether her identification of the sound is direction-specific. If so, in the first case she should begin to respond as soon as the speakers are far enough apart that she can identify the sound as two separate, effective patterns coming from different directions. In the second case she should cease to respond as soon as she can detect that the two components of the sound are coming from different directions.

The pattern of the song of *Chorthippus biguttulus* (von Helversen 1972) is such that two suitable artificial pattern combinations can easily be constructed, as illustrated in Fig. 1. A pattern that very effectively elicits a response of female *Chorthippus biguttulus* is a simple series of noise pulses (syllables), 80 ms in duration and separated by 20-ms pauses (termed pattern *80*/20). This syllable-pause sequence was presented for 5 s (giving a total of 50 syllables). When two such patterns are presented 180° out of phase, the result is a *30*/20 pattern, in which relatively loud syllables alternate with lower-intensity 'pauses' (see Fig. 1, upper left). A *30*/20 pattern is entirely ineffective for female *Ch. biguttulus*, even if the 20-ms pauses are silent.

Conversely, two patterns can be found that are in themselves ineffective, whereas together they produce the effective *80*/20 pattern. Two *40*/60 patterns (40-ms syllables, 60-ms pauses) are timed such that the syllables are contiguous, forming a continuous 80-ms noise pulse (Fig. 1, upper right).

Figure 1 shows the results of this experiment. The effective pattern *80*/20, when presented alone over one of the two speakers, regularly elicits a response (hatched columns in the left half of the picture). When the same pattern is also presented over the second speaker, but 50 ms shifted in time with respect to the first, as expected the female fails to respond (white columns, left half of the picture). When the angle between the two speakers is increased she still does not respond – even when the speakers are opposite one another, on the right and left sides of the animal (as can be seen, e.g., in Fig. 5).

Evidently the female grasshopper cannot distinguish the patterns coming from different directions; whatever the positions of the loudspeakers, the sounds they emit are superimposed to form an ineffective pattern.

The behavior of a female presented with a sound in which two ineffective patterns combine to give an effective pattern is consistent with this result (right half of Fig. 1). Regardless of the angle between the two speakers, the grasshopper always responds to the composite sound (black columns). That is, the females respond to components that come from different directions and at the tympanal organ superimpose to form an effective pattern, just as though this pattern were from a single source. Together with the result of the first experiment, this behavior demonstrates that the information reaching the pattern-recognition apparatus is the sum of the signals arriving from various directions, the total input function of a tympanal organ.

The grasshopper, then, is not capable of dissecting a sound pattern into its component directions before it is classified.

How do the inputs to the two tympanal organs interact in pattern analysis?

The preceding experiment shows that no directional analysis of the components of a sound signal precedes its processing in the pattern-recognition apparatus.

Taking the experiments a step further, we can learn whether the grasshopper will still respond even when each of the two tympanal nerves is transmitting an ineffective pattern, so that the two ineffective patterns can combine to form an effec-

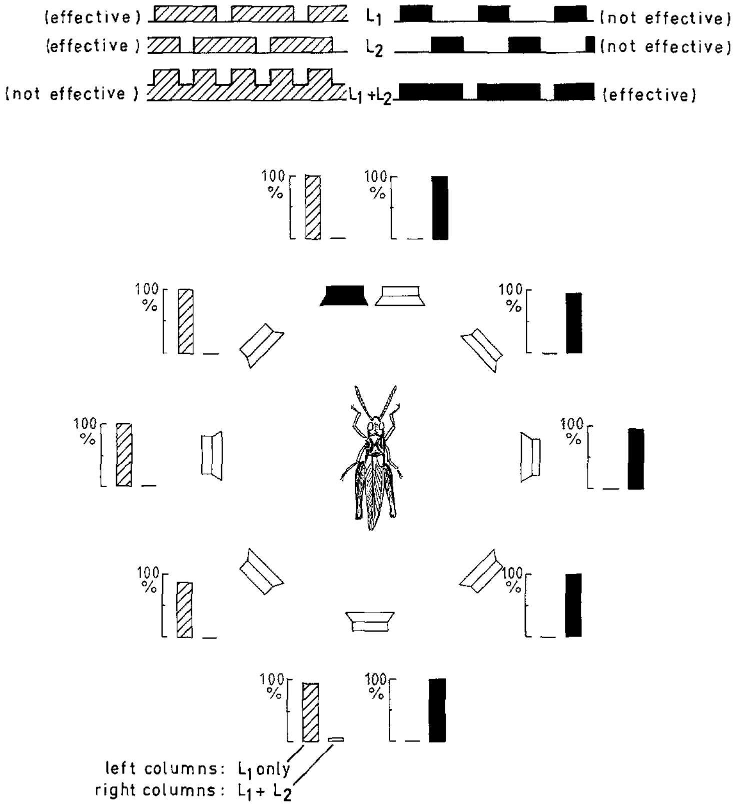

Fig. 1. Response frequencies of *Chorthippus biguttulus* females to patterns from two loudspeakers. Loudspeaker L1 (black) was fixed at a distance 1 m in front of the grasshopper, while loudspeaker L2 was moved in 30° steps along a circle centered on the animal. The bar graphs at each L2 position show the frequency of responses to L1 alone (left bar in each graph) and to L1 + L2 (right bar in each graph) as a percentage of the stimuli presented (25–28 tests at each position). In the left half of the circle two effective stimulus patterns combined to give an ineffective pattern, in the right semicircle two ineffective patterns combined to give an effective one (see schematic representations of the sound at the top of the picture)

tive one only inside the animal, at the neuronal level.

This experiment requires that each tympanal organ is stimulated independently, which could be done with miniature earphones. However, it is impossible to attach such earphones to a freely moving grasshopper. The situation can be simulated, though, by presenting loudspeaker stimuli at an intensity just great enough to elicit a response on the side toward the sound source but too low to activate the side away from the source.

To do such an experiment, one must know the directional characteristic of the tympanal organ. Moreover, the attenuation of the sound by the animal's body must be sufficient, in comparison to the slope of the threshold curves. The following sections describe this attenuation and the slope of the threshold curves as measured in several females.

Attenuation of laterally incident sound. The degree to which sound coming from one side is attenuated on the opposite side by the grasshopper's body can be measured in a behavioral experiment, by comparing the threshold curves for response of unilaterally deafened females to sounds coming from the two sides. The difference between the two curves corresponds to the attenuation. The attenuation was measured with the same artificial sounds – the same carrier-frequency spectrum, in particular – as in the other experiments reported here, to facilitate comparison.

In order to leave both tympanal organs completely intact, so that their sound-attenuating properties would be retained, the measurements were done with two females, in each of which one tympanal nerve had been transected. Despite this surgery, both animals continued to respond in the experimental situation for many days. The two threshold curves were found by presenting stimuli from the right and left sides in continuous alternation.

In Fig. 2 the threshold curves so obtained (see Methods) from female 81-bl are shown as an example. Measurements were taken on two days, and although the thresholds were different (because of differences in motivation) the distances separating the two curves, the measure of attenuation, were nearly identical, 8.5 and 9 dB.

Comparable results were obtained with 5 other females in which, for earlier measurements, the receptor cells and the tympanal membrane near them had been destroyed mechanically and by the action of heat (see Table 1). On the average, then, the attenuation of laterally incident sound at the side away from the source can be taken as about 8 dB.

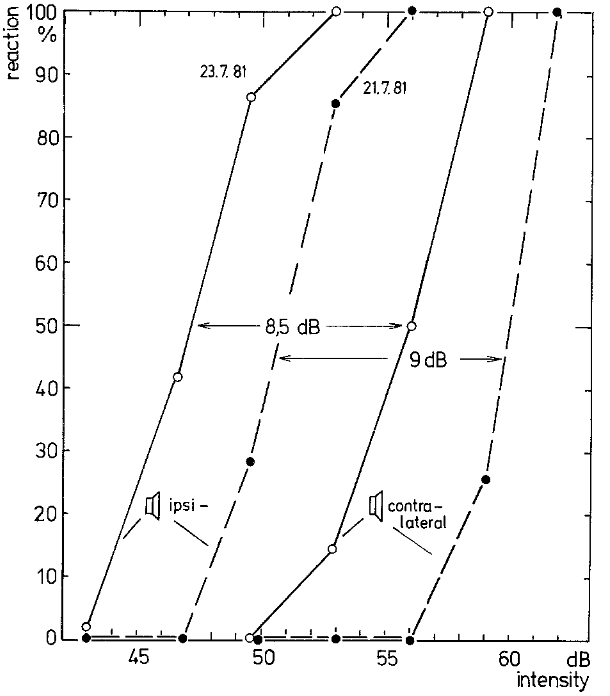

Fig. 2. Threshold curves for the response to laterally presented sound signals (carrier frequency spectrum ca. 3–40 kHz) of a female *Ch. biguttulus* with transected left tympanal nerve. The female was tested on two days. On 23.7 the threshold was lower, but the distance between the curves for sound from the left and from the right remained the same. Transitions between not responding and responding are plotted cumulatively (see Material and methods), with 21 and 22 transitions on 21.7 and 38 and 34 on 23.7

Table 1. See text

Animal	Method of eliminating tympanal input	Attenuation from ipsi- to contralateral
♀ 77-s	Tympanal membrane pierced, cells of tympanal organ destroyed by heat	8 and 9.5
77-19		7.4
77-23		8.4
80 li Fe bl		7.5
80 r Fe bl		6 and 6.5
81-bl	Tympanal nerve transected	9
81-r		8.5 and 9

With one of the unilaterally deafened animals (♀ 77-23), after the lateral attenuation had been measured a complete directional characteristic (in 30° steps) was obtained. The result is shown in Fig. 3.

The threshold curves of 7 females, all highly motivated, are shown in Fig. 4. In all cases the response saturates at ca. 6–8 dB above the threshold intensity. Therefore, if an intensity is chosen at which the response probability is just at the 100% level or slightly below it, it can be assumed

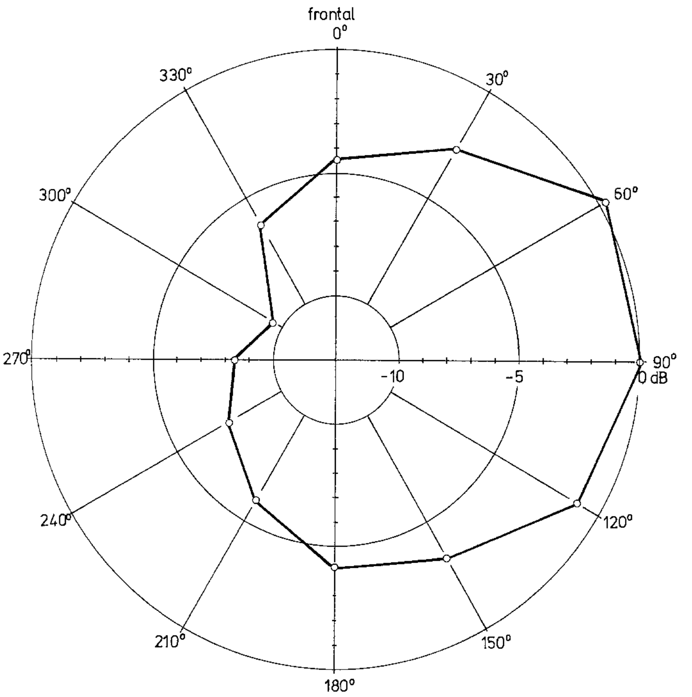

Fig. 3. Directional characteristic of the tympanal organ of a unilaterally deafened female *Ch. biguttulus*, measured with a stimulus pattern having a carrier-frequency spectrum from 3 to 40 kHz. At each position the intensity was raised from a low level in 3-dB steps, until a level was reached at which the female began to respond. Each point represents the mean of 8 to 14 such trials, with the positions tested in various sequences

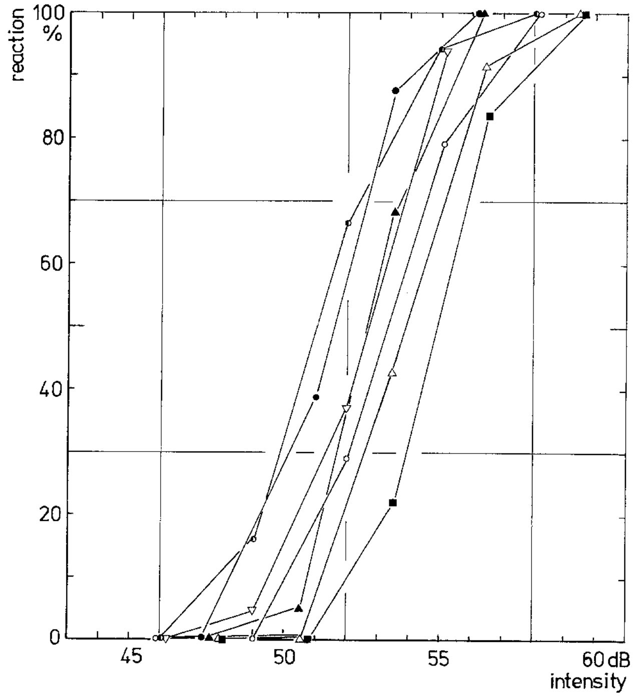

Fig. 4. Threshold curves for the singing response of 7 intact female *Ch. biguttulus* to pattern *80/20* presented from the side. The individual curves are based on between 17 and 45 transitions between not responding and responding (see Material and methods)

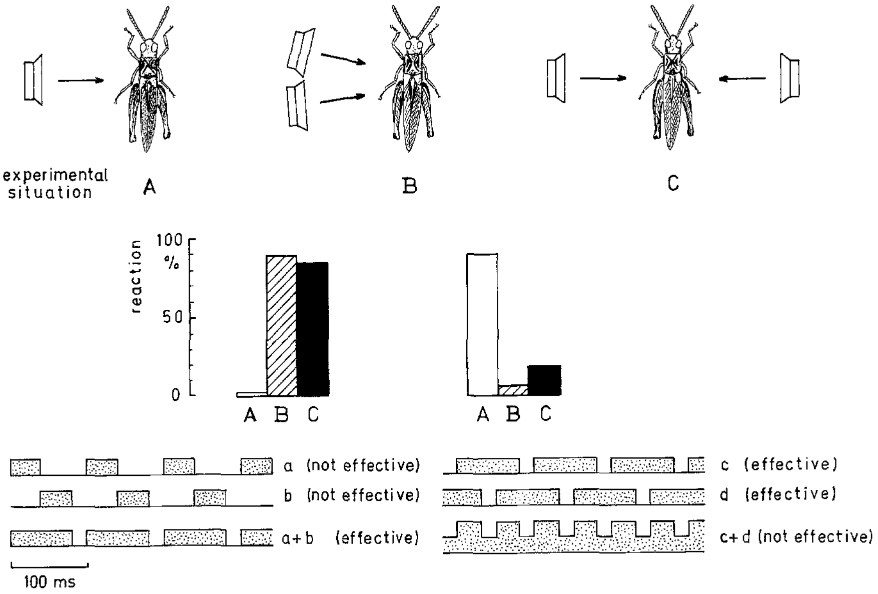

Fig. 5. Effectiveness of composite artificial sound stimuli from two directions. The upper row of drawings (A, B, C) shows positions of the loudspeakers with respect to the female for which the response frequencies shown in the middle were obtained. Left bar graph corresponds to the pattern *40*/60 shown at lower left, which together formed the effective pattern *80*/20. In the right bar graph the patterns shown at lower right were tested: two effective patterns *80*/20 combined to form an ineffective pattern

that the intensity at the side away from the sound source will be so attenuated as to elicit very few or no responses. This allows to study the interaction of two acoustical inputs from both sides of the animal, each of which is only suprathreshold on the side of the sound source.

Interaction of binaural inputs. It follows from the above considerations that the intensity of sound from a loudspeaker on one side of the animal can be adjusted so as to be suprathreshold (for a behavioral response) on that side and subthreshold on the other. With two such loudspeakers, one on each side of the animal, independent patterns can be presented to the two sides, and the question whether an effective pattern of excitation can be generated *within* the animal by two ineffective stimuli can be investigated.

This experiment is illustrated in Fig. 5. The speakers are 1 m apart, one on each side of the female. The stimuli were the same sound patterns as in Fig. 1, but now emitted lateral to the animal at an intensity adjusted individually for each animal so that it was just under the saturation level of the threshold curve.

First consider the result of presenting the two ineffective patterns (again *40*/60), superposition of which produces an effective pattern. In this situation – as expected – the single pattern alone elicits hardly any response (case A), whereas the grasshopper responds strongly to the composite pattern produced with the speakers side by side (case B). In the critical experiments, in which both sides are stimulated with ineffective patterns (case C), the animal also responds. The effectiveness of the combined stimulus was only slightly less in case C than in case B. And precisely the reciprocal result is obtained with two effective patterns that in combination form an ineffective one: in arrangement C the grasshopper hardly responds, even though each tympanal organ in itself receives an effective pattern.

This outcome means that the two tympanal inputs must be put together somehow in the CNS of the grasshopper before pattern analysis occurs. That is, the grasshopper is responding to a pattern that has only been completed on the neuronal level within its CNS.

Control experiment. A fundamental requirement for the experiment illustrated in Fig. 5 is that the tympanal organ contralateral to each loudspeaker not be exposed to a suprathreshold stimulus from that speaker (because of its directional characteristic). If this condition is not met, the interpretation of the result can be called into question. In experiments on intact animals, 'suprathreshold' can mean only a behavioral threshold – in this case the singing response of the female. Clearly, a sound intensity too low to elicit a behavioral response might still be exciting some or even many units in the tympanal nerves, so that their subthreshold influence might have made itself felt in the special situation imposed by the experiment. As a check on the binaural-mixing experiment, therefore, another experiment was done in which the line of argument does not require that the excitation on the contralateral side be subthreshold, as follows.

Consider the situation in which speakers arranged as in Fig. 5C, one on each side of the ani-

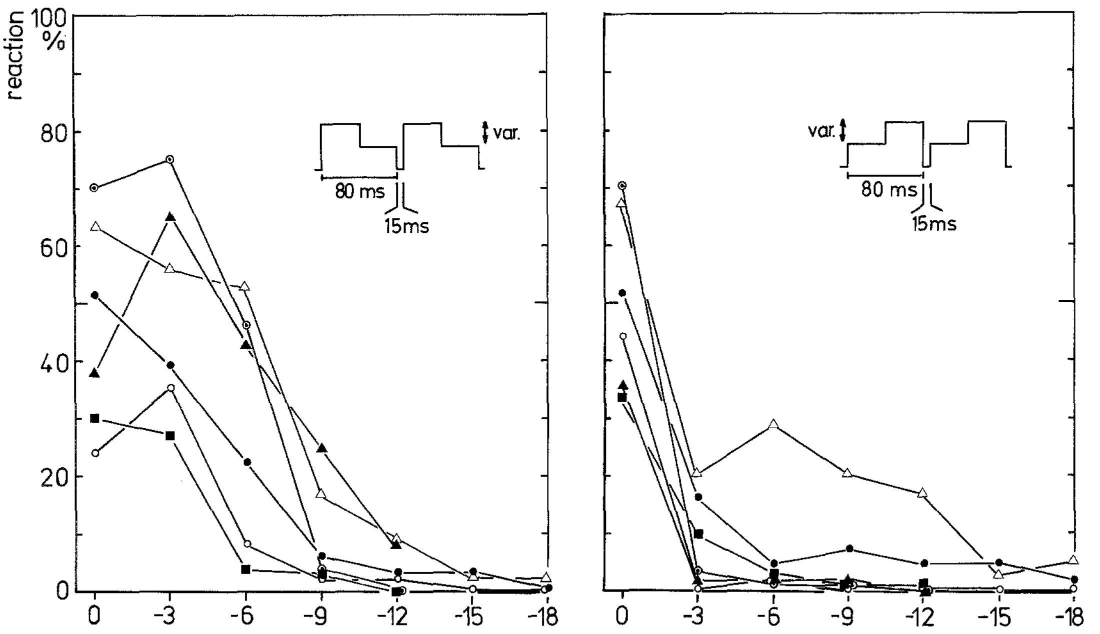

Fig. 6a, b. Effectiveness of simulated songs with graded pulse amplitudes. Pattern *80*/15 was modified by reducing the intensity of the second half of the syllable (**a**) or the first half (**b**) in 3-dB steps. (The curves for the individual females are based on 40–200 stimulus presentations per data point)

mal, are emitting the sound patterns shown on the left in Fig. 5. The patterns produced at the two tympanal organs are then mirror images of one another. On the side of the speaker first activated the first half of the syllable is unattenuated and therefore louder than the second, which undergoes 8 dB attenuation by the body of the animal. On the other side the second half of the syllable is louder, by the same amount, than the first. The assumption in the above binaural-mixing experiment was that the lower-intensity half of each syllable is not detected by the tympanal organ as it was below the threshold. If, on the contrary, the responses observed resulted not from internal mixing but from detection of the entire composite syllable by each tympanal organ, one ought to be able to elicit equivalent responses by presenting similar 'graded-intensity' syllables to only one tympanum. If graded-intensity syllables prove ineffective in unilateral presentation, it follows that the effectiveness of bilaterally presented phase-shifted pulses is due to internal processing rather than to superposition at the periphery.

The response to graded-intensity patterns was measured within intact females in a computer-controlled testing device. The two mirror-image patterns have very different effects on the females. When the beginning of the syllable is less loud than the rest, even by only a small amount, the pattern becomes much less effective (Fig. 6b). Conversely, if the syllable is loud at the beginning and becomes softer only in the second half, its effectiveness is no less and can be even greater when the intensity difference is small. Attenuation of the second half by 9 dB, however, makes the signal unattractive (at intermediate intensities) to most females (Fig. 6a).

This experiment therefore leaves open the possibility that the female in the experiment of Fig. 5 might have been responding to the graded-intensity pattern to which the tympanum on the side of the speaker first activated was exposed (i.e., louder in the first half of the syllable). Therefore a further test was required, as illustrated in Fig. 7. Here threshold curves were obtained simultaneously for the same female under three conditions: (a) with phase-shifted half syllables of equal intensity from speakers opposite one another on either side of the animal (situation C of Fig. 5); (b) with phase-shifted half syllables of equal intensity from speakers next to one another on one side of the animal (control, corresponds to situation B in Fig. 5); (c) with phase-shifted half syllables from speakers next to one another on one side of the animal, the second half syllable being attenuated by 6 or 8 dB (simulation of the pattern produced on one side in (a)).

Figure 7 shows that the threshold curves for (a) and (b) practically coincide with one another, whereas with the graded-intensity patterns asso-

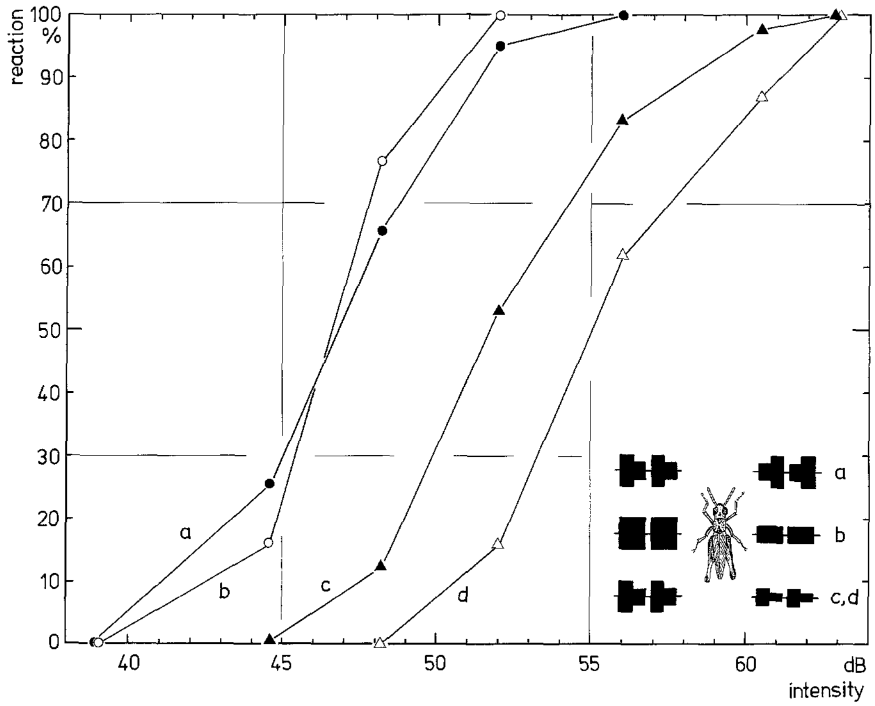

Fig. 7. Threshold curves for the response of a *Ch. biguttulus* female to pattern *80/20* coming from a single direction (b) or produced by superposition of patterns from the right and left (a). Curves (c) and (d): threshold curves for patterns with graded amplitudes (second half of the syllable reduced by 6 (c) and 8 (d) dB, respectively), which when presented on one side simulate the pattern produced at the tympanal organ in the stimulus situation of (a). Inset illustrates schematically the patterns produced at the grasshopper's tympanal organs. (Number of transitions between not responding and responding for curves a to d: 60, 61, 62 and 24)

ciated with curves (c) and (d) the overall intensity has to be increased by ca. 6 and 8 dB, respectively, to make them equally effective. Evidently, then, the latter patterns become effective only when the less loud parts of the pattern become suprathreshold.

When the stimulus intensity was below the threshold for the curve (c), therefore, the female must have been responding to patterns generated in the CNS by putting together the two inputs, which confirms the result described in the previous section.

Discussion

Directional characteristic

In the large acridid species (*Locusta* and *Schistocerca*) the directional characteristic of the tympanal organ has been measured by several authors, chiefly with electrophysiological methods. With regard to the right-left difference of interest here, Autrum et al. (1961) found 15–22 dB in *Locusta* (multi-unit recording at 7 kHz). Römer (1976) found that single receptor cells tuned to low frequencies had right-left differences between 8 and 24 dB, whereas the high-frequency receptors (measured at 20 kHz) all exhibited larger differences, between 18 and 28 dB. In his multi-unit recordings from the tympanal nerve Adam (1977) found that on average 8 dB was the maximum difference at 6 kHz, and Miller (1977) made a corresponding finding. Michelsen (1971) and later, more extensively, Miller (1977) studied the tympanal organ with both electrophysiological and physical methods. It turned out that at low frequencies a considerable amount of sound was transmitted through the grasshopper body, so that the tympanal organ was operating as a pressure-gradient receiver, whereas at high frequencies little sound was transmitted through the body, which thus casts an appreciable sound shadow. As a consequence of these different effects, the sound-pressure-level difference between sounds from ipsi- and contralateral sources over the entire frequency range is about 9 dB.

The disadvantage of the experiments done previously was that the measurements required some dissection of the grasshoppers; for example, the hindlegs were almost always amputated. But the hind femora are immediately in front of the tympanal organs, shadowing them in certain positions of the legs, so that removing them or even fixing them in a not-quite-natural position could have considerable influence on the directional characteristic (Adam 1983).

For this reason, and because the results in *Locusta* cannot necessarily be applied directly to a considerably smaller animal such as *Ch. biguttulus*, it seemed advisable to measure the right-left difference and a directional characteristic by behavioral criteria with freely moving animals. To make these measurements comparable with the other experiments described here, broad-band noise was used (ca. 3–40 kHz), so that the results presumably reflect an average over the two physical effects that predominate in different parts of this range. The mean value of 8 dB is also confirmed by multi-unit recordings from the tympanal nerve of *Ch. biguttulus* done in collaboration with Adam.

No direction-specific pattern recognition

Our experiments show that the filter-system for species specific song of the grasshopper is not capable of distinguishing different simultaneously presented acoustic signals by their direction. In principle, therefore, if two males were singing simultaneously (and equally loudly and not in phase) the song of each would make that of the other unrecognizable. It is questionable whether this situation arises very often in nature, because the patterns of two males would be unlikely to be superimposed in precisely such a way as to disguise an entire chirp, and because the distances of the singers from the female would usually be different, so that the pattern of the nearer male could be distinguished. But this finding should not be ignored in discussions of the 'choral singing' of insects. In experiments with tape-recorded sound simulating two or more simultaneously singing males as done by Morris et al. (1978) and Otte (1979) the phase relation of the signals may greatly influence the effectiveness of the simulated song, if it produces patterns that do not correspond closely to the conspecific pattern. On the assumption that a male does not join in the song of another male specifically in order to disturb the latter's signal, one way for this concealment of the pattern by superposition to be avoided would be for the singers to synchronize their songs exactly. Indeed, synchronization has been observed in many species in the field (Walker 1969; Alexander 1975). In the case of *Chorthippus biguttulus*, however, the period of the pattern, at most ca. 100 ms (with pauses lasting only 10–20 ms), would probably be too small for exact synchronization of the song of two males. Male *Ch. biguttulus* can be observed to incide one another to sing, which in the field often leads to a chorus-like buildup of the singing of an entire small population, but males sitting close to one another tend to join in the song of a neighbor only after a relatively long latency, so that there are always fairly long periods during which only one animal is singing.

It is interesting to consider whether tettigoniid and gryllid crickets are also incapable of directionally selective recognition. When gryllids hear two different simulated signals presented simultaneously over two loudspeakers, they choose one of the patterns and track it phonotactically (see, e.g., Popov et al. 1977; Weber et al. 1981). When identical simulated songs are presented (with the chirps alternated so as to avoid acoustical interference) at equal intensity from two directions, the crickets could select one of the two sound sources, but they changed course fairly often, aiming first toward one and then toward the other (Weber et al. 1981). However, cricket tympanal organs are movable with respect to the body and the cricket was allowed to adjust its body axis freely, so that the demand of equal intensities on both sides could not be maintained throughout the experiment. These slight differences in loudness caused by the gryllids' turnings might have sufficed to extract the effective pattern from the superimposed.

Summation of the stimulus pattern at the two tympanal organs

The experiments have shown that the grasshopper evidently responds to a pattern that can be generated at the earliest in its metathoracic ganglion. Evidently there is some kind of addition (not necessarily in the exact mathematical sense) of the information carried in by the two tympanal nerves, before the information is sent on to the 'pattern detector'. The effectiveness of patterns thus generated in the CNS is usually not as great as that of the same pattern presented externally on one side of the animal (cf. Fig. 5). This effect would be understandable on the assumption that the addition process includes phasic components already present in the pattern. For example, at the summation point an on-excitation would coincide with an off-excitation, and these might by no means compensate but rather produce and deliver to the pattern-recognition system a pattern that was not quite 'right'.

The neuronal addition of signals arriving from the two sides could take place at a level as low as one of the auditory neuropils in the metathoracic ganglion. Kalmring (1975) found various interneurons in *Locusta* that summate contra- and ipsilateral excitation (and in some cases operate in a fairly intensity-independent manner). It is conceivable that interneurons of this sort are inputs to the 'pattern-recognition system'.

Directional hearing and pattern recognition

When female *Chorthippus biguttulus* respond to patterns with components coming from different directions, this of course does not mean that the grasshoppers are unable to discern the direction of a sound source but only that the pattern-recognizing apparatus cannot distinguish the directions of the components. If a female is sufficiently motivated, for example, she can make her own way to a singing male. Unfortunately, females presented with a male chirp do not exhibit a characteristic, reliably elicited directional response, so that it is difficult to determine experimentally a female's directional perception of a composite stimulus pattern originating in two places. Males, on the other hand, have a very characteristic turning response toward a perceived female chirp. Their excellent lateralization ability requires only very small sound-intensity differences between the right and left organ (about 1 dB; von Helversen and Rheinlaender, in preparation). When experiments like those described here are done with male *Ch. biguttulus,* a pattern ineffective in itself being presented on each side so that the superposition of the two produces an effective signal equivalent to the female chirp, it is evident that the male's innate releasing mechanism for female chirps does respond to composite sound patterns from different directions. The males give the typical turning reaction and begin to sing, whereas either component presented alone elicits neither turning nor singing. The observation that turns to the right and left are equally common, and that forward jumps frequently occur, indicates that the incomplete patterns presented at the same intensity on the two sides are perceived by the male grasshopper as an effective pattern coming from in front (or behind) of him.

It would seem, then, that the two important neuronal evaluating processes, direction analysis and pattern analysis are to a large extent independent of one another. The same inputs to the two tympanal organs are used for both tasks: whereas directional hearing is essentially based on reciprocal inhibition of the two inputs (see, e.g., Rheinlaender and Mörchen 1979), the channels carrying excitation to the pattern-analyzing filter evidently receive excitatory inputs from both sides. It is conceivable that the paths leading to the two processes might diverge immediately after the sense cells, at the level of the first synapses or at the latest just before entering the 'pattern-recognition-network'. In any case, directional hearing and pattern recognition must involve largely independent and parallel processing of the same input functions.

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