Single spikes may suffice

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IT IS WELL-ESTABLISHED THAT the vast majority of information is carried through the brain by action potentials. Exactly how this information is embedded within the spike train, however, has been a topic of some debate. Potential codes fall roughly into three categories: rate, timing, and synergy. In a rate code, the only thing that matters is the number of spikes that occur in a particular interval; different stimuli are coded by different numbers of spikes. As a corollary, two stimuli that evoked the same number of spikes would be indistinguishable. A timing code, on the other hand, posits that it is not just the number of spikes that carries information, but also the timing of those spikes: two stimuli that elicit the same number of spikes may be distinguished if those spikes occur, on average, at different times. In a synergy code, information is carried not by the spiking statistics of individual neurons but rather by the relative alignment of spikes across neurons.

Obviously, these categories are not mutually exclusive. Synergy codes do not rule out information transfer in single neurons, they merely posit that the population carries more information than the sum of its parts. Meanwhile, the difference between rate codes and certain timing codes is often just a matter of scale: with rate coding, readout neurons with coarse temporal resolution are sufficient to extract information; with a timing code, finer temporal discrimination is necessary. Why, then, is it so important to work out how information is laid down in spikes? This is a crucial question in neuroscience because the answer places clear constraints on the types of neural circuitry required to read out and manipulate the information. To know the code is to know almost everything about the processing capabilities of the system: its information capacity; its resolution, detection, and discrimination capabilities; even its metabolic demands.

In this issue of the Journal of Neurophysiology, Storchi and colleagues (2012) weigh in on this question by investigating first-spike latency (FSL) coding in the ascending whisker pathway of the rat. FSL codes are a special case of timing codes in which the timing of the first spike in response to a stimulus carries information about the attributes of that stimulus. The advantages of FSL codes are twofold. First, they are superfast: in a world where reflex times matter, they represent one of the most rapid methods of information transmission from one area to another. Second, they have a large capacity: since time is a continuous variable, the number of different discriminable states is limited only by the noise, or jitter, in that first spike time, and in the subcortical whisker system of the rat, neurons can fire with submillisecond precision (Montemurro et al. 2007). The main problem with FSL codes has to do with the onset reference. To compute the latency between stimulus onset and the arrival time of the first spike, the subject needs to have some kind of independent reference of when stimulus onset actually occurred. For certain tasks, like bat echolocation or eye saccades, there are clear motor signals that can be used as the onset reference for incoming spikes. How can a similar reference be found for purely sensory tasks, where the subject does not control the stimulus onset?

One answer is that stimulus onset can be decoded from the population. Unlike stimulus intensity, which would typically shift the entire population to respond earlier as intensity increases, Storchi et al. (2012) investigate the encoding of whisker deflection direction. If the response latency at the preferred direction of a neuron depends only weakly on direction, there will always be a subset of cells that responds at a roughly constant time with respect to the time of deflection. Expanding on previous work by Chase and Young (2007), Storchi et al. (2012) use a simulated leaky integrate-and-fire neuron that receives input from the entire population of cells and spikes when a stimulus is detected. They find that by using this hypothesized onset detector as the stimulus reference, they can decode 91% of the information from FSL compared with what they would be able to decode from the true onset time. Furthermore, their onset detector was remarkably reliable over a large range of simulation parameters, adding credibility to its potential biological implementation.

Of course, showing that information is carried by a particular type of response is one thing; proving that the brain actually uses that information is something else entirely. As Cariani (1995) argues in his treatise on temporal coding, to qualify as a neural code, the brain must use the information in that response modality to inform behavior. How does one show that particular neural codes are actually implemented? This is, in general, a very hard problem with no fixed solution. Strong forms of evidence for various codes can come from careful dissection of the anatomic and physiological processes of the neurons responsible for readout, as when Carr and Konishi (1990) established the anatomic implementation of Jeffress’ (1948) delay-line coding for interaural timing differences within the auditory brain stem of the barn owl. Other evidence can rule in (or, more commonly, out) particular codes. Van Rullen and Thorpe (2001), for example, have argued that behavioral responses to visual stimuli occur so quickly that the information must be conveyed by the very first spikes. Meanwhile, Jacobs et al. (2009) have investigated the ability of mice to perform a particular visual discrimination task and then recorded the responses of retinal ganglion cells in vitro to the same stimuli in a preparation that allowed them to record simultaneously from the entire population of cells. Because these cells act as a bottleneck on all visual information flowing into the brain, they could construct optimal Bayesian classifiers based on different assumed coding schemes and evaluate how well each classifier performed the same discrimination task. If the proposed coding scheme cannot differentiate the stimuli at least as well as the behavior indicates, the mice must not rely solely on that code. [Jacobs and colleagues (2009) found that rate codes could not reproduce the behavioral capabilities of their subjects.] Circumstantial evidence

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disciplinary interests can come from theoretical investigations into the types of computations that can be performed in biological systems. These considerations motivated Gütig and Sompolinsky’s (2006) development of the tempotron, a readout neuron that can learn to spike based on particular spatiotemporal combinations of inputs. They showed that biologically plausible learning rules could be used to sensitize neurons to particular spatiotemporal patterns of inputs, including spike latency. Similarly, Shamir (2009) showed that a particular readout mechanism, the “temporal winner-take-all,” could provide very accurate discrimination of the directional movement of visual stimuli based only on FSL.

Storchi and colleagues’ (2012) findings suggest that the FSL coding they observe is not merely an epiphenomenon. First, they show that neurons in both the trigeminal ganglion and the ventroposteromedial thalamus, two stops on the ascending processing pathway, carry information about whisker direction in FSL. Although still not proof that the FSL code is used, at the very least this finding rules out the thalamus as the site of the FSL readout and demonstrates that the system meets a necessary condition for FSL use: that the information be preserved in the spike train until readout. Furthermore, in previous work, they have demonstrated that FSL coding of whisker direction is maintained all the way to cortex (Bale and Petersen 2009). Second, they show that latency codes provide far more accurate stimulus reconstruction than spike count codes for small populations of neurons. If one believes that feasible codes should also be sparse (Olshausen and Field 2004), FSL becomes a good contender.

This paper is the latest in a long line of research from Rasmus Petersen, who together with long-time collaborators Stefano Panzeri and Matthew Diamond has published more than 20 papers using information theoretic tools to evaluate systematically the representation of whisker movement information along the entire ascending somatosensory pathway. Their findings support the emergent view of a system poised to communicate information as rapidly as possible: although the reliability and precision of spike timing may change across brain areas, overall the system represents individual whisker deflection events in remarkably small numbers of spikes per neuron. For this system, at least, it seems that single spikes may indeed suffice.

DISCLOSURES
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S.M.C. drafted manuscript.

REFERENCES