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Neural Code: Another breach in the wall?

*Response to the target article by **Romain Brette**:
Is coding a relevant metaphor for the brain?*

Chloé Huetz, Samira Souffi, Victor Adenis, Jean-Marc Edeline

NeuroPSI, UMR CNRS 9197, Dept Cognition & Behavior

Université Paris-Sud, 91405 Orsay, France

chloe.huetz@u-psud.fr

samira.souffi@u-psud.fr

victor.adenis@u-psud.fr

jean-marc.edeline@u-psud.fr

<http://neuro-psi.cnrs.fr/>

Abstract

Brette presents arguments that query the existence of the neural code. However he has neglected certain evidence that could be viewed as proof that a neural code operates in the brain. Albeit these proofs show a link between neural activity and cognition, we discuss why they fail to demonstrate the existence of an invariant neural code.

By questioning the existence of the neural code, Romain Brette opens again a strong debate between representational views of the brain (cognitivism and computationalism) and sensorimotor/enaction theories (O'Regan and Noë, 2001, Varela et al 1991), his preference being the latter. According to his view, all cognitive functions, particularly action and perception are viewed as means to interact with the world, without the need to build internal representations of it. Neural activity during perception should be viewed as the result of the organism's interaction with the world taking into account all possible influences, such as its internal state and its actions resulting in a given percept. Therefore, as the brain does not manipulate representations, it is senseless to try to decipher any code supposed to encrypt representations in neural activity. The results of three research fields focusing on proving that a particular neural code is at play should be addressed by Brette's review to strengthen his point.

First, in sensory physiology, research on tuning curves has been extended to naturalistic stimuli and is divided into two complementary approaches: encoding and decoding. Based on models of the stimulus-response function, these approaches rely on the idea that neural activity encodes some features of the external world. Successful reconstructions of complex stimuli based on neural responses (decoding), or successful predictions of responses to new stimuli (encoding) are viewed as proofs that the neural code has been cracked. Interpreting these results in light of Brette's arguments seems necessary. Initially, the stimulus reconstruction method (decoding) was performed either with simple artificial stimuli (Bialek et al. 1991) or in peripheral sensory systems (Warland et al 1997, Rieke et al 1995). More recently, studies have reconstructed natural stimuli from cortical responses (Miyawaki et al 2008, Naselaris et al 2009, Akrabi et al 2019), opening the spectacular expectation to read subjects' percepts. In the auditory modality, encoding models were used to investigate neural selectivity to a variety of acoustic properties such as phonetic features (Mesgarani et al, 2014), pitch (Oxenham 2018), timbre and rhythm (Woolley et al 2009). To achieve good performance, the stimulus/response models used in decoding/encoding approaches rely on features such as trial averaging, statistics of natural stimuli, starting time of the stimulus. Thus, the right interpretation should be that an "ideal observer" with an a priori knowledge of the experimental design can infer the stimulus (in the decoding approach) or the neural response (in the encoding approach). Noteworthy, this field has led to an interesting drift from the idea of a fixed relationship between stimulus and

neural responses to a more dynamic model, and is now tackling the mechanisms by which sensory responses are modulated by learning, context and history (Williamson et al, 2016; Fritz et al 2005; Holdgraf et al. 2016).

Second, the field of neuroprosthetic devices offers demonstrations of causal links between neural code and brain functions. The most successful of these devices, cochlear implant (CI), operates with blunt stimulations of auditory nerve terminals. Despite a large current spread in the tympanic ramp, CI allows implanted subjects to have percepts and recover speech understanding. Even though there are huge differences between normal cochlea and CI, the fact that CIs restore hearing can be viewed as a proof that the neural code at play in the periphery has been deciphered and is successfully implemented in a prosthetic device. However, the CI settings that leads to speech comprehension considerably differ from one subject to another, as do the strategies leading to the largest evoked responses in auditory cortex (Adenis et al 2018). Thus, in contrast with the genetic code that is invariant across cells and species, the neural code (understood as changes in neural activity in adaption to a CI) is probably specific for each individual and/or each type of neuron. In line with sensorimotor theories, success of CI shows that the brain is using a new input in a way it can interact again with the environment, which might be the basis of hearing restoration.

A third important field investigates the effect of disrupting a particular feature of neural activity on a cognitive skill. In the visual system, disruption of physiological activity in the primate area MT during presentation of moving stimuli bias the perceptive judgment of a behaving animal (Salzman et al 1990; Salzman & Newsome 1994) thus making the first link between neural code (understood as a pattern of activity of specific neurons) and behavioral performance. More recently, studies performed in the hippocampus have showed that disrupting the replay of spiking patterns occurring across neuronal ensembles during the sharp wave ripples profoundly alters the memory of previously acquired information (Girardeau et al 2009; Ego-Stengel & Wilson 2010). These data reinforce the notion that neuronal activity patterns do correlate with the acquired information. More importantly, associating a rewarding stimulation of the medial forebrain bundle with an hippocampal place cell activity induced a place preference at the place cell location (Lavilléon et al 2015), demonstrating causal links

between a particular place cell's firing rate and a specific location memory. In all these examples, the exact neural activity feature (its firing rate or its temporal spike patterns) correlated with the animal's location is unknown, but causal relationships do exist. Yet, causality is not enough to define a neural code.

Clearly, more caution is necessary when discussing the neural code as overstatements made (Ferster & Spruston 1995; Panzeri et al 2017) tend to generate the illusion that (1) the same code operate in any sensory and motor systems, which is obviously not the case and (2) the brain's cognitive functions consist of manipulating encoded representations of the world, a theory that is controversial. Does this mean that the concept of neural code should be abandoned or should it be used to describe studies linking neural activity to brain function? We believe that the neural code definition should be freed from the notion of representation and we should clarify what we refer to when investigating the neural mechanism of brain functions.

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