# Feature extraction by multiple neurons in a topographical sensory map

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## ABSTRACT

We have shown that burst-like spike patterns of single electrosensory neurons in the hindbrain of weakly electric fish reliably indicate the occurrence of behaviorally relevant stimulus features. Here, we demonstrate that the reliability of feature extraction improves even further when the coincident activity of nearby cells is evaluated. Correlated firing of these cells was mostly stimulus-induced and not attributable to shared synaptic inputs. Since the time scales of interspike intervals within bursts and those of the best coincidence time window were very similar (5-15 ms), we suggest that coincident spikes can be considered "distributed bursts".

## SUMMARY

Topographically organized maps are a common feature of many sensory systems. An important question for understanding the functioning of topographical maps is how information transmission by groups of nearby cells compares to the performance of single cells. Weakly electric fish are an excellent model system to study this question, because electrosensory input to

their brain is processed in several experimentally accessible maps representing the body surface. Here, we asked specifically how stimulus encoding and the extraction of behaviorally relevant stimulus features by pairs of nearby neurons in a hindbrain map compare to the corresponding performance of single cells.

Weakly electric fish generate electric fields and monitor field distortions that are induced by nearby prey or the signals of conspecifics. P-receptor afferents relay information about the amplitude of the electric field from electroreceptors in the skin to the hindbrain. There, P-receptor afferents excite E-type pyramidal cells and, via interneurons, inhibit I-type pyramidal cells. E-units therefore respond to increases in electric-field amplitude with excitation, while I-units respond with inhibition, analogous to the physiology of ON- and OFF-cells in the visual system.

Using a stimulus estimation approach, we demonstrated in our earlier work that the primary afferents faithfully encode the stimulus time course, consistent with an instantaneous firing-rate code. Single pyramidal cells, on the other hand, encode the time course of amplitude modulations only poorly. Applying methods derived from signal-detection theory, we found instead that they reliably indicate the occurrence of upstrokes (E-units) and downstrokes (I-units) in amplitude. In this feature extraction task, spikes occurring in bursts perform significantly better than isolated spikes (1-3).

To tackle the question how information transmission by groups of nearby neurons compares with the performance of single cells, we recorded simultaneously from pairs of nearby pyramidal cells with overlapping receptive fields while presenting random amplitude modulations (RAMs) of a mimic of the fish´s own electric field.

Pairs of the same type (E-E, I-I) showed clearly correlated firing. Cross-correlogram peaks were centered around 0 ms and had a width at half-height of between 40 and 160 ms. To determine if these correlations were mainly due to stimulus-locked responses or to shared synaptic input, we also computed the shuffle corrector and subtracted it from the raw cross-correlogram. The resulting shuffle-corrected cross-correlograms were virtually flat. Similarly, all cross-correlograms computed for spontaneous activity, that is in the absence of amplitude modulations, were flat. We conclude that the correlations found for our data set were mainly stimulus-induced and not driven by shared input, be it from the primary afferents or from feedback loops. This conclusion implies that there is only little divergence from primary afferents to pyramidal cells. To anatomically estimate the level of afferent divergence, we labeled P-receptor afferents with Neurobiotin and measured the spread of their terminal fields. The results suggest that one afferent fiber diverges onto 3 to 8 pyramidal cells. Considering all the excitatory and inhibitory inputs converging onto a pyramidal cell [6 to 15 P-receptor afferents, intrinsic and commissural interneurons, extrinsic feedback (4)], it is conceivable that the effect of shared input on the joint-firing probability of two neighboring pyramidal cells is insignificant. On the other hand, we may have failed to record from cell pairs sufficiently close to each other to receive a sizable amount of shared input.

We quantified the encoding of the RAM time course by estimating the stimuli from the simultaneously recorded spike trains. The quality of stimulus reconstruction was significantly higher than for single pyramidal cells, however, it was still inferior to the performance of single P-receptor afferents. Even when we extrapolated our data to estimate the stimulus from up to 20 spike trains (two cells; ten repetitions of the same stimulus), reconstruction quality was still significantly lower than for single primary afferents.

Next, we studied how reliably the correlated activity of pairs of pyramidal cells driven by the same stimulus was able to indicate the occurrence of upstrokes (E-units) and downstrokes (I-units) in RAMs. To this end, we used an extension of the before-mentioned feature-extraction analysis. We found that spikes of pyramidal cell pairs coinciding within a time window of a few milliseconds performed significantly better at detecting up- and downstrokes of the stimulus compared to isolated spikes and even spike bursts of single cells. The time scales of interspike intervals within bursts of single neurons (7-15 ms) and of the best coincidence time window (5-10 ms)were remarkably similar. This suggests that integration of both, burst-like spike patterns arriving on single neurons and coincident spikes on groups of pyramidal cells may have contributed to the detection of stimulus features. Therefore, temporally correlated activity of groups of pyramidal cells may be considered "distributed bursts".

Similar to earlier findings for single pyramidal cells (2, 3), pairs of I-units performed better than pairs of E-units. A reason for this difference may be that the homogeneous electric field used in our study probably maximally activated the inhibitory commissural fibers responsible for common-mode rejection (5). These fibers terminate on E-units, possibly lowering their performance. Preliminary observations support this hypothesis, since the difference in feature-extraction performance observed for homogeneous global RAMs disappeared when the stimuli were delivered via small local probes positioned within the receptive field.

In conclusion, the findings of the present study suggest that stimulus encoding by primary electrosensory afferents is transformed into feature extraction at the next stage of processing. There, stimulus-induced coincident activity of nearby cells can improve the extraction of behaviorally relevant features from the stimulus.

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