1. Author of target article: Romain Brette

2. Word count: 60 (abstract); 999 (main text); 116 (references); 1,242 (entire text)

3. The Origin of the Coding Metaphor in Neuroscience

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10. Abstract: In order to assess Brette's proposal to expunge "coding" from the neuroscientist's lexicon, we must consider its origins. The coding metaphor is largely due to British nerve physiologist Edgar Adrian. I suggest two ways that the coding metaphor fueled his research. I conclude that the debate today should not be about the "truth" of the metaphor but its continuing utility.

11. Main text:

Brette, in his provocative article, gives a number of arguments for his proposal that we expunge the coding metaphor from the neuroscientist's lexicon. To properly evaluate his proposal, however, we should consider the metaphor's *origins*. When did neuroscientists begin describing the neural response to a stimulus as a coded message? Why did they begin using that metaphor? What benefit, if any, did they derive from using the metaphor?

I have investigated these questions extensively, and concluded that the British nerve physiologist Edgar Douglas Adrian (1889-1977) deserves most of the credit for introducing the metaphor (Garson 2015). Adrian's most notable accomplishment was his recording, in 1925, of the action potential of a single sensory neuron (Adrian and Zotterman 1926). This was the achievement for which he was awarded the Nobel Prize in Physiology and Medicine in 1932. Additionally, he formulated what he understood to be the basic laws governing the action potential: the all-or-none principle, rate coding, and adaptation (see Rieke et al. 1997, pp. 3-8). Following his achievement, he spent the next decade attempting to demonstrate the universality of these basic laws across different neuron types and in different species.

1925 marked another turning point in Adrian's work. From that time onwards, his work was permeated with coding metaphors. He described the neural response in terms of the

transmission of *messages*, *signals*, and *codes*. In a revealing analogy, he noted that these messages are "scarcely more complex than a succession of dots in the Morse Code" (Adrian 1932, p. 12). In his use of linguistic metaphors he distinguished himself from his contemporaries, such as Charles Sherrington, Herbert Gasser, and Alan Hodgkin, who, at the time, preferred the colorless language of "impulses," "reactions," "activity," and "disturbances" to describe the neural response.

This is not to say that nobody before Adrian had described the nervous system as a communication device. That analogy dates back to the middle of the 19th century, when pioneers like Hermann Helmholtz and Emil du Bois-Reymond, in their popular writings, compared the nerves to a telegraph system that shuttles news and instructions from the body to the brain and back. Adrian's use, however, was quite distinctive. Unlike his predecessors, he attributed a highly specific, language-like code to the neuron. For Adrian, neural responses were, as Brette puts it, "hieroglyphs to be deciphered."

We can speculate on the historical, sociological, and technological context that might have prompted Adrian to think about the neuron as a coding device. I have argued that the widespread military use of radio communication during World War I played a role in this terminological innovation. But that is hardly the issue here. The issue here is this: Did the coding metaphor actually benefit Adrian's research? Did it meaningfully advance neuroscience? Was it, in its time, a scientifically fruitful metaphor?

I think the answer to these questions is a decisive "yes." The metaphor let Adrian formulate and test questions that had never been systematically posed before. There were at least two fields of investigation that the coding metaphor opened for him. First, it allowed Adrian to shift his attention away from the mechanistic details of the action potential (for example, how the impulse propagates through narcotized nerve), and toward the *abstract correspondences* between the pattern of sensory stimuli and the neuron's patterned response (for example, how a rapidly changing stimulus modulates the neural response). By posing questions about these abstract correspondences, Adrian was able to gather evidence for what later became known as "rate coding:" for some sensory neurons, spike frequency approximates an exponential function of the intensity of the stimulus. It is hard to see how one would even formulate such questions without using the coding metaphor.

Second, the metaphor allowed him to pose questions about the *purpose* or *end* of various "coding" schemes. Put differently, it allowed him to reason teleologically about the brain. Why does the brain use rate coding, rather than some other coding principle, to represent rapidly changing stimuli? Consider, for example, the principle of adaptation, which describes how some sensory neurons eventually stop responding to an unchanging stimulus. For Adrian, this principle could be explained teleologically, as a bulwark against the pointless, and metabolically costly, production of redundant messages (Adrian 1928, p. 99). Some biologists bristle at the mention of "teleology," but the simple fact is that teleology cannot be eliminated from biology (Garson 2019). Every time we ask a question about the *function* of a trait (what is the function of zebra stripes?) we are engaged in teleological reasoning. Moreover, such reasoning is usually harmless, as

teleological questions can often be restated as respectable evolutionary questions (why did zebra stripes evolve?), rather than questions about the intentions of a divine being.

I have discussed the origins of the coding metaphor, but how does this bear on Brette's proposal to expunge "coding" from neuroscience? For everything I have said here, Brette might still be correct that the coding metaphor is otiose. He might insist that, while the metaphor might have been useful in the early days of the neurosciences, it is no longer so. Since I am a philosopher and not a neuroscientist, I am hardly in a position to survey the current state of the science and make a pronouncement of such scope. Still, thinking about the origins of the coding metaphor can helpfully frame what I expect to be an ongoing and lively debate. It seems to me that the question of eliminating "coding" should not be a referendum on the *truth* of the coding metaphor, but on its *utility*. In other words, in assessing Brette's proposal, we should not get bogged down wondering whether the brain "really" encodes information about the world. It does not. It is a metaphor; like all metaphors, it gives us a partial and imperfect picture of what the brain is doing. The question, rather, is this: is the metaphor still useful for us, today? Does the usefulness of the metaphor outweigh its inaccurate connotations? Or, has it outlived its usefulness entirely?

12. Reference list

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