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ORIGINAL PAPER

Intensity invariance properties of auditory neurons compared to the statistics of relevant natural signals in grasshoppers

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Abstract The temporal pattern of amplitude modulations (AM) is often used to recognize acoustic objects. To identify objects reliably, intensity invariant representations have to be formed. We approached this problem within the auditory pathway of grasshoppers. We presented AM patterns modulated at different time scales and intensities. Metric space analysis of neuronal responses allowed us to determine how well, how invariantly, and at which time scales AM frequency is encoded. We find that in some neurons spike-count cues contribute substantially (20–60%) to the decoding of AM frequency at a single intensity. However, such cues are not robust when intensity varies. The general intensity invariance of the system is poor. However, there exists a range of AM frequencies around 83 Hz where intensity invariance of local interneurons is relatively high. In this range, natural communication signals exhibit much variation between species, suggesting an important behavioral role for this frequency band. We hypothesize, just as has been proposed for human speech, that the communication signals might have evolved to match the processing properties of the receivers. This contrasts with optimal coding theory, which postulates that neuronal systems are adapted to the statistics of the relevant signals.

Keywords Spike-train metric · Decoding · Acoustic communication · Optimal coding · Evolution

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Introduction

All communication systems face the problem that signals must be interpreted correctly in a broad range of intensities. This robustness can be attained by employing two, not mutually exclusive, strategies depending on whether the signal processing hardware or the signals themselves exhibit more evolutionary plasticity. On the one hand, the receiver's signal processing hardware can adapt to the statistics of relevant signals, such that successive stages of feature extraction operate on a representation which has "corrected" for most intensity induced changes in the signal (e.g., Chander and Chichilnisky 2001; Benda and Hennig 2008). On the other hand, in the evolution of communication systems the signals themselves can adapt to rely on features, which are per se less intensity dependent or which exploit some invariance properties of existing neuronal networks (e.g., Guilford and Dawkins 1993; Ryan et al. 2001; Arnqvist 2006).

This problem is of special relevance for grasshoppers, which use acoustic communication signals to identify, evaluate, and locate their mates. Signal recognition depends on the signal's temporal pattern of amplitude modulations (AM). Signals in a broad intensity range between 40 and 80 dB SPL are accepted (von Helversen and von Helversen 1997), underlining the need for intensity invariant processing of sound patterns. The peripheral auditory system of grasshoppers is a feed-forward network. It is therefore ideally suited to track the transformation of information and possible changes in coding along consecutive processing stages (Vogel et al. 2005; Vogel and Ronacher 2007). Basic properties of this system have been investigated by stimulating with sinusoidal AM patterns and constructing modulation transfer functions (Wohlgemuth and Ronacher 2007; Weschke and Ronacher 2008),

as well as with natural communication signals and song models (Stumpner and Ronacher 1991; Stumpner et al. 1991; Machens et al. 2003; Neuhofer et al. 2008). In this study, we present a combined analysis of neuronal intensity invariance and of the statistics of behaviorally relevant signals to collect cues as to how the problem of intensity invariance might have been solved by grasshoppers. The hypothesis formulated thus possibly applies to animal communication systems in general.

How can one quantify neuronal intensity invariance? The only source of information an animal has in order to infer stimulus "identity" is neuronal spike trains. We mimic this by decoding stimulus identity, that is the AM pattern imposed by a sinusoidal modulation, from single-cell spike responses recorded from auditory neurons. If decoder performance is robust to changes of stimulus intensity, then we consider the neuronal response intensity invariant given this decoder. Extensive behavioral experiments have shown that the computations grasshoppers perform on the stimulus rely on the temporal pattern of amplitude modulations of stimuli, not on signal periodicity (von Helversen and von Helversen 1998; Schmidt et al. 2008). The decoder employed here is based on a spike distance metric after van Rossum (2001) and incorporates this knowledge. The metric allows us to probe and to interpolate between two of the most widely hypothesized neural codes: a spike-timing code, where the pattern of spike times is available for the decoding of stimulus identity; and a spike-count code, where only the number of spikes over a long time window is available. There is evidence that a spike-timing as well as a spike-count code are employed at different stages in the auditory pathway of grasshoppers (Machens et al. 2001; Creutzig et al. 2009; Stumpner and Ronacher 1994).

Methods

Animals, electrophysiology, and acoustic stimulation

The animals used in the experiments were adult locusts (*Locusta migratoria*) of both sexes, which were obtained from a local supplier and held at room temperature (22–25°C). Intracellular electrophysiological recording methods are described in detail in Vogel et al. (2005) and Weschke and Ronacher (2008). After completion of the stimulation protocol, we stained neurons with Lucifer Yellow and identified them by their characteristic morphology (Römer and Marquart 1984). We present data from the three consecutive levels of processing, located in the thoracic ganglia, which constitute an important stage of auditory information processing (Stumpner and Ronacher 1994). Information from the population of auditory receptors enters into a network of local interneurons, which in turn connects to a set of ascending interneurons. These forward the information to decision centers in the brain. Different cell types were pooled into four classes based on abundance in the data set and assignment to processing stages. Auditory receptors comprise the first class ($N = 6$). Local interneurons were divided into two classes: T-shaped neuron TN1 and the segmental neuron SN1 ($N = 16$) comprise a class of primary-like interneurons, whereas the bi-segmental neuron BSN1 forms a class with more derived response properties ($N = 7$). Ascending interneurons (fourth class, $N = 11$) are an inhomogeneous group with respect to physiological properties but were pooled into one class due to their position at the output stage of the thoracic network to the brain. Representatives included are AN1, AN2, AN3, AN4, AN11 and AN12 (terminology after Römer and Marquart 1984).

Note, that the same neuron types are found in other acridid grasshoppers, and exhibit not only compelling morphological similarities, but also share their physiological characteristics (Römer et al. 1988; Ronacher and Stumpner 1988; Stumpner and Ronacher 1991; Stumpner et al. 1991). A recent study has demonstrated a strong evolutionary conservation of coding properties of identified thoracic auditory neurons between the locust used in this study (*Locusta migratoria*) and a gomphocerine grasshopper, *Chorthippus biguttulus* (Neuhofer et al. 2008; see also Ronacher and Stumpner 1988). This close correspondence in processing characteristics between these species allows us to relate the neuronal data presented here to acoustic signal characteristics and behavioral performance in other grasshopper species.

As stimuli we used broadband noise that was sinusoidally amplitude modulated (SAM, modulation depth 100%) in a broad frequency range (10 stimuli, 5–1,000 Hz, logarithmic spacing, see Weschke and Ronacher 2008). The rationale for this choice was the observation that in many grasshopper species the temporal structure of the signal envelope is crucial for signal recognition (von Helversen and von Helversen 1997; von Helversen and von Helversen 1998; Schmidt et al. 2008). In order to investigate how changes in intensity affect the neural responses, we stimulated the neurons with SAM stimuli at 2–3 different intensities. Intensity was defined by dB SPL peak. As the neurons considered here vary widely in their dynamic ranges, we adjusted the peak intensities such that they covered comparable parts within the dynamic range of each neuron. This was done by determining the rate-level curve for each neuron from responses to a 100 ms constant-amplitude broadband noise (see Fig. 1a for an example). The first (lowest) intensity at which we presented the SAM stimuli was set to lie at the middle of the first rising part of the cell's rate-level curve. The second intensity was set to lie at the end of the first rising part of the rate-level curve, shortly before

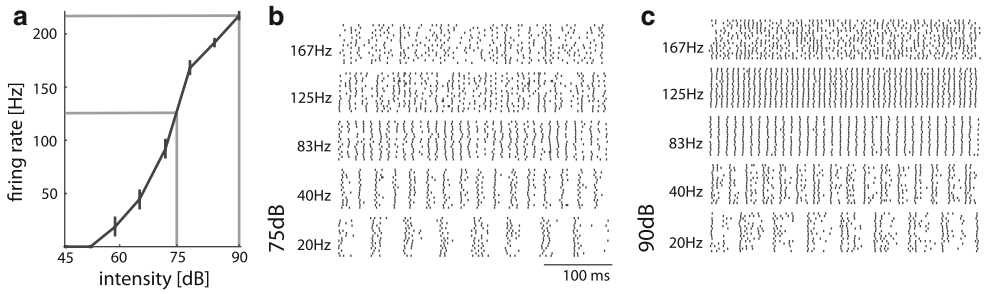

Fig. 1 **a** Rate-level curve for a local interneuron (TN1) measured with rectangularly modulated 100 ms noise pulses. Peak intensity of the SAM stimuli used to quantify intensity invariance was chosen such that the cell was either moderately (75 dB) or strongly (90 dB) driven (*grey lines*). Plotted is the mean firing rate. *Error bars* indicate standard deviation. **b** and **c** Responses of a local interneuron (TN1) to a subset of the AM frequencies presented at two different intensities: one intensity, which lies at ~50% (**b**, 75 dB) and one, which lies at ~100% (**c**, 90 dB) of the cell's dynamic range 129 × 39 mm (600 × 600 DPI)

saturation. Thus, we assessed the cell's coding properties when it was driven either moderately or strongly. If possible, an additional intensity was placed either halfway between the two other intensities or further into the saturating part of the rate-level curve. For cells exhibiting more complex or optimum-like intensity tuning, we probed coding properties for the first rising part only. Additionally, we assured that the stimuli were spaced approximately evenly along the intensity axis. Note, that the above protocol changes both stimulus mean intensity as well as stimulus variance.

Data analysis

General classification algorithm

We applied a classification algorithm based on the spike-train metric after van Rossum (2001). The algorithm assesses how well stimuli can be discriminated from the neuronal responses, and allows us to quantify the information about AM frequency contained in a neuronal response via the classification performance (Machens et al. 2003). Spike trains were convolved with an α function: $\alpha(t) = \Theta(t)t\exp(-at)$, where $\Theta(t)$ is Heaviside's function. The parameter $\tau = 2.54/a$ represents the temporal resolution, as measured by the function's width at half maximum, with which spike trains are read out (Machens et al. 2003). The Euclidean distance between two convolved spike trains is a measure of spike-train dissimilarity. Repeating this procedure for all pairs of spike trains yields a distance matrix whose structure depends on the spike trains themselves and the temporal resolution parameter τ. Based on the distance matrix, spike trains were then classified according to the stimulus' AM frequency by a supervised nearest-neighbor cluster algorithm as in Machens et al. (2003). The algorithm itself operates as follows: out of each stimulus class, one spike train was chosen randomly as a template. Each remaining non-template spike train was assigned to the class, which the nearest template was in. Repeating this to cover all possible combinations of templates, and counting the frequency with which a spike train from a given class was assigned to any class resulted in a confusion matrix: rows correspond to the presented stimulus class, columns to the decoded stimulus class. The values at the confusion matrix' main diagonal indicate correctly and off-diagonal values falsely classified ("confused") spike trains (Fig. 2a–c). Frequency-resolved classification performance was derived from the values at the confusion matrix' main diagonal. Overall classification performance was taken as the fraction of correctly classified spike trains (the main diagonal's mean). Chance level is 0.1 (one over the number of AM frequencies).

Classification performance depends crucially on the choice of the temporal resolution τ at which spike trains are evaluated. Hence, by varying τ we gain insight into the time scale(s) at which information about AM patterns resides: small to intermediary τ correspond to a spike-timing code, very large τ (>500 ms) correspond to a spike-count code. We tested a broad range of τ values ranging from 0.6 to 1,800 ms spaced evenly on a logarithmic scale. All performance values are taken at the optimal τ for each cell and task. However, the τ curves usually exhibited rather broad peaks, and, hence, performance did depend only little on the exact τ value (see Fig. 5a). Furthermore, optimal τ changed only little with the specific task.

Quantifying invariance through decoding

We aimed at quantifying the intensity invariance of the neuronal representation of AM frequency by applying the algorithm outlined above. Our notion of intensity invariance implies that a neuron should retain the features of its response necessary for the decoding of AM frequency under changes of stimulus intensity.

A procedure to quantify intensity invariance would then be to train a decoder at a certain intensity, validate it at that training intensity ("self-validation") and at other intensities

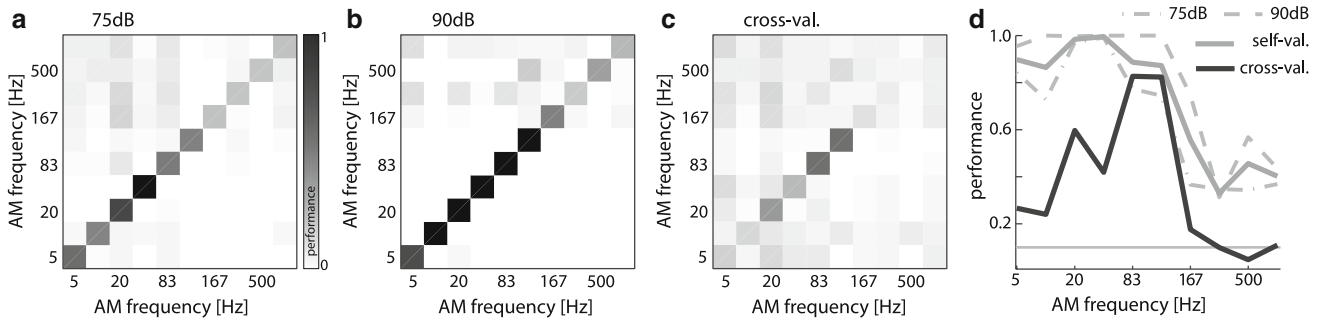

Fig. 2 Exemplary data analysis for a local interneuron: **a** and **b** confusion matrices for the self-validation task at both intensities. AM frequency is decoded for the set of responses of the same TN1 as in Fig. 1 at 75 and 90 dB separately. The outcome of the decoding algorithm is presented in a confusion matrix. The grey value corresponds to the probability with which a presentation of a given AM frequency y is decoded as AM frequency x (for color legend see 3a). A perfect classification would lead to all entries being concentrated along the main diagonal. **c** Confusion matrix for the cross-validation task, when AM frequency is decoded across intensities (see "Methods" for details). **d** Classification performance as a function of AM frequency for the three confusion matrices in **a**, **b**, **c**: AM classification performance at 75 and 90 dB (*dash-dotted* and *dashed grey lines*) differ only slightly in their average performance and in their frequency dependence. The mean of both curves over intensities (*grey*) is a measure of how well each AM frequency is decoded on average. Cross-validation performance (*black line*) is lower in general and exhibits a more band-pass like frequency dependence: performance is much worse at both low and high frequencies and high in an intermediate frequency range around 83 Hz. The ratio of the grey and the black curve's frequency average yields a measure of overall intensity invariance. *Grey line* at 0.1 indicates chance level 173 × 44 mm (600 × 600 DPI)

("cross-validation"). The comparison of the performance obtained in the self-validation and in the cross-validation task yields a measure of intensity invariance: a fully invariant neuron would exhibit no decrease of performance in the cross-validation, leading to a performance ratio of 1. A neuron whose responses change such that different response aspects underlie decoding at different intensities would exhibit a large decrease in performance and hence a ratio $\ll 1$. By this, intensity invariance is not only a property of the neuron under study but also of the decoding scheme employed.

Applied to a distance-based decoder, we required the responses to a given AM frequency to be nearer to each other than to other AM frequencies, irrespective of intensity. We did this first by classifying AM frequency using templates from the same intensity as the target responses. This self-validation served to quantify base-line performance of the cell. Second, we classified AM frequency with templates obtained by stimulation with intensities different from those of the target responses. By this cross-validation, we evaluated performance when the same pattern was present at varying intensities, a task the animal faces in its natural environment.

Self-validation

To quantify classification in the self-validation task, we classified frequency for each intensity presented separately such that both template and target responses came from the same intensity. This produced confusion matrices (Fig. 2a, b), reflecting the outcome of the algorithm for each intensity. Self-validated performance of frequency classification was then taken as the mean performance over all intensities and frequencies. We chose the same τ for all intensities such that the mean performance over all intensities was maximal. Note that "self-validation" does not imply that we use the same data for training as for validating. Rather, "self" relates to intensity being the same in the training and the validation data.

Cross-validation

We applied a cross-validation procedure to estimate invariance. Using the responses from all intensities, we quantified how well the responses to an AM frequency at a certain intensity allowed to classify the AM frequency at other intensities (Fig. 2c). That is, we modified the clustering algorithm to exclude not only the template response from the set of spike trains to be classified. Rather, we excluded all responses to an AM frequency, which had the same intensity as the template response for that AM frequency. By this, we ensured that template and target responses always came from different intensities. We then calculated intensity invariance by taking the ratio of the performance obtained by cross-validation and by self-validation. A cell with near-chance performance in both tasks could score falsely invariant. To avoid this, we excluded all cells, which did not exhibit more than twice the chance level performance (i.e., more than 0.2) in the self-validation task from the analysis.

Frequency-resolved intensity invariance

The intensity invariance taken as the ratio of the mean performance in the self- and cross-validation tasks over all

frequencies told us how intensity invariant a cell is on *average overall AM frequencies*. In order to pinpoint AM frequencies where intensity invariance was exceptionally high—i.e., AM frequencies, which yield spike responses more robust to changes in intensity—we applied a frequency-resolved measure. The ratio of the performance in the self- and the cross-validation task at each frequency was taken as the frequency-resolved intensity invariance (see Fig. 2d).

We then computed the mean and its standard error over all cells in a class. In order to avoid domination of the class' mean by highly invariant cells, we rescaled each cell's curve to vary between 0 and 1 prior to the averaging. By this, we lose all level information and are sensitive to changes of invariance with frequency only.

Analysis of natural signals

One major function of the grasshopper's auditory system is species recognition (e.g., Stumpner and von Helversen 2001). We analyzed the envelopes of the songs of 17 species of the taxon *Chorthippus* to explore the statistics of relevant natural stimuli (one song per species, kindly provided by M. Bauer and O. von Helversen, see Fig. 4a–q for species names and AM amplitude spectra).

We extracted song envelopes by the root mean square method: the raw signals (sampling frequency 100 kHz) were squared, filtered by a flattop window of duration 2.5 ms and square-rooted. Amplitude spectra of these envelopes (Fig. 4a–q) were sampled down to 30 linearly spaced values between 5 and 200 Hz.

Where in the AM spectrum does this set of natural stimuli exhibit large variations across species, indicating frequency ranges potentially suitable for species recognition and discrimination? To answer this question we performed factor analysis (FA) (see e.g., Lawley and Maxwell 1971 or Martinez 2004). This method seeks to explain a set of observed variables in terms of a few latent variables or factors. In our case, the observed variables $\vec{x} = \{x_1, \ldots, x_{30}\}^T$ are vectors having the AM amplitude at each of the 30 frequencies as entries, whose correlation structure across species is to be represented by 4 latent variables $\vec{f} = \{f_1, \ldots, f_4\}^T$. FA assumes a linear model of the form $\vec{x} = \Lambda\vec{f} + \vec{e}$. $\vec{e}$ describes observation noise and $\Lambda = \{\vec{\lambda}_1, \ldots, \vec{\lambda}_4\}^T$ is a 4 × 30 (rows × columns) matrix containing the factor loadings. We are not interested in the factors $\vec{f}_i$, but in common patterns among the AM spectra of the songs of different *Chorthippus* species as revealed by the loadings $\vec{\lambda}_i$. These loadings take the form of template spectra and show the frequency content of correlated power in the signals. The four factors used here account for 64% of the total variance. To generate error bars for the factor loadings, we performed leave-one-out subsampling: We did the FA using only 16 of the 17 songs and calculated the standard error over the 17 possible subsets. While principal component analysis is equally successful in terms of dimensionality reduction, it accounts for approximately the same amount variance (67%) we chose FA over principal component analysis. We did this because the concept underlying FA is more close to our goal, which is to explain the AM spectra in terms of few, latent or generative factors.

All analysis was performed in Matlab 2009a.

Results

Intensity invariance of AM frequency classification is generally low

To illustrate the analysis performed here, we show an example in Figs. 1 and 2. We presented the set of AM frequencies at two different intensities lying either at the middle or at the end of the rising part of the cell's rate-level curve (75 and 90 dB, respectively; Fig. 1a). From the response obtained in this way (Fig. 1b, c), we calculated spike train distances (at a temporal resolution of $\tau = 7$ ms) and used them to classify AM frequency for each intensity separately, resulting in two confusion matrices: one for 75 dB and one for 90 dB (Fig. 2a, b). The values at the main diagonal of the confusion matrix indicate the probability of correctly classifying AM frequency: both diagrams show that performance over AM frequency was mostly low pass, with high values at low frequencies and a cutoff frequency around 83–125 Hz after which performance was significantly worse (Fig. 2d, dashed and dash-dotted line). The curves for both frequencies were similar apart from an increased general performance and a higher cutoff frequency for 90 dB. The average performance over intensities yielded the cells' performance in the self-validation task (Fig. 2d, continuous grey line). To quantify intensity invariance, we classified AM frequency for the whole set of responses obtained at 75 and 90 dB in the cross-validation task. This yielded a single confusion matrix (Fig. 2c), the main diagonal of which quantifies how well the cell performed when the same AM frequency was presented to the classifier at different intensities. Frequency dependence of cross-validation performance was strongly band pass, with low performance both at low and high frequencies (Fig. 2d, black line). Yet, there existed a range of intermediary frequencies around 83 Hz where performance was greater than 80%. This was in stark contrast to the low-pass performance curves for the self-validation task (compare grey and black lines in Fig. 2d): here, performance was high for low frequencies at both intensities. Hence, although the cell presented here carried

information about low frequencies at both intensities, this information was not robust to changes in intensity.

General classification performance for AM frequency as quantified by self-validation was highest for the intermediate layer of local interneurons, and lowest for the input (receptors) and the output layer (ascending interneurons) of the network considered here (Fig. 3a, Kruskal–Wallis test $p < 0.002$; Tukey–Kramer post hoc test $p < 0.05$ for TN1 and BSN1 against ascending interneurons, all other pairs not significant). Cross-validation performance was significantly lower than self-validation performance for each cell class (Wilcoxon's signed rank test p between 6×10^{-5} and 0.04, box plots for cell classes in Fig 3b).

Intensity invariance, calculated as the ratio between self- and cross-validation performance for each cell, was generally poor for all cell classes (Fig. 3c, median invariance: receptors 0.37; the two local interneurons TN1 0.48 and BSN1 0.56; ascending interneurons 0.49; no significant differences between cell classes; Kruskal–Wallis test $p = 0.33$). 60% of the cells (22/37) exhibited an intensity invariance <0.5. This means that the changes in the neuronal responses introduced through different intensities degraded frequency classification performance by more than 50%. Only 5% of the cells (2/37) exhibit intensity invariance >0.9. This is in strong contrast to recent findings in songbird field L, where 22% of the cells recorded have been found to be highly intensity invariant (Billimoria et al. 2008).

Intensity invariance is confined to specific frequency bands

Intensity invariance of single neurons was rather low at all processing levels. However, the systematic differences in the exemplary performance curves in Fig. 2d suggest that intensity invariance is not uniform across frequencies. We therefore examined the frequency dependence of intensity invariance.

We obtained frequency-resolved measures for each cell class by comparing the performance obtained in the self and the cross-validation task at each frequency (see "Methods" for details), that is, at each AM frequency we calculated the ratio between the performance achieved in the cross-validation task and the performance reached in the self-validation task. In the example in Fig. 2d this amounted to taking the ratio between the solid grey and black curve at each frequency.

Figure 3d shows a remarkably high-intensity invariance of 0.75 and 0.87 at 83 Hz for TN1 and BSN1, respectively. A Kruskal–Wallis test revealed that there existed significant changes of invariance over frequency for TN1 and BSN1 (Fig. 3d; $p < 0.001$ and $p < 0.05$, respectively) but not for receptors and ascending interneurons ($p > 0.37$). A comparison of the invariance values at 83 Hz to those at 10 and 167 Hz further suggests that the frequency dependence of TN1 and BSN1 is band-pass like (Wilcoxon's signed rank, p between 1×10^{-4} and 0.04). Thus, although intensity invariance is low when averaged across frequencies, for local interneurons there exists a frequency band around 83 Hz where the decoding of AM pattern is robust to changes in intensity.

Intensity invariance coincides with the statistics of natural signals

Behaviorally relevant information of grasshopper songs resides particularly at two frequency bands: low AM frequencies, between 10 and 50 Hz, carry information about the gross syllable-pause structure and species identity (von Helversen and von Helversen 1998; Safi et al. 2006; Schmidt et al. 2008). A second frequency band, between 60 and 110 Hz, provides additional information about envelope fine structure, which is used to infer physical condition, sex, and species identity (von Helversen 1972; Kriegbaum 1989; von Helversen and von Helversen 1997; Machens et al. 2001; Safi et al. 2006; see Fig. 4). FA (see "Methods") of the AM spectra of songs from 17 species of the *Chorthippus* group illustrated this nicely: while the first and fourth factors were mostly loaded at low frequencies <50 Hz, the factors two and three exhibited concentrated power in a band between 60 and 110 Hz (Fig. 3e, black line and grey-shaded area).

In order to examine whether there exists a correspondence between natural signals and neuronal properties as suggested by theories of optimal coding, we compared frequency dependence of intensity invariance to the statistics of natural signals. The coding properties of the neurons considered here are highly conserved between *Locusta migratoria* and *Chorthippus biguttulus* (Ronacher and Stumpner 1988; Neuhofer et al. 2008). This allows us to compare electrophysiological data obtained from *Locusta* with natural signals relevant to the *Chorthippus* group. Although the stimuli used to quantify intensity invariance consist of rather simple sinusoidal amplitude modulations and neurons are known to be non-linear (see e.g., Machens et al. 2004), neurons can often be well approximated as linear encoders (see e.g., Rieke et al. 1999; Machens et al. 2001 for the case of auditory receptors of grasshoppers). Furthermore, the periodic structure of the sinusoidally amplitude modulated stimuli used here is not unlike the structure of natural songs (see the harmonic content of the spectra in Fig. 4r, s). Thus, we consider it plausible to extrapolate our findings to natural stimuli.

Most remarkably, for receptors and local interneurons the invariance had its maximum within the behaviorally relevant frequency band around 83 Hz: the species-specific natural signals exhibited considerable variation in a frequency range coincident with the one where neuronal

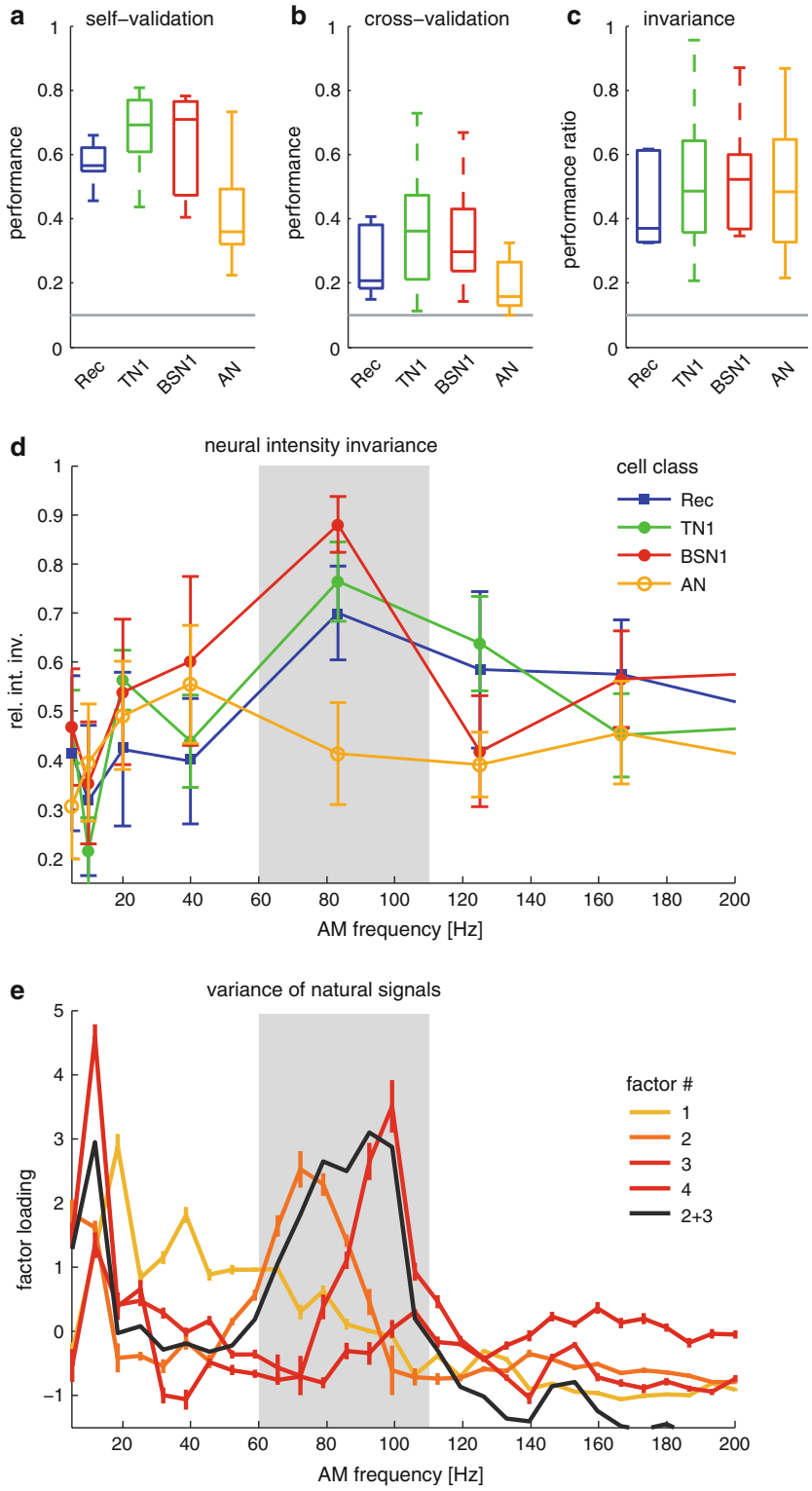

Fig. 3 Cell-class wise performance, intensity invariance and its frequency dependence: **a** Self-validation performance for each cell class: AM frequency was decoded at each intensity separately. The *grey line* indicates chance level at 0.1 in this and the following two plots. **b** Cross-validation performance for each cell class: AM frequency was decoded across several intensities. **c** Intensity invariance: the ratio of each cell's values in **b** and **c** yields a measure of how strong the loss of performance due to changes in intensity is. **d** Frequency dependence of intensity invariance: shown is the mean ± standard error for each cell class. To allow a better comparison of differently performing cells, each individual cell's curve was rescaled to vary between 0 and 1 before taking the class mean. Thereby, we lost all absolute level information and focused on the changes of intensity invariance with frequency. The two classes of local interneurons (*green and red*) exhibit elevated intensity invariance in a frequency band around 83 Hz. **e** Statistics of natural communication signals as determined by factor analysis. *Error bars* indicate the standard error of each factor, calculated by leave-one-out subsampling. While the first factor is rather broadband with a peak at 20 Hz, the next two most important factors (*2* and *3*) clearly peak in a frequency band between 60 and 110 Hz. This frequency band coincides with the one where neuronal intensity invariance of local interneurons is maximal (*grey-shaded area*)
92 × 186 mm
(600 × 600 DPI)

intensity invariance was maximal (compare Fig. 3d green and red line with Fig. 3e black line and grey-shaded area in both plots). Thus, there appears to exist a good match between the AM frequency content of natural signals and the AM frequency dependence of invariance properties of auditory interneurons.

Spike-count cues are not robust to changes of intensity

Besides the quantification of decoding performance, the van Rossum metric allowed us—by varying the temporal resolution parameter τ—to gain insight into the time scales at which classification-specific information resides. For

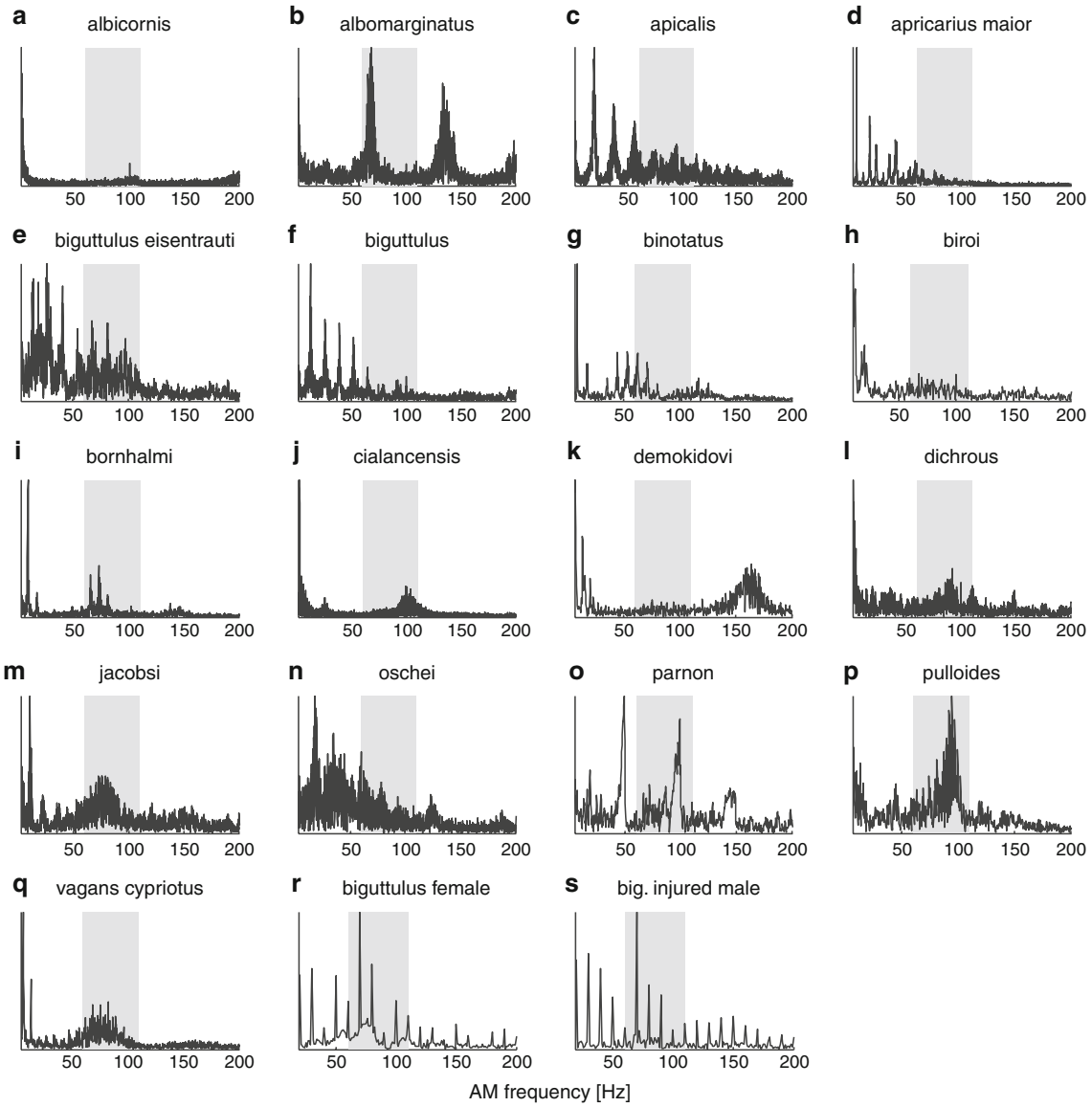

Fig. 4 AM frequency spectra of songs of members of the *Chorthippus* group. The *grey area* in each plot indicates the frequency band between 60 and 110 Hz where intensity invariance is high. **a–q** The AM spectra of songs of 17 species of the *Chorthippus* group used for factor analysis (see "Methods"). Species name indicated above each plot. **r** and **s** Spectrum of a female (**r**) and an injured male (**s**) of *Chorthippus biguttulus* (envelopes kindly provided by S. Wohlgemuth). Note that the songs of intact males (**f**) do not possess considerable power in the frequency band between 60 and 110 Hz 136 × 131 mm (600 × 600 DPI)

small to intermediate τ (5–30 ms for our cells), this corresponds to a spike-timing code. For very large τ relative to the time scales of the stimulus fluctuations ($\tau \geq 500$ ms), this amounts to a spike-count code (Theunissen and Miller 1995; van Rossum 2001). We now want to examine which time scales were suited for the decoding of AM frequency at a single intensity and whether these time scales changed when intensity was not held fixed in the stimulus ensemble. This is especially interesting with respect to observations of an increase of the role of spike-count changes at higher processing levels in grasshoppers (Vogel et al. 2005; Wohlgemuth and Ronacher 2007) as well as vertebrate auditory systems (e.g., Joris et al. 2004). Hence, we examined how robust such spike-count cues were to changes in signal intensity.

Figure 5a shows the decoding performance in the self-validation (grey line) and cross-validation (black line) task as a function of the temporal resolution parameter τ for the same local interneuron TN1 as in Fig. 1. We subtracted chance level from all performance values for the analysis of the contribution of spike count. The optimal time scale for both tasks was $\sim$7 ms, indicating that optimal decoding of AM frequency relied on a spike-timing code. However, a look at the performance for very large

$\tau > 500$ ms, where only differences in spike count contribute to the decoding (van Rossum 2001), revealed a discrepancy: performance at large τ was ~ 0.15 for the self-validation task (decoding of AM frequency at a single intensity), but zero for the cross-validation task (decoding of AM frequency across intensities). Hence, while a decoder based on spike count yielded moderate performance at a single intensity, it completely failed when the same temporal pattern was presented at different intensities. In the latter case, changes in spike count evoked by AM frequency could not be disambiguated from those evoked by changes in intensity.

To explore this more systematically, we quantified the contribution of spike count to the overall decoding performance (after chance level has been subtracted) as the ratio between the maximal performance at the optimal τ (usually 5–30 ms) and the performance at $\tau = 512$ ms. Figure 5b and c show histograms of the contribution of spike count for both tasks. For the self-validation task, spike count contributed 10–65% to overall performance (Fig. 5b) suggesting an important role of spike-count cues in the encoding of AM frequency. However, in the cross-validation task, spike count contributed less than 1% for 26/37 cells (less than 20% for 35/37 cells, see Fig. 5c). For two ascending interneurons (AN4 and AN11), contribution of spike count is even higher than in the self-validation task (Fig. 5c, two rightmost orange bars). This indicates that the temporal pattern of spikes changes strongly with intensity for these cells.

Thus, we can rule out a general transformation of the code from spike timing to spike count for the decoding of AM frequency in the metathoracic ganglion, as it is not robust to changes in the signal's intensity.

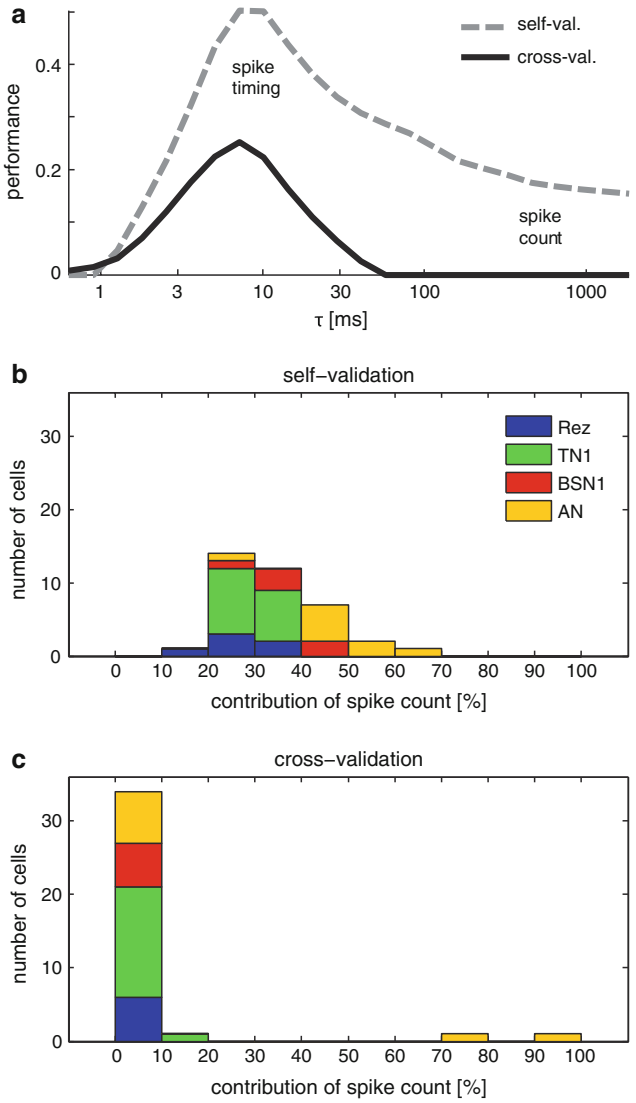

Fig. 5 Contribution of spike count to performance in different decoding tasks: **a** Dependence of decoding performance on time scale τ in the self- and the cross-validation task (*black and grey line*, respectively) for the same TN1 as in Fig. 1. The contribution of spike count is taken as the ratio between the maximal performance and the one achieved at $\tau = 512$ ms. Chance level was subtracted and is therefore zero. **b** Contribution of spike count to the decoding of AM frequency at a fixed intensity (self-validation): most receptors and local interneurons (TN1, BSN1) rely on spike count to 20–50%. The contribution of spike count for ascending interneurons is mostly >40%. **c** Contribution of spike count to the decoding of AM frequency across intensities (cross-validation): all but 2 cells rely to less than 20% on spike count 72 × 129 mm (600 × 600 DPI)

Discussion

In the analysis presented here, we investigated the problem of intensity invariant decoding of AM frequency. The two main findings were (1) a low general intensity invariance of the system, and (2) a range of AM frequencies around 83 Hz for which intensity invariance was remarkably high for local interneurons. In order to examine whether there exists a correspondence between natural signals and neuronal properties as suggested by theories of optimal coding (see e.g., Barlow 1961; Machens et al. 2005), we compared the AM frequency dependence of intensity invariance with the statistics of natural signals in different grasshopper species. To put this comparison on firm ground, we have to emphasize that the coding properties of homologous thoracic auditory neurons are indistinguishable between the locust and *Chorthippus biguttulus*, a European grasshopper species, for which detailed behavioral data exist (Ronacher and Stumpner 1988; Neuhofer et al. 2008). Based on this strict evolutionary conservation of the thoracic auditory pathway we can take the locust's auditory pathway as a model system for other gomphocerine grasshoppers. Before we proceed to this comparison, however, we will discuss another aspect of our analysis. Intensity invariance cannot be treated independently of the neuronal coding schemes. By variation of the temporal resolution parameter

τ, the decoding algorithm based on the van Rossum metric allows one to consider invariance under the two most commonly assumed neuronal codes: a spike-timing code and a spike-count code.

Spike-count codes

Two previous studies found a decrease of spike-timing precision and an increasing role of spike-count cues for the discrimination of temporal patterns at the transition from local to ascending interneurons: first, a general increase of spike-train variability has been observed between local and ascending interneurons, hinting at spike-timing cues getting less reliable (Vogel et al. 2005). A follow-up study investigated the discrimination of SAM stimuli based on metric distances of spike trains (Wohlgemuth and Ronacher 2007). This study reported a decrease of classification success from $\sim$80% in receptors and primary-like local neurons to $\sim$50% or less in ascending neurons. For the latter neurons, the contribution of spike timing to the decoding of AM frequency decreased drastically, while the contribution of spike count increased (Fig. 7 in Wohlgemuth and Ronacher 2007). This suggests a change from a temporal to a spike-count code. A similar transformation of the coding scheme is discussed for vertebrate auditory systems (Lu et al. 2001; Joris et al. 2004; Narayan et al. 2006). Here, we show that spike-count cues are not robust to changes of intensity (see Fig. 5) and hence unlikely to be employed in general at that stage in the auditory system of grasshoppers. As intensity itself heavily influences the number of action potentials elicited by a stimulus, a spike-count code for AM frequency is viable for the decoding at a narrow intensity range only. The situation may be different, however, if not a broad range of stimuli but only specific features have to be encoded. One example is the gap detection response of the AN4 neuron. This neuron responds in a phasic-tonic manner to natural songs or to block stimuli, but ceases to spike if the stimulus exhibits small gaps of a few millisecond duration (Ronacher and Stumpner 1988; Franz and Ronacher 2002). Hence, by its spike count this neuron can encode the presence/absence of gaps. However, the specific spike-count-based encoding of gaps by the AN4 neuron is not restricted to a single intensity only, although its specific response depends on intensity. At lower SPL, only larger gaps can be detected, and the neuronal data closely parallel the behavioral data (Ronacher and Stumpner 1988).

Dealing with poor intensity invariance: behavioral relevance

The low overall intensity invariance (Fig. 3c) seemed rather surprising: a system whose task is to classify auditory signals highly relevant for mate recognition should be less liable to intensity changes. For example, Billimoria et al. (2008) found song-specific neurons in songbird field L, which were highly intensity invariant.

However, this need not necessarily pose a problem for behavioral performance. A more general intensity invariant recognition could be achieved by two different strategies: either by appropriate neuronal processing at subsequent processing stages in the brain or through specific design of the relevant signals.

The metathoracic ganglion is only the first, nonetheless important, processing stage for auditory information. Its output is transmitted via ascending neurons to the brain where behavioral decisions are made (Bauer and von Helversen 1987). Hence, it is conceivable that appropriate processing at subsequent stages located in the brain leads to an improved intensity invariant representation of auditory stimuli in the brain. Adaptive processes (e.g., Abbott et al. 1997; Benda and Herz 2003; Benda and Hennig 2008; Hildebrandt et al. 2009) and divisive inhibition (Koch 1998; Uchida and Mainen 2007) are known to lead to intensity invariance. Furthermore, in this study we were exclusively concerned with intensity invariance at the level of single cells. Yet, it has been shown that intensity invariance can emerge as a result of an optimal readout of cells exhibiting band-pass intensity and frequency tuning in primary auditory cortex of marmosets (Sadagopan and Wang 2008). The nicely staggered, band-pass intensity tuning in the auditory system of a bushcricket suggests that one might generalize this to insect auditory systems as well (Römer 1987). However, the intensity tuning of ascending interneurons in grasshoppers seems not to be organized in such orderly fashion (Stumpner and Ronacher 1991; Stumpner et al. 1991). In addition, the temporal specificity of ascending interneurons is highly diverse (e.g., Stumpner and Ronacher 1994; Wohlgemuth and Ronacher 2007; Creutzig et al. 2009), further complicating an intensity invariant readout of temporal pattern. Whether such processes leading to intensity invariance at the population level really take place in the grasshopper's brain must await further study by applying more sophisticated decoding algorithms.

A different solution to the problem of intensity invariance would be to adjust the relevant signals to properties of the receiver. This road may pertain specifically to communication systems, which are shaped in a reciprocal coevolution of sender and receiver. By restricting relevant signal features to specific frequency bands, a certain degree of intensity invariance can indeed be attained, as indicated by the results of Fig. 3. Our frequency-resolved analysis revealed that there exists an AM frequency band around 83 Hz where intensity invariance is high. We observed a close correspondence between this frequency band and the

frequencies, at which communication signals vary much across species, indicating a potential role of this band in species separation (compare Fig. 3d and 3e).

The position of the optimal frequency band has probably to do with basic neuronal properties: around 83 Hz, neuronal phase locking to the AM envelope is most precise (Wohlgemuth and Ronacher 2007; see our Fig. 1a). Thus, stimuli containing power around 83 Hz evoke highly reproducible and phasic response patterns in receptors and local interneurons. This might lead to spike patterns being stable across intensities and, hence, enhanced intensity invariance. Note, that we found the peak of neuronal intensity invariance at 83 Hz only for local interneurons but not for receptors and ascending interneurons. That is, we could not show that the population of ascending interneurons investigated here propagates this invariance directly to the brain. This could indicate that the increased intensity invariance is an epiphenomenon without any relevance for subsequent computations and behavior. However, two features of the ascending interneurons could have prevented us from detecting it with the methods applied here. This group of cells probably does not encode the full stimulus waveform but specific features of the stimulus. For instance, the aforementioned AN4 is specifically inhibited by gaps as short as 3 ms in the AM envelope (Stumpner and Ronacher 1994). Due to this inhibition the full stimulus pattern can be retrieved only very incompletely from the cell's response. In addition, the neural code of ascending interneurons is probably more complex and possibly non-linear. Likely, the simple metric applied here is not able to extract the full information contained in such complex codes. A well understood exemplar is AN12, which encodes the syllable-pause ratio in the number of spikes in its bursts (Creutzig et al. 2009). While the response at the level of single spikes is intensity variant, the burst component of the response might turn out to be highly intensity invariant. Nevertheless, our data show that information in the frequency band between 60 and 110 Hz is available in a way, which may allow the ascending neurons to extract feature-specific information in an intensity invariant manner. This hypothesis could be tested by exploring the intensity invariance of the presentation of specific, behaviorally relevant features rather than that of the overall AM pattern as done in this study.

A set of additional observations indicates that the high intensity invariance at 83 Hz is indeed exploited and employed in the communication of grasshoppers. In the grasshopper *Chorthippus biguttulus*, sex recognition relies partly on the fact that female songs contain brief pauses within the noise syllables, while these pauses are masked in the songs of males by a phase shift between movements of the left and right hind leg (von Helversen and von Helversen 1997). Males that have lost one hind leg, however, do produce gaps in their songs, and females strongly reject such signals (Kriegbaum 1989). The gaps in the songs of injured males as well as the brief pauses in female songs have similar time scales, being associated with signal power at 60–110 Hz (see Fig. 4r, s). Thus, both sexes evaluate information in this frequency range and benefit potentially from increased intensity invariance. In addition, other species (see Figs. 3e, 4a–q) produce signals, which contain different amounts of power in this high-frequency band, thereby potentially contributing to species separation. Thus, evidence from behavioral studies and the statistics of relevant natural signals fits well with the restricted invariance properties of the receiver's auditory system unveiled in our study. This suggests that signal evolution of gomphocerine grasshoppers may have exploited a specific frequency channel of the receiver that exhibits best robustness against intensity changes. In order to test the behavioral relevance of our results directly, one should test behavioral intensity invariance with stimuli whose frequency content is manipulated as to either contain or lack signal power around 83 Hz.

An alternative view on optimal coding

Finally, we want to hypothesize about the match between neuronal invariance and natural signals in terms of the evolution and optimization of communication signals and the sensory networks processing them. Optimal coding theory (e.g., Attneave 1954; Barlow 1961; Atick 1992; Smith and Lewicki 2006) or the matched filter concept (Wehner 1987) both predict that coding properties of neurons were shaped by the statistics of natural signals they process. Indeed, there are reports that sensory neurons have adapted their response characteristics to the statistics of natural stimuli (e.g., Simoncelli and Olshausen 2001; Lewicki 2002; Laughlin and Sejnowski 2003). The adjustment of sensory receivers to the properties of relevant signals may be the normal situation in evolution, as the receiver cannot "control" the properties of environmental signals.

Here, we argue in the spirit of the sensory exploitation hypothesis (Ryan et al. 2001) that the situation may be different for communication systems: the coevolution of sender and receiver in a communication system entails a continuous reciprocal adaptation of both partners. Depending on the evolutionary plasticity of the sender and the receiver as well as the selective pressures acting on both, either the signal's structure or the receiver's processing properties may adapt more rapidly.

For communication systems subject to sexual selection, selective pressures are usually distributed asymmetrically between the sexes. In the case of the gomphocerine grasshoppers in the *Chorthippus* group, a male's aim is to

reach as many females as possible with their calling songs. As the females are spaced randomly, the signals will impinge on each female with different intensity. Thus, the selective pressure acting on males to produce signals, which appear attractive over a broad range of intensities, may have favored males that exploited the intensity invariance properties of the females.

In addition, the communication signals are evolutionary young as compared to the age of the neural network examined here. The morphological and physiological properties of the metathoracic network are conserved for ~50 million years (Flook and Rowell 1997; Neuhofer et al. 2008). In contrast, many species of the *Chorthippus* group included in our study originated relatively recently, probably through rapid radiation (Bridle et al. 2002; Bugrov et al. 2006). This suggests that the species-specific courtship signal is a highly plastic trait, whereas the neuronal hardware is a static trait in this group. This might be because the auditory system of grasshoppers is subject to multiple constraints as it is used not only during courtship but also for predator avoidance (Stumpner and von Helversen 2001).

In summary, evidence from neurophysiology, natural signal statistics, and evolutionary history of the communication system (Neuhofer et al. 2008) suggests that the signals are adapted to the intensity invariance properties of the receiver. Under this hypothesis, grasshoppers chose to solve the problem of intensity invariant object recognition in a different way than predicted by the optimal coding hypothesis (Barlow 1961, 2001). We propose that natural communication signals may have evolved to optimally match the properties of the neuronal hardware of animals (Lewicki 2002). Possibly, this is particularly relevant for signal design and evolution in taxa, where rapid radiation of species is driven by a diversification of communication signals as in Hawaiian crickets (Mendelson and Shaw 2005) and *Drosophila* (Hoy et al. 1988), songbirds (Price 1998), cichlids (van Alphen et al. 2004) and anurans (Gerhardt and Huber 2002). This applies to the evolution of human speech as well (Lewicki 2002).

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