

Synchronous spikes are necessary but not sufficient for a synchrony code in populations of spiking neurons

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This manuscript was compiled on January 13, 2017

Synchronous activity in populations of neurons potentially encodes special stimulus features. Selective readout of either synchronous or asynchronous activity allows formation of two streams of information processing. Theoretical work predicts that such a synchrony code is a fundamental feature of populations of spiking neurons if they operate in specific noise and stimulus regimes. Here we experimentally test the theoretical predictions by quantifying and comparing neuronal response properties in tuberous and ampullary electroreceptor afferents of the weakly electric fish *Apteronotus leptorhynchus*. These related systems show similar levels of synchronous activity, but only in the more irregularly firing tuberous afferents a synchrony code is established, whereas in the more regularly firing ampullary afferents it is not. The mere existence of synchronous activity is thus not sufficient for a synchrony code. Single-cell features such as the irregularity of spiking and the frequency-dependence of the neuron's transfer function determine whether synchronous spikes possess a distinct meaning for the encoding of time-dependent signals.

synchrony | oscillations | population code | electric fish | mutual information

Neurons are the inherently noisy computing devices of the brain. Repeated stimulation with identical stimuli evokes similar but not identical neuronal responses [e.g. 1]. Noise from internal and external sources induces substantial variability in the number and the timing of fired action potentials [2]. Because of the strong non-linearity of the spiking threshold neural noise can be beneficial by improving the representation of stimuli in populations of spiking neurons [3–7]. Noise reduces the precision with which spikes lock to the stimulus [1]. In populations of neurons that share a common input, for example by having overlapping receptive fields, noise as well as population heterogeneity have the advantage to decorrelate the responses [8, 9]. That is, only those stimulus features that drive the population strongest could synchronize the response across neurons and thereby signal the presence of a particularly important stimulus.

The role of synchronous activity in the cortex is widely discussed [6, 10–12], e.g. as a possible solution for the binding problem [for review see e.g. 13, 14], as a separate information channel to relay visual information from thalamus to visual cortex [15], as a mechanism for gain control in visual cortex [16], or as a code for odor categories in zebrafish olfactory bulb [17].

A synchrony code requires that asynchronously firing populations are synchronized or, vice versa, synchronization is escaped under certain conditions or by specific stimuli. In weakly electric fish, changes in the level of synchronization

are considered an important cue for the detection of communication signals on the level of the receptor afferents [18–21] and subsequent processing in hind- and midbrain neurons [22, 23]. Middleton and colleagues [24] demonstrated that reading out population activity of electrosensory neurons with either integrators or coincidence detectors results in two distinct representations of sensory stimuli. Integrators encode low stimulus frequencies, approximately matching frequencies characteristic for prey detection and navigation. Coincidence detectors discard low-frequency information and encode predominantly higher frequencies matching the ones of communication signals (for alternative mechanisms of such information filtering, see [25]). In a theoretical study the conditions for such a synchrony code have been analyzed in the limit of low signal amplitudes and exemplified for leaky integrate-and-fire neurons [26]. In particular, subtle effects of intrinsic noise on the shape of peaks in the neuron's response power spectrum have been identified as an important parameter influencing a potential synchrony code.

We experimentally investigate the role of noise in shaping a synchrony code by comparing populations of two closely related subsystems of the electrosensory system of the weakly electric fish *Apteronotus leptorhynchus*. These animals employ an actively generated electric field (the electric organ discharge, EOD) to detect prey, navigate and communicate [e.g. 27–

Significance Statement

Populations of sensory neurons convey information about the outside world to the brain. Post-synaptic neurons may read out their total activity or, alternatively, by focusing only on synchronous activity, they might extract specific features from the same sensory information. But does synchronous activity always encode special features of the stimulus? This question was experimentally addressed in in vivo recordings from two closely related populations of electrosensory neurons of a weakly electric fish. Despite having similar amounts of synchronous activity, only in one population of neurons did synchronous spikes carry specific information about the stimulus. A detailed spectral analysis reveals that too low levels of intrinsic noise paired with too little frequency locking of the neural oscillator destroys a synchrony code.

JG and JB designed the experiments, JG recorded the data, JG and AK analyzed the data, JG drafted the paper, all authors discussed and revised the paper.

The authors declare no conflict of interest.

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29]. The tuberous electroreceptors of the active system are tuned to the frequency of their own field [30], and the most prominent type of receptors afferents, the P-units, mainly encode amplitude modulations of this carrier [31–33]. The second system is the passive or ampullary system that is most sensitive for low-frequency fields like those emitted by muscle activity of e.g. prey organisms [e.g. 34, 35]. The two electrosensory systems thus offer a unique opportunity to analyze the information filtering in closely related but sufficiently different populations of sensory neurons within the same species.

Our results show that similar levels of synchrony can be observed in both cell types while only the P-units of the active system show a synchrony code consistent with the theory. To understand this difference we describe and compare characteristics of the spontaneous baseline activity as well as the encoding of dynamic stimuli. The two systems, though related, show distinct differences in various response features. In particular, the level of response variability and the strength of the resonance in the input-output correlation are much higher in the active system. It is exactly the combination of stronger noise in the P-units and a more pronounced peak in its cross-spectrum with the stimulus that allows for a separation of information channels, i.e. to establish a synchrony code.

Results

While the main type of electroreceptor afferents of the active system, the P-units, have received much attention [e.g. 18, 31–33, 36] the response characteristics of the ampullary afferents of South American species of weakly electric fish have not been described in comparable detail [but see 34, 37]. We thus first compare the fundamental properties of the baseline and stimulus-driven activity of both cell types, and then analyze the impact of these differences on the information contained in the synchronous activity of populations of such neurons.

Baseline activity Both types of afferents are spontaneously active in the absence of an external stimulus. P-units show an irregular baseline firing pattern while the baseline activity of ampullary afferents appears much more regular (figure 1 A). The response regularity can be quantified with the coefficient of variation ($C_V = \sigma_T / \bar{T}$) of the interspike intervals T . A C_V of zero would indicate perfect regularity with all interspike intervals being equal, random Poisson firing results in $C_V = 1$. The baseline activity of the depicted P-unit has a broad interspike interval histogram (figure 1 B, left) and a coefficient of variation of 0.33 (average firing rate of 177 Hz), indicating the irregularity of the P-unit's baseline activity. For the regularly firing ampullary afferent, on the other hand, the $C_V = 0.08$ (average baseline firing rate of 130 Hz) is indeed close to zero matching the narrow distribution of the interspike intervals (figure 1 B, right). Also, the power spectral density (PSD) of the baseline activity of both cell types differs strongly. The P-unit PSD (figure 1 C, left) has a peak at the baseline firing rate (arrow). The most prominent peak, however, is at the EOD frequency. This peak is a consequence of spike-time locking to the self-generated electric field which is also the reason for the multimodal structure of the P-unit interspike-interval histogram. The EOD peak of the power spectrum is symmetrically flanked by peaks resulting from the interaction of the EOD peak and the baseline frequency. The ampullary PSD (figure 1 C, right), on the other hand, is dominated by

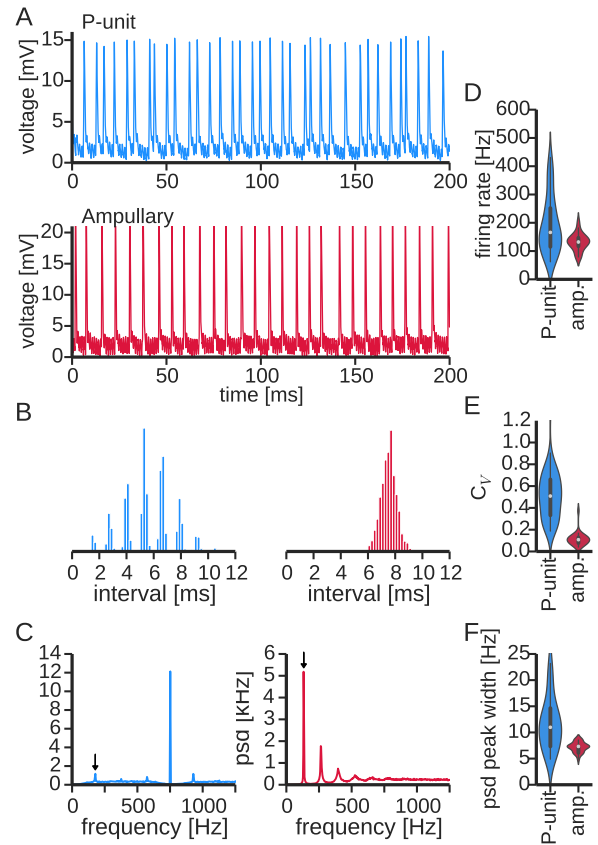


Fig. 1. Baseline activity of P-type and ampullary electroreceptor afferents. **A** top: Intracellular recording of spontaneous activity of a P-type electroreceptor afferent (P-unit, cell 2012-03-30-ah) in the absence of an external stimulus. bottom: Spontaneous activity of an ampullary afferent (cell 2012-03-23-ad). Note that the sub-threshold modulations of the membrane potential are a contamination of the recording with the fish's own EOD. **B** Interspike interval histograms of the example cells shown above. **C** Power spectra of the baseline activity of the P-unit (left) and ampullary afferent (right) shown above. Arrows indicate the baseline firing rates at 177 Hz and 133 Hz, respectively. While the power spectrum of the P-unit is dominated by a peak at the EOD frequency (752 Hz), indicating tight locking of P-unit spikes to the fish's own field, a respective peak is absent in the power spectrum of the ampullary afferent (EOD frequency of 907 Hz). The power spectrum of the ampullary baseline activity, however, is dominated by the sharp peak at the firing rate. **D** Violin plots depicting the distributions of observed firing rates across all recordings of P-units and ampullary afferents ($n = 57$ and 25 , respectively). Width of the violin indicates density of the data points. Within the violin an abstraction of a box plot is shown, where the white dot marks the median firing rate. **E** Distributions of the observed C_V s of the interspike intervals across cells. **F** Distributions of the width of psd peaks at the firing rates observed in all cells.

peaks at the baseline firing rate and its harmonics. The strong and narrow peaks are a consequence of the regularity of the baseline firing. A peak at the fish's EOD frequency is missing since the ampullary afferents are not driven by the EOD.

Differences in population heterogeneity. On the population level, across all cells recorded in this study, the baseline characteristics discussed above vary to different degrees for P-units ($n = 57$) and ampullary afferents ($n = 25$) (figure 1 D–F).

While the medians of the observed baseline firing rates do not differ significantly (Mann-Whitney U-Test, $p > 0.05$), the population heterogeneity is significantly larger in P-units than in ampullary afferents (figure 1 D, $p < 0.001$ Levene test centered on the median). P-unit firing rates are very

heterogeneous, their firing rates vary from about 50 to more than 450 Hz (199 ± 104 Hz, mean $\pm$ std), similar to previously reported values [38]. Ampullary afferents, on the contrary, are more homogeneous with firing rates ranging from 80 to 200 Hz (131 ± 29 Hz, mean $\pm$ std).

The C_V s of the interspike intervals of P-units are significantly higher than the ones of ampullary afferents ($p < 0.001$, Mann-Whitney U-Test), confirming their generally more irregular firing pattern. In addition, the P-unit population is also more heterogeneous regarding the irregularity of their baseline activity. P-unit C_V s range from 0.33 to 0.66 while C_V s of ampullary afferents are more homogeneous with values ranging from 0.08 to 0.13 (figure 1 E, variances significantly different, $p < 0.001$, Levene test centered on median).

Reduced irregularity of the baseline activity of ampullary afferents is reflected in a smaller width of the first peak in the PSD at the baseline firing rate (arrows in figure 1 C). On the contrary, in P-units the peaks vary a lot and are on average wider than in ampullary afferents because of their more irregular firing pattern (figure 1 F, significant difference in median $p < 0.001$, Mann-Whitney U-Test, Levene test yields a $p < 0.001$ for the differences in variance).

Encoding of dynamic stimuli by ampullary and P-type electroreceptor afferents. The responses to dynamic stimulation with band-limited Gaussian white noise reflect the differences in the baseline properties shown above. The cutoff frequencies of the stimuli were adjusted to cover the full coding range of the cells (300 and 150 Hz for P-type and ampullary electroreceptor afferents, respectively, figure 2 A, B).

The example P-unit shown in figure 2 A has a mean firing rate of 147 Hz and encodes the stimulus intensity with changes of its firing rate around the mean firing rate. The time-dependent firing rate was estimated by convolution with a Gaussian kernel ($\sigma = 2.5$ ms, Eq. (3)) and is referred to as the peri-stimulus-time-histogram, PSTH, from here on. The depth of the PSTH modulation is quantified by the response modulation (Eq. (4), i.e. standard deviation of the PSTH over time). In this particular recording the response modulation is 60 Hz. The ampullary afferent shown in figure 2 B also follows the temporal pattern of the stimulus by modulating its firing rate around an average rate that is in the same range (127 Hz). The response modulation is weaker (35 Hz) in this example recording.

Different response modulations result from different stimulus intensities, different sensitivities of the cells, and in particular from different positions and orientations of the cells relative to the stimulus (supplementary figure S1). For the following analysis and the comparison with predictions from theory it is, however, only relevant how strongly a cell was effectively driven by the stimulus. In the following we therefore use the response modulations as a proxy of the effective stimulus intensity.

The properties of the baseline activity (figure 1) suggest that P-unit responses are more variable than those of ampullary afferents. The response variability (Eq. (5), i.e. standard deviation of the PSTH over trials) illustrated as the shaded band in the PSTH in the single-cell examples (figure 2 A, B) suggests that the same mechanisms that cause high baseline variability in P-units also affect the encoding of dynamic stimuli. In the whole population of recorded cells the P-units indeed show a higher response variability than the ampullary

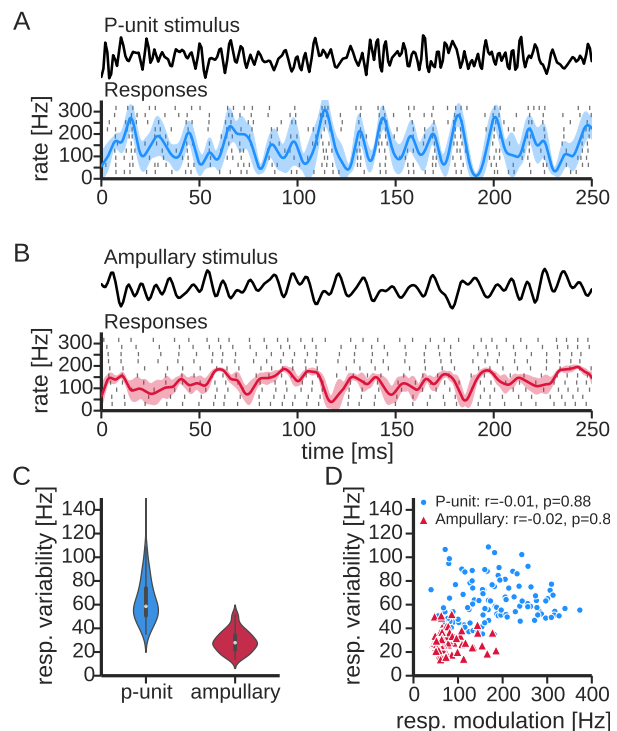


Fig. 2. Encoding of dynamic stimuli in electroreceptor afferents. **A** Responses of an example P-unit (cell 2010-12-07-ad, selected for the similar average firing rate). Cutoff frequency of the stimulus was at 300 Hz, its standard deviation was calibrated to 10% of the EOD amplitude. In the rasterplot each dash marks the occurrence of a spike in ten consecutive trials (rows). Superimposed on the spike raster is the average PSTH (solid line) and its standard deviation (shaded area). The PSTH was estimated by convolving the spike trains with a Gaussian kernel ($\sigma = 2.5$ ms). **B** Same as panel A but of an ampullary electroreceptor afferent (cell 2012-03-23-ad, same as in figure 1) to a band-limited white noise stimulus (top, cutoff at 150 Hz). Standard deviation of the stimulus was calibrated to 5% of the EOD amplitude. **C** Distributions of the response variability in P-type and ampullary electroreceptor afferents. Variability was estimated as the time-averaged across-trial standard deviation of the PSTH (Eq. (5)). P-units show a significantly higher degree of response variability than ampullary afferents ($p < 0.001$, t-test). **D** Same data as in C but the response variability is plotted as a function of the response modulation (i.e. the modulation of the PSTH, Eq. (4), a proxy of the effective stimulus intensity) for P-type (dots) and ampullary electroreceptor afferents (triangles). Correlation between the response variability and the response modulation is estimated using Pearson's r and given in the legend. The response variability is uncorrelated with response modulation.

afferents (62 ± 19 Hz and 27 ± 9 Hz, mean $\pm$ standard deviation, $p < 0.001$, t-test, figure 2 C).

For both cell types response variability is independent of response modulation, i.e. effective stimulus intensity (figure 2 D, Pearson's $r = -0.01$ ($p = 0.88$) and $r = -0.02$ ($p = 0.87$), for P-type and ampullary electroreceptor afferents, respectively). There is very little overlap of the distributions of response variabilities even for ranges of the response modulation that is covered by both cell types (below approximately 150 Hz).

Thus far we have described two populations of sensory afferents within the same sensory system in the same species that exhibit distinct differences in their response variability. In the following paragraphs we analyze how these differences affect the efficiency of a synchrony code for both populations.

Synchrony code. First, the synchrony code of P-units [24] is reviewed in light of theoretical predictions [26], in particular its dependence on stimulus amplitude. Further, the comparison

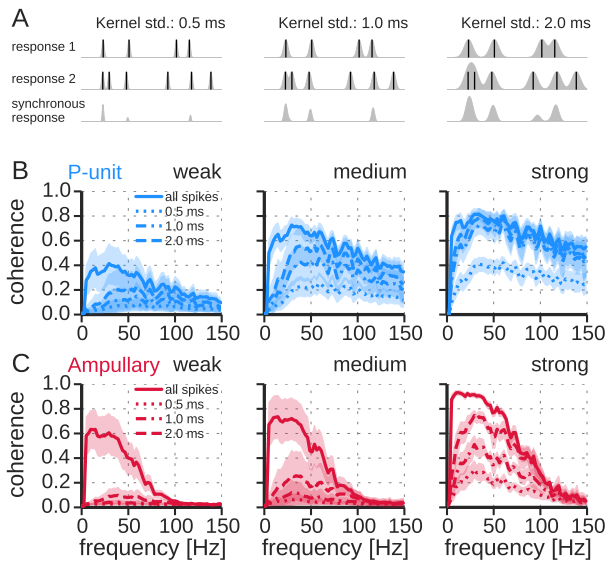


Fig. 3. Stimulus-response coherence for synchronous responses versus all-spike responses in dependence on response amplitude. **A** Calculation of the synchronous response. Spike trains of pairs of responses were combined by replacing spike events (solid vertical lines) with Gaussian kernels (gray shaded). The responses were then multiplied to yield the synchronous response. Kernels with standard deviations of $\sigma \in \{0.5, 1.0, 2.0\}$ ms were used. For illustrative purposes kernels are scaled to their maximum in the figure. See methods for details and Eq. (1) and Eq. (7) for normalization of kernels. **B** Coherence spectra of P-unit responses computed from all-spike response (solid line) and synchronous response (dashed lines) using three different window sizes defining synchrony for the multiplication method as indicated. Plotted are average coherences $\pm$ standard deviation for the three categories *weak*, *medium* and *strong* response modulations (compare supplementary figure S1). Note the elimination of low-frequency coding of synchronous spikes for weak stimuli. **C** Same as B but for responses of ampullary afferents.

to the ampullary afferents with their less variable spike activity allows to assess the impact of noise and other cellular properties on the efficiency or the existence of a synchrony code. The stimulus response coherence (Eq. (8), methods) is used to quantify how well the stimulus is represented in the responses. The coherence is a spectral measure that quantifies the (linear) correlation between stimulus and response in a frequency resolved way. A coherence of 1 indicates a perfect linear correlation. If there is no such linear correlation, the coherence assumes values close to zero.

The way how pre-synaptic spike activity is read-out potentially affects the stimulus-response coherence. Integrating all spikes (all-spike responses) yields a stronger representation of low-frequency information while selectively reading out synchronous spikes (synchronous responses) shifts the best frequency, the position of the coherence peak, to higher frequencies and discards low-frequency information [24].

Previous studies used a “binning method” to estimate the synchronous responses (supplementary figure S2 A). Here, synchronous responses were computed by a convolution of the individual spike trains with Gaussian kernels of different widths and subsequent multiplication of the responses [26] (figure 3 A).

Synchrony code in P-units is strongest for weak stimuli. For weak response modulations the shape of the stimulus-response coherences of synchronous responses qualitatively differs from the ones of all-spike responses in P-units (figure 3 B, left panel).

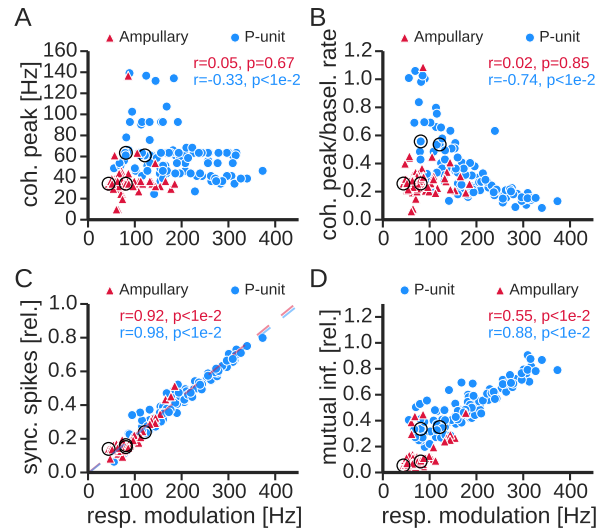


Fig. 4. Properties of synchrony codes. Scatter plots compare properties of the coherence of synchronous spikes between ampullary (triangles) and P-type electroreceptor afferents (dots) as a function of response modulation, i.e. effective stimulus intensity. As a synchrony criterion a window of 1 ms width was used. Legend indicates corresponding Pearson's correlation coefficient and significance of the correlation. Circles mark the example cells shown in figure 5. **A** Position of the peak of the coherence of synchronous spikes. **B** Same data as in A, but the peak position of the coherence spectrum was normalized to the baseline rate of the respective cell. **C** The firing rate of synchronous spikes relative to the average firing rate during stimulation. Dashed lines are linear regressions for the two types of electroreceptor afferents. **D** Mutual information between stimulus and synchronous spikes relative to the mutual information of all-spike responses. A lower bound of mutual information was estimated from the coherence spectra according to Eq. (10) in the frequency range from 0 to 150 Hz.

Confirming previous results [24] low-frequency information is suppressed in synchronous spikes, leading to a shift of the peak of the coherence to higher frequencies — a synchrony code is established.

However, for stronger responses, i.e. higher response modulations, the coherence of synchronous responses becomes more and more similar to the coherence of all-spike responses (figure 3 B, middle and right panel). The peak of the coherence of synchronous responses shifts to lower frequencies — the synchrony code vanishes, as predicted by Sharafi and coworkers [26]. This is supported by a negative correlation between the position of the coherence peak and the response modulation (figure 4 A, dots). In each category of response modulations we observe that the width of the synchrony window (see methods), i.e. the strictness of the synchrony detector, affects the amplitude of the coherence spectra. The coherence amplitude is reduced with smaller synchrony windows. At *medium* and especially at *weak* response modulations a stronger shifting effect can be observed with smaller synchrony windows (figure 3 B).

Theoretical work predicts that the peak of the synchronous response coherence should shift towards the baseline firing frequency in the limit of weak stimuli [26]. Normalizing the peak position of the coherence to the baseline firing rate shows that in P-units the coherence peak indeed moves towards baseline firing rate for weak response modulations, in accordance with the expectation (note the strong negative correlation between normalized position of coherence peak and the response modulation, figure 4 B, dots).

No synchrony code in ampullary afferents despite similar synchronous activity. In ampullary electroreceptor afferents the position of the peak of the synchronous response coherence is only slightly shifted to higher frequencies in comparison to the all-spike response coherence (figure 4 A, triangles). This shift does not depend on response modulation and peak positions are far from the baseline firing rate (figure 4 B). No synchrony code is established in ampullary afferents. In contrast to what is observed in P-units, increasing the temporal precision of the synchrony estimation scales the coherence functions down, but does not affect the position of the peak.

This absence of a synchrony code cannot be explained by differences in the firing rates of the synchronous responses. For low response modulations, where we expect P-units to show a synchrony code, the fraction of synchronous spikes is exactly the same for P-units and ampullary afferents (figure 4 C).

Although ampullary responses compared to P-unit responses have the same amount of synchronous spikes, synchronous spikes in ampullary afferents do not carry specific information.

Synchronous response in ampullary afferents carries less information. Extracting the synchronous spikes from ampullary responses leads to a more pronounced drop in stimulus-response coherence than observed for P-units (figure 3). Accordingly, the amount of information contained in the synchronous responses is much more reduced in ampullary than in P-type electroreceptor afferents (lower-bound estimation of the mutual information according to Eq. (10)). Synchronous spikes of ampullary afferents contain only 12% (median, 9% and 19% lower and upper quartile) of the information contained in the all-spikes response. On the other hand, synchronous responses of P-units carry a significantly larger proportion (median 73%, 58% and 86% lower and upper quartile, $p \ll 0.001$, Mann-Whitney U test) of the all-spikes information (figure 4 D), despite similar fractions of synchronous spikes (figure 4 C). In both cell types there is a positive correlation between the relative mutual information and the response modulation. The stronger the cell is driven, the less pronounced is the attenuation of the low-frequency coherence (figure 3 B, C, right panels) and the coherence peak is less shifted (figure 4 B). Thus, the spectra become more similar and hence synchronous and all-spike responses carry increasingly similar information.

The results shown above are based on the comparison of pairs of responses but are also valid for larger populations in which spikes in m-out-of-n trials have to be synchronous [39] (supplementary figure S3).

Discussion

We experimentally reproduced the previously described information filtering of synchrony detection in P-type electroreceptor afferents [24] and analyzed the preconditions of such a synchrony code in more detail. In particular, we verified the predicted dependence of a synchrony code on effective stimulus amplitude [26] and studied the influence of cellular properties, such as neural response variability, on synchrony codes by comparing our findings on P-units to a related population of sensory interneurons, the ampullary afferents which exhibit less variable responses. Although they have the same fraction of synchronous spikes as the P-units, the synchronous spikes

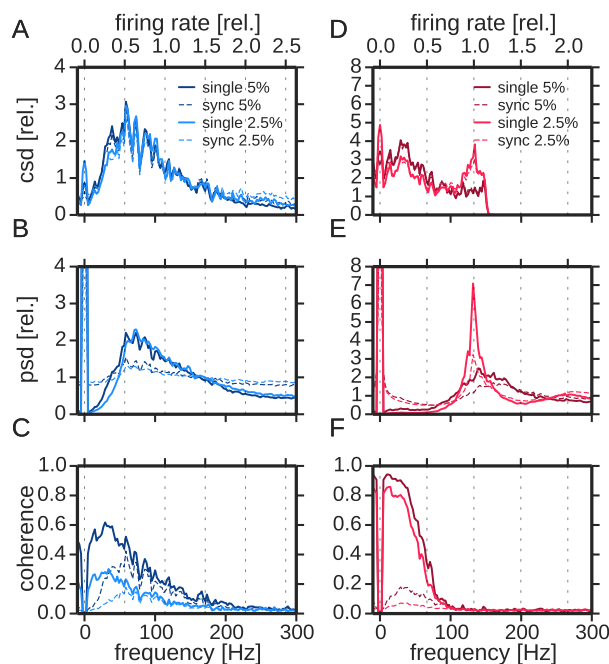


Fig. 5. Comparison of response spectra of P-type and ampullary afferents. A–C Cross-, power and coherence spectra of an example P-unit (2012-03-23-ae). In each panel the respective spectra of the single-trials (solid lines) and the synchronous responses (broken lines) at two different stimulus intensities (contrast, see methods) are depicted. All spectra were calculated from response segments of 8192 points (approximately 0.41 s) width with 50% overlap. Hanning windows were applied to each segment. Segments were not de-trended leading to the large 0 Hz power. Cross- and power spectra are normalized to their average in the frequency range from 10 to 150 Hz for easier comparison of the shape. Second frequency axis on top is scaled according to the baseline firing rate. D–F Same analysis for an example ampullary afferent (2012-03-23-ad). Cells were selected to allow for a comparison at the same two stimulus intensities.

in ampullary afferents do not encode different aspects of the stimulus in comparison to the information carried by all spikes.

Why P-units allow for a synchrony code and ampullary afferents do not.

The differential effect of synchrony detection in P-units and ampullary afferents can be qualitatively understood by comparing the relevant spectra. The stimulus-response coherence (Eq. (8)) is essentially determined by the ratio of squared stimulus-response cross-spectrum and response power spectrum (the white stimulus does not contribute to the frequency dependence of the coherence). For two sample cells stimulated at two different levels (2.5 and 5% contrast, lighter and darker lines, respectively) we show the respective spectra for the single spike train (solid line, qualitatively similar to the all-spikes statistics shown above) and the synchronous output (dashed lines) in figure 5.

The cross spectra (figure 5 A, D) relate stimulus and response and, because of the white spectrum of the stimulus, are proportional to the transfer function. As expected from theory [26], the cross-spectra are similar for the synchronous response and the single trial response (dashed and solid lines in figure 5 A, D agree apart from a scaling factor). In P-units they reveal a broad but pronounced peak at a frequency that is about 60% of the firing rate. This is typical for a leaky integrator cell in a mean-driven mode that is subject to a moderate amount of intrinsic noise [40, 41]. The ampullary

afferent on the contrary has a small peak (for small stimulus intensity) or no peak at all (for the larger stimulus intensity) — the latter behavior can be expected for a perfectly integrating cell [3, 41]. The form of the small and narrow peak, however, suggests that this cell is subject to less intrinsic noise than the P-unit, which is in line with the baseline activity discussed above. The differences in the cross-spectra of P-units and ampullary afferents are a consequence of the level of intrinsic noise and the leakiness of the respective cell.

Turning to the power spectra, we first note that the spectra of the synchronous spikes (dashed) differ from those of the single trials (solid). The synchronous spikes can be approximated by multiplying the single spike trains (supplementary figure S2). According to the convolution theorem this multiplication translates into a convolution of the single-trial power spectrum (including its DC peak) with itself. Such a convolution flattens the power spectrum, especially, when the original spectrum has a sufficiently broad peak [26]. Since the single spike train power spectrum of the ampullary afferent is narrowly peaked (in particular for the lower stimulus level), this flattening is not pronounced. In contrast, the synchronous power spectrum of the P-unit exhibits a rather flat shape because of the comparatively broad peak in the single spike train spectrum.

Dividing a peaked function (the squared stimulus-synchrony cross-spectrum of P-units) by a flat function (the synchronous output power spectrum of P-units), yields a likewise peaked function. If the power spectrum is flat, the coherence simply inherits the peak from the squared cross-spectrum. Depending on the specific level of intrinsic noise and on other biophysical parameters of the neuron, the cross-spectrum peaks in a range of 40–110% of the firing rate, which corresponds to the range of coherence peak frequencies observed in figure 4B. For the ampullary afferent the same mechanism cannot work because there is (i) not a pronounced peak in the cross-spectrum in the first place, (ii) the convolved spectrum (i.e. the synchrony spectrum) is predominantly increased at low frequencies, where the single spike-train power spectrum is exceptionally small. The latter effect leads to a strong overall reduction of synchrony coherence at low frequencies compared to the single spike train coherence (cf. the strong drop from solid to dashed lines in figure 5F) and can thus explain the strong reduction of the information rate (figure 4D, red symbols).

We have tested whether a similar behavior can be found in leaky integrate-and-fire (LIF) models. By adapting the level of intrinsic noise and the value of an effective leak parameter, we were able to qualitatively reproduce the spectral features seen in the real cells (compare figures 5 and supplementary figure S4). In this picture, the P-unit corresponds to an IF neuron with stronger leak current and higher noise level than the ampullary afferent.

These results suggest that the biophysical properties of the respective cell (leak current, channel noise) might be matched to its biological function for encoding specific aspects of time-dependent sensory signals. Ampullary afferents encode low-frequency components of a stimulus in an excellent manner, however, their synchronous spikes do neither encode very much nor do they show a very different frequency preference than the summed output. This suggests that stimulus-driven synchrony is not used in ampullary afferents. For P-units the encoding performance of the summed activity of pairs of neurons is less

impressive in magnitude but extends over a larger frequency band. Moreover, the higher intrinsic noise level (responsible for the lower overall coherence) permits the P-units to use two codes and to encode stimulus components of different frequency bands in the summed activity and in the synchronous spikes, respectively. These effects are strongest in a regime of weak stimuli.

Behavioral relevance of the weak stimulus regime. Behavioral observations of communication scenes in weakly electric fish of a closely related species *Apteronotus rostratus* in the field show that electric fish communicate at the limits of sensation [42]: (i) In aggression contexts rivals are assessed and attacks are initiated at animal distances of up to more than 1 m. At such distances the electric field intensities are extremely low (0.1 μ V) and therefore electroreceptor stimulation is weak. (ii) In courtship contexts the spatial distances between communication partners are low and the signals strong but a mismatch between the signal frequencies and the electroreceptor tuning again leads to weak activation of P-type afferents [20, 42, 43]. (iii) During foraging prey items like the crustacea *Daphnia* are detected by electric signals created through muscle activity (stimulating the ampullary afferents) and the amplitude modulations induced by their resistive properties (stimulating the P-units) which are in the 0.2–1 μ V range [44–47]. The weak stimulus regime where a synchrony code is distinct from a simple population code can thus be considered a behaviorally relevant regime in which communication and prey signals need to be encoded and separated from other signals.

Readout of electrosensory information in the weakly electric fish. Electroreceptor afferents project to the electrosensory lateral line lobe (ELL) in the hindbrain of the fish. The P-units trifurcate and synapse onto postsynaptic cells in three somatotopically organized maps, the so called lateral, centro-lateral, and centro-medial segments (LS, CLS, and CMS, respectively, 48–51). The target cells in the ELL are the pyramidal neurons which constitute an information bottleneck since all electrosensory information passes this stage. The coding properties of these neurons are well investigated [e.g. 8, 52–56]. Across maps the spectral tuning changes from low-pass behavior in the CMS to high-pass behavior in the LS [52, 55, 56]. In the context of a synchrony code this suggests that LS pyramidal cells might read out synchronous spikes only and CMS pyramidal cells integrate all their input spikes [24]. Read out of synchronous spikes could be achieved by coincidence detection where the summed postsynaptic potentials (PSP) need to cross a threshold higher than a single PSP [57]. This would lead to much lower firing rates in synchrony detectors if they would integrate the same number of inputs as a pyramidal cell with lower firing threshold that encodes the information contained in all input spikes [24]. In fact, cells in the CMS integrate over a few tens of electroreceptor afferents only, they have small receptive fields, and have low thresholds. On the other extreme, LS pyramidal neurons integrate over about 30 times more afferents, they receive input from large receptive fields, and have higher thresholds [51, 58]. These evidences suggest that the processing of electrosensory information in the active subsystem is split up into several processing streams, based on reading out different levels of synchrony in the P-unit population, thereby exploiting the specific information carried by synchronous spikes.

The ampullary afferents of the passive system project onto

a single map only, the medial segment (MS) of the ELL [48]. Little is known about the internal structure and the coding properties of the pyramidal cells in the MS of *A. leptorhynchus* [for *Eigenmannia* see 37]. Like the maps of the active system, the MS shows a somatotopic arrangement, rendering it unlikely that there are sub-populations of pyramidal cells that show distinct differences regarding their frequency tuning. This would match our finding that ampullary responses do not allow the extraction of distinct information from synchronous spikes.

High- and low-noise afferents in the vestibular system. Two anatomically distinct firing sub-populations of vestibular afferents in primates show characteristics that qualitatively match the properties of ampullary and P-type electroreceptor afferents. Both sub-populations show a spontaneous baseline activity that is very regular in the one and irregular in the other sub-population. It has been concluded that the regularly firing afferents encode self-motion using a time-code while the irregularly firing afferents employ a rate-code [59]. We suggest that the high irregularity allows for a combined rate and time-code when synchronous events in populations of afferents are taken into account.

Oscillations, noise, and synchrony. Regular neuronal firing with precise locking of spike times to a driving oscillation is observed in various systems, for example, locking to pure tones in the auditory system [60, 61], internal oscillations in electroreceptors [62] or cold receptors [63]. If the periodic drive results from internal oscillations the coding performance at this frequency is reduced [3]. Accordingly, the ampullary afferents of the paddlefish show a dip in the stimulus-response coherence at this frequency [62].

The ampullary afferents recorded here have a very regular baseline firing generated by a limit-cycle oscillation (figure 1). Thus the power spectrum of the response to white-noise stimuli shows a strong peak at the baseline firing rate, if the system is driven in the weak-stimulus regime (figure 5 E). Ampullary receptor afferents need to encode low-amplitude and low-frequency signals of prey items as reliable as possible [46, 62, 64, 65]. Accordingly, across species, ampullary afferents show a clear tuning to low stimulus frequencies [e.g. 35, 62, 66–68] (figure 3 C). Because there is no need to encode stimulus frequencies beyond the firing rate, a reduced intrinsic noise level and thus a minimum response variability is beneficial.

In P-units, on the other hand, the frequency range of behaviorally relevant signals is much wider. During foraging and navigation low-frequency signals dominate [e.g. 29, 46, 69] while in communication contexts relevant frequencies extend up to about 400 Hz [e.g. 20, 42, 43]. The P-unit system must cover a much broader frequency range that exceeds the baseline firing rate. In this case, intrinsic noise improves encoding of the stimulus by escaping the entrainment of the limit-cycle oscillation [3]. Indeed, P-unit responses are much more variable than the ones of ampullary afferents (figure 1). Such higher noise levels smear out the peak at the firing rate in the response power spectrum and as a result the stimulus-response coherence is not reduced at the firing rate (figure 5). The information provided by ampullary and P-type electroreceptor afferents were concluded to contribute equally to the multimodal task of prey detection [46, 64]. Increased levels of noise in P-units may be compensated for by the larger number of

P-type electroreceptors and the integration over large receptive fields [51, 64, 70].

In addition to the limit cycle oscillation, P-units are strongly driven by the oscillating self-generated electric field, the EOD (figure 1 C). The P-unit spikes lock to the EOD, but the intrinsic noise induces stochastic skipping of EOD cycles and this way enables encoding of small changes in EOD amplitude [71]. Stochastic skipping is also known from auditory nerve fibers [e.g. 60, 72] and cold receptors [63, 73, 74] and relies on the right amount of intrinsic noise [75]. This similarity with P-units suggests that in these systems a synchrony code is also possible. In cold receptors, however, temperature modulations change the frequency of the driving oscillation and thereby change the time scale on which synchronous spikes could be read out [63, 73, 74]. In the auditory system, on the other hand, where auditory nerve fibers encode amplitude modulations in similar ways as P-units, a synchrony code might indeed be exploited by neurons in the cochlear nucleus.

Conclusions. The active and passive electrosensory subsystems of weakly-electric fish are closely related but the electroreceptor afferents of the two systems differ in their response variability, population heterogeneity, and encoding properties. This makes them the ideal model system for analyzing the effect of response variability on a synchrony code. Differences in intrinsic noise and leakiness define whether or not a synchrony code is established. Despite similar rates of synchronous activity, information filtering by extracting synchronous spikes does not work in the ampullary afferents of the passive system. Thus, the presence of synchronous spikes is necessary but not sufficient to establish a synchrony code.

Materials and Methods

This study includes data from *in vivo* recordings of P-units and ampullary electroreceptor afferents gathered from 44 individuals of *Apteronotus leptorhynchus* of either sex. Fish were obtained from a commercial fish dealer (Aquarium Glaser, Rodgau, Germany) and were kept in colonies of up to 20 individuals. Animals were kept in a 12h:12h day — night cycle, water temperatures were 26 °C to 27 °C and water conductivity was adjusted to 180 $\mu\text{S cm}^{-1}$ to 200 $\mu\text{S cm}^{-1}$. All experimental protocols complied with national and European law and were approved by the Ethics Committees of the Ludwig-Maximilians Universität München (permit no: 55.2-1-54-2531-135-09) and the Eberhard-Karls Universität Tübingen (permit no: ZP 1/13).

Electrophysiology.

Surgery. Prior to surgery animals were anesthetized by submerging them into tank water containing 150 mg L^{-1} MS 222 (PharmaQ, Fordingbridge, UK) until gill movement ceased. Animals were then respired with a constant flow of tank water provided through a piece of tubing introduced into their mouth. Respiration water contained 150 mg L^{-1} MS 222 to ensure anesthesia. Those parts of the skin that were to be cut were locally anesthetized by cutaneous application of liquid Lidocainhydrochloride 2% (bela-pharm GmbH, Vechta, Germany). A plastic rod was glued to the exposed bone of the skull for fixating the head. Dorsal to the operculum the lateral line nerve was exposed. After surgery fish were immobilized by intramuscular injection of 25 μL to 50 μL of tubocurarine (5 mg mL^{-1} dissolved in fish saline, Sigma - Aldrich, Steinheim, Germany). Respiration was then switched to normal tank water and the fish was transferred to the experimental tank. Water temperature in the experimental tank was adjusted to 26 °C. During the experimental session local anesthesia was renewed about every two hours by carefully applying lidocaine to the skin surrounding the wounds.

Recording. Intracellular recordings of electroreceptor afferents were done using sharp glass electrodes pulled on a P97 puller (Sutter Instruments, Novato, CA, USA). Electrodes had resistances in the range 40 MΩ to 80 MΩ when filled with 1 mol L⁻¹ KCl. Electrode potentials were amplified (SEC-05 amplifier, npí electronics, Tamm, Germany, operated in bridge mode) and low-pass filtered at 10 kHz and digitized at 20 kHz (NI-PCI 6259, National Instruments, Austin, TX, USA). Recordings and stimulation were controlled by the “efish” plugins of RELACS (www.relacs.net).

Measurement of electric fields. The electric organ discharge (EOD) of the fish was recorded in two ways. First, the so called “global” measurement was obtained by measuring the fish’s head-to-tail EOD using two carbon rods (8 mm diameter) placed at the head and the tail of the fish. The electrodes were placed iso-potential to the stimulus electrodes not to pick up the electrical stimuli applied (see below). The second measurement of the fish’s field was recorded using a dipole of silver wires (spaced 1 cm) which was oriented perpendicular to the animal’s longitudinal axis and was placed just behind the operculum close to the body of the fish. This “local” measurement contained the fish’s own field as well as the stimulus and is taken as an estimate of the transdermal potential stimulating the electroreceptors. Global as well as local measurements were differentially amplified and bandpass filtered (DPA-2FXM; npí-electronics, 3 Hz and 1.5 kHz lower and upper cutoff, respectively). All signals were digitized at 20 kHz.

Stimulation. Electroreceptors were stimulated with band-limited white noise stimuli with upper cutoff frequencies of 300 Hz or 150 Hz for P-type and ampullary afferents, respectively. P-units were stimulated with amplitude modulations (AM) of the fish’s own field: the desired AM waveform was multiplied (MXS-01M, npí-electronics, Tamm, Germany) with the global measurement of the fish’s field. Ampullary electroreceptors were stimulated with directly applied electrical stimuli. In both cases, the stimuli were isolated from ground (ISO-02V, npí-electronics, Tamm, Germany) and delivered into the recording tank via two carbon rods (30 cm length, 8 mm diameter) which were placed parallel to the longitudinal axis of the fish at a distance of approximately 20 cm and fully submerged in the water. Signals were calibrated relative to the local measurement (see above) of the field by proper attenuation (ATN-01M, npí-electronics, Tamm, Germany).

Data analysis. Spikes were detected online by RELACS using the peak-detection algorithm proposed by Todd and Andrews [76]. Raw-data as well as spike times were stored for subsequent offline analysis. Data sets used in this study are publicly available in the open NIX data format (<https://github.com/g-node/nix>, [77]) and are publicly available (<http://dx.doi.org/10.12751/g-node.5b08du>). Data were analyzed with custom routines written in C++ and Python using routines of matplotlib [78], numpy/scipy [79], pandas [80], and seaborn (<https://web.stanford.edu/~mwaskom/software/seaborn>) packages.

Basic spike train analysis. The firing rate as a function of time, $y_k(t)$, was estimated by convolving spike responses $x_k(t) = \sum_i \delta(t - t_{k,i})$ of trial k with spikes at times $t_{k,i}$ with a Gaussian kernel

$$F(t) = \frac{1}{\sqrt{2\pi\sigma_{gauss}^2}} e^{-\frac{t^2}{2\sigma_{gauss}^2}} \quad [1]$$

with σ_{gauss} the standard deviation of the kernel which was 0.5 ms if not otherwise stated. The single trial firing rate then reads

$$y_k(t) = x_k(t) * F(t) = \int_{-\infty}^{+\infty} x_k(t') F(t - t') dt', \quad [2]$$

where $*$ denotes convolution. The Peri-stimulus-time histogram (PSTH, $y(t)$) is then calculated by averaging across trials:

$$y(t) = \langle y_k(t) \rangle_k. \quad [3]$$

Estimating the response modulation as a proxy for effective stimulus amplitude. In response to dynamic stimuli the firing rate is modulated around an average firing rate that is close to the baseline firing rate of the cell (figure 2 A, C). We quantified this response modulation as the standard deviation of the PSTH over time

$$\sigma_{mod} = \sqrt{\langle (y(t) - \langle y(t) \rangle_t)^2 \rangle_t}, \quad [4]$$

where $\langle \cdot \rangle_t$ denotes averaging over time. $\langle y(t) \rangle_t$ is the time-average of the PSTH, i.e. the average firing rate.

The response modulation rather than the stimulus intensity quantifies directly the effectiveness of a stimulus to drive a particular cell (e.g. supplementary figure S1 A). For the further analyses we therefore use the response modulation as a measure for effective stimulus intensity, since we were interested in the effects a stimulus has on the neuron. Three categories of *weak*, *medium*, and *strong* responses were selected to separate the whole response range (zero to maximum observed response modulation) into equally large ranges irrespective of the number of neurons or trials contributing to each category (supplementary figure S1 B, C).

Response variability was quantified by the standard deviation of the single-trial firing rates $y_k(t)$, Eq. (2), across trials averaged over time:

$$\sigma_{psth} = \left\langle \sqrt{\langle (y_k(t) - y(t))^2 \rangle_k} \right\rangle_t, \quad [5]$$

with $y(t)$ the PSTH, Eq. (3).

Analysis of synchronous and all-spikes response. In line with the analysis by Middelton et al. [24] and Sharafi and colleagues [26], we estimated the *All-spikes* and *Synchronous spikes responses* from all pairwise combinations of repeated trials recorded in the same neuron.

The *All-spikes* responses were estimated by adding pairs of single-trial responses $y_k(t)$ and $y_j(t)$

$$y_a(t) = y_k(t) + y_j(t). \quad [6]$$

Synchronous spikes responses were estimated in two ways: (i) From each pair of spike trains one spike train was convolved with a box kernel of a given duration d_{box} ($d_{box} = 0.25, 0.5, 1.0, 2.0$ ms). Whenever a spike of the second response fell into the box a spike in the synchronous response was noted at the respective average spike time in response 1 and 2 (supplementary figure S2 A) [24]. (ii) Single trial responses $y_k(t)$ were computed according to Eq. (2), with the standard deviation $\sigma_{gauss} = d_{box} \sqrt{12}$ of the Gaussian kernels Eq. (1) matching the standard deviation of the box kernels. Pairs of single-trial responses $y_k(t)$ and $y_j(t)$ were point-wise multiplied to estimate the synchronous response

$$y_s(t) = \alpha y_j(t) y_k(t), \quad \alpha = 2\sqrt{\pi} \sigma_{gauss}. \quad [7]$$

The synchronous response is zero for times in which the kernels do not overlap and positive in overlapping epochs, indicating synchronous activity (figure 3 A, supplementary figure S2 B). The normalization factor α ensures that perfectly overlapping spikes result in a Gaussian with integral one [26].

The mean response amplitudes (comparable to an average firing rate) of both methods were very similar (supplementary figure S2 C) and all further analyses yielded similar results irrespective of the applied measure (not shown). For the rest of this work we show only results from the multiplication method (supplementary figure S2 B).

Spectral analysis. To analyze the encoding of electrosensory stimuli in a frequency-resolved manner we computed the stimulus-response coherence [e.g. 81]

$$C_{sr}(f) = \frac{|S_{sr}(f)|^2}{S_{rr}(f) S_{ss}(f)} \quad [8]$$

between the stimulus $s(t)$ and the neural response $r(t)$, i.e. single trial spike trains $y_k(t)$ or synchronous responses $y_s(t)$. Power and cross-spectra were defined in terms of the Fourier transform $X(f) = \int_0^T x(t) e^{2\pi i f t} dt$ of a time series $x(t)$ by the formulas

$$S_{sr}(f) = \langle S^* R \rangle / T, \quad S_{rr}(f) = \langle R^* R \rangle / T, \quad S_{ss}(f) = \langle S^* S \rangle / T, \quad [9]$$

where $*$ denotes the complex conjugate and $\langle \cdot \rangle$ indicates averaging across segments. To estimate spectra and to determine the coherence, stimulus and responses were cut into segments of 8192 data points (≈ 0.4096 s) length and a Hanning window of the same length was applied to each segment. Segments had an overlap of 50%. As the response time series the single trial PSTH was taken (Eq. (2), spike train convolved with a Gaussian kernel, $\sigma = 0.5$ ms).

From the coherence spectra a lower bound estimate of the mutual information between stimulus and response was estimated according

to:

$$MI = - \int_0^{f_c} \log_2(1 - C_{sr}(f)) df \quad [10]$$

with f_c the cutoff frequency of the frequency band for which the mutual information is estimated.

ACKNOWLEDGMENTS. We thank Henriette Walz and Franziska Kämpfbeck for recording parts of the data. JB and JG were funded through BMBF grant 01GQ0802 to JB. AK and BL are funded through DFG grant LI 1046/2-1 and BMBF 01GQ1001A.

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DRAFT

Supporting information

Response modulation. The response modulation rather than the stimulus contrast, its strength relative to the fish's own field, was taken as a proxy for the stimulus intensity. To which extent a stimulus drives a particular neuron varies strongly. The observed response modulations at different stimulus contrasts strongly overlap (figure 1 A). For several comparisons the cells were classified according to the response modulation (figure 1 B, C).

Detection of synchronous spikes. Synchronous spikes were detected by a convolution of the individual spike trains with Gaussian kernels and subsequent multiplication of the responses [26] (figure 2 B). This approach is different from the one chosen by Middleton et al. [24] (figure 2 A). Both approaches, however, give similar firing rates in the synchronous responses for both cell types (figure 2 C).

Existence of synchrony code does not depend on population size. In addition to the synchronous-spikes response for pairs of spike responses we estimated the synchronous responses for situations in which spikes in m -out-of- n trials have to be synchronous [39]. Each spike train of the population is convolved with a box kernel of a certain width Δ (height 1) and the resulting traces are summed up. The synchronous response is then estimated by simply thresholding the summed spike trains and normalizing with the width of the box kernel. The selection of the threshold defines how many neurons of the population have to fire in synchrony to evoke a synchronous response. In our analysis we created 50 unique populations of $n = 10$ spike trains of each neuron by randomly combining selected trials. For each population we estimated the synchronous response when m out of 10 neurons were firing synchronously in a time window of width Δ . Chosen values were $m \in \{2, 3, 4, 5, 6, 7, 8, 9, 10\}$ and

$\Delta \in \{0.25, 0.5, 1.0, 2.0\}$ ms).

Pyramidal neurons in electrosensory lateral line lobe in the hindbrain (ELL) receive information from more than two electroreceptor afferents [e.g. 51]. In the following analysis we therefore enlarged the population size to $n = 10$ by randomly selecting 10 trials recorded in any recorded neuron. For a synchrony criterion we required spikes from m out of n trials to occur simultaneously within a given time window (see methods). Requiring more spikes to be synchronous makes the synchrony criterion harder. Only if the stimulus is potent enough to drive the population sufficiently strong, a synchronous event is observed. Hence, the firing rate of the synchronous response of the population drops with increasing m . Analogous to the results shown above (figure 4 B) the position of the peak coherence was estimated relative to the baseline firing frequency. For ampullary cells the required number of synchronous spikes and the response modulation do not have a pronounced effect on the position of the coherence peak; the surface plot is almost flat (figure 3 A). In P-units, however, increasing m shifts the best coding frequency (peak of the stimulus-response coherence) closer towards the baseline firing rate, resulting in a stronger synchrony code (figure 3 B). For weak responses, i.e. weak effective stimuli, the shift is larger than for strong responses, irrespective of the number of required synchronous spikes (compare to figure 4 B).

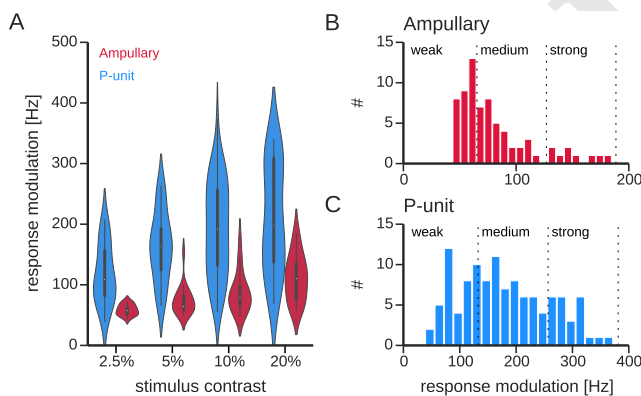


Fig. 1. Relation of response modulation and stimulus contrast. **A** Neuronal responses of ampullary and P-unit electroreceptors were evoked by stimuli of four different contrasts, i.e. standard deviations of the random AM stimuli relative to the EOD amplitude measured by the local electrode. Violin plots show the distributions of the resulting response modulations for the different stimulus contrasts for both cell types. The response modulation, Eq. (4), is the standard deviation of the PSTH over time. High modulations indicate a high gain with which the cell responds to the stimulus. Within the violins, a boxplot indicates median, interquartile range, 10 and 90% percentiles. **B, C** Distributions of observed response modulations for ampullary electroreceptor afferents and P-units, respectively. The full range of response modulations is divided into three categories (weak, medium and strong responses, vertical dashed lines). Since many cells were stimulated with stimuli of different contrasts individual cells can contribute to more than one category.

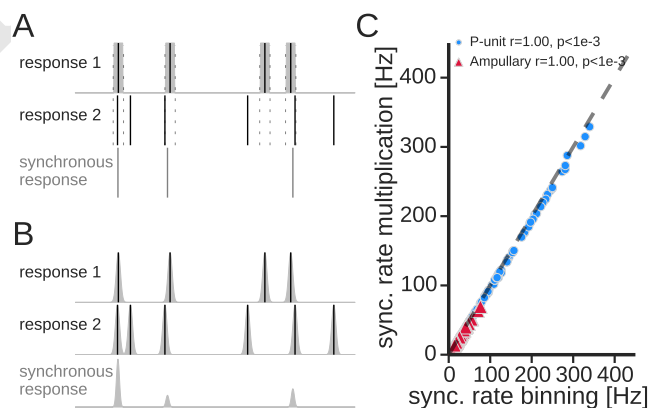


Fig. 2. Computation of the synchronous response of pairs of responses. **A** Binning method: The spikes of response 1 (solid vertical lines indicate the occurrence of each spike) were convolved with a box kernel. If a spike of response 2 fell into the box of the first response a spike in the synchronous response (bottom trace) was noted between the spikes of response 1 and response 2. **B** Multiplication method: Spikes of both responses were convolved with Gaussian kernels. The synchronous response is obtained by multiplying both responses. **C** Comparison of the mean synchronous response (comparable to the average rate of synchronous spikes) estimated with both methods. Data show results from both type of electroreceptors analyzed in this study. Dashed line is the bisecting line. 'r' values in the figure legend represent Pearson's correlation coefficient.

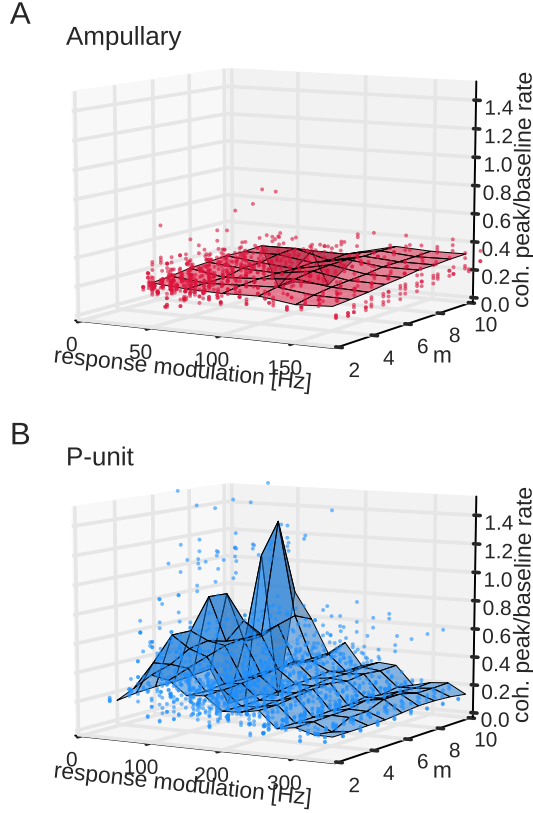


Fig. 3. Synchrony code in homogeneous populations of 10 neurons. Shown is the position of the coherence peak of synchronous spikes relative to baseline rate as a function of response modulation and number m of simultaneously synchronous spikes. The peak of the stimulus-response coherence was estimated from synchronous responses where spikes from m out of 10 trials were required to occur simultaneously within 2 ms (see methods). The position of the coherence peak was then normalized to the baseline firing rate. Dots show data points for each cell which is an average over 50 artificial populations constructed by randomly selecting 10 trials. The surface plot shows the average value in 25 Hz bins of the response modulation. **A** Independent of response modulation and number of synchronous spikes the coherence peak of ampullary afferents is only slightly shifted towards the baseline firing rate. **B** In P-unit electroreceptors a stronger synchrony criterion (higher m) results in a stronger shift of the coherence peak towards the baseline firing rate. Similar to the case of synchronous spikes in two trials (fig. 4 B) the synchrony code is more pronounced at lower response modulations.

Spectral effects can be explained by combinations of leak and noise in leaky-integrate-and-fire neurons. In order to better understand the spectral statistics of ampullary cells and P-units (see figure 5) and the efficiency of a synchrony code for these cell types, we simulated pairs of leaky integrate-and-fire (LIF) neurons obeying the simple voltage dynamics

$$\dot{v}_k = -\alpha v_k + \mu + s(t) + \sqrt{2D_i} \xi_k(t), \quad k = 1, 2, \quad [1]$$

complemented by the fire-and-reset rule: Whenever the voltage crosses the threshold $v_t = 1$, a spike is generated and the voltage is reset to the value $v_r = 0$. In eq.[1], μ is the

constant base current, $\{\xi_k\}_{k=1,2}$ are independent Gaussian white noise processes with zero mean and correlation function $\langle \xi_k(t) \xi_{k'}(t') \rangle = \delta_{k,k'} \delta(t - t')$, and D_i is the intrinsic noise intensity. The parameter α can be regarded as setting the leak conductance of the membrane. The common stimulus $s(t)$ is modeled by broad-band Gaussian white noise with cutoff

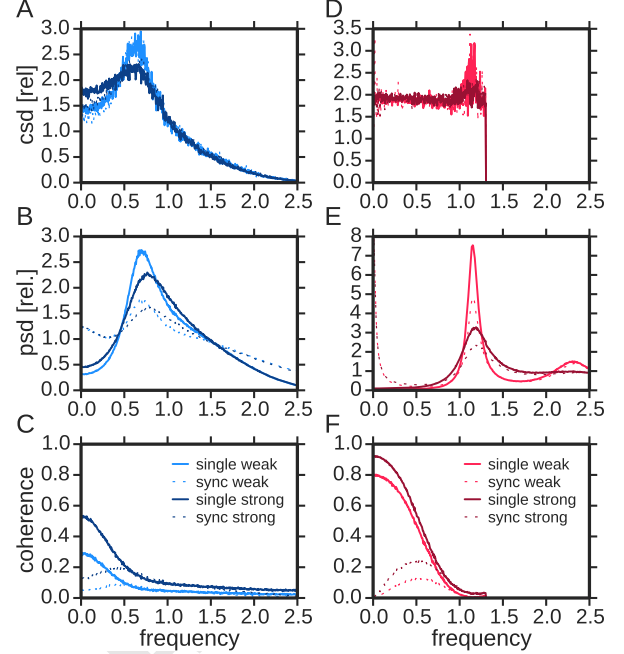


Fig. 4. Spectral analysis of model neuron. **A–C** Cross-, power and coherence spectra of LIF neuron Eq. (1) with $D_i = 0.02$, $\alpha = 1.0$ and $f_c = 3.0$. **D–F** Same analysis for $D_i = 0.002$, $\alpha = 0.1$ and $f_c = 1.3$. In each panel the respective spectra of the single-trials (solid lines) and the synchronous responses (broken lines) are shown for two different stimulus intensities $D_s = 0.01$ ('weak') and $D_s = 0.03$ ('strong'). Cross- and power spectra are normalized to their average. Remaining parameters: $\mu = 1.2$, width of box-kernel d_{box} was chosen, such that the product between baseline firing rate and d_{box} equals 0.2. Parameters were selected to qualitatively resemble experimental results in fig. 5.

frequency f_c and noise intensity D_s , i.e. its power spectrum is given by $S_{ss}(f) = 2D_s$ for $f \leq f_c$ (and is zero for $f > f_c$).

Figure 4 shows that we can find parameters such that the spectra of the simulated model neurons look similar to the ones of the example cells presented in figure 5. This similarity is achieved by changing only two parameters: the leak parameter α and the intrinsic noise intensity D_i turn out to be the key parameters to mimic the different spectral statistics of the P-units and ampullary cells. An ampullary-cell-like behavior is obtained for low intrinsic noise intensity and a small leak term, resulting in a low coefficient of variation and a comparatively flat cross-spectrum (see right column in figure 4: $D_i = 0.002, \alpha = 0.1 \rightarrow C_V = 0.06$). A dynamics similar to the one observed in P-units is obtained by setting the intrinsic noise and leak to higher values, leading to a higher CV and a peaked cross-spectrum (see left column in figure 4: $D_i = 0.02, \alpha = 1 \rightarrow C_V = 0.31$).