

B. Ronacher · R. M. Hennig

Neuronal adaptation improves the recognition of temporal patterns in a grasshopper

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Abstract The recognition of the temporal structure of sound patterns by grasshopper males was investigated in behavioural experiments. Males were tested with short (165–335 ms) song models in which the characteristic subunit pattern of syllables and pauses was modified either at the beginning or at the end of the stimuli. The highly specific responses of the animals indicate that neuronal adaptation has a substantial influence on the detection of the pauses which are essential cues for the subunit structure: pauses were less likely detected shortly after the beginning of a song model than at later positions. Even adaptation in auditory neurons that was induced by unspecific stimulation (with unmodulated noise) facilitated the processing of sound envelopes. The effects of stimulus prolongation and introduction of pauses appeared to combine linearly, similar to the effects of introducing two pauses instead of a single one. In the responses to some song models large interindividual differences were observed. Comparison across stimuli and repeated testing of a smaller number of individuals indicated a considerable consistency of behavioural preferences. However, the data yielded no clear evidence for the existence of individually distinct processing types among males, that conceivably would focus on different features of the stimuli.

Keywords Adaptation · Amplitude modulation · Grasshopper · Pattern recognition · Temporal integration

Introduction

A common observation when recording neuronal signals in the auditory pathway of various species is that most neurons, on different levels of processing, respond with higher spike rates at stimulus onset, while during longer stimuli their response is gradually diminished by adaptation (e.g. Westerman and Smith 1984; Yates et al. 1985; Epping 1990; Givois and Pollack 2000; Benda 2002). Adaptation may reduce the spike rates by more than 50%, and can also lead to substantial shifts in first-spike latencies and spike timing during ongoing stimuli (Stumpner and Ronacher 1991; Ronacher and Krahe 1998; Givois and Pollack 2000; Krahe et al. 2002). Shifts in spike timing in turn should affect the processing of temporal patterns on later stages of the auditory pathway. Furthermore, the adaptional influences often differ between different neuron types, which may pose problems for relational spike codes—at least from the view point of an observer. Thus, while adaptation is certainly important for an adjustment of the cell's dynamic range to varying stimulus levels at time scales of seconds or minutes, it may interfere with the processing of acoustic signals on short time scales (< 300 ms), especially if fast amplitude modulations are of relevance (e.g. Epping 1990; Clague et al. 1997).

How can we assess whether adaptation improves or impedes the neuronal processing of temporal patterns? One way to investigate such questions is to focus on the final output of the processing system, i.e. a behaving animal that reliably indicates whether it has identified a signal or not. The temporal pattern can then be modified either at the beginning or near the end of test stimuli, and any changes in behavioural responses elicited by these manipulations can be observed. The acoustic communication system of the grasshopper *Chorthippus biguttulus* is ideally suited for this kind of experiments since (1) the recognition of communication signals depends primarily on their precise time structure (von Helversen and von Helversen 1997, 1998), and (2)

B. Ronacher (✉) · R. M. Hennig
Department of Biology, Humboldt University,
10099 Berlin, Germany
E-mail: Bernhard.Ronacher@rz.hu-berlin.de
Tel.: +49-30-20938806
Fax: +49-30-20938859

the males of this species react very specifically and reliably to female songs with a characteristic turning response, which is the first step of their phonotactic approach towards the female (von Helversen 1993, 1997; von Helversen and von Helversen 1997). This turning response is exclusive to female songs, and is therefore an excellent indicator that a male has recognized and correctly classified a signal (von Helversen 1993, 1997; Ronacher and Krahe 1998). Here we use this behaviour as a tool to investigate how adaptation influences the precision of neuronal processing of temporal patterns.

Neuronal adaptation is most prominent during the first 200–300 ms in many auditory interneurons of grasshoppers (Stumpner and Ronacher 1991; Ronacher and Krahe 1998; Krahe et al. 2002), and to a lesser extent also in auditory receptors (Benda 2002). Since *Ch. biguttulus* males respond very well to signals as short as 250 ms (Ronacher and Krahe 1998), it is possible to focus the behavioural experiments specifically on the initial segments of the signal in which the strongest changes of spike rates and spike timing will occur. We ask what influence neuronal adaptation has upon the detection of the species-specific temporal structure at the very beginning of a song. In this context also the questions will become important of whether individuals with deviant recognition requirements exist, and to what degree the behavioural measures are stable over time (cf. Gerhardt 1992; Reinhold et al. 2002).

Materials and methods

Animals

Experiments were performed in 1998 on a total of 47 males of *Ch. biguttulus* L. (Gomphocerinae, Acrididae, Orthoptera) caught in the field around Berlin, near Göttingen or in Northern Bavaria.

Characteristic features of *Ch. biguttulus* songs

The songs of *Ch. biguttulus* females exhibit the species-specific pattern of syllables and pauses, which is, with some modifications, also typical for songs of males of this species (Fig. 1a). This syllable-pause pattern is crucial for the recognition of songs by conspecifics (von Helversen and von Helversen 1997). In addition, three song characteristics are important for the classification of a song as stemming from a female and not from a male (von Helversen 1993): (1) the sound pulses of female songs are characterized by a slow rise of several milliseconds, in contrast to the steep onset of sound pulses in male songs; (2) the sound pulses in female songs are separated by small gaps of a few milliseconds, while in male songs these gaps are normally masked by a phase shift between the two hindlegs (Elsner 1974; von Helversen and von Helversen 1997); and (3) female songs have a relatively low spectral power in the high-frequency range (Meyer and Elsner 1997). Males respond more frequently with a phonotaxis to songs that lack strong high-frequency components (von Helversen and von Helversen 1997, Figs. 9 and 10). Apart from this, however, recognition is primarily based on the characteristic temporal pattern of the amplitude envelope of the signals (von Helversen and von Helversen 1997, 1998).

Modifications of temporal patterns introduced in song models

In order to have attractive song models, the basic characteristics of female songs were kept: the ramped shape of female sound pulses, their separation by small gaps, and a relatively low energy in the high-frequency range (von Helversen 1993). The principal changes that were introduced to test for conceivable effects of adaptation concerned the characteristic syllable-pause pattern, which was varied by removing onset accentuation and pauses. The crucial experiments tested whether the recognizability of the pauses between syllables differed for different positions of the pauses.

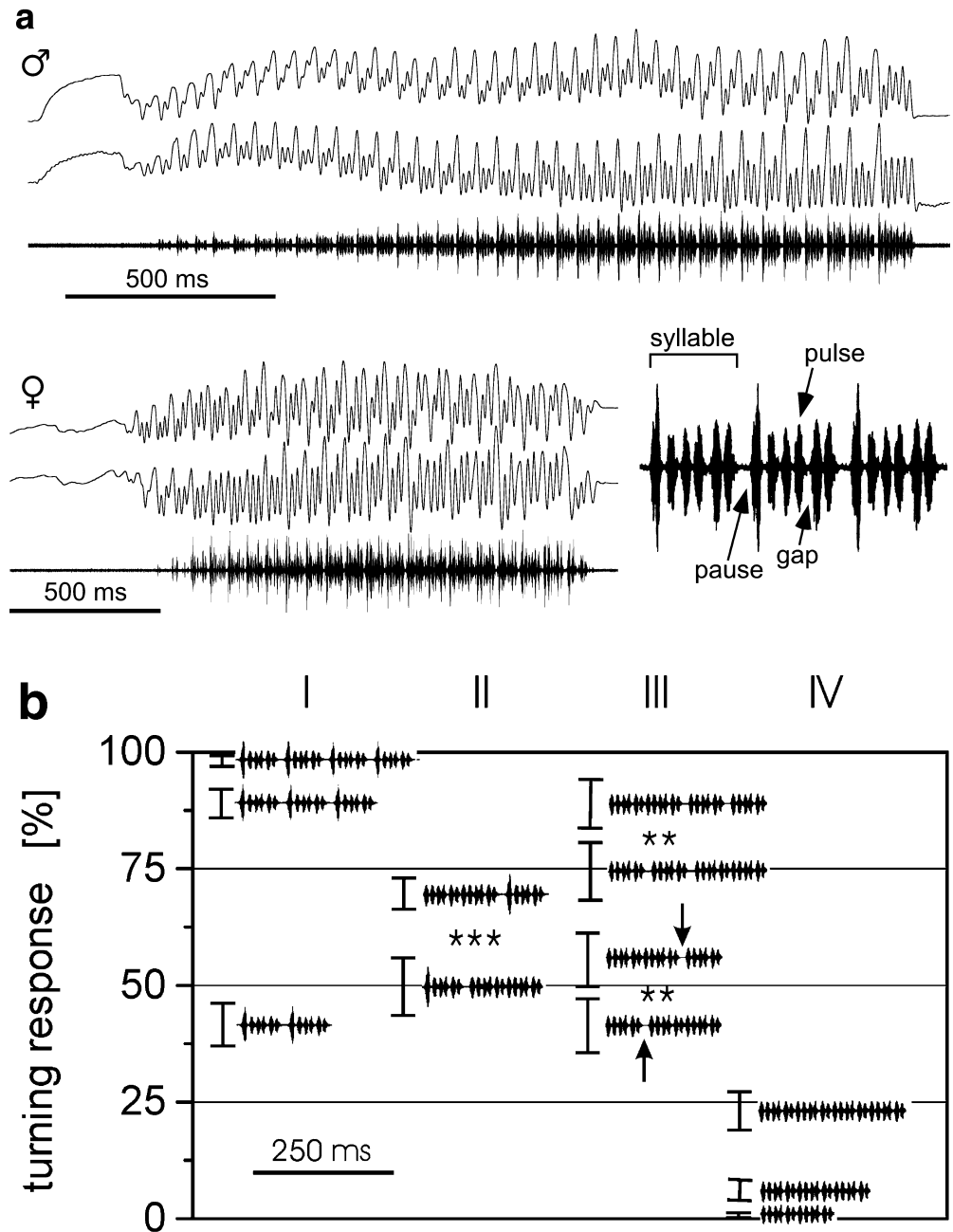
Our standard control stimuli were the same female song models as used in an earlier investigation (Ronacher and Krahe 1998). These models were composed of 4, 3 or 2 identical subunits, their durations were 335, 250 and 165 ms, respectively (Fig. 1b, column I). Stimuli that were completely devoid of the syllable-pause structure served as another control (these stimuli consisted of 12, 18 or 24 sound pulses, without longer pauses; Fig. 1b, column IV). In a first test series the basic 3-subunit model was modified by removing either the first pause (the pronounced first pulse of the following syllable was also replaced by a softer one) or the second pause. Hence these models consisted of 12 sound pulses followed by a pause and a normal syllable, or of a single syllable plus pause followed by 12 sound pulses of equal amplitude (Fig. 1b, column II). In a second experiment we replaced the pronounced first sound pulses by pulses of normal amplitude and then removed one of the pauses (Fig. 1b, column III). In a third series segments of unstructured noise (165 ms) were presented immediately before or after a model song (Fig. 2).

Experimental setup and test procedure

All experiments were run with single males in a room lined with sound-reflection attenuating foam material. The temperature during the experiments was kept at 29–32°C. The set up was the same as described in Ronacher and Krahe (1998) and in Ronacher et al. (2000). The stimuli were modified using the programme Turbolab (Stemmer) and stored digitally. Following digital-to-analog conversion the signals were routed through a computer-controlled attenuator and a custom made audio amplifier to the speaker (Vifa Type D26NC-05-06; speaker diameter 30 mm). Males were tested on a table (90×90 cm) carpeted with 5-cm-thick foam material and covered by untreated cotton. The female song models were broadcast via a single movable loudspeaker that was positioned laterally to the animal (at a distance of 20 cm), to provide good lateralization cues. Sound pressure of the signals was 49 (±1) dB SPL (sound pressure level) calibrated with a Brüel & Kjaer sound level meter (2235; fast reading; 1/2" condenser microphone type 4133) at the position of the animal. As in earlier experiments the female song models were low-pass filtered (at 10 kHz, KEMO VBF8; for spectra and details of the apparatus see Ronacher and Krahe 1998).

A first group of males ($n=14$) was tested with the stimuli shown in columns I, II and IV of Fig. 1b (the short unstructured stimuli were only tested on males that showed a non-zero response to the longer ones). A second group of different males ($n=13$) was tested with the stimuli shown in the columns I, III and IV of Fig. 1b, and a third group ($n=20$) was tested with the stimulus set shown in Fig. 2. Normally all stimuli of a series were tested in a single session; percentage values are based on at least 10–20 stimulus presentations. As the responses of each animal had to be sampled across several stimuli to allow for meaningful comparisons, it was important to control for any shifts of motivation during the experiments. This was done by repeatedly presenting the standard 3-subunit stimulus as a control. In addition, critical tests, e.g. the two of column II (Fig. 1b), were interleaved in order to have the animal in the same principal motivational status.

Fig. 1 a Songs of a *Ch. biguttulus* male and female. *Upper two traces*: leg movements recorded with an optoelectronic camera, *lower trace*: sound pattern. Note the repetition of regular subunits—"syllables" and pauses—as well as the increase in amplitude during the beginning of the male song and the less regular, pulsed structure of the female song (courtesy of O. von Helversen and Maria Bauer). Inset shows the syllable pause pattern of the 3-subunit female song model. **b** Results of tests with song models that varied in duration and/or the position of pauses (see *insets*). The respective *y*-position of a song model indicates the mean response percentage of the males to this model. A 100% value means that the males had shown the turning response to every stimulus presentation. The data of column I and IV were very similar between the two groups of individuals tested (see Materials and methods), and therefore the combined data are shown. *Vertical bars* show \pm SEM. *Asterisks* indicate significance levels determined according to Wilcoxon's matched pairs test. *** $P < 0.001$; ** $P < 0.005$. Further explanations in text



Data analysis

As each male was tested with several stimuli the experiments corresponded to a repeated measures design. This allowed for paired comparisons (e.g. of the responses of column II in Fig. 1b). Since several of the response distributions were skewed and one of them even bimodal, a nonparametric test was used (Wilcoxon's matched pairs signed rank test; Sachs 1999; extensive tables in McCornack 1965). In case of multiple comparisons (Fig. 2) a Bonferroni correction was applied.

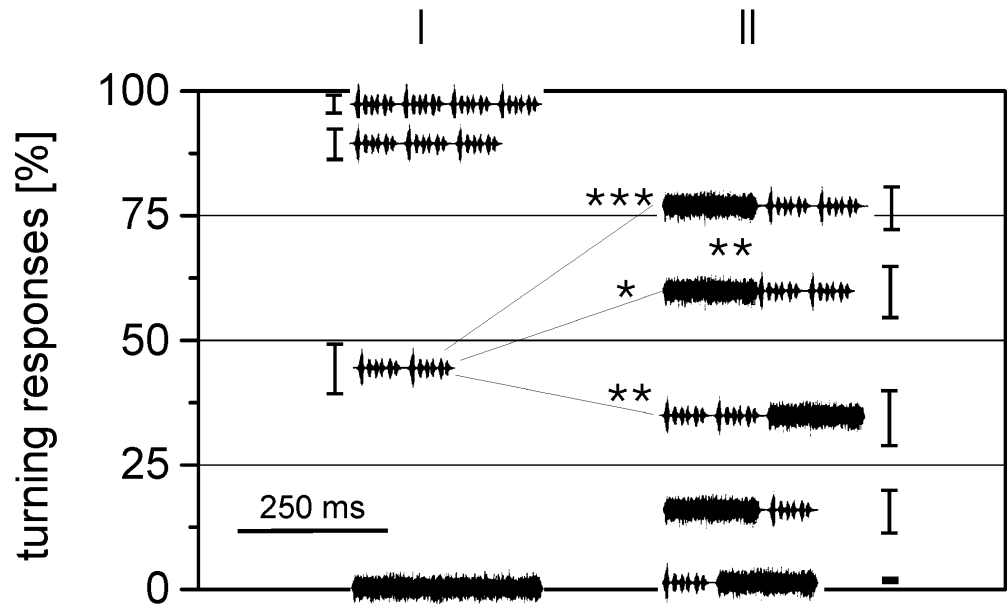
Results

The stimuli used in this study kept the basic cues for the discrimination of female and male songs (von Helversen

1993; von Helversen and von Helversen 1997): the ramped shape of female sound pulses, their separation by small gaps, and a relatively low energy in the high-frequency range. To test for conceivable effects of adaptation rather subtle modifications were introduced only in the species-specific subunit pattern, by changing the subunit structure at different positions in the stimulus. In Figs. 1b and 2 the results of tests with different song models are summarized in a way that the *y*-position of a song type depicted in the diagram symbolizes the mean percentage of turning responses to this stimulus.

Recognition of the control stimulus, a 3-subunit female song model, was near perfect: two thirds of the males responded to at least 90% of the stimulus

Fig. 2 Tests with song models combined with noise segments. Plot as in Fig. 1b. *** $P < 0.001$; ** $P < 0.01$; * $P < 0.02$



presentations, one half of the males even showed a 100% response (mean value = 89.6%, median = 100%; Fig. 1b, column I). Interestingly, even a 2-subunit model elicited on average ca. 40% turning responses, although in this case the distribution of individual response levels was bimodal (see Fig. 4a). Note that this is the shortest model still exhibiting the species-specific syllable-pause pattern.

Effects of modifying the subunit structure at different positions

Modification of the 3-subunit model by removal of a single pause (Fig. 1b, column II) led to different response levels, depending on whether the first or second pause was concerned. Removal of the first pause reduced the response level by ~20 points (from 90 to 70), while the absence of the second pause led to a reduction of 40 points (difference between the two conditions: $P < 0.001$, Wilcoxon matched pairs test). As these two stimuli differed also in the presence of the pronounced first sound pulse of a subunit, we repeated this experiment with stimuli in which all sound pulses had equal amplitudes (Fig. 1b, column III). These tests confirmed that song models in which the subunit structure at the beginning was removed yielded higher response levels than stimuli in which the pause was missing in later parts of the model (arrows in Fig. 1b; response differences between the two respective stimulus types significant, $P < 0.005$; Wilcoxon's matched pair test). When the subunit structure was completely absent (Fig. 1b, column IV) the males did not or only rarely respond to these signals: an 18-pulse model led to a mean of only 6% turning responses (median = 0); the longer unstructured model consisting of 24 pulses yielded a mean response level of 23% (median = 20). In conclusion, the effectiveness of

the species-typical syllable-pause combination obviously depended on its position within the stimulus (pulse train), a later position being advantageous.

Our hypothesis was that neuronal adaptation which is especially strong at the beginning of a sound stimulus, might be responsible for the differential effects of removing the subunit structure at different times after stimulus onset, and that the detection of a pause may become more difficult near the beginning of a stimulus. In order to test this hypothesis unspecific noise was used to adapt the auditory pathway. In this experiment the song model was preceded (or followed) by a 165-ms segment of noise. To avoid a saturation of responses, this experiment was conducted mainly with a 2-subunit song model (Fig. 2), and in addition with a 1-subunit model. Unmodulated noise was used in order not to present any song-typic temporal envelope cues. Indeed, the noise alone was completely ineffective in eliciting any responses of the males (Fig. 2). If neuronal adaptation was responsible for the unequal salience of pauses depicted in Fig. 1b then the expectation was that a leading noise segment could—by adaptation of the auditory pathway—improve the response to a short 2-subunit model, while a following noise segment should have no such beneficial effect. Two versions of this model were used, one that had a short pause between noise and the song while in the other version the song model was following the noise segment immediately (see insets in Fig. 2). The preceding noise had indeed the expected effect, the response level was significantly increased as compared to a 2-subunit stimulus ($P < 0.001$ and 0.02, Wilcoxon with Bonferroni correction). This was true even for the most crucial model, in which there was no pause between the noise and the first subunit. If the noise segment was lagging the model, the response level even decreased (the difference to the 2-subunit model was significant: $P < 0.01$; Wilcoxon with Bonferroni

correction). Tests with stimuli that had the noise combined with a single song-subunit showed a similar effect, although starting from a very low response level (a single subunit alone does not elicit turning responses). These results confirm those of Fig. 1b, that the recognition of the song subunit pattern is improved after a certain time span from stimulus onset, probably because the detection of pauses is more difficult shortly after stimulus onset.

Influence of pauses and stimulus duration on the detection of subunit structure

In the song models used here the species-specific song structure has been modified in two basic ways: by adding (or removing) a subunit, or by inserting (or removing) a pause. The following data analysis was intended to separate the effects of these different manipulations. In several stimulus combinations a prolongation by one subunit occurred. When calculating the respective improvement in response level, however, one has to be aware of possible ceiling effects. This becomes immediately evident by comparing the increase in response levels from a 2-subunit to a 3-subunit model and from a 3-subunit model to a 4 subunit model (column I in Fig. 1b). In order to circumvent this problem the data were analyzed as indicated in Fig. 3a. For each individual the increase of its response level, from a 2-subunit to a 3-subunit model, is plotted against the response to the 2-subunit stimulus. The (broken) -45° line indicates the limits imposed by response saturation. In this picture the data corresponding to abscissa values of less than 40% appear not to be influenced by saturation. Considering only these values, the average increase in response level by adding one female song subunit is 57.5% (for comparison: simply calculating the difference between the respective mean values of Fig. 1b yields 48%). The columns in Fig. 3b indicate the respective increases in response levels determined that way (Fig. 3a), for the stimulus combinations depicted on the right. For example, by adding a subunit (row 5) both a prolongation of the total duration occurred and a pause was introduced. To separate the respective contributions, one has to refer to the 18-pulse and 24-pulse stimuli, in which a prolongation of the stimulus occurred without introducing additional subunit structures (row 7). To a 18-pulse model without subunit structure the animals did respond only very rarely (Fig. 1b), and the additional pulses yielded a moderate increase in response of 18.8 points. Introduction of a single pause (row 6) led to a relatively large increase in stimulus effectiveness, compared to the unstructured model. Interestingly, the response improvement in row 5 (48.5%) is rather exactly the sum of rows 6 and 7 (30.6+18.8), indicating that the two effects of introducing a single pause and stimulus prolongation by 6 pulses sum up linearly in the response probabilities. The experiments of the rows 4 and 3 can be interpreted as the

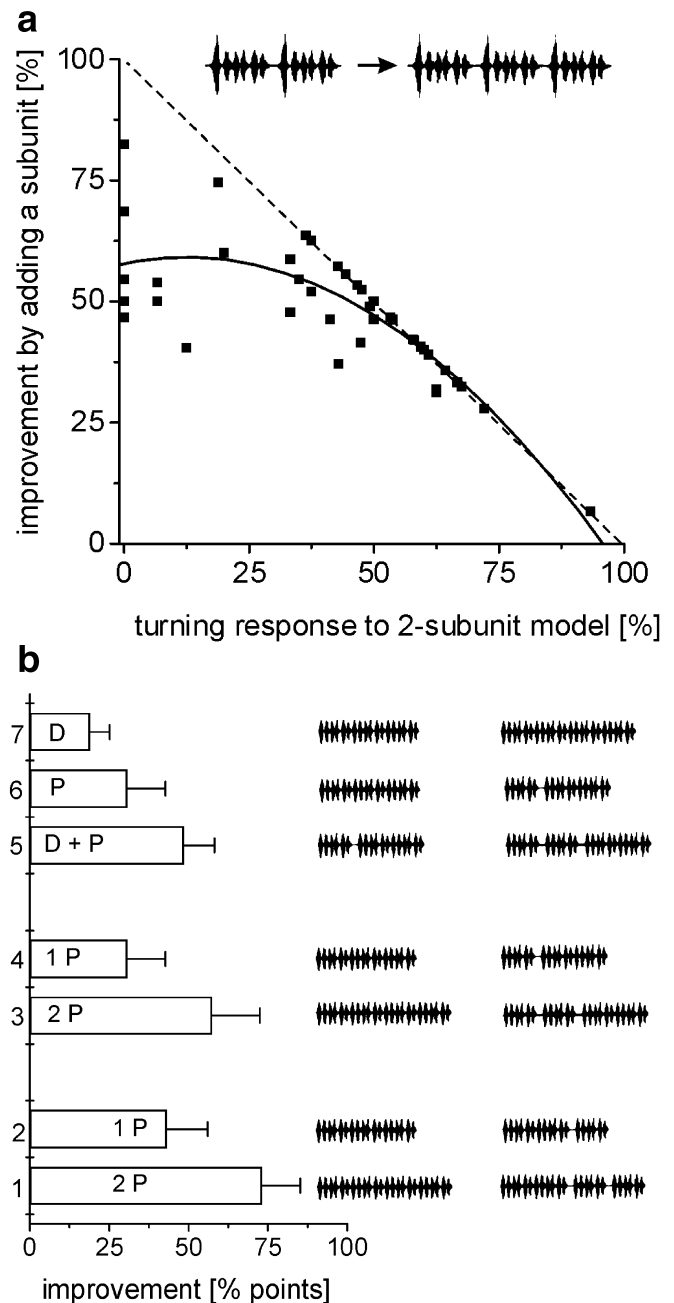


Fig. 3 a Improvement in response level of individual males between a 2-subunit model and a 3-subunit model. *Abscissa*: response to 2-subunit stimulus. *Ordinate*: improvement, i.e. difference between responses to 3-subunit model and 2-subunit model (curve represents a polynomial fit; $r^2=0.678$). **b** Improvement in response levels for selected stimulus combinations (indicated on the right). *D*, *P* indicate a change in duration and insertion of a pause, respectively. *Bars* indicate 95%-confidence intervals. Further explanation in text

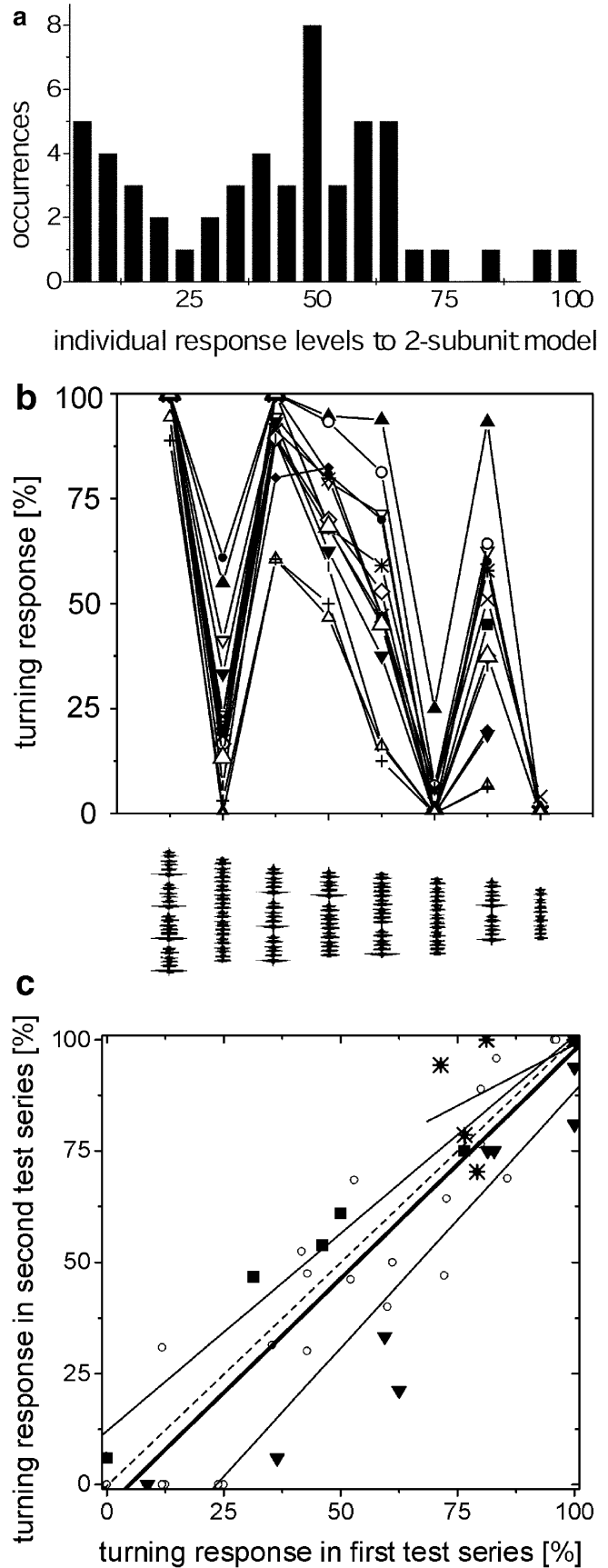
insertion of a single pause into an unstructured series of 18 pulses, or of two pauses in a 24-pulse stimulus (after the 6th and after the 12th pulse). Rows 2 and 1 show the situation for introduction of pauses after pulse 12 and 18. The introduction of a single pause into a 18-pulse stimulus yielded an improvement of 30.6 or 43.1 points,

Fig. 4a–c Responses of individuals. **a** Bimodal distribution of response levels of individual males to a 2-subunit female song model (the data of 7 individuals tested twice on different days are shown separately). **b** Response levels of individuals to different stimuli (indicated *below* abscissa). **c** Tests for stability of individual responses. Comparison of responses of 7 individuals that completed the test series twice, on different days. Each point corresponds to a test with a certain song model. Data of three individuals are shown separately (*larger symbols, thin regression lines*). Both, an improvement or a deterioration of response levels occurred. *Stippled line* indicates perfect agreement between first and second test series. *Thick line*: regression for complete data set ($r=0.928$; slope 1.026)

depending on the position of the pause (Fig. 3b, rows 4 and 2). Introducing two pauses into a 24-pulse stimulus yielded an increase of 57.3 or 73.1 points (rows 3 and 1). Thus, two pauses seem to be nearly twice as effective as a single one (30.6 versus 57.3%) when introduced at the beginning of a stimulus (compare rows 3 and 4). Later on, the two pauses are only 1.7 times as effective as the single one (rows 1 and 2).

Individual response types?

It has already been mentioned above that the distribution of responses to a 2-subunit female song was bimodal (Fig. 4a). About a quarter of the males responded only rarely to this model (<20%), while another third of the males responded to more than 50% of the stimulus presentations. This entails the question of whether different recognition types among the males might exist, similarly as recently reported for females of this species (Balakrishnan et al. 2001). Figure 4b presents some data on the interindividual variability of male responses to the stimuli of one test series (from Fig. 1b). The stimuli are put in order according to their number of sound pulses, and to allow comparison data of individuals are connected by thin lines. Three trends are obvious: (1) there were clear ceiling effects, e.g. towards 100% for the 4-subunit stimulus, or towards 0% for the 18-pulse stimulus. (2) Between these extremes were stimuli with very large interindividual variations in response level (e.g. the 24-pulse model, 1 subunit-12-pulse model, 2-subunit female model). However, there seemed to exist a continuum of responses rather than clearly disjunct response types. (3) There was a tendency that low responders performed at low levels with all stimuli. In order to further examine this trend on the whole data set, such individuals were selected that showed low response percentages to the standard 3-subunit female song. For eight animals the responses to this model deviated by more than 1 standard deviation (SD) from the mean. Each of these animals showed low level responses to the (5–9) other test stimuli as well: in 36 tests their response was more than 1 SD below the mean for the respective stimuli; in another 12 tests their response was still below the respective means; in only 2 cases (out



of 50) their response level exceeded the respective means of all individuals for this stimulus. Thus, the (low) response level to the 3-subunit standard was also a good predictor for the relative responses to other stimuli.

Consistency of responses

With seven individuals (nearly) complete test series were conducted on two different days (with a pause of 1–6 days in between). In Fig. 4c the data of 51 test replicas on these animals are shown as small open circles; the data of 3 animals are shown separately (larger symbols and thin regression lines). For some individuals a moderate improvement, for others a moderate deterioration of response levels was observed. The respective percentages of the replicas correlate rather well; the slope of the regression line for all data is 1.026 (thick line), and the correlation coefficient $r=0.928$ (when saturating values are excluded—100% response in both tests—the overall correlation coefficient is still very high: $r=0.893$). The correlation coefficients for data of individuals range—with one exception ($r=0.52$, stars in Fig. 4c)—from 0.91 to 0.99. However, although these very high correlations suggest a remarkable stability of individual responses, they must be interpreted with care, since they depend also on the choice of the stimuli that in general covered the total response range from near 0 to 100% response. Note that the correlation coefficient was much smaller for that individual which showed a high response level for all stimuli (stars in Fig. 4c). We therefore applied an alternative evaluation, by determining the three most potent stimuli for each individual in the first test series (i.e. the stimuli chosen with the highest percentage, the second highest and the third highest). This was then repeated for the second test series, and the correspondence between the two was determined. For example, if the order of the stimuli with highest response percentages was C, A, F, a complete correspondence (=3) would be that on the second test day the animal also preferred stimuli in the same order C, A, F. If the order had been C, F, A the correspondence would be only 1. In 17 cases (out of 21 comparisons; 81%) the animals preferred the same three stimuli, in the same order, on both days, in only 4 cases there occurred shifts (most of them were caused by small differences in response percentages). Although from a very small sample, these data nevertheless suggest a high consistency of the response behaviour of individual males.

Discussion

The experiments presented here aimed at analyzing the capabilities of grasshopper males to detect small deviations from the normal song pattern during the first segments of a communication signal, during which the effects of adaptation are strongest. In view of the profound changes in spike rates and spike timing observed in

most auditory neurons (Stumpner 1988; Stumpner and Ronacher 1991; Stumpner et al. 1991; Krahe et al 2002) it is the more remarkable that the animals are able to recognize shortened communication signals so precisely. It has to be emphasized that even a single presentation of short signal segments (165–250 ms) induced high response levels (Fig. 1b). A sampling over several stimulus presentations thus is not necessary and obviously the recognition mechanism operates very fast, in real time. It is amazing that the animals are so selective, even with such short signals. An alternative tactic, in particular since the males suffer from a high inter-male competition, could be to respond to anything that bears even a remote likeness to a female song. The present results, however, confirm earlier results showing that even males are very choosy, and that their nervous system is extraordinarily fast and precise in processing temporal patterns, and in detecting any deviations from the normal pattern.

Do individual ‘recognition types’ exist?

In a careful behavioural analysis Balakrishnan et al. (2001) have demonstrated the existence of different recognition types among *Ch. biguttulus* females. Whether individual females responded to a song model or not depended on the respective values of syllable onset accentuation and on the offset level between the end of the syllable and the following pause. Some of the females responded only if a distinct offset was present, while for others an onset accentuation even without any offset was sufficient to elicit responses. In view of these results the bimodal distribution of responses shown in Fig. 4a was of interest. However, the data presented in Fig. 4b, as well as the evaluation of low-level responders, did not support the contention that clearly distinguishable male types exist able to evaluate different song features. At present, a more parsimonious explanation of the differences between males visible in Fig. 4 would be that these data reflect differences in their overall willingness to respond (their motivational status) rather than individually different specific requirements for certain song features. Alternatively, there might exist a broad distribution of male types, some of them requiring higher levels of reliability in the recognition process than others. In order to elucidate this question of individual response types, systematic and larger variations of stimulus parameters should be repeatedly tested (cf. Gerhardt 1992; von Helversen and von Helversen 1997; Reinhold et al. 2002). The data in Fig. 4c indicate a remarkable stability of individual responses (see also Fig. 13 in von Helversen 1972), so that individual recognition types, if existing at all among males, should in principle be detectable.

Inferences on stimulus processing from behavioural data

The stimuli used in the behavioural tests of this study can be interpreted as modifications of two different

features of the female song: shortening or prolongation by a subunit, or removing or introducing of syllable pauses. The effects of these manipulations were considered separately in order to obtain possible hints to the neuronal detection of different song features (Fig. 3). The data presented in Figs. 1 and 2 show that recognition essentially depends on the detection of pauses, which then allow for a structuring of the sound event into recognizable subunits. The data summarized in Fig. 3b indicate that the effects of introducing a single pause and of prolongation by 6 pulses sum up linearly, and also that two pauses are detected with approximately twice the probability as a single one (compare with the concept of “heterogeneous stimulus summation” or “Reizsummenphänomen” introduced by Seitz 1940, p 79). This suggests that the animals perform a kind of repeated sampling, corresponding to the “multiple looks” model of Viemeister and Wakefield (1991) but on rather short time scales, and that the detection probabilities summate linearly across these events.

Assuming that a response to an unstructured model corresponds to a false alarm (e.g. that in these cases the animal’s CNS did hallucinate a pause, due to an irregular spike train), we can conclude that a pause in the second half of the stimulus is detected with at least 43% probability, a pause in the first half with 31%. These values rather constitute lower bounds for detection probabilities, since there may other factors—e.g. the short overall stimulus duration—that may induce the animals sometimes not to show their phonotaxis response. With an unstructured 24-pulse stimulus there is a higher “false alarm rate” (mean 23%). This may be due to the spike trains becoming more irregular at later times after stimulus onset (Stumpner 1988; Stumpner et al. 1991; Ronacher and Stumpner 1993; Krahe et al. 2002). New neurophysiological data must be obtained that can directly be compared with the detection probabilities derived from behaviour.

Influence of adaptation

A main conclusion of this study is that adaptation improves the detection of pauses, on which the recognition of subunits and acceptance of a song model depends. This inference is based on two results: (1) the differential effects of the position of the pause in Fig. 1b (columns II and III), and (2) the effects of unstructured noise preceding a song model (Fig. 2). The two stimulus combinations of column III in Fig. 1b differed only in the position of the pause (arrows), without changes in the stimulus duration or the number of sound pulses. Hence, the differences in response level are indicative for the pure effects of adaptation, as were repeatedly reported also for orthopteran insects (Stumpner and Ronacher 1991; Ronacher and Krahe 1998; Givois and Pollack 2000; Krahe et al. 2002; Benda 2002). An additional inde-

pendent confirmation are the experiments with unmodulated noise, which increased the attractiveness of a 2-subunit model, if the noise was immediately preceding the song model (Fig. 2). Since the noise alone did not induce turning responses (cf. Ronacher and Hoffmann 2003), this shows that even an adaptation process in auditory neurons started by unspecific stimulation may facilitate the processing of sound patterns, in particular the detection of pauses which separate the subunits. Whether long-term inhibitory processes, as found in interneurons of crickets and bushcrickets may contribute to these adaptational effects seems rather unlikely, due to the different time scales involved (Pollack 1998; Sobel and Tank 1994; Römer and Krusch 2000).

Interestingly, a similar trend in the detectability of pauses along stimulus duration as described here for grasshoppers was found in gap-detection experiments on humans. Gaps inserted at 30 ms after stimulus onset were clearly more difficult to detect than those inserted at 150 ms (total stimulus duration 300 ms). Minimal detectable gap widths were 3.2 ± 0.35 ms for the earlier position, and 1.9 ± 0.42 ms for the later position (Immke 1999; cf. also Phillips et al. 1997).

The observation that adaptation has a beneficial effect on the detection of pauses situated later in the pulse train can also be seen the other way round: that the strong onset response of auditory neurons may have detrimental effects upon the detection of pauses. This could have been an evolutionary incentive for grasshoppers to produce songs that start soft and gradually increase in intensity, as found in many grasshopper species (Fig. 1a, see also Elsner 1974; von Helversen and von Helversen 1994, 1997). This common feature of grasshopper songs may be due to a lesser degree to constraints imposed by the motor pattern generation of the sender. Rather, it may be an adaptation to the requirements of the auditory processing equipment of the receiver, namely to avoid too strong onset effects of spiking responses in the receiver’s auditory system.

It should be mentioned that these data also yield caveats to modeling and stimulus reconstruction studies in which the mathematical tools require that there are no long-term shifts in neuronal responses, for which reason usually the first several hundred milliseconds of the spike trains are excluded from the analysis (cf. Machens et al. 2001; Ronacher et al. 2004). Thus, such procedures do not capture those parts of the responses which are, as the present experiments show, nevertheless important or even crucial for recognition.

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