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Analyzing neural responses with vector fields

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ABSTRACT

Analyzing changes in the shape and scale of single cell response fields is a key component of many neurophysiological studies. Typical analyses of shape change involve correlating firing rates between experimental conditions or "cross-correlating" single cell tuning curves by shifting them with respect to one another and correlating the overlapping data. Such shifting results in a loss of data, making interpretation of the resulting correlation coefficients problematic. The problem is particularly acute for two dimensional response fields, which require shifting along two axes. Here, an alternative method for quantifying response field shape and scale based on correlation of vector field representations is introduced. The merits and limitations of the methods are illustrated using both simulated and experimental data. It is shown that vector correlation provides more information on response field changes than scalar correlation without requiring field shifting and concomitant data loss. An extension of this vector field approach is also demonstrated which can be used to identify the manner in which experimental variables are encoded in studies of neural reference frames.

1. Introduction

Since Sherrington first described variations in afferent responses resulting from tactile stimulation to different parts of the body surface (Sherrington, 1906) neurons have been characterized by their response fields, constructs which relate the firing frequency of action potentials (and more recently frequency bands of the power spectra of local field potential signals) to sensory, motor or cognitive variables. In the sensory domains (visual, auditory, etc.) these response fields are typically referred to as 'receptive fields' and in the motor realm as motor or 'movement fields'. Similarly, hippocampal and entorhinal 'place fields' can be considered cognitive response fields or cognitive maps as they represent a memory trace of an animal's experienced position in its environment (McNaughton et al., 2006; O'Keefe and Nadel, 1978). Importantly, these response fields are not fixed entities but can change in shape and/or scale as a function of time and/or task conditions (Kusunoki and Goldberg, 2003; Taylor et al., 2002), general brain state (Worgotter et al., 1998), experience (Mehta et al., 2000), or attention (Womelsdorf et al., 2008).

Various methods have been used to quantify experimentally induced changes in response field shape. On the sensory side, these methods often assume either implicitly or explicitly that the response field is an approximate Gaussian or sigmoid function of the experimental variable being investigated. For example, in the study by Womelsdorf et al. (2008), changes in visual receptive fields were quantified by the extent to which the center of the field shifted when attention was diverted toward a location outside the field (see also Britten and Heuer, 1999; Raiguel et al., 1995). Responses were fit by two-dimensional Gaussians which were parameterized by their centers, orientations (main elliptical axis), and standard deviations along their two axes. These investigators also quantified response fields nonparametrically via spine interpolation of response surfaces, using the center of mass of the area above one-half of the maximum response and the square root of this area as measures of response field center and size respectively.

Arm movement fields are typically characterized by changes in mean firing rate as a function of movement related parameters such as direction and/or amplitude (Fu et al., 1993; Messier and Kalaska, 2000). In the motor cortex for example, many arm movement related neurons can be described as 'cosine-tuned' to the direction of hand movement, and can be further characterized by their preferred directions, a vector quantity that roughly corresponds to the 'peak' of this cosine function (Georgopoulos et al., 1982). Significant changes in these fields due to experimental manipulation can be determined by quantifying the degree of rotation of these preferred directions. At the population level, rotations of the 'population vector' (the vector sum of the contribution of each individual neuron along its preferred direction) can also be quantified as can changes in the length of this vector, which is thought to represent changes in movement velocity (Georgopoulos et al., 1986; Schwartz and Moran, 1999).

In studies designed to examine the reference frames underlying spatial representations in the brain, correlation methods are

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often used to quantify changes in response field shape (Batista et al., 1999; Buneo et al., 2002; Chang and Snyder, 2010; Mullette-Gillman et al., 2005). In some cases direct scalar correlation of the response fields has been used. For example, Batista et al. (1999) recorded the responses of parietal neurons in an arm reaching task where goal locations were the same in eye-centered coordinates but different in limb-centered coordinates and correlated these data with those obtained when locations were the same in limb coordinates but different in eye coordinates. No shifting of the response fields was performed; instead these investigators simply compared the correlation coefficients obtained for the two comparisons. Using this approach, statements can be made about which of the two coordinate frames being examined best explains the data but it is difficult to arrive at more definitive conclusions. That is, this approach does not allow direct investigation of the "intermediate", "mixed," or "hybrid" reference frames that have been reported in some studies (Buneo et al., 2002; Chang and Snyder, 2010; Mullette-Gillman et al., 2005).

Another scalar correlation method involves shifting the response fields or tuning curves (in the case of one dimensional data) in increments of the sampled workspace and correlating the data at each step (Cohen and Andersen, 2000). This 'cross-correlation' approach results in a vector of coefficients, with the maximum of that vector taken as the location in space where the data are best aligned. Fig. 1 illustrates the procedure in the context of an experiment where visual receptive fields are mapped along the horizontal dimension at two different gaze positions. Fig. 1B depicts these receptive fields as one-dimensional Gaussian tuning curves with peak responses centered on each fixation position (i.e. they are retinotopic). Fig. 1C show the cross-correlation function that is obtained by incrementally shifting (in both directions) the 'gaze right' tuning curve with respect to the 'gaze left' tuning curve. The cross-correlation function demonstrates a sharp peak at a shift of -8, as expected given the shapes and locations of the peak responses in each tuning curve. In principle this shifting method is superior to the direct correlation approach mentioned above, as it allows for examination of intermediate reference frames, but the method suffers from the fact that the shifting procedure necessarily results in data vectors which are progressively non-overlapping (i.e. data loss). This is illustrated in Fig. 1D, where the number of data points used to derive the cross-correlation function in 1C is plotted as a function of shift. The gradually decreasing number of correlated data points for shifts away from zero shift is associated with a decreasing likelihood of obtaining a statistically significant correlation (Zar, 1996), which can substantially affect the conclusions drawn from such an analysis. In addition, such correlation methods assume implicitly that response fields are symmetric and remain so during shifting. However, response fields are not always well approximated as symmetric Gaussians and such "skewness" has implications for how these data and subsequent analyses are interpreted (Mehta et al., 2000). As a result, if cross-correlation is to be used to quantify response field similarity then skewness should also be explicitly quantified. Alternatively, skewness or other asymmetries in response field shape can be taken into account implicitly using other nonparametric methods (see below).

The data loss resulting from cross-correlation can be ameliorated somewhat by sampling a sufficiently large number of locations during an experiment. However, in awake, behaving animal preparations the time associated with maintaining stable recordings is often the limiting factor determining the number of locations and trials that can be sampled. For studies involving multiple locations sampled in two-dimensions this problem is even more acute. Thus, methods are required which allow quantification of the degree of relatedness of neural response fields while also obviating sampling unnecessarily large numbers of locations and/or cross-correlating response fields.

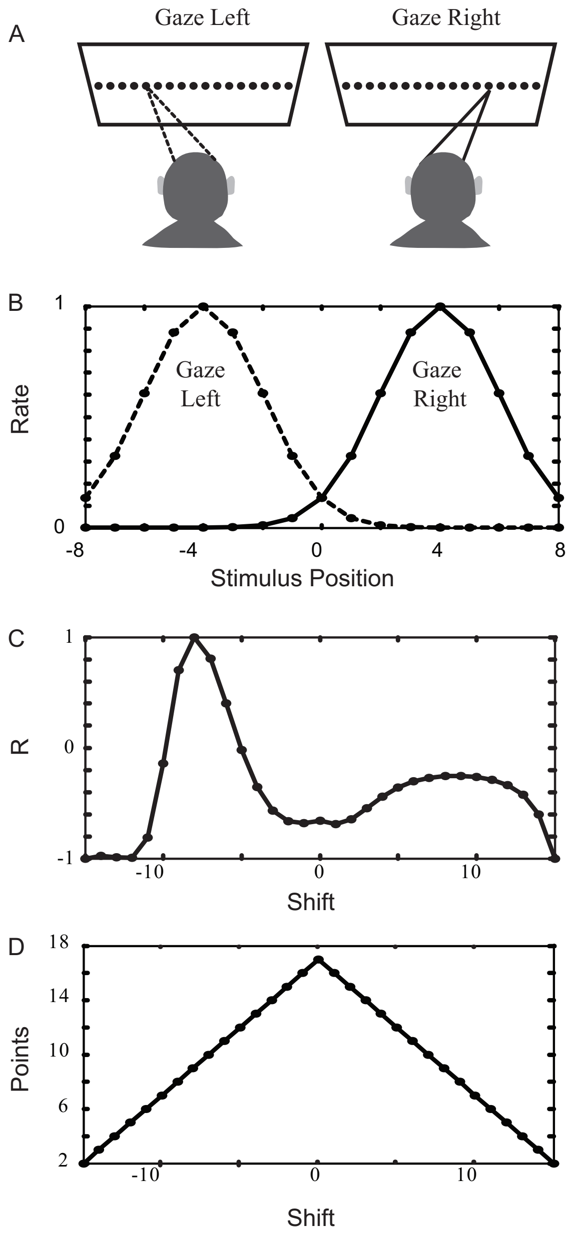

Fig. 1. Cross-correlation of one-dimensional response fields. (A) Illustration of an experiment involving visual receptive field mapping at two gaze positions. (B) Response fields corresponding to the two gaze positions in (A), plotted in world/screen coordinates (arbitrary units). (C) Correlation coefficient (R) plotted as a function of response field shift. (D) Number of points correlated as a function of shift.

Here a nonparametric method for quantifying changes in the scale and shape of neural response fields is described, one that naturally accounts for irregularities/asymmetries in the fields such as skewness. This method involves converting a matrix of scalar firing rates into gradients, then correlating these vector fields using methods originally derived for the quantification of geographic data (Hanson et al., 1992). The calculations produce a correlation coefficient that is analogous to scalar correlation but also provide a measure of the rotational or reflectional relationship between two vector fields and a measure of their scaling relationship. It is shown that vector correlation provides information about the degree of relatedness between two-dimensional response fields that cannot be obtained via simple scalar correlation, and that this information can be obtained without response field shifting. The basic method