Parallel coding as a mechanism for the resolution of ambiguity in the adaptive code

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Our senses enable us to experience our surroundings through vision, touch, taste, smell, and sound. Such a multitude of sensations burdens our nervous system with the problem of encoding sensory information efficiently. One of the most basic ways in which neurons encode information is in their firing rate (Panzeri et al., 2010), but sensory stimuli often contain characteristics that vary over more orders of magnitude than the firing rate can encode. For example, the intensity of light outside on a clear winter day is much greater than it is indoors, and our eyes need some time to adjust when moving from outside to inside. This adjustment highlights an efficient mechanism for the encoding of light intensity, and is called adaptation. A neuron adapts to a certain stimulus by changing its coding strategy to suit the current distribution of the stimulus (Wark et al., 2007). However, adaptation brings a problem of its own, which is ambiguity: given a certain firing rate, we cannot determine the absolute value of the stimulus it encoded without more information about its context.

There is much discussion on how the nervous system resolves the ambiguity problem. In experiments on the fly visual system, Fairhall and colleagues (2001) have demonstrated that ambiguity can be fully resolved at the level of the individual cell. They claim that the more rapid features of the rate code, such as individual spikes, encode relative information, while the steady state features, such as firing rate, encode context. Other researchers such as Hildebrandt and colleagues (2015) describe a circuit-level approach. Through experiments in the grasshopper auditory system, they showed that adaptation in both downstream and upstream neurons establishes context at the beginning of a stimulus, while the rest of the stimulus is encoded relative to that context.

Our hypothesis is that ambiguity is resolved also at the level of the neural circuit. We believe that distinct populations of cells encode different features of a stimulus, an idea known as parallel coding (McGillivray et al., 2012). Thus, while one population of neurons may adapt to a stimulus, another population may not adapt and preserve the context of a stimulus. We tested this hypothesis using an animal model, the weakly electric fish *Apteronotus leptorhychus*. These fish emit an electric field that can sense nearby peers by interfering with their electric fields (Krahe and Maler, 2014). This interference is sensed by peripheral receptors, which project onto pyramidal cells in an area of the hindbrain known as the electrosensory lateral line lobe, or ELL (Chacron et al., 2011). The ELL contains three parallel segments: the centro-medial (CMS), centro-lateral (CLS), and lateral (LS) segments (Figure 1A,B).

Although adaptation to the presence of another fish in electroreceptor afferents have been characterized (Benda et al., 2005), adaptation in the ELL to changes in the position of another fish has not yet been explored. Due to differences between the segments (Chacron et al., 2011), we predict that cells in CMS should adapt very little, while cells in LS should adapt much more. Additionally, since feedback is a mechanism for adaptation (Drew and Abbott, 2006), we predict that superficial cells, receiving large amounts of feedback from higher areas (Chacron et al., 2005), should adapt more so than deep cells.

My project involved performing extracellular recordings of cells in the ELL while the fish is receiving a stimulus that mimics the position of another fish. In particular, I switched the position of the simulated fish from near to far, periodically (Figure 1C). By averaging over multiple presentations of the switch, I observed how the firing rate of different cells in the ELL adapted to changes in position.

Figure 1D shows averaged responses from deep and superficial cells in LS, and Figure

1E shows responses from CMS. In general, in response to a fish moving close, the firing rate increases but decays as the cell adapts to the new position of the fish, and in response to a fish moving away, the firing rate decreases but then increases. What is interesting is that only superficial LS cells adapt strongly to position, whereas deep LS, superficial CMS, and deep CMS cells adapt very little or not at all. This result agrees with our parallel coding hypothesis: as superficial LS cells adapt their coding strategy to the stimulus, other cells are less willing to adapt, creating channels to store information about the context of the stimulus. A larger representation of weakly- and non-adapting cells in the ELL suggests that preservation of absolute stimulus features is a priority in the electrosensory system. This makes sense as the electrosensory system is used to sense nearby objects, including potential predators, prey, and mating partners, the positions of which are important and can be rapidly changing.

While the ambiguity problem can potentially be solved by the parallel coding hypothesis, further analysis can be done to understand the relative contributions of adapting and non-adapting channels. One method could be to mathematically simulate a neural network consisting of cells with adaptation parameters obtained from the experiments. From the simulations, we can calculate the ability of the network to distinguish between different types of stimuli, such as different positions of fish, as we adjust the relative amounts of adapting and non-adapting cells.

In the end, there must always be a balance between efficiently encoding and preserving the maximum amount of information from the environment. In our system, we see that the balance is struck between channels that process information differently. While one channel efficiently encodes a wide range of stimuli by adapting, other channels keep track of the absolute features of the stimulus by not adapting. By encoding a stimulus in this manner, neurons can convey accurate information about the environment while reducing the generation of redundant spikes, allowing an efficient encoding of sensory information.

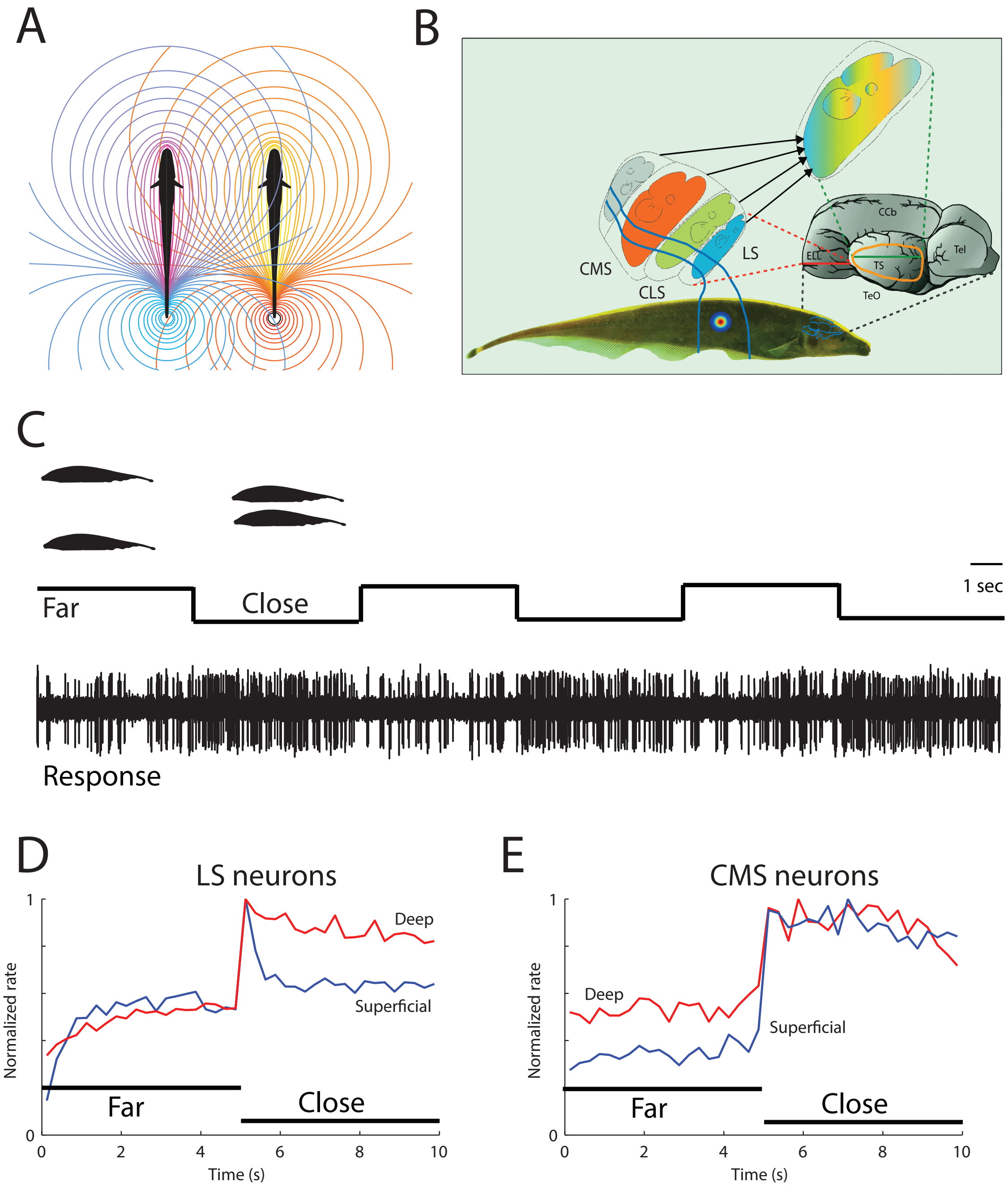

Figure 1: (A) Schematic depicting the EOD of two fish. The electric fields overlap to create interference waves that can be sensed by each fish. (B) Receptors along the surface of the fish transmit electro-sensory information onto three parallel maps in the hindbrain: LS, CLS, and CMS. These segments then project onto higher areas. (C) Sample response from a lateral segment neuron to the position of another fish that switches from far to close in a period of 10 s. The second fish is simulated by artificially interfering with the fish's electric field. (D) Averaged firing rates for representative cells in LS and (E) CMS.

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