Converting neural signals from place codes to rate codes

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Abstract. The nervous system uses two basic types of formats for encoding information. The parameters of many sensory (and some premotor) signals are represented by the pattern of activity among an array of neurons each of which is optimally responsive to a different parameter value. This type of code is commonly referred to as a place code. Motor commands, in contrast, use rate coding: the desired force of a muscle is specified as a monotonic function of the aggregate rate of discharge across all of its motor neurons. Generating movements based on sensory information often requires converting signals from a place code to a rate code. In this paper I discuss three possible models for how the brain does this.

1 Introduction

Sensory maps or place codes are ubiquitous throughout the brain. For information processing, several features of this style of representation are of critical importance. First, the individual neurons that make up sensory maps respond maximally to different “preferred” values of the sensory parameter being encoded, and their responses decrease if the actual stimulus either exceeds or falls short of that particular favorite parameter value. These non-monotonic response functions dictate the second key feature of sensory maps: the representation of the sensory parameter must be distributed across an array of neurons with different preferred parameter values. The discharge rate of any one neuron is ambiguous – except at the peak of the tuning curve, the same response level corresponds to at least two possible values of the sensory parameter. Thus, only by examining the responses of a population of such receptors is it possible to deduce what the stimulus actually looks, sounds, feels, smells, or tastes like. If these tuned neurons are topographically organized according to their preferred parameter values, a given stimulus will evoke activity at a given site in the population, hence the term place code.

The neural representation of motor commands shares some similarities with sensory systems. Each muscle exerts force along a particular direction, and the motor neurons that control those muscles show tuning for these pulling directions. The overall direction of movement is represented by the ratio of activity in different groups of motor neurons controlling muscles with different pulling directions. However, motor commands differ from sensory maps in how the magnitude of the force of each muscle group is controlled. To move a body part farther or faster requires a monotonic increase in motor neuron activity. This can occur by increasing the activity level of a given set of motor neurons, by recruiting additional motor neurons, or both. It does not involve activating a completely different set of motor neurons, as is the case for place codes. Because this monotonic discharge rate can be an unambiguous signal of a parameter of interest, this type of code is commonly referred to as a rate code.

Motor commands do not have a monopoly on rate coding: the responses of sensory neurons can also vary as a monotonic function of certain sensory parameters. Visual neurons, for example, are usually tuned for the location of a visual stimulus (the receptive field), but the response can vary monotonically with the intensity of the stimulus. Indeed, the responses of many if not all sensory neurons can be influenced by more than one sensory parameter, and show place coding for some parameters and rate coding for others. I will consider these issues in more detail later, and concentrate for the moment on those individual sensory parameters that are represented through place codes. Guiding movements based on this kind of sensory information requires translation of place-coded sensory signals into rate-coded motor commands.

In this article I will discuss three models for how this place-to-rate transformation may be accomplished by the brain. I will draw heavily on examples involving oculomotor responses to sensory stimuli, but similar issues apply for more complex skeletal movements such as
reaching movements in which the body interacts with objects in space. A preliminary report of this work has been presented elsewhere (Groh 1997).

2 Methods

Simulations were conducted using Matlab (Mathworks, Natick, Mass.). Interneurons and output neurons were simulated as linear threshold units. Weights were assigned in the principled manner described in detail below. Inhibitory synapses were treated either as divisive (the weighted average model) or as multiplication by zero (the summation-saturation model, Koch 1999). The consequences of these assumptions are discussed in detail below.

3 Results

3.1 Model 1: weighted summation

The simplest way to convert place-coded signals into a rate code is to multiply the level of activity \( (a) \) of each neuron in the place code by a synaptic weight \( (w) \) that represents that neuron’s preferred value, and sum the totals.

\[
\text{output} = \sum_i w_i a_i
\]  

(1)

This is essentially the same calculation that computers perform when converting a binary number into a voltage level for an analog output channel. A network of neurons can perform this type of weighted summation calculation very easily (Fig. 1a).

This type of network has been proposed previously (e.g., Van Gisbergen et al. 1987; Scudder 1988; Groh and Sparks 1992; Lefevre et al. 1998), and has a certain elegant simplicity. Indeed, graded anatomical projections of the type needed to perform such a computation have been identified in the brain (Moschovakis et al. 1998). However, it also has some obvious problems. One major problem concerns what happens when there are multiple sites of activity in the place code. This situation might arise naturally when more than one value of a sensory parameter is present. Suppose, for example, that two (or more) visual stimuli are present in the visual

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**Fig. 1.** a The weighted summation model for converting signals from a map of tuned neurons into a rate code. Each neuron in the map is tuned for a different parameter value. The synaptic weights \( (w) \) of the projections onto the rate code unit scale monotonically with the preferred parameter values. The rate code unit calculates the weighted sum of its inputs. b The weighted average model. A second set of projections with a uniform pattern of synaptic weights (denominator channel) is divided into the output of the first set (numerator channel), yielding an overall output that is normalized for the total amount of activity in the map, and corresponds to the average location of activity within the map. c The summation-saturation model. The activity in the numerator and denominator channels will charge up until the denominator channel reaches a certain threshold. This triggers an inhibitory neuron, which shuts off the input to the numerator channel. The numerator channel will then ignore any additional activity in the map, but will hold steady at a value that indicates the average location of the activity that occurred up until that point.