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Spike Packet Coding: Lessons from Electric Fish*

Ángel Ariel Caputi†

Abstract

Spike packet code is one of the least explored in the brain. Packet coding is based on three principles: 1) Sensory flow is composed of a series of discrete self-generated sensory image whose precise timing is separately encoded in the brain. 2) Images are encoded in the temporal structure of spike evoked trains, defined by onset time, inter-spike intervals, and spike number. 3) Packet information should be stored in some manner that allows memories to operate with subsequent sensory inputs. This form of coding may facilitate neural computations underlying natural behaviors, encompassing aspects such as novelty detection and boundary recognition. This article reviews some contributions from weakly electric fish that have advanced both the experimental and theoretical understanding of the spike packet neural code.

Keyphrases

Spike timing, synaptic plasticity, active sensing.

Introduction

Ocular micro-saccades are followed by short-latency cortical evoked potentials (Gaarder et al. 1964). Gaarder (1966) posited that these potentials are used for the detection of borders, coining the phrase "packet information transmission". Under this hypothesis, the reafferent consequences of self-generated shifts of retinal images are incorporated in visual signals, thereby fragmenting the continuous stream of light into series of discrete and compact units (packets) of information that can be encoded, transmitted, stored, and manipulated. This notion was further substantiated by subsequent research involving monkeys freely looking at natural visual stimuli. Fixation-related spike synchronization occurs at the early phase of a rate response in some neurons of the primary visual cortex (Maldonado et al. 2008; Ito et al. 2011). This suggests that the oculomotor command might drive a corollary signal enabling precise timing of the earliest spike after every saccade. More recently, the concept of packet information transmission has been generalized and applied to the cortical processing of various sensory modalities, including audition, olfaction, and somatosensation (Luczak et al. 2015). The conceptualization of information packaging as spike trains carries significant theoretical implications: 1) The stream of information is segmented by precisely timed, discrete, and transient self-generated actions. 2) Individual images are encoded in packets consisting of spike timing probability distributions after the self-generated action. 3) Packet information may be retained in some manner that allows memories to operate with subsequent sensory inputs. In this article, I propose that these memories may be supported by temporally precise alterations in synaptic weights which work together as packet operands that process the next neuronal input to the same neuron. I present empirical evidence that substantiates this hypothesis within cerebellum-like sensory networks (the electrosensory lobes, ELs), typically present in two analogous yet non-homologous active electrosensory systems, and I elaborate on how the interplay of self- generation, spike packet encoding, storage, and operational mechanisms orchestrates novelty detection.

Pulsatile electric discharges carry discrete self-generated electric images

African Mormyriformes and American Gymnotiformes emit electric organ discharges (EODs) converging into two main evolutionary basins: some species generate sinewave-like continuous electric fields while other generate series of brief pulses showing a species-specific time course separated by silences (wave and pulse fishes, respectively, Fig. 1). In the case of pulse fishes each EOD provokes the polarization of nearby

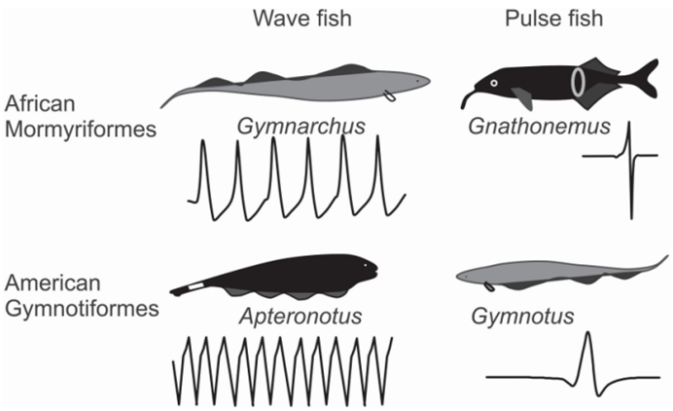

Figure 1: Species specific electric organ discharges (EODs) Four species belonging either to African and American taxa and exhibiting either wave or pulse electric discharges (adapted from Á. A. Caputi (2017)).

objects which, in turn, behave as virtual sources projecting electrosensory images on a cutaneous mosaic of electroreceptors. Here I focus on two paradigmatic species of pulse fish Gymnotus omarorum and

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†Correspondence to caputiangel@gmail.com.

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Gnathonemus petersii.

Sensory images are encoded as packets of post-EOD spike firing probabilities

The electrosensory mosaics of African pulse fish (Bell 1989; von der Emde and Bleckmann 1992) and American pulse fish (Á. A. Caputi and Aguilera 2019) comprise clusters of receptors specifically tuned to the typical time course of the species' EOD. These electroreceptors are innervated by primary afferent neurons that transduce and encode the temporal profile and amplitude of the local transcutaneous field into a burst of spikes (Fig. 2, bottom). The alteration in the time course (Fig. 2, color insets) or in the root mean square (rms) value of an EOD in the series elicits a well-defined behavior characterized by an abrupt and pronounced reduction of a few inter-EOD intervals followed by a gradual reversion to the preceding baseline (behavioral novelty response, BNR). In both taxa, these primary afferents project onto a laminar cerebellum-

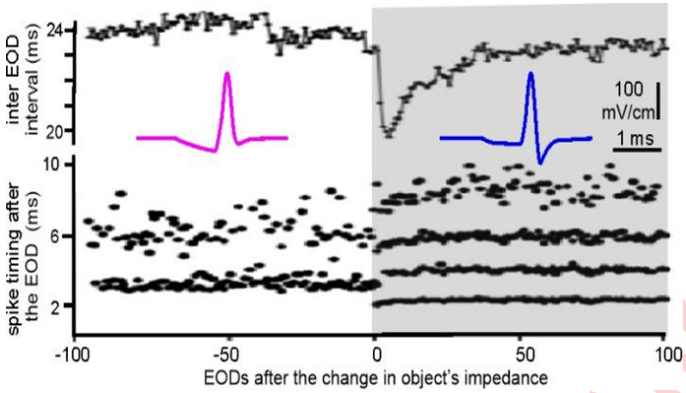

Figure 2: Peripheral encoding of the time course of the stimuli. Changes in the time course of the EOD maintaining stimulus intensity (insets) alters the spiking pattern of the primary afferent (bottom) and elicits a BNR (top, adapted from Borde and Á. A. Caputi (2025)).

like network localized in the lower brainstem. These electrosensory lobes (ELs) are extensively interconnected with the contralateral EL and with neighboring praeminentialis nuclei (PNs), collectively forming a complex for early processing of electrosensory signals (Bell and Maler 2005). The downstream target is the torus semicircularis (TS), which serves as a crucial sensory hub participating in the regulation of electro-motor, skeletal-motor, and intricate behavioral responses. In G. omarorum, peri-EOD histograms of EL neurons firing in the absence of external objects reveal that deeply located neurons exhibit a sharp firing pattern approximately 10 ms after the main peak of the EOD (Fig 3A and B), whereas superficially located neurons show a delayed and more dispersed probability distribution (Fig 3C and D). Deep and superficial neurons display two distinct types of responses to increases in stimuli, "center on" and "center off". These resemblances have prompted their functional classification in wave fish (Clarke et al. 2015). Typically, in all neuron types, peri-EOD histograms show a silence spanning between 6 to 9 ms after the EOD (Fig. 3 gray bar, Pereira et al. (2014); Rodríguez-Cattáneo et al. (2024). This silence can be attributed to a significant inhibition elicited by the primary afferent volley. This inhibition is partly mediated by large multipolar neurons that project onto the basilar dendrites of both deep and superficial "on neurons", accompanied by an augmentation in the activity interneurons that in-

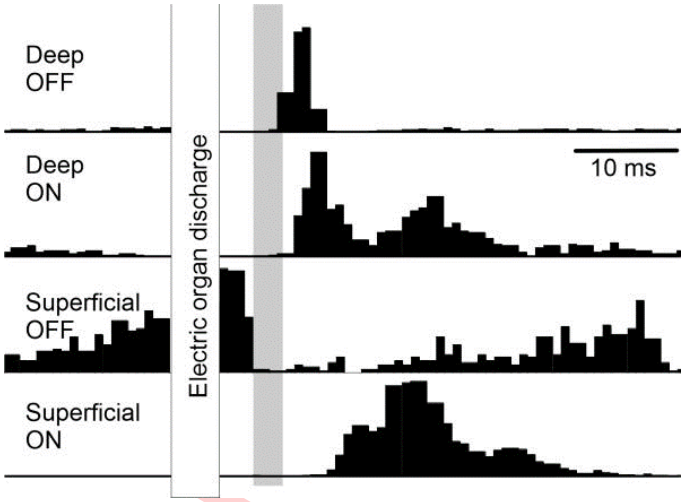

Figure 3: Post-EOD firing patterns in G. omarorum. Note a) the blanked interval corresponding to the EOD and b) the lack of firing in all histograms between 6 and 9 ms (gray bar).

hibit "off neurons" (Berman and Maler 1998). Inhibition of "on neurons" typically attenuates - or completely blocks - the excitatory synaptic effects of the primary afferent volley along the basilar dendritic trunks. Deep "center on" neurons, which lack an apical dendritic tree, originate a feed-forward functional pathway. They project onto a subset of PN neurons, which in turn project to the eminentia granularis posterior, where they activate the granule neurons that give rise to the parallel fibers driving the distal branches of the apical trees of superficial neurons. Image processing in the EL of G. petersii shows notable similarities. Strikingly, in addition to the hindbrain circuitry, African species show an EOD command corollary discharge (EOCD) which is extensively distributed throughout the brainstem, including both the ELs and the PNs. There are two EOCD components (Bell 1989): The gating EOCD acts on deeply located neurons and facilitates the response of "center on" neurons to the EOD (Fig 4A). The plastic EOCD consist of a synaptic pattern elicited by the activation of a data-bus of parallel fibers and elicit synaptic patterns in which excitatory and inhibitory post-synaptic potentials counterbalance according to the changes in their relative weights (Bell, A. Caputi, and Grant 1997).

Spike packets can be stored as and operated with synaptic expectations

Figure 4B illustrates the increase in late excitatory EOCD synaptic potentials after pairing the EOCD with peripheral stimulus evoking a large inhibition in a "center off neuron" of G. petersii (Bell, A. Caputi, Grant, and Serrier 1993; Bell, A. Caputi, and Grant 1997). This anti-Hebbian plastic effect is also elicited when the EOCD is paired with intracellular stimuli administered at varying delays (Fig. 4C). The interpretation via Occam's razor suggests that prior neuronal spiking activity is preserved as a modulation of the EOCD synaptic potentials occurring at spike-specific timing. Strikingly, as the data bus conveys a vast temporal array of activities to all traversed apical dendritic arbors, the pattern of spike timing probabilities is deftly reflected in the synaptic potential profile. Essentially, a negative counterpart of the input packet is retained, prepared to engage with the forthcoming spiking pattern. This phenomenon is particularly significant in certain interneurons, where the

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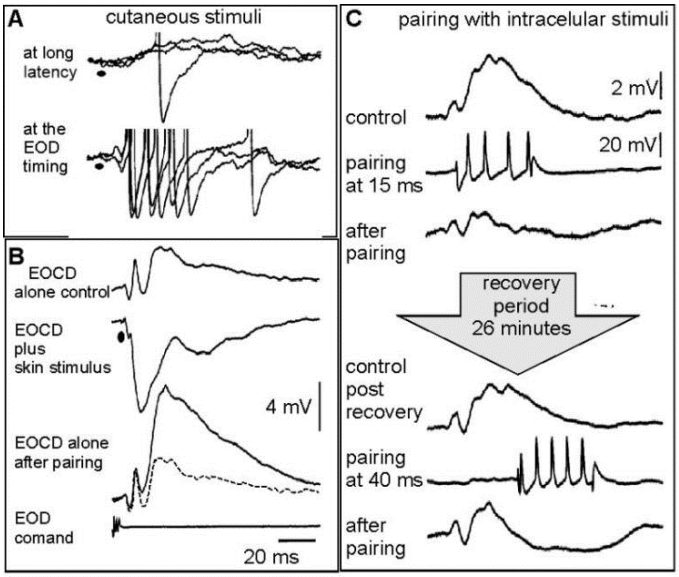

Figure 4: Corollary discharges in G petersii. In A and B the EOD was suppressed. A) "Center on" neuron responding to an electrosensory stimulus applied at long (top) and short (bottom) delays after the EOD. B) Response to EOCD of a "center off" neuron. Top: in the absence of stimulus. Middle: while an electrical stimulus was applied at the center of the neuron receptive field. Bottom: in the absence of stimuli after a period of stimulation (dotted line represents control response) C) Evolution of the EOCD synaptic potentials when pairing with intracellular stimuli applied at different delays in the same neuron as in B (adapted from Bell, A. Caputi, and Grant (1997)).

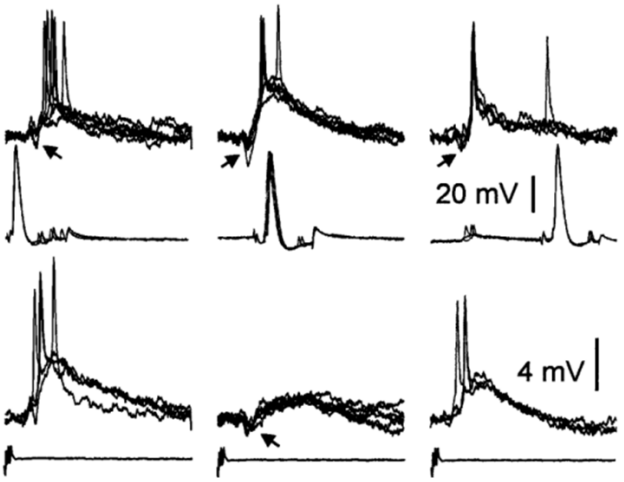

Figure 5: Anti-Hebbian spike timing dependent plasticity. The top and third row respectively represent the EOCD synaptic potentials before and after intracellularly evoking a dendritic spike (second row) either before (left column), during (middle column) and after (right column). The EOD was suppressed the remaining neural command (bottom row) was used to trigger the stimulus (adapted from Bell, A. Caputi, and Grant (1997)).

temporal coincidence between synaptic activity and dendritic spiking induces synaptic depression, while timing discrepancies either before or after coincidence foster synaptic potentiation. This "Mexican hat time pattern" of the plastic mechanism, augments temporal precision, thereby optimizing packet storage (Fig. 5). This particular form of plasticity, first shown in preparations in vivo of G. petersii (Bell, A. Caputi, Grant, and Serrier 1993; Bell, A. Caputi, and Grant 1997), is currently designated as "spike time dependent plasticity". In vitro studies indicate that the temporal architecture of the "Mexican hat" plastic adaptation is realized through the synergistic interplay of a synapse-specific mechanism and a non- specific mechanism (Grant et al. 1996; Bell, Han, et al. 1997). Subsequent research the cerebral cortex of mammals have revealed analogous plastic phenomena, albeit exhibiting a Hebbian induction rule (Markram et al. 1997).

Role of spike packet code in novelty detection

Behavioral experiments conducted on G. petersii, wherein the EOD was suppressed and replaced by an artificial EOD administered at varying delays post-command while preserving all other EOD parameters suggested that anti-Hebbian plasticity is involved in novelty detection (Hall et al. 1995). The relationship between novelty detection at the ELs and BNRs was explored in more detail in G. omarorum. In this species, comparable BNRs of the same amplitude are provoked by equivalent augmentations in EOD amplitude, yet they are elicited by singular deviant stimulus or under a step-and-hold paradigms (Fig. 6 A and B). In both cases, the amplitude of the BNR (BRNa) is a logarithmic function of the increase in the initial deviant EOD (Á. A. Caputi, Aguilera, and Castelló 2003). When the baseline stimulus is longer than 30 s the

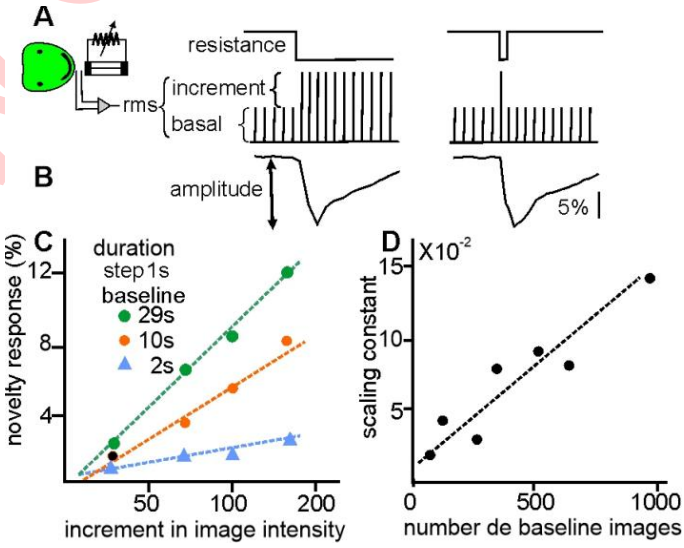

Figure 6: Behavioral novelty responses. A) Experimental schematics. B) Novelty responses elicited by step and hold and deviant stimulus. C and D) BNR amplitude increases with stimulus intensity and the scaling constant positively correlates with baseline duration and number of images (adapted from Á. A. Caputi, Aguilera, and Castelló (2003)).

amplitude of the amplitude of the BNR is independent of the duration stimulus baseline. However, when the stimulation pattern consisted of duty cycles in which the stimulation pattern consisted in two periods of low (baseline) and high (test) object resistance, the slope of the fitted line increased with the number of EODs in the baseline (Fig. 6). Simulation of the electro-sensoriomotor loop fits the experimental results. Novelty detection at the EL was conceptualized as a first-order concentrated parameter system. In biological terms, the output of the EL

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compares the present afferent input with an expectation constructed by leaky integrating preceding images (Á. A. Caputi, Rodríguez-Cattáneo, et al. 2023; Á. A. Caputi, Waddell, et al. 2023). Confirming this hypothesis, local field potential recordings in the EL (LFP) show that the first stimulus deviant from a constant amplitude baseline evoked a local novelty potential which amplitude predicted the amplitude of the BNR either when the stimulus amplitude or the baseline duration was manipulated (Figure 7, Á. A. Caputi, Waddell, et al. (2023)). The present hypothesis posits that the time delay instantiated by the feed-forward pathway in G. omarorum conveys the expectation signal synaptic at the right moment to be compared with the afferent input. First, primary afferents activate excitatory contacts with thw basilar dendritic branches of "on neurons". Second, this excitatory input is counterbalanced by inhibitory projections from the ipsi- and contra- lateral deep inhibitory neurons, resulting in the typical silence that precedes the onset of the spike packet (Berman and Maler 1998). Third, subsequent to the cessation of inhibition, the residual effects of basilar excitation are integrated with the synaptic inputs on the apical dendritic tree, elicited via the feed-forward PN pathway. This signal integration is modulated by a feedback TS-PN pathway that project on the stems of the apical dendritic trees (Bastian et al. 2004). Although definitive evidence for anti-Hebbian plasticity in the apical dendritic tree of "on neurons" in G. omarorum remains elusive, such phenomena have been documented in wave Gymnotiformes (Bastian 1999). Spike time-dependent synaptic plasticity within the apical dendritic arbor may modulate the intricate interplay between current inputs conveyed through afferent pathways and recent historical inputs preserved as modifications in synaptic efficacy, alongside the regulation of apical-somatic coupling. This adaptive filtering mechanism may enable the EL-PN circuit to attenuate stable components of reafferent signals as well as other predictable patterns of sensory input, all while preserving responses to novel stimuli.

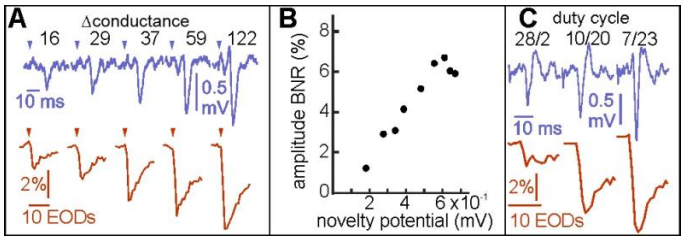

Figure 7: BNRa is predicted by the amplitude of the novelty potential A) Responses to different strength of the stimulus, BNR (brown) novelty potential (blue). A) Responses to different strength of the stimulus, B) Responses to different stimulation duty cycles, C) Correlation between BNR and novelty potential at the EL (adapted from Á. A. Caputi, Waddell, et al. (2023). B) Correlation between BNR and novelty potential at the EL C) Responses to different stimulation duty cycles (adapted from Á. A. Caputi, Waddell, et al. (2023)).

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Affiliations

Ángel Ariel Caputi, caputiangel@gmail.com; Sistema Nacional de Investigadores, W. Ferreira Aldunate 1219 Pando, CP 15600 Montevideo, Uruguay.

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