Synergistic population coding of natural communication stimuli by hindbrain electro-sensory neurons

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Statement of Contributions

The thesis is based on the refereed journal article:

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This study was designed by Dr. Maurice Chacron. All data collection, analysis, and figure generation were performed by Ziqi Wang. The thesis was written by Ziqi Wang, with edits by Dr. Maurice Chacron.
**Abstract**

Understanding how neural populations encode natural stimuli with complex spatiotemporal structure to give rise to perception remains a central problem in neuroscience. Here we investigated population coding of natural communication stimuli by hindbrain neurons within the electrosensory system of weakly electric fish *Apteronotus leptorhynchus*. Overall, we found that simultaneously recorded neural activities were correlated: signal but not noise correlations were variable depending on the stimulus waveform as well as the distance between neurons. Combining the neural activities using an equal-weight sum gave rise to discrimination performance between different stimulus waveforms that was limited by redundancy introduced by noise correlations. However, using an evolutionary algorithm to assign different weights to individual neurons before combining their activities (i.e., a weighted sum) gave rise to increased discrimination performance by revealing synergistic interactions between neural activities. Our results thus demonstrate that correlations between the neural activities of hindbrain electrosensory neurons can enhance information about the structure of natural communication stimuli that allow for reliable discrimination between different waveforms by downstream brain areas.
Résumé

Comprendre comment les populations neurales codent des stimuli naturels avec une structure spatio-temporelle complexe pour donner naissance à la perception reste un problème central en neurosciences. Ici, nous avons étudié le codage de population de stimuli de communication naturelle par les neurones du cerveau postérieur dans le système électrosensoriel de poissons faiblement électriques Apteronotus leptorhynchus. Dans l'ensemble, nous avons constaté que les activités neuronales enregistrées simultanément étaient corrélées: les corrélations du signal mais pas du bruit étaient variables en fonction de la forme d'onde du stimulus ainsi que de la distance entre les neurones. La combinaison des activités neuronales à l'aide d'une somme de poids égal a donné lieu à des performances de discrimination entre différentes formes d'onde du stimulus qui étaient limitées par la redondance introduite par les corrélations de bruit. Cependant, l'utilisation d'un algorithme évolutif pour attribuer des poids différents aux neurones individuels avant de combiner leurs activités (c'est-à-dire une somme pondérée) a donné lieu à une performance de discrimination accrue en révélant des interactions synergiques entre les activités neuronales. Nos résultats démontrent ainsi que les corrélations entre les activités neuronales des neurones électrosensoriels du cerveau postérieur peuvent améliorer les informations sur la structure des stimuli de communication naturels qui permettent une discrimination fiable entre les différentes formes d'onde par les zones cérébrales en aval.
**Introduction**

Under the pressure for survival and reproduction, animals are evolved to adapt to their living habitats by developing specialized senses and skills. For example, an emperor penguin coming back from fishing needs to find its mate and chick, and it is not an easy task because emperor penguins live in large colony, whose members are visually identical as much to human as to penguins themselves. Luckily, the emperor penguins can produce unique vocal calls, which can be discriminated from calls that are simultaneously produced by other members of the colony (i.e., noise) and recognized by their mates. This task, which is a highly sophisticated “cocktail party problem”, requires specialized auditory streaming. Different animals are evolved to have different specialized senses, e.g., mice and rats used in laboratory studies have highly specialized olfactory sense. Animals perceive the external environments in their natural habitats and generate behaviors using sensory information processed in different sensory modalities. Therefore, how sensory information from the naturalistic environment is represented in the brain and used to guide perception and natural behaviors has been one of the key questions in system neuroscience (Einhauser & Konig, 2010; Kayser et al., 2004; Nelken, 2004).

One of the animal models that is suitable to answer that question is the weakly electric fish. These fish have relatively poor vision, but instead, they have specialized electrosense. They actively generate electric fields using the electric organ and detect the perturbations of the fields through the electrosensory receptors (Hitschfeld et al., 2009; Krahe & Maler, 2014). One vital function of the electrosensory system is to detect and process the communication signals sent by other conspecifics, usually in the context of either aggression or courtship (Hupe & Lewis, 2008; Smith, 2013). These electro-communication signals can be easily mimicked using laboratory setups, unlike natural stimuli for other systems which tend to have complex spatiotemporal structures. How the electrosensory system processes naturalistic, behaviorally relevant communication signals is therefore an ideal question for the investigation of sensory processing of natural stimuli and answering this question can offer insights into the principles of neural coding.
In this work, we studied how communication stimuli are encoded by the hindbrain electrosensory neurons in the weakly electric fish *Apteronotus Lepterynchus* (the brown ghost knifefish). Instead of studying encoding at the single neuron level, we investigated how populations of neurons in the electrosensory hindbrain encode the communication stimuli. While a single neuron is not fully informative about the stimuli, the neuronal populations can offer more accurate representations, which can be decoded by the downstream neurons that receive synaptic inputs from the populations. Understanding of population coding is complicated by the fact that neural activities are not independent of each other but are instead correlated (Averbeck et al., 2006; Cohen & Kohn, 2011; Kohn et al., 2016). The correlations seen in the neural responses, especially correlations in the trial-to-trial variability (i.e., noise correlation), were shown to have impact on population coding (Averbeck et al., 2006). Whether or not noise correlations exist in neural responses to electro-communication stimuli, and if so, how noise correlations impact the encoding of such stimuli are therefore questions of specific interests. Before we present our work, we will go over some background information and previous literatures about, e.g., the electrosensory system and population coding, in the next segment.

**Backgrounds and Reviews of Relevant Literatures**

**Natural stimuli vs artificial stimuli**

Through evolution, the perceptual system of an organism is shaped by the physical environment (Geisler, 2008). The sensory processing of the brain is determined by the stimuli organisms encounter naturally in their habitats. Therefore, from an evolutionary perspective, the sensory systems should be understood through the processing and computations of natural stimuli. However, most of our understandings of the sensory systems to date are based on the studies of artificial stimuli. For examples, the orientation selectivity of primary visual cortex (V1) was discovered and extensively investigated using bars and gratings (Ferster & Miller, 2000). While the studies of artificial stimuli contribute tremendously to our understandings of how sensory neurons represent stimuli with different physical properties, they have certain limitations. First of all, artificial stimuli might not be optimally encoded by the sensory neurons: For example, a study investigating stimuli selectivity in midbrain superior colliculus of bats showed that natural
stimuli have better response selectivity than artificial stimuli with matched properties (Wohlgemuth & Moss, 2016). More importantly, artificial stimuli are not behaviorally relevant, therefore the information of these stimuli might not be decoded by downstream neurons to guide perception and behaviors. More recently, sensory processing of natural stimuli has been one of the key interests of system neuroscience (Einhauser & König, 2010; Kayser et al., 2004; Nelken, 2004). Most recent studies have started to look at population coding of natural stimuli (Koren et al., 2020; Yoshida & Ohki, 2020). However, the natural stimuli tend to have complex spatiotemporal structures, so that using such stimuli to design well-controlled hypothesis-driven experiments is difficult (Rust & Movshon, 2005). In this work, to study the population coding of natural stimuli, we used an animal model where the natural communication stimuli are relatively simple and easily mimicked using laboratory setups. This will be introduced in the following section.

**Natural electro-communication in weakly electric fish**

In this project we used a species of wave-type weakly electric fish as our animal model. The electrosensory system of the weakly electric fish is well characterized in terms of anatomy and physiology (Chacron et al., 2011; Clarke et al., 2015; Maler, 2009a, 2009b). These fish are nocturnal and have poor vision, so they rely heavily on their active electrosense. They can generate weak electric discharges in the range of a few millivolts using the electric organ - either neurogenic or myogenic - for sensing the environment (e.g., navigation and prey localization) and communicating with conspecifics (Hitschfeld et al., 2009; Krahe & Maler, 2014). The weakly electric fish used in this project is *Apteronotus leptorhynchus* (i.e. brown ghost knifefish), whose EOD is a continuous pseudo-sine wave.

When two fish encounter, their EOD are modulated by each other’s EOD in amplitude sinusoidally, i.e. forming a beat. The fish can detect the prey and communicate through the perturbations of its EOD (Henninger et al., 2018; Scheich et al., 1973). In this project we focused on the sensory processing of natural electro-communication stimuli which are the transient frequency excursion of the EOD (also referred to as “chirps”). There are many subtypes of chirps, and the most common types are Type 1 chirps (or “big chirps”) and Type 2 chirps (or
“small chirps”) (Engler et al., 2000; Engler & Zupanc, 2001; Hupe & Lewis, 2008; Smith, 2013; G. K. Zupanc et al., 2006). In the context of opposite-sex courtship (or the encounter of one dominant and one submissive fish), the fish will elicit Type 1 chirps which have high frequency excursion (300-900 Hz) and relatively long duration (>20 ms), accompanied by an amplitude reduction. In the context of same-sex aggression, the fish elicit Type 2 chirps that have short duration (10-20 ms) and relatively small frequency excursion (50-180 Hz).

Male fish produce significantly more chirps (both Type 1 and Type 2 chirps) than female fish, and both genders produce more Type 2 chirps than Type 1 chirps (Hupe & Lewis, 2008). In the context of aggression, Type 2 chirps production of a fish is related to a decreased rate of physical attacks, while the production of abrupt frequency rises (repeated events of frequency increase and subsequent decrease) are related to a high attack rate (Hupe & Lewis, 2008). Chirps produced by the receivers usually follow the chirps of the senders with a latency of 500 to 1000 ms (G. K. Zupanc et al., 2006), which are known as the “echo responses”. The echo responses to Type 2 chirps show a high degree of invariance in terms of duration, frequency excursion and phase (Metzen et al., 2016, 2020). In this project, we focused on the population coding of Type 2 chirps, which will be referred to as simply “chirps” for the remaining sections.

**Electroscopic system of weakly electric fish**

The weakly electric fish we used can sense both frequency and amplitude modulations of the electric fields (Carlson & Kawasaki, 2006). Since the interactions and electro-communications between two fish will cause global modulations in the amplitude of EOD (G. K. H. Zupanc & Maler, 1993), we focused on the study of EOD amplitude modulations in this work. The EOD amplitude modulations are detected by the tuberous electroreceptors P-units on the skin (Chacron, 2006). The Electroscopic Afferents (EA) send the information to Electroscopic Lateral Line lobe (ELL) in the hindbrain, which is a cerebellum-like structure with laminar organization and the first and only site of termination of EA in this specie (Berman & Maler, 1999; Krahe et al., 2008). ELL has four parallel segments, and three of them - centro-medial segment (CMS), centrolateral segment (CLS) and lateral segment (LS) - process inputs coming from tuberous electroreceptor afferents. ELL pyramidal cells, which are neurons receiving inputs
from P-units, can be classified into ON cells which receive inputs from EA directly, and OFF cells which receive inputs from EA indirectly through intermediate inhibitory interneurons (Maler, 1979). ON and OFF cells reside in three layers - superficial, intermediate, and deep layers. Pyramidal cells are the major output neurons of ELL, which project to neurons in midbrain torus semicircularis (TS) (Maler, 1979). Electrosensory information is sent from these neurons to the forebrain and gets further processed to guide perception and behaviors.

Besides the feedforward/ascending pathways described above, there are also extensive feedback/descending pathways in the electrosensory system (Hofmann & Chacron, 2019). There are two major sources of feedback onto ELL pyramidal cells: the direct pathway and the indirect pathway. For the direct pathway, midbrain TS neurons project onto stellate cells in nucleus praeminentialis (nP) which then directly project back to ELL pyramidal with excitation and inhibition via local interneurons. This pathway forms a closed loop and the feedback onto pyramidal cells through this pathway is topographically organized (Bratton & Bastian, 1990). For the indirect pathway, deep pyramidal cells project onto the multipolar cells in nP and these cells then project to granule cells in eminentia granularis posterior (EGp), which form parallel fibers connections with mainly superficial and intermediate pyramidal cells. This pathway, unlike the direct pathway, forms an open loop, and the feedback onto pyramidal cells through parallel fibers is diffuse (Bastian & Bratton, 1990).

**Encoding of electro-communication stimuli at different levels**

Here we briefly review the previous studies of sensory processing of chirps at the levels of sensory periphery (EAs), the hindbrain (ELL), and in the midbrain (TS).

The peripheral EAs increase the firing rate when the amplitude and frequency of AM are increased. Chirps, as introduced above, are transient increases in the AM frequency, and will thus increase the responses of EAs (Benda et al., 2005). Since EAs’ responses faithfully follow the waveforms of AMs, chirps will elicit either an excitatory response (when occurring at beat phase < 180°) or an inhibitory response (when occurring at beat phase > 180°) (Metzen et al., 2016). Also, chirps elicit synchronous spiking of the EAs (Benda et al., 2006). While the firing
rate of EAs gets modulated differentially by frequency excursion, duration and phase of the chirps, the correlated activities of EA population are more invariant across all chirp waveforms (Metzen et al., 2016, 2020). Previous studies have shown that EAs respond to higher beat frequencies with increased phase-locking due to their high-pass frequency tuning (Chacron et al., 2005a; Xu et al., 1996). Due to this property, the phase invariant coding of correlated activities is decreased with higher beat frequency (Metzen & Chacron, 2017).

The EAs send electrosensory information to the ELL, which has heterogeneous populations of pyramidal cells, lying across different maps (CMS, CLS, LS), residing in three layers (superficial, intermediate, deep), and having ON and OFF cells which respond asymmetrically. Superficial and intermediate pyramidal cell receive extensive feedback on their apical dendrites while deep cells are the source of the feedback and themselves receive little feedback (Bastian & Bratton, 1990). ON cells increase the firing rate in response to chirps at beat phase < 180° and similarly, OFF cells increase the firing rate to chirps at beat phase > 180° (Metzen et al., 2016). However, only the superficial ON-type pyramidal cells in LS respond to chirps robustly with a stereotyped burst due to the activation of feedback, while OFF cells, ON cells in other layers and cells in other maps respond to beat and chirps with similar firing rate (Marsat et al., 2009). Different chirp attributes can be discriminated based on the responses of ELL pyramidal cells (Vonderschen & Chacron, 2011). While the discriminability of single ELL neurons is decreased compared to that of single EAs, the responses of pyramidal cells provide a more invariant representation for chirps of different attributes than the single EAs (Metzen et al., 2016, 2020).

Next, the electrosensory information is sent from the ELL pyramidal cells to the midbrain TS. TS neurons can be categorized into dense and sparse neurons. The dense neurons respond to stimuli very much like the ELL pyramidal cells, while sparse neurons respond selectively to a certain type of stimuli and remain silent to other stimuli (M. K. J. Sproule et al., 2015; Vonderschen & Chacron, 2011). For chirps encoding, the sparse neurons are the ones that show a higher level of phase invariance compared to ELL pyramidal cells and EAs, because they will only respond to chirps, not the beat (Metzen et al., 2016; Vonderschen & Chacron, 2011). This invariant response can be explained by these neurons receiving balanced inputs from ON and OFF type cells in the ELL (Aumentado-Armstrong et al., 2015). Dense and sparse neurons are
thought to have complementary functions: while sparse neurons accurately detect the chirp occurrence, dense neurons can transmit the contextual information about the identity of the chirp (Metzen et al., 2016).

**Population coding and neural correlations**

Recent technological advances have enabled simultaneous large-scale recordings of populations of neurons. With up to hundreds and thousands of neurons recorded simultaneously, analysis beyond single-neuron firing statistics can be done to help us understand how a neuronal population represents information. Specifically, there has been a keen interest in analyzing pairwise correlations between neurons in a population. Pairwise correlations are easy to quantify and can imply higher-dimensional correlations (Shlens et al., 2006). There are two types of correlations between neural responses of two neurons: signal correlations and noise correlations. Signal correlations quantify similarities between the mean responses of two neurons to stimuli and arise due to similar properties of neurons (e.g., similar tuning curves). Noise correlations, on the other hand, are correlations between the trial-to-trial variabilities of neural responses to repeated presentations of a given stimulus and arise due to shared noisy synaptic inputs (note that the shared inputs can come from bottom-up/feedback, top-down/feedback, and recurrent connections). In this work, we specifically studied noise correlations because previous studies have shown that noise correlations can impact population coding (Averbeck et al., 2006).

There is a history of studying how noise correlations limit information. In a pioneering work, Zohary et al. (1994) found that correlated variability can limit signal-to-noise ratio by preventing cancellation of noises when pooling responses of a population of neurons. Also, they found that noise correlations are higher for neurons with similar stimulus selectivity. Theoretical studies that employed this limited-range correlations (i.e., noise correlations decrease as stimulus selectivity of the pairs becomes more dissimilar) in a homogeneous population (i.e., neurons with tuning curves that are identically shaped) also found noise correlations to be information limiting (L. F. Abbott & P. Dayan, 1999; Sompolinsky et al., 2001). How exactly do noise correlations cause information to saturate as the number of neurons in a population keeps growing? Moreno-Bote et al. (2014) found that only correlations that are related to the derivatives of the tuning
curves, which are termed “differential correlations”, can limit information growth. This is true for both heterogenous and homogenous populations (limited-range correlations of homogeneous populations contain differential correlations). Geometrically, noise correlations are information limiting if the vector formed by derivatives of the tuning curves points predominantly in the long directions of the covariance ellipse. Recent experimental evidence showed that information-limiting correlations exist in large neural populations (Bartolo et al., 2020; Kafashan et al., 2021).

However, not all noise correlations are information limiting. More generally, when comparing a population that has correlated noise with the one that has independent noise, noise correlations can be detrimental, beneficial, or play no effect on information coding. Information-limiting correlation is just an extreme case of noise correlation being detrimental. Experimentally, some studies showed that noise correlations introduce redundancy to population information (Averbeck & Lee, 2006; Ecker et al., 2010), while other studies showed that noise correlations can be beneficial (Franke et al., 2016; Lin et al., 2015; Zylberberg et al., 2016). How noise correlations affect information coding was shown to be dependent on the relationship between signal and noise correlations: If noise and signal correlations have the same signs (i.e. both positive or both negative), the effect is likely detrimental; if noise and signal correlations have opposite signs, the effect is beneficial (Averbeck et al., 2006). Here we want to emphasize that noise correlation can be plastic/state-dependent: It depends on multiple factors such as stimulus features (Chacron & Bastian, 2008), attentional state (Cohen & Maunsell, 2009; Mitchell et al., 2009), adaptation (Gutnisky & Dragoi, 2008) and training (Gu et al., 2011). According to Doiron et al. (2016), input correlations, internal fluctuations and response gain are the three mechanisms underlying the modulations of noise correlations. This plasticity of noise correlation can complicate its effect on population coding (Franke et al., 2016). We also noticed that while signal correlation is usually defined using derivatives of tuning curves, there are alternative definitions, e.g., as correlations between the entire tuning curves, or the correlations between the binned responses of a single time-varying stimulus. Previous studies quantifying signal correlations under these alternative definitions also showed that the relationship between signal and noise correlations affect population information (Gu et al., 2011; Minces et al., 2017). However, simply quantifying the relationships between signal and noise correlations is not
enough to explain the effect of noise correlations. According to Hu et al. (2014), if all pairs in a population have signal and noise correlations with opposite signs, the coding is improved; however, a beneficial correlation structure, or even an optimal correlation structure, can violate this rule. Also, the opposite of the rule (i.e., coding is degraded if all pairs have signal and noise correlations with the same signs) only holds true for weak noise correlations - stronger correlations could play no effect or even become beneficial. The effect of noise correlation is also dependent on the choice of decoder, e.g., a subtraction decoder instead of an addition decoder can make positive noise correlations between neurons beneficial (Romo et al., 2003), and a suboptimal decoder can make the information saturate while the correlations are not information-limiting (Moreno-Bote et al., 2014).

Eventually, information in a population is decoded and used for computations. Therefore, it is also crucial to study the effect of noise correlation on the decoding perspective – whether downstream neurons need to know correlations in order to optimally decode (Averbeck et al., 2006; Averbeck & Lee, 2006). More directly, one can quantify the importance of noise correlations on perception and behaviors. For example, this could be done by quantifying noise correlations using PCA and determining whether the corresponding principle component can predict the behavioral outcome on a trial-by-trial basis (Ni et al., 2018).

Methods

Animals

The South American wave-type weakly electric fish *Apteronotus leptorhynchus* (N = 2) was used in this study. Animals were purchased from tropical fish suppliers and were housed in groups (2 – 10) at controlled water temperatures (26-29°C) and conductivities (300-800 µS*cm⁻¹) according to published guidelines (Hitschfeld et al., 2009). All animal procedures were approved by McGill University’s animal care committee.
Surgery and recording

Surgical procedures have been described in details previously (Chacron et al., 2003). Briefly, animals were immobilized by injection of 0.1-0.5 mg of tubocurarine (Sigma) intramuscularly. The animals were then transferred to an experimental tank (30 cm x 30 cm x 10 cm) containing water from the animal’s home tank and respirated by a mouth tube providing constant flow of oxygenated water at a flow rate of 10 mL*min⁻¹. Before surgery, the animal’s head was locally anesthetized with lidocaine ointment (5%; AstraZeneca, Mississauga, ON, Canada). Craniotomy (a ~ 5mm² window) was performed to partially expose the hindbrain. Neuropixel probes (Imec inc., Leuven, Belgium) were inserted into the brain along the rostral-caudal axis and a 45° angle with respect to the sagittal plane at transverse slice T-4 of the brain atlas (Maler et al., 1991) laterally near the praeminentialis efferent tract (labeled “P-Cb” on the atlas), as done previously when recording from single ELL pyramidal cells within the lateral segment (LS) of the ELL (Huang et al., 2018, 2019; Krahe et al., 2008), and the tip moved to a depth of 1500 µm. We waited at least one hour after inserting the probe before starting to record to allow brain tissue to settle following probe insertion and to improve recording stability. Accounting for the fact that the first recording site is located 175 µm away from the tip along the probe shaft, as well as the fact that recordings were typically obtained on recording sites ranging between 13 and 97, this gives approximate recording depths between 355 µm and 1195 µm, which are within the range reported from a previous study where location within LS was confirmed by histological post-processing (Krahe et al., 2008; M. K. Sproule & Chacron, 2017). Thus, based on probe geometry, anatomy (Maler et al., 1991), and our experience recording from LS ELL pyramidal cells (Huang et al., 2018, 2019), it is likely that most of our recordings were from LS. However, we cannot reject the hypothesis that some of our recordings were from the centrolateral segment (CLS). The distance between recorded units was computed as the physical distance between the recording sites on which the spikes shapes of both units displayed the largest amplitude, which is approximate. However, since a given unit was most often recorded from the nearest neighbors to the primary recording site, the error is at most 40 µm based on probe geometry. We note that this is much smaller than the range of distances over which recordings were obtained.
**Stimulation**

The electric organ discharge (EOD) of *A. leptorhynchus* is neurogenic, and therefore is not affected by injection of curare. Stimuli consisted of amplitude modulations (AM) of the animal’s own EOD were produced by triggering a function generator to emit one cycle of a sine wave for each zero crossing of the EOD as done previously (Bastian et al., 2002). The frequency of the emitted sine wave was set slightly higher (30 Hz) than that of the EOD, which allowed the output of the function generator to be synchronized with the EOD. The emitted sine wave was subsequently multiplied with the desired AM waveform (MT3 multiplier; Tucker Davis Technologies, Alachua, FL, USA), and the resulting signal was isolated from the ground (A395 linear stimulus isolator; World Precision Instruments, Sarasota, FL, USA). The isolated signal was then delivered through a pair of chloritized silver wire electrodes located 15 cm away from the animal on each side of the recording tank perpendicular to the fish’s rostro-caudal axis. In this study, 5 Hz beat frequency and 14ms chirp duration were used. Chirps were generated with different attributes by systematically varying the excursion frequency (30, 60, 90 and 120 Hz) and the phase (0, 90, 180 and 270° of the underlying beat cycles at which the chirp occurs). As such, a total of 16 chirps were used (4 different chirp amplitudes, 4 different chirp phases). Parameter ranges were chosen to contain those observed in previous studies (Engler & Zupanc, 2001; G. K. H. Zupanc & Maler, 1993). To measure the stimulus intensity, a dipole was placed near the animal’s skin. Stimulus intensity was adjusted to produce changes in EOD amplitude that were ~20% of the baseline level, as done previously (Metzen & Chacron, 2017; Metzen et al., 2016). Each type of chirp stimulus was presented 40 times (i.e., 40 trials).

**Data analysis**

Spike times for each individual neuron were sorted using Kilosort and manually curated using Phy 2. The spike times were converted into binary sequences $X_i(t)$ sampled at 2 kHz (i.e., 1 if a spike occurred during a given binwidth of 0.5 ms and 0 otherwise). Neurons were classified into either ON- or OFF-type based on spike-triggered average (STA) of a low-pass filtered (0-120Hz) noise stimulus as done previously (Martinez et al., 2016). The strength of the neural response...
was quantified through the STA amplitude (i.e., the distance between the maximum and minimum values) (Huang et al., 2018).

We quantified correlations between neuronal activities using spike count sequences $N_i$ that were obtained from each spike train by counting the number of spikes occurring during 4 successive and non-overlapping 10ms time windows that were always aligned with respect to 8ms after the onset of the chirp stimulus in order to account for transmission delays. We then computed the correlation coefficient between pairs of spike count sequences using Pearson’s correlation coefficient:

$$r_{ij} = \frac{\text{Cov}(N_i, N_j)}{\sqrt{\text{Var}(N_i)\text{Var}(N_j)}} \quad [1].$$

where $<>$ represents an average over trials (i.e., each presentation of a given chirp stimulus is one trial). To compute signal correlations, spike count sequences were first randomly permuted based on the order of trials to obtain shuffled spike counts. Signal correlations were then computed on the shuffled spike counts using eq. [1] and were averaged over 50 independent realizations of the shuffling procedure. Noise correlations were computed as the correlation coefficient between the spike count residual sequences, which were obtained by averaging over trials and subtracting the mean spike count sequence from the spike counts for each trial (Metzen & Chacron, 2021). Thus, correlations were computed for each individual chirp stimulus.

For correlations at the population level, we divided the entire population into two subpopulations through partial sums: we summed the binary sequences $X_i(t)$ of 50% of the neurons in the entire population to form the first subpopulation and then the activities of the other 50% of the neurons to form the second subpopulation. Correlations were then computed as described above and error bands for signal and noise correlations were generated for 300 bootstrap samples of partial sums.

The single neuron PSTHs $R_i(t)$ were calculated by low-pass filtering the binary sequences $X_i(t)$ with a 10 ms boxcar window. The population PSTHs were obtained by summing the single neuron PSTHs $R_i(t)$ with either equal weights or unequal weights obtained through an evolutionary algorithm (described below):
equal - weight \( PSTM = \sum_{i=1}^{N} R_i(t) \) \[2\]
unequal - weight \( PSTM = \sum_{i=1}^{N} w_i R_i(t) \) \[3\]

where \( w_i \) is the weight of neuron \( i \). We note that, as the weights can be negative, the population PSTM obtained using unequal weights can also be negative. For each stimulus, the population PSTM of each trial was then normalized by the maximal value of that trial. The mean and standard deviation of the normalized population PSTHs across different trials were then obtained.

To quantify the similarity of mean responses of the population to different stimuli, we computed the inter-response distance (Aumentado-Armstrong et al., 2015):
\[
D(x, y) = \frac{\sqrt{<(x-y)^2>}}{\max\left(\frac{\max(x) - \min(x)}{\sqrt{2}}, \frac{\max(y) - \min(y)}{\sqrt{2}}\right)} \quad [4],
\]

where \( x \) and \( y \) are means of normalized population PSTHs across different trials of two different stimuli, \(<...>\) denotes an average over an evaluation window of 40 ms after chirp onset. For each stimulus, we calculated the inter-response distance of the stimulus to the rest of the stimuli individually, and then took the average to obtain the averaged distance to other stimuli for this stimulus. For boxplots in Fig.6c, the interquartile range (Q3=0.25, Q4=0.75) was taken to rule out stimuli whose averaged distances to other stimuli are either overly high or low, which hinder our comparisons.

To quantify the response variability of the population activities, we averaged the standard deviation of responses across different trials over all stimuli:
\[
RV = \sum_{i=1}^{n} \frac{\sigma(k_n)}{n} \quad [5],
\]

where \( \sigma(k_n) \) is the standard deviation of normalized population PSTHs across different trials of each stimulus and \( n \) is the number of stimuli. The response variability at each time point was normalized by the maximal value of variability across the entire evaluation time window. For boxplots in Fig.6d, the interquartile range (Q3=0.25, Q4=0.75) was taken to rule out times at which variability values are either overly high or low.
Classifier

We used a classifier to quantify the performance of ELL pyramidal cells at stimulus discrimination. We combined activities of individual neurons using either weighted or un-weighted sums for each chirp stimulus. For each chirp stimulus, the averaged population activity of all trials was chosen as a template. Next, each combined response was assigned as being generated by the stimulus that gave rise to a given template based on whether the distance between the combined response and the template was minimum. We thus constructed a “confusion matrix” whose element $(i, j)$ gives the probability that a response was assigned as being generated by stimulus $j$ given that it was actually generated by stimulus $i$ (Jamali et al., 2019; Jamali et al., 2016; Vonderschen & Chacron, 2011). The diagonal elements of this matrix are the probabilities that a stimulus was correctly assigned, whereas non-zero off-diagonal elements indicate misclassification. For each confusion matrix we computed the discrimination performance by averaging over the diagonal elements, as done previously (Jamali et al., 2019; Jamali et al., 2016; Metzen & Chacron, 2021; Vonderschen & Chacron, 2011). The discrimination performance can thus vary between 0 (no discrimination) and 1 (perfect discrimination). Note that the chance level for discrimination performance was 0.0625 (that is, 1/16) because we used a total of 16 different chirp stimuli. The distance between combined neuron activities was computed using the van Rossum metric (van Rossum, 2001). First, the combined neural activities were convolved with a decaying exponential kernel with time constant $\tau$:

$$f(t) = \sum_{i=1}^{M} H(t - t_i) e^{-\frac{(t-t_i)}{\tau}} \quad [6],$$

where $t_i$ is the $i^{th}$ spike time, $M$ is the total number of spikes and $H(t)$ is the Heaviside step function ($H(x) = 0$ if $x<0$ and $H(x) = 1$ if $x>=0$). The distance was then computed as the Euclidian distance between convolved combined neural activities $f_{Rj}$ and $f_{Rk}$:

$$D(f_{Rj}, f_{Rk}) = \sqrt{\frac{1}{\tau} \int \left[ f_{Rj} - f_{Rk} \right]^2 dt} \quad [7].$$

We varied $\tau$ between 1 and 100 ms to evaluate the effects of precise spike timing on classification. When $\tau$ is small, the metric takes into account spike timing whereas, when $\tau$ is larger, the metric takes into account slower changes in firing rate. If not specified otherwise, $\tau = 3$ ms was used.
Evolutionary Algorithm

In order to determine whether performing a weighted sum of neural response gave rise to better classification than an equal-weight sum, we trained an evolutionary algorithm (EA) using the population responses on a randomly selected 60% of trials for each chirp stimulus as a training dataset. We then measured the classification accuracy of the trained classifier on the entire dataset. We chose the recording session that contained the greatest number of neurons recorded simultaneously (n = 21).

Specifically, each neuron was assigned a weight $w_i$ which varies between -2 and 2 and the goal was to choose a set of weights that maximizes the performance of the classification algorithm described above. The EA is described in detail in a previous study by our group (Aumentado-Armstrong et al., 2015; Metzen & Chacron, 2021). Specifically, a set of weight vectors (i.e., “agents”) is allowed to evolve by minimizing a fitness function $F_{fit}$ over a series of iterations (i.e., “generations”). In keeping with the notation used in previous studies (Aumentado-Armstrong et al., 2015), we denote $X^r_k(i)$ as parameter $i$ for agent $r$ of generation $k$. First, the population of $K$ individuals is randomly initialized with weight values that are uniformly distributed with zero mean and restrained within [-2 2]. For each individual at every generation, a new individual is constructed by “differentiation”: the $r^{th}$ new parameter vector $X^r_{k,trial}$ is built by combining three other individuals $X^{r_1}_k$, $X^{r_2}_k$, and $X^{r_3}_k$, where $r_1 \neq r_2 \neq r_3$:

$$X^r_{k,trial} = X^r_k + \left( X^{r_2}_k - X^{r_3}_k \right) F, \ \forall \ r = 1, ..., N$$  \hspace{1cm} \text{[8]},

where the differential weight $F = 0.5$, and the three individuals are chosen based on a probability distribution that is preferentially weighted for more fit (i.e., lower fitness score) individuals:

$$p^r_k = \lambda \exp \left( \frac{-F_{fit}(X^r_k)}{\max_j(1-F_{fit}(X^j_k))} \right), \ \forall \ r = 1, ..., N$$  \hspace{1cm} \text{[9]},

where $\lambda$ is a normalization constant such that the sum of probability values is equal to one. Random mutations are then performed as follows:

$$X^r_{mut}(i) = \begin{cases} X^r_{k,trial}(i), & \text{if } u < CR \\ X^r_k(i), & \text{otherwise} \end{cases}, \ \forall \ r = 1, ..., N; i = 1, ..., D$$  \hspace{1cm} \text{[10]},

where $u$ is a random variable generated from a uniform distribution $U(0,1)$ and with crossover probability $CR = 0.9$. Selection is finally performed to produce the next generation via:
\[ X_{k+1}^r = \begin{cases} X_{mut}^r, & \text{if } F_{fit}(X_{mut}^r) < F_{fit}(X_k^r) \\ X_k^r, & \text{otherwise} \end{cases}, \forall r = 1, ..., N \quad [11]. \]

In this study, the fitness function for a given individual was defined as:

\[ F_{fit}(X_k^r) = 1 - DP_{X_k^r} \quad [12], \]

where \( DP_{X_k^r} \) is the discrimination performance estimated by computing the precision of events (i.e., spikes) of our neuronal population in response to our set of 16 chirp stimuli. The EA was terminated if the change in population discrimination performance was less than 0.0001 in 10 consecutive iterations. The algorithm was repeated 30 times, and each time a different set of weights was obtained because of different initial conditions and the randomness in generating new individual and mutations. The weights were normalized so that the sum of weights of all neurons equals to 1. The weights that gave rise to the best performance out of the 30 runs were used for Fig. 6 and 7. As mentioned above, this methodology is the same as that used previously for midbrain neurons (Metzen & Chacron, 2021), which allows for a direct comparison between these previous results and those obtained in the current study for hindbrain neurons. In general, we found significant correlations between weight magnitude and STA amplitude to noise stimulus for ON \((r=0.92, p=6.4*10^{-7})\) and OFF cells \((r=0.95, p=0.013)\).

Results

Previous studies have primarily focused on understanding how single electro-sensory neurons respond to chirp stimuli (Benda et al., 2006; Metzen et al., 2016) and used these recordings to study population coding (Marsat et al., 2009; Vonderschen & Chacron, 2011). However, a limitation is that, because the neural recordings were not performed simultaneously, the effects of noise correlations were not considered. Importantly, ELL pyramidal cells display correlations between their activities in the absence of stimulation (Hofmann & Chacron, 2017), which tend to give rise to noise correlations during stimulation (Chacron & Bastian, 2008; Simmonds & Chacron, 2015). Here, to investigate how correlations affect population coding of chirps by ELL pyramidal cell populations, we used multi-channel Neuropixels probes to record simultaneously the activities of multiple ELL pyramidal cells in response to chirp stimuli.
Experimental setup and example responses

Here we investigated how ELL pyramidal cell populations encode chirps with different attributes. During social interaction, interference between the EODs of two fish form a beat (i.e., a sinusoidal modulation in EOD amplitude; Fig. 1a, top left). Chirps consist of transient increases in the EOD frequency of one fish (i.e., the emitter fish) and will give rise to a transient modulation of the beat waveform as sensed by the receiver fish. Differences in the duration of the frequency increase, its excursion, and the beat phase at which the chirp occurs will thus give rise to different stimulus waveforms (Metzen, 2019). Fig. 1b shows three example chirp stimulus waveforms (top) as well as raster plots of ON and OFF cells (middle) and population peri-stimulus time histograms (population PSTHs; bottom) in response to each stimulus. We recorded the activities of multiple ELL pyramidal cells simultaneously using Neuropixels probes (Fig. 1a, right) in response to chirp stimuli that were delivered to the fish through a pair of electrodes located on either side of the fish (Fig. 1a, bottom left). We considered responses to chirps within a 40 ms time window that started 8 ms after chirp onset to account for transmission delays (see Methods).
Figure 1: Neuropixels probes were used to record extracellular activities of ELL pyramidal cells responding to chirps. (a) Left: Schematics demonstrating chirps stimuli used in the experiments and experimental set up. Right: recorded activities from example channels using Neuropixels probes with spikes of different neurons highlighted in colors. (b) Left: Stimulus waveform (top) consisting of a 5 Hz beat with a chirp (vertical red dashed line), raster plot of ON and OFF cells (middle), and the mean and standard deviation (shaded areas) of normalized population PSTHs across different trials (see Methods) (bottom) for chirp with 30Hz excursion frequency at 0° of beat phase. The grey rectangle indicates the 40ms chirp evaluation time window. Middle: Same plots for chirp with 30Hz excursion frequency at 180° of beat phase. Right: Same plots for chirp with 60Hz excursion frequency at 180° of beat phase.
**Signal but not noise correlations vary with distance and stimuli**

As previous studies have shown that the correlation structure (i.e., the relationship between signal and noise correlations) strongly impacts population coding (Averbeck et al., 2006), including in ELL pyramidal cells but for stimuli other than those considered here (Chacron & Bastian, 2008; Hofmann & Chacron, 2018), we first investigated signal and noise correlations between ELL pyramidal cell pairs during chirp stimulation. Signal correlations represent similarities between the mean responses of two neurons to a given stimulus (Fig. 2a, left), while noise correlations are instead correlations between the trial-to-trial variabilities of neural responses to repeated presentations of a given stimulus and arise due to shared noisy synaptic inputs (Fig. 2a, right).

We found that ELL pyramidal cells displayed both signal and noise correlations in their activities in response to chirp stimuli. Specifically, signal correlations of same-type (i.e., pairs containing either ON cells or OFF cells) and opposite-type pairs (i.e., pairs containing both ON and OFF cells) were on average positive and negative respectively (Fig. 2b, compare top and bottom panels). In contrast, noise correlations were similarly distributed around 0 for both same-type and opposite-type pairs (Fig. 2c, compare top and bottom panels). Interestingly, for same-type pairs, signal correlations first decreased and then increased with increasing distance between the probe sites on which both neurons were recorded (Fig. 2b top, from 0 to 550 µm: linear regression, $r=-0.74$, $p=0.011$; from 400 to 1000 µm: linear regression, $r=0.91$, $p=4.2\times10^{-3}$). For opposite-type pairs, the opposite trend was observed in that signal correlation first increased and then decreased with increasing distance (Fig. 2b bottom, from 0 to 550 µm: linear regression, $r=0.66$, $p=0.030$; from 400 to 1000 µm: linear regression, $r=-0.81$, $p=8.3\times10^{-3}$). However, noise correlations were largely independent of distance for both same-type and opposite-type pairs (Fig. 2c, same-type pairs: linear regression, $r=0.020$, $p=0.96$; opposite type pairs: linear regression, $r=0.42$, $p=0.10$).
Figure 2: Signal but not noise correlations varied with distance. (a) Schematics showing how signal and noise correlations arise. While signal correlation arises from similarity in mean responses to stimuli (left), noise correlation instead arises from shared noisy synaptic inputs (right). (b) Top: Signal correlations of same-type pairs (i.e., pairs of either ON or OFF cells) as a function of distance (blue dots) for all chirp stimuli used. Distance was discretized into 20 bins (50 microns per bin) and signal correlations for pairs that fall within the same bin were averaged (black dots, error bars indicate standard deviation). Signal correlations first decreased and then increased with distance (from 0 to 550 microns: linear regression, \( r=-0.74, p=0.011 \); from 400 to 1000 microns: linear regression, \( r=0.91, p=4.2 \times 10^{-5} \)). Bottom: Signal correlations of opposite-type pairs (i.e., pairs containing one ON and one OFF cell) as a function of distance (red dots). Signal correlations first increased and then decreased with distance when the data was averaged within bins (from 0 to 550 microns: linear regression, \( r=0.66, p=0.030 \); from 400 to 1000 microns: linear regression, \( r=-0.81, p=8.3 \times 10^{-4} \)). We note that qualitatively similar results were obtained when performing linear regression on the data directly before averaging (same type: from 0 to 550 microns: linear regression, \( r=-0.26, p=4.7 \times 10^{-37} \); from 400 to 1000 microns: linear regression, \( r=-0.34, p=2.8 \times 10^{-26} \); opposite type: from 0 to 550 microns: linear regression, \( r=0.18, p=2.2 \times 10^{-13} \); from 400 to 1000 microns: linear regression, \( r=-0.32, p=2.0 \times 10^{-14} \). (c) Top: Same as (b), but for noise correlations. There was no significant correlation between noise correlations and distance for both same-type pairs and opposite-type pairs (same-type pairs: linear regression, \( r=0.020, p=0.96 \); opposite type pairs: linear regression, \( r=0.42, p=0.10 \)). When performing a linear regression on the data without averaging, we found a negligible but significant relationship between noise correlations and distance both for same type pairs (slope=\(-1.3 \times 10^{-5} \), \( r=-0.045, p=0.014 \)) and for opposite type pairs (slope=\(2.5 \times 10^{-5} \), \( r=0.096, p=2.2 \times 10^{-5} \)). In panels b and c, correlation coefficient values that were deemed non-significant at the \( p=0.05 \) level using the function “corrcoeff” in Matlab are plotted in green.

Next, we looked at whether and, if so, how signal and noise correlations varied as a function of the different chirp stimulus waveforms used in this study. We found that for the population with only ON cells, the distributions of signal and noise correlations were significantly different from one another for different chirps (Fig.3a left, Friedman’s test, \( p=4.0 \times 10^{-44} \); Fig.3b left, Friedman’s test, \( p=0.020 \)). However, for the population with both ON and OFF cells, while the distributions of signal correlation were significantly different (Fig. 3a right, Friedman’s test, \( p=1.1 \times 10^{-16} \)), noise correlation distributions did not change significantly (Fig. 3b right, Friedman’s test, \( p=0.17 \)). Furthermore, we noticed that noise and signal correlations were not independent of each other. The signal and noise correlations of ON-ON pairs and all pairs are shown in Fig. 3c and, overall, there were positive but weak correlations between signal and noise correlations for both cases (Fig. 3c left, linear regression, \( r=0.060, p=1.3 \times 10^{-3} \); Fig.3c right, linear regression, \( r=0.11, p=6.0 \times 10^{-15} \)). Thus, our results at this stage show that while signal correlations were strongly dependent on distance and chirp stimulus waveform, this was not the case for noise correlations.
Decoding ELL pyramidal cells activities with equal-weight sum and weighted sum

We next quantified the performance of a classifier at correctly discriminating between neural responses generated by a given chirp stimulus waveforms (see Methods). In short, neural activities of all neurons were combined in different manners to obtain the population activity. The population activities obtained in response to different chirp waveforms were then compared across different stimulus trials using the van Rossum metric (van Rossum, 2001). Thus, a given population activity was assigned as being generated by a certain stimulus $i$ if the distance between this activity and the chosen template for stimulus $i$ was lower than all other distances computed using chosen templates for other stimuli (see Methods). In practice, the trial-averaged population activities were chosen as templates. The performance of the classifier is represented by a confusion matrix where each entry $(i,j)$ is the probability that a response which was actually generated by stimulus $i$ is classified as generated by stimulus $j$. As such, the diagonal elements of the confusion matrix give the amount of correct classification whereas the off-diagonal elements instead give the amount of incorrect classification.

First, we combined the neural activities by performing a linear sum giving the same weight to each neuron (Fig. 4a). To quantify the effects of noise correlations, the performance of the classifier was evaluated on the neural responses as well as neural responses that were randomly shuffled with respect to trial order (see Methods). Performances obtained with and without noise correlations were significantly above chance level (with noise correlations, one-sample t-test,
p=3.9*10^{-50}; without noise correlations, one-sample t-test, p=1.5*10^{-54}). We quantified the effect of timescale of encoding used in the van Rossum metric on the performance. This is important as small timescales put more emphasis on precise spike timing whereas larger timescales instead place more emphasis on slower variations in the firing rate (van Rossum, 2001). We found that maximal performance was observed using a timescale of ~3ms (Fig. 4b left), indicating that precise spike timing can be used to reliably discriminate between different chirp stimulus waveforms. The performance when noise correlations were removed was higher than that obtained for the raw data (Fig. 4b right, one-way ANOVA, p=1.3*10^{-4}), indicating that noise correlations have a detrimental effect on discrimination performance. Next, we analyzed how discrimination performance varied as a function of population size. We separated the entire population into ON cells and OFF cells and increased the population size by adding either ON cells or OFF cells first. We found that when increasing population size by first adding the ON cells, the performance increased when ON cells only were first considered and actually decreased when OFF cells were added to the pool (Fig. 4c). Interestingly, when increasing population size by first adding the OFF cells, the performance started with low values and increased slowly, but later increased drastically when ON cells were added (Fig. 4d). We found that ON cell populations had much better performance than OFF cell populations (Fig. 4d inset, one-way ANOVA, p=1.0*10^{-66}). These results were consistent with the previous findings that single ON cells instead of single OFF cells better respond to chirps (Marsat & Maler, 2010).
Figure 4: Discrimination performances of population activities when using an equal-weight sum to combine neural activities. (a) Schematics showing how the responses of ELL pyramidal cells were summed with equal weights. (b) Left top: Confusion matrices where each entry is the probability of a stimulus $i$ predicted as stimulus $j$ (prediction based on distance between neural responses quantified by van Rossum metric with timescale $\tau$, see Methods for details) for a population of 21 neurons consisting of 16 ON cells and 5 OFF cells with $\tau = 1, 3$ and 100ms. Left bottom: Discrimination performance as a function of $\tau$. The shaded areas represent standard deviation when using 30 different sub-trials (60% of all trials), and same for (c) and (d). The range of $\tau$ values for which performance was higher than 90% of the maximum is 6ms. Right: Boxplots showing that equal-weight sum of neural activities without noise correlations (right) had better performance than that with noise correlations (left; one-way ANOVA, $p=1.3*10^{-4}$). (c) The effect of population size on discrimination performance. ON cells were first considered before OFF cells. Top: Confusion matrices for populations of 1 ON cell, 11 ON cells, and all cells (16 ON cells and 5 OFF cells) with $\tau = 3$ms. Bottom: Discrimination performance as a function of population size. (d) Same as (c) but OFF cells were first considered before ON cells. Top: Confusion matrices for populations of 1 OFF cell, 5 OFF cells, and all cells (16 ON cells and 5 OFF cells) with $\tau = 3$ms. Bottom: Discrimination performance as a function of population size. Inset: Boxplot showing that 5 ON cells had better performance than 5 OFF cells (one-way ANOVA, $p=1.0*10^{-66}$).
Next, we combined the neural activities of all neurons using a weighted sum (i.e., a sum with unequal weights) (Fig. 5a). To find the weights that give rise to the best discrimination performance, we used an evolutionary algorithm (see Methods; Fig. 5a). The effect of timescale of encoding on performance was similar as in the case of the equal-weight sum (Fig. 5b left). Overall, the performance improved significantly when performing a weighted sum as compared to that obtained with equal-weight sum with and without noise correlations (Fig. 5b right top, equal-weight with noise correlations vs. weighted with noise correlations, one-way ANOVA, p=1.1*10^{-39}; equal-weight without noise correlations vs. weighted without noise correlations, one-way ANOVA, p=8.7*10^{-19}). Weight distributions for ON and OFF cells were largely mirror images of one-another (Fig. 5b right bottom, ON cells: mean=0.12, std=0.16; OFF cells: mean=-0.19, std=0.15) and were significantly different (two-sample Kolmogorov-Smirnov test, p=9.0*10^{-62}). Further, we noticed that, unlike the equal-weight case, noise correlations were actually beneficial as removing them significantly reduced performance (Fig. 5b right, weighted with noise correlations vs. weighted without noise correlations, one-way ANOVA, p=5.3*10^{-19}).

For the effect of population size on performance, adding OFF cells to the ON cells population did not decrease the performance (Fig. 5c), in contrast to the equal-weight case (Fig. 4c); however, a population with only OFF cells still had a poor performance in the weighted case (Fig. 5d). It is important to note that population consisting of only ON cells displayed much better performance in the weighted case than in the equal-weighted case (compare Figs. 5c and 4c). As such, the improvement in performance is not due to considering both ON and OFF cells with opposite weights. Rather, such improvement is largely due to heterogeneities within the ON cell population.
after variability in their responses. Sums were confirmed only when weighted by the taking of different simulations of the evolutionary algorithm (30 in total), and same for (c) and (d). The range of values for which performance was higher than 90% of the maximum is 5.3 ms, which is similar to that obtained in the equal-weighted case (Fig.4b). Right top: Boxplots showing that weighted sums of neural activities improved performance for both with and without noise correlations (with noise correlations, one-way ANOVA, p=1.1*10^{-9}; without noise correlations, one-way ANOVA, p=8.7*10^{-19}); also, equal-weight sum of neural activities without noise correlations had better performance than those with noise correlations (one-way ANOVA, p=1.3*10^{-4}), while weighted sum of neural activities with noise correlations had better performance than those without noise correlations (one-way ANOVA, p=5.3*10^{-19}). Right bottom: The probability distributions of weights assigned for different neurons. The weights were generated by an evolutionary algorithm. If the weights generated gave a better performance, they replaced the previous weights; if the weights generated didn’t improve the performance for 10 iterations (performance maximized), the evolutionary algorithm was terminated (see Methods for details). (b) Left Top: Confusion matrices where each entry is the probability of a stimulus i predicted as stimulus j (prediction based on the distance between neural responses quantified by van Rossum metric with timescale $\tau$, see Methods for details) for a population of 21 neurons consisting of 16 ON and 5 OFF cells with $\tau = 1$, 3 and 100ms. Left Bottom: Discrimination performance as a function of $\tau$. The shaded areas represent standard deviation of performance from different simulations of the evolutionary algorithm (30 in total), and same for (c) and (d). The range of $\tau$ values for which performance was higher than 90% of the maximum is 5.3 ms, which is similar to that obtained in the equal-weighted case (Fig.4b). Right top: Boxplots showing that weighted sums of neural activities improved performance for both with and without noise correlations (with noise correlations, one-way ANOVA, p=1.1*10^{-9}; without noise correlations, one-way ANOVA, p=8.7*10^{-19}); also, equal-weight sum of neural activities without noise correlations had better performance than those with noise correlations (one-way ANOVA, p=1.3*10^{-4}), while weighted sum of neural activities with noise correlations had better performance than those without noise correlations (one-way ANOVA, p=5.3*10^{-19}). Right bottom: The probability distributions of weights assigned to ON cells and OFF cells over 30 runs of the evolutionary algorithm. (c) The effect of population size on discrimination performance. ON cells were first considered before OFF cells. Top: Confusion matrices for populations of 1 ON cell, 11 ON cells, and all cells (16 ON cells and 5 OFF cells) with $\tau = 3$ms. Bottom: Discrimination performance as a function of population size. (d) Same as (c) but now OFF cells were first considered before ON cells. Top: Confusion matrices for populations of 1 OFF cell, 5 OFF cells, and all cells (16 ON cells and 5 OFF cells) with $\tau = 3$ms. Bottom: Discrimination performance as a function of population size.

Why is there an overall performance increase when using a weighted sum vs. an unweighted sum? Intuitively, increases in performance can occur when the set of responses elicited by different stimuli become more distant from one another and thus more discriminable. However, increases in performance can also occur if the size of these sets decreases (Fig. 6a). Fig. 6b shows three example stimulus waveforms (left top panel) as well as population PSTHs when taking equal-weight (left middle panel) and weighted (left bottom panel) sums. It was seen that the population activities were more different from each other (see dashed rectangle) when taking weighted sums, partly because a weighted sum with both positive and negative weights can lead to negative population activities while population activities obtained with equal-weight sum can only be positive by definition. Quantification of the distance between responses (see Methods) confirmed that greater values were obtained when considering weighted sums than equal-weight sums (Fig. 6c, one-way ANOVA, p=4.5*10^{-4}). We next tested whether weighted neural responses were less variable than their equal-weight counterparts. To do so, we quantified the variability in the response using both weighted and equal-weight sums, as well as before and after removing noise correlations (see Methods). We found that weighted sums reduced overall
variability of neural activities, both with and without noise correlations (Fig. 6d, equal-weight with noise correlations vs weighted with noise correlations, one-way ANOVA, $p=3.9 \times 10^{-29}$; equal-weight without noise correlations vs weighted without noise correlations, one-way ANOVA, $p=3.4 \times 10^{-17}$). We also noticed that removing noise correlations reduced overall variability in the equal-weight case and increased overall variability in the weighted case (Fig. 6d, equal-weight with noise correlations vs equal-weight without noise correlations, one-way ANOVA, $p=3.1 \times 10^{-9}$; weighted with noise correlations vs weighted without noise correlations, one-way ANOVA, $p=0.040$).
Weighted sums of ELL pyramidal cells activities eliminate redundancy and introduce synergy

Why is the performance greater for weighted sums before removing noise correlations? Previous theoretical studies have shown that noise correlations can be beneficial to information transmission when their sign is opposite to that of signal correlations (Averbeck et al., 2006). In order to study the correlation structures at a population level beyond two neurons, we combined the activities of subsets of neurons. Specifically, we divided our dataset into two subpopulations and considered correlations between the summed (either equal-weight or weighted) activities of both subpopulations (Franke et al., 2016) (see Methods). We found that, for equal-weight, signal and noise correlations were both predominantly positive (Fig. 7a, 78.3% of points in upper-right quadrant). However, this was much less the case for weighted sums, as more data points with signal and noise correlations having the opposite signs were observed (Fig. 7b, number of points in upper-left quadrant increased from 18.4% to 34.5%, while number of points in upper-right quadrant decreased from 78.3% to 61.0%). These findings thus confirm our hypothesis and explain why removing noise correlations led to lower performance when considering equal-weight sums but instead led to increased performance when considering weighted sums.

Figure 6: Weighted sums maximized the performance by increasing distances between trials-averaged responses to different stimuli and reducing trial-to-trial variability. (a) Schematics showing that weighted sums of neural activities maximize the performance by increasing the inter-response distance (i.e., distances between trials-averaged responses to different stimuli) and reducing response variability. (b) Top: Three example chirp stimuli. The waveforms are shifted to the right by 8ms to account for the common synaptic delay of chirp responses. Middle and bottom: The means and standard deviations (shaded areas) of normalized population PSTHs across different trials of the example chirp stimuli under equal-weight and weighted sum. Horizontal dashed line indicates zero. Dashed squares indicate that responses to different stimuli under weighted sum are more different from each other compared to responses under equal-weight sum. (c) Boxplots showing that weighted sums of neural activities had higher inter-response distance than equal-weight sums of neural activities (one-way ANOVA, p=4.5*10^{-4}). (d) Boxplots showing that weighted sums of neural activities had lower response variability than equal-weight sums of neural activities (with noise correlations, one-way ANOVA, p=3.9*10^{-29}; without noise correlations, one-way ANOVA, p=3.4*10^{-17}); also, equal-weight sums of neural activities without noise correlations had lower response variability than equal-weight sums with noise correlations (one-way ANOVA, p=3.1*10^{9}) while weighted sums of neural activities without noise correlations had higher response variability than weighted sums with noise correlations (one-way ANOVA, p=0.040).
Discussion

Summary of results

In this study, we investigated for the first time how ELL pyramidal cell populations encode natural electro-communication stimuli by simultaneously recording the activities of multiple
neurons. We first demonstrated that the activities of ELL pyramidal cells were correlated pairwise under chirp stimulation. Specifically, while signal correlations varied as a function of the physical distance between recording probe sites as well as stimulus waveform, noise correlations were instead largely independent of both distance and stimulus waveform. There was furthermore a positive relationship between signal and noise correlations. We next quantified the performance of a classifier at correctly discriminating which stimulus waveform was presented based on the combined neural activities of ELL pyramidal cells. When the activities were combined using an equal-weight sum, we found that ON cells have better discrimination performance than OFF cells with a combined (ON and OFF cells) correct discrimination performance around 75%. Noise correlations were overall detrimental to discrimination performance as their removal increased performance. When instead considering weighted sums and using an evolutionary algorithm to optimize the weights, we found increased performance up to 85%. Interestingly, noise correlations were then beneficial as removing them decreased performance. Further analysis revealed that the improved performance by weighted sum was the result of maximizing distance between trial-averaged responses to different chirp stimuli and minimizing overall variability. By considering correlations between the activities of subpopulations, we found that signal and noise correlations tended to have the same sign when considering equal-weight sums, which is detrimental to discrimination. In contrast, signal and noise correlations with opposite signs became relatively more dominant when considering weighted sums, which is beneficial to discrimination. Our results thus showed that ELL pyramidal cells display significant correlations in their activities during chirp stimulation that can be either beneficial or detrimental to discriminability depending on how these activities are decoded by downstream brain areas.

**Large-scale in-vivo electrophysiology in weakly electric fish**

To date, most studies of sensory processing in the electrosensory system in weakly electric fish were done using single-unit recordings. There were studies which investigated correlations of neurons in the electrosensory system using simultaneous recording with multiple electrodes (Chacron & Bastian, 2008; Hofmann & Chacron, 2017; Litwin-Kumar et al., 2012). However, only a few neurons can be recorded simultaneously in one experiment with this technique, and
the effect of population size on information coding cannot be quantified. Also, the dependence of correlations on distance between neuron pairs cannot be measured. In this project, we demonstrated that Neuropixels probes can be used to record activities of neuronal populations in the hindbrain without damaging the brain tissues, while other multielectrodes arrays which were designed to be used in animals with larger brains might cause considerable damages and bleeding to the fish brain. By using the Neuropixels probes, we were able to record from more than 20 neurons simultaneously, and the distance between these neurons can be estimated by the relative distance between the recording channels. Future studies can utilize Neuropixels probes to simultaneously record from neurons across different layers (superficial, intermediate and deep) and sensory maps (LS, CLS and CMS) of ELL. This would make the quantification of correlations within and across different layers/maps possible and help elucidate how heterogeneities of ELL neurons contribute to population coding.

**Origins of signal and noise correlations**

Our results have shown that signal correlation magnitude first decreased with distance then increased. While the decrease can be explained by increasing dissimilarity in the receptive fields of neurons with increasing distance, the increase of signal correlations as the distance further increased is more puzzling. One possible explanation is that descending inputs from higher brain areas (i.e., feedback) modulate chirp responses to increase signal correlations. Indeed, ELL pyramidal cells receive abundant feedback consisting of both topographic and diffuse sources (Hofmann & Chacron, 2019). In particular, diffuse feedback was shown to affect signal correlations in ELL pyramidal cells to beat stimuli (Simmonds & Chacron, 2015) and enhance single neuron responses to chirps (Marsat & Maler, 2012). Such feedback originates from cerebellar granule cells, which make the ELL a cerebellum-like structure (Bell et al., 2008). As such feedback originates from afferent inputs located far away from the cell within the non-classical receptive field (Chacron et al., 2003; Chacron et al., 2005b), we hypothesize that this might explain the increase in signal correlations observed for larger distances. Alternatively, the decrease and increase in signal correlations could be due to the fact that the recording probe went across different maps of ELL, from the lateral segment (LS) into the central lateral segment
(CLS) thereby recording from cells in different segments that receive similar feedforward inputs from electroreceptor afferents. Further studies are needed to test these predictions.

In contrast, our results showed that noise correlations were invariant as the physical distance between neurons increased. These observations agree with previous findings in the visual cortex that noise correlations do not depend on the contact distance (Hansen et al., 2012). In general, noise correlations can arise from both bottom-up and top-down inputs as well as recurrent connections (Doiron et al., 2016). The amount of common inputs from electroreceptive afferents to ELL pyramidal cells decreases as the distance between neurons increases (Chacron & Bastian, 2008; Hofmann & Chacron, 2017). Thus, if noise correlations were caused by common feedforward inputs, they would likely decay as distance between neurons increases. Therefore, it is likely that the descending inputs from cerebellar granule cells mentioned above strongly contribute to shaping noise correlations during chirp stimulation. Indeed, previous studies have shown that feedback can modulate noise correlations in response to beat stimuli (Simmonds & Chacron, 2015). The fact that a previous study of cerebellum found that parallel fibers can synchronize neural activities and no difference in correlations was found across pairs with different distance (Vos et al., 1999) is consistent with our hypothesis.

**Population coding of natural communication stimuli: Comparisons within the electroreceptive system**

Our study investigated the population coding of chirp stimuli in the ELL, which is the first stage in the brain for processing electroreceptive stimuli. A recent study by Metzen and Chacron (2021) which also utilized Neuropixels probes investigated the population coding of chirp stimuli in the midbrain structure TS, which receive direct synaptic projections from ELL pyramidal cells. By comparing this study with ours, we noted that noise correlations of neurons in ELL and TS in response to chirp stimuli have similar structures – they do not depend on the distance between neurons and are invariant across different chirp waveforms. Also, in both areas, noise correlations are detrimental to discrimination performance when neural activities are combined with equal-weight sum. Both ELL and TS have highly heterogenous neuronal populations: ELL pyramidal cells can be classified into ON and OFF cells, and TS neurons can be loosely classified based on their responses to chirp stimuli – for example, there are “chirp responders”
which selectively respond to chirps but not beats, “beat responders” which respond to the beats and the perturbation of beat, and “beat-chirp responders” which respond to both beats and chirp (Metzen & Chacron, 2021). In ELL, we found that ON cells contribute more to the discrimination performance of chirp stimuli than OFF cells. This is not surprising because previous studies have shown that individual ON cells respond better to the chirp stimuli than individual OFF cells (Marsat et al., 2009). In TS, surprisingly, the “beat responders” instead of the “chirp responders” are the ones that contribute the most to the discrimination performance of the chirp stimuli (Metzen & Chacron, 2021). The “chirp responders”, while being less informative, were shown to invariantly represent chirp stimuli (Metzen et al., 2016; Vonderschen & Chacron, 2011). The “beat responders” and “beat-chirp responders” in TS behave like ELL pyramidal cells in terms of their responses to chirps. Therefore, we hypothesize that these neurons in TS inherit the chirp discriminability of ELL pyramidal cells, forming a pathway for estimating different chirp stimuli, while the “chirp responder” form another parallel pathway that is responsible for chirp detections.

**Effects of noise correlations on population coding**

In this study, we demonstrated that noise correlations were beneficial for population coding when the neural activities were combined using weighted sums. The beneficial effect of noise correlations was observed both theoretically (e.g., Ecker et al. (2011), da Silveira and Berry (2014)) and experimentally in other sensory systems, (e.g., the visual system: Franke et al. (2016)). The modulations of noise correlations under different stimuli (i.e., correlation plasticity) was also shown to affect coding performance (Franke et al., 2016). In the electrosensory system, the plasticity of noise correlations due to different stimulations was observed, e.g., local stimuli increase noise correlations while global stimuli decrease noise correlations (Chacron & Bastian, 2008). In our study, the plasticity of noise correlation was not observed for different chirp waveforms. However, most of the cells recorded in this study were superficial cells (i.e., those with relatively low baseline firing rate). Deep cell (i.e., those that have relatively higher baseline firing rate) receive little descending feedback compared to intermediate and superficial cells (Bastian & Bratton, 1990), and therefore can have different correlation structures. Noise correlations between deep cells and cells across different layers might be more plastic than the ones we quantified using mostly superficial cells, and future
studies are required to verify this prediction. Furthermore, we noted that the effect of noise correlations on discrimination performance was dependent on the decoders we used to combine the neural activities: While noise correlations were detrimental for the equal-weight sum of neural activities, a weighted sum can instead make noise correlations synergistic. The decoder-dependent effect of noise correlation on coding performance was found previously in other studies too (Moreno-Bote et al., 2014; Romo et al., 2003).

**Optimized decoding of ELL pyramidal cells activities**

Our results showed that a weighted sum of neural activities can improve discrimination performance, which was due in part to synergistic effects of noise correlations. These findings agreed with the previous studies showing that, rather than averaging neuronal responses by weighting them equally, weighting neurons differently can provide more information (Butts & Goldman, 2006; Jazayeri & Movshon, 2006; Marsat, 2019). In this case, the weights were generated using an evolutionary algorithm to maximize the discrimination performance of electro-communication stimuli. We note that such “combinatorial codes” can recover much more information about the stimulus and are thus advantageous (L.F. Abbott & P. Dayan, 1999; Liu et al., 2013; Osborne et al., 2008; Pitkow et al., 2015; Reich et al., 2001; Sanger, 1996; Seung & Sompolinsky, 1993). In general, the amount of information extracted by the algorithm was an upper-bound. However, it is unclear how such weights can be assigned physiologically. Possible biological implementations of neural decoding with weighted sums have been investigated in previous studies (Berkowitz & Sharpee, 2019; Lewis & Kristan, 1998). For example, a model of population decoding with weights determined by the activity levels of upstream neurons can well capture the experimentally observed behaviours (Lewis & Kristan, 1998). In the electrosensory system, midbrain neurons of *torus semicircularis* in general integrate synaptic inputs from both ON- and OFF-type ELL pyramidal cells although the relative proportion varies greatly across individual neurons (McGillivray et al., 2012). How these midbrain neurons discriminate between ON and OFF cells and assign synaptic weights accordingly requires further investigation. While a recent study showing that some midbrain neurons can reliably discriminate between different chirp stimulus waveforms (Metzen & Chacron, 2021) provides support for the hypothesis that TS
neurons respond to a weighted sum of ELL inputs, further investigation is needed to fully test this hypothesis, and, if true, determine how these weights are assigned.

Our results showed that ELL pyramidal cell populations can discriminate between chirps occurring at different phases of the beat. This is consistent with previous results showing good discriminability in peripheral electroreceptor afferents (Walz et al., 2014) as these faithfully follow the detailed time course of the chirp stimulus (Metzen et al., 2016, 2020). In general, phase discriminability decreases at the single neuron level relative to that of afferents when considering single ELL pyramidal cells (Allen & Marsat, 2018; Metzen et al., 2016, 2020). Our results showed that considering correlations between ELL pyramidal neuron activity can improve discriminability in the unequal-weighted case. Finally, we note that previous studies have shown other types of synergistic neural codes based on synchrony in both afferents (Benda et al., 2006; Grewe et al., 2017) and ELL pyramidal cells (Middleton et al., 2009). While behavioral studies have shown that fish can detect chirps with different attributes (Allen & Marsat, 2018; Metzen et al., 2016, 2020), whether fish can discriminate between different chirp stimulus waveforms remains unknown as the behavioral responses were mostly invariant (i.e. the same) when varying chirp attributes such as amplitude, duration, and the phase of the beat at which the chirp occurs at (Metzen et al., 2016, 2020).

It is also important to note that our study focused on natural electrocommunication signals termed Type II chirps (i.e., “small chirps”) that tend to occur on top of low frequency beats (Bastian et al., 2001; Zakon et al., 2002). There are other types of electrocommunication signals with different characteristics, e.g., Type I chirps (i.e., “big chirps”) that instead tend to occur on top of high frequency beats (Bastian et al., 2001). Interestingly, recent studies have shown that small chirps can also occur on top of high frequency beats (Henninger et al., 2018). Moreover, a previous study that considered population coding of both small and big chirps but did not consider the effects of noise correlations has found results qualitatively similar to our own when varying the timescale of encoding (Marsat & Maler, 2010). Further studies are needed to understand how correlations influence coding of big chirps as well as small chirps occurring on top of higher frequency beats by ELL pyramidal cell populations. Moreover, future studies should consider other behaviorally relevant stimulus classes (e.g., prey). We also note that the
stimulation protocol using two electrodes on each side of the animal gives rise to stimulation patterns that are more homogeneous than those typically encountered during social interactions (Kelly et al., 2008). Future studies should consider such patterns of stimulation when studying sensory processing by neural populations.

**Discrimination vs invariance**

There has been an ongoing debate in terms of whether chirp stimuli can be well discriminated in the ELL. On the one hand, some studies showed that chirp stimuli can be discriminated by ELL pyramidal cells when only the frequency excursion and duration of the chirps are varied, but cannot be well discriminated when they are allowed to occur at different phases (Allen & Marsat, 2018; Marsat & Maler, 2010). However, on the other hand, another study showed that ELL pyramidal cells can discriminate chirp stimuli with varying phases (Vonderschen & Chacron, 2011). There are two shortcomings with these previous studies: First, the activities of different neurons were only summed linearly, i.e., using equal weights; second, the activities of different neurons were collected using non-simultaneous recordings, so noise correlations were not considered. Our study showed that there were noise correlations between ELL pyramidal cells in response to chirp stimulations, and when combined with a weighted sum, the neural activities can well discriminate different chirp stimuli due in part to the beneficial effect of noise correlations. Therefore, our results demonstrated that the information about different chirp stimuli is available to and can potentially be used by the fish.

In addition to discrimination, the invariance coding of chirps was also studied. Studies showed that neural representations of chirp stimuli became more invariant from peripheral to downstream brain areas in the electrosensory system (Metzen & Chacron, 2017; Metzen et al., 2016, 2020). Furthermore, these studies also showed that the behavioral responses to chirps, i.e., the “echo response”, were highly invariant in terms of frequency excursion, duration, and different phases. However, these results did not imply that the fish cannot discriminate between different chirps. Previous studies showed that both sparse neurons, which respond to chirp stimuli invariantly, and dense neurons, which respond to chirp stimuli differentially therefore enabling chirps discrimination, exist in the midbrain TS (M. K. J. Sproule et al., 2015; Vonderschen & Chacron, 2011). The dense neurons inherit the discriminability of ELL
pyramidal cells, suggesting that discriminability does not just stay upstream, but is passed down to downstream neurons and can be potentially utilized by the fish. The existence of both sparse and dense neurons in midbrain TS strongly suggests the existence of parallel pathways for detecting and estimating chirp stimuli. Our results, together with results from a recent study showing that population activities of midbrain TS neurons transmit information that enable chirps discrimination (Metzen & Chacron, 2021), further demonstrate the possibility that such parallel pathways exist.

**Implications for other systems**

Previous studies have shown that the electrosensory system processes information similarly to other sensory systems (e.g., contrast coding (Clarke et al., 2015), sensory adaptation (Huang et al., 2019)). Sensory processing of natural communication stimuli has been widely studied in other animals (e.g., songbirds (Narayan et al., 2006; Woolley et al., 2006), grasshoppers (Creutzig et al., 2009; Machens et al., 2001), the grassfrog (Epping & Eggermont, 1986)). We note that there are also similarities between the electrosensory system and other systems in terms of sensory processing of communication stimuli: For example, the midbrain torus semicircularis in the grassfrog contains neurons that selectively respond to natural mating calls (Epping & Eggermont, 1986), while in the torus semicircularis of weakly electric fish A. leptorhynchus, neurons selectively respond to chirps were also found (Metzen & Chacron, 2021). Therefore, we predict that our results are applicable to population coding of communication stimuli in other systems.

Our results further demonstrated the ON-OFF asymmetry of ELL pyramidal cells in terms of chirp discrimination. Previous studies showed symmetry between ON and OFF pyramidal cells in terms of their responses to different chirps (i.e., ON cells increase their firing rates while OFF cells decrease their firing rates in response to increases in stimulus amplitude) (Clarke et al., 2015; Metzen et al., 2016). While the chirp stimuli we delivered contained equally phases that ON cells prefer and those that OFF cells prefer, ON cells still perform much better than OFF cells in discriminating different chirps, which is in agreement with previous studies (Marsat et al., 2009). Since we only used chirps with four different phases, future studies of chirp stimuli with more phases used can be done to further confirm an asymmetry in coding of chirp stimuli.
by ON and OFF type cells. ON and OFF type cells are found in other sensory modalities (e.g., visual (Gjorgjieva et al., 2014; Wassle et al., 1981), auditory (He, 2001), olfactory (Chalasani et al., 2007)). Other types of ON-OFF asymmetries have also been found previously in the visual system (de Monasterio, 1979; Freed, 2017; Jiang et al., 2015; Leonhardt et al., 2016). Our results thus add further evidence supporting the hypothesis that ON-OFF asymmetries are general property across different sensory modalities.

Methodologically, we used an evolutionary algorithm that runs iteratively to find weights that maximize discrimination performance, as was done recently for midbrain neurons (Metzen & Chacron, 2021). The same algorithm was used previously to optimize model parameters (Aumentado-Armstrong et al., 2015). The algorithm takes both spike timing and firing rate into account, therefore extracts information in not only the spike counts but the structures of spike trains. This algorithm can be easily adapted to analyze activities of neurons in other systems and help determine the upper-bound of information that the spiking activities of neurons can carry. We note that a similar approach was also used to optimize weights to maximize discriminability (Marsat, 2019).

**Final Remarks**

In this study, through analysis of simultaneous recordings of the ELL pyramidal cells population activities, we obtained three key understandings about the population coding of natural communication stimuli by the hindbrain electrosensory neurons: (1) There are noise correlations between the ELL pyramidal cells’ responses to communication stimuli. (2) The population activities of ELL pyramidal cells can be decoded using a weighted sum to well discriminate the communication stimuli with different attributes. (3) Noise correlations are beneficial when using such weighted sum to decode the population activities. Our study is among the first to elucidate the effect of noise correlations on population coding in the electro sensory system. Since our study suggests that communication stimuli can be discriminated by the fish, future studies can further investigate the behavioral significance of discriminating these stimuli, i.e., how the fish utilize the detailed information about different communication signals to guide perception and
behaviors. New behavioral assays, possibly for freely-swimming fish, should be designed to answer this question.
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