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. 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.

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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
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. 18 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.

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 reflexional 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

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.
is demonstrated using idealized and real response fields in the context of reference frame experiments. In addition, an extension of the method is discussed in the context of separable/inseparable fields that are encountered in the analysis of spatio-temporal and movement related responses.

2. Methods

2.1. Vector field correlation

2.1.1. Neural responses

Both idealized and real neural responses were used to illustrate the vector field analyses. The real neural responses were obtained from the posterior parietal cortex (PPC) of the monkey during arm movement studies investigating the frames of reference for visually presented targets presented in a vertical plane (Buneo et al., 2008). As a result, idealized responses were generated with similar experiments in mind. Neural responses were generally simulated as Gaussian functions of target position along two spatial dimensions (i.e. 2D Gaussians). For more complex fields, combinations of sigmoid functions and Gaussian functions were used. For the simple 2D Gaussian fields, neural responses were described by the following equation:

\[ f(X, Y) = Ae^{-(X^2/2\sigma_x^2 + Y^2/2\sigma_y^2)} \] (1)

where \( X \) and \( Y \) represent position along two arbitrary orthogonal axes. To generate sets of idealized data similar to the real neural reference frame experiments the following procedure was used. A scalar neural response field was first generated for one set of 'experimental' conditions (e.g. eyes fixated straight ahead, arm to the left of the fixation point). A set of 'shifted' responses was then produced for the second set of conditions, i.e. a response field with the same tuning structure but with a peak response that was associated with a different location. Once the shifted responses were generated the corresponding gradients were numerically determined for both scalar fields (Matlab, The Mathworks). After generating the gradients the correlation between the vector fields was calculated as described below.

2.1.2. Correlation analysis

Numerous measures of vector correlation have been defined in the literature, both parametric and non-parametric (reviewed by Hanson et al., 1992). With few exceptions (Shadmehr and Mussa-Ivaldi, 1994), these methods have been used to analyze vector-valued data outside the realm of neuroscience, such as wind speeds and ocean currents. Here the vector correlation method of Hanson et al. (1992) was used, which was originally developed for the analysis of geographic data. This method produces a correlation coefficient that is analogous to the scalar Pearson product–moment correlation coefficient in the sense that it is formed as a ratio of the covariances to the product of the variances. The vector correlation coefficient (\( \rho \)) can be computed as follows:

\[ \rho = s \sqrt{\frac{\sigma_{xx}^2 + \sigma_{yy}^2 + \sigma_{xy}^2 + \sigma_{yx}^2 + 2\xi}{(\sigma_{xx}^2 + \sigma_{yy}^2)(\sigma_{xy}^2 + \sigma_{yx}^2)}} \] (2)

where

\[ \xi = \sigma_{xx}\sigma_{yy} - \sigma_{xy}\sigma_{yx}, \]

\[ s = \frac{\xi}{|\xi|} \] (4)

and \( \sigma_{xx}, \sigma_{yy}, \sigma_{xy}, \) and \( \sigma_{yx} \) represent the variances of \( x, y, u \) and \( v \) and \( \sigma_{xx}, \sigma_{yy}, \sigma_{xy}, \) and \( \sigma_{yx} \) represent the four component covariances. The vector correlation \( \rho \) is analogous to the scalar (Pearson's product–moment) correlation coefficient in the sense that it is formed as a ratio of the covariances to the product of the vari-
ances. The quantity $\xi$ is a rotation/reflection index; if $\xi$ is positive it implies that the relationship between the two sets of vectors is better explained by rotational dependence and if $\xi$ is negative then reflection is a better fit. Lastly, $s$ is simply a sign variable that is used to help automate the calculations.

Two additional quantities can also be computed, a scale factor

$$\beta = s\sqrt{\frac{\sigma_{x}^{2} + \sigma_{y}^{2}}{\sigma_{x}^{2} + \sigma_{y}^{2}}}$$

and a phase angle

$$\theta = \tan^{-1}\left(\frac{\sigma_{xy}}{\sigma_{xx} - \sigma_{yy}}\right).$$

$\beta$ is formed from the ratio of the variances of the two sets of vectors and thus describes their scaling relationship (under rotation or reflection). The phase angle $\theta$ represents the angle of reflection or rotation required to best align the two sets of vectors.

The correlation coefficient $\rho$ ranges from $-1$ to $1$, with $1$ representing a perfect rotational relationship, $-1$ representing a perfect reflectational relationship and $0$ representing no relationship (Hanson et al., 1992). Thus, correlating a field with itself would be representing a perfect rotational relationship,

$$\rho = \frac{\sum(X_i - \bar{X})(Y_i - \bar{Y})}{\sqrt{\sum(X_i - \bar{X})^2} \sqrt{\sum(Y_i - \bar{Y})^2}}.$$
Fig. 3. Idealized scalar response fields and vector fields. (A) Left: Idealized response field with a peak response (white square) at the left middle region of the workspace (top). Middle: Vector field representation of the scalar data. Gradient converges toward the peak response. Right: Vector field plotted in polar format. (B and C) Idealized response fields and vector fields with peaks in the center and right middle portion of the workspace. Correlating the scalar responses in (A) and (C) with those in (B) gave (in both cases) an $r = 0.18$. Correlating the vector fields in (A) and (C) with those in (B) gave $\rho$, $\theta$, and $\beta$ of $-0.59$, $90^\circ$, and $0.9$, respectively.

The examples described above suggest that when response fields undergo relatively large changes in structure, vector correlation generally indicates a reflectional relation between the fields. To investigate more generally the properties of vector correlation under response field shifting, 2D Gaussian fields were generated with peak responses located at 25 equally spaced positions in the workspace, and vector correlations were calculated between each of these ‘shifted’ fields and a reference field centered at 0, 0 (i.e. the one shown in Fig. 3B). Plots of each of the correlation parameters as a function of shift are depicted in Fig. 4. For this relatively simple response field structure the behavior of all parameters was relatively easy to interpret. That is, the correlation coefficient ($\rho$), was moderately high and positive for relatively small shifts of the field away from the center position (4A) and then quickly reversed sign for larger shifts. Regarding the phase ($\theta$), small shifts resulted in virtually no rotation. Larger shifts to the far right (and up) resulted in moderate degrees of positive rotation while those to the right and down resulting in counterclockwise rotations of the field. Scale factors ($\beta$) showed the most sensitivity to shifting, being generally high for the smallest shifts and rapidly diminishing in magnitude for larger shifts (4C).

The discussed trends will of course depend on the particular shape of the response field, including its width. To illustrate the effects of the latter the results of the field shifting analysis are shown in a different format in Fig. 5. Here the parameters are plotted as a function of field shift, quantified as the Euclidean distance between the peaks of the correlated response fields. Results for three different response field widths are shown: the one illustrated in Fig. 3 ($\sigma^2 = 2$), as well as fields with half or double that width. Wider response fields ($\sigma^2 = 4$) resulted in generally higher correlations ($\rho$) and scale factors ($\beta$) for smaller shifts but otherwise all three field widths exhibited the same pattern of decay/reversal with field shift. The phase angle was surprisingly insensitive to variations in field width. For simplicity of presentation, only the negative phase angles are shown for the rotation parameter. Although this parameter also changed abruptly with large field shifts, the behavior was similar for the different widths, i.e. the plot lines representing different field widths are largely superimposed for this parameter.

These examples suggest that vector correlation can provide important information about the degree of relatedness of response fields that can substantially augment scalar correlation analyses. Not surprisingly the scalar correlation coefficient ($r$) degrades in a manner similar to $\rho$ as two fields are systematically shifted with respect to one another (e.g. see Fig. 1). However, the phase and scale parameters arising from vector correlation provide additional
Fig. 4. Variation in vector correlation parameters with response field shifts along the X and/or Y axes. (A) Vector correlation coefficients (ρ), plotted as a pseudocolor map, with redder hues indicating stronger (positive) correlations. (B) Phase (θ): redder hues indicate positive (counterclockwise) rotations. (C) Scale (β): redder hues indicate higher scale factors, indicating greater similarity in scale. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

information regarding precisely how the field is changing (shape vs. scale) and the sign of the phase parameter provides information about the extent of these changes. This information would be particularly useful for interpreting the results of experiments probing frames of reference. That is, two response fields that are shifted by small amounts with respect to one another appear to be associated with relatively strong correlations and low to moderately positive phase angles. Allowing for experimental and neural variability, these would be consistent with the idea that responses in these conditions reflect an encoding of information in the same reference frame. In contrast, low correlations and negative (reflexional) phase angles appear to imply large-scale changes in shape that are inconsistent with a common reference frame.

Clearly, more complex patterns of variation in the vector correlation parameters can be observed under different circumstances. This is illustrated in Fig. 6 which shows the results of the field shifting analysis for an idealized neuron with a more complex field structure than the one in Fig. 3; here the response was simulated as a sigmoidal function of X and a Gaussian function of Y. Although some similarities can be observed between the plots in this figure and those in Fig. 4, there are clearly some substantial differences as well. That is, although vector correlation parameters indicated a relatively high degree of similarity between fields when shifts were small, as demonstrated for the more symmetric 2D Gaussian fields, the pattern of decay with shift was more anisotropic for both the correlation and scale parameters. In instances where real responses exhibit such complex structure, augmentation of vector correlation with simulation procedures might be necessary to assist in interpreting changes in response field shape.

Fig. 5. Variation in vector correlation parameters with response field shift. Data for 2D Gaussian response fields of various widths are shown. Field shift is defined as the norm of the vector joining the peak of a shifted 2D Gaussian with an identical 2D Gaussian located at the center of the workspace.

Fig. 7 shows the vector correlation analysis applied to a real posterior parietal neuron with a relatively simple field structure. These data were recorded in an experiment where a monkey made reaching movements to visual targets on a vertically oriented board of pushbuttons. Four experimental conditions were interleaved in this
Fig. 6. Variation in vector correlation parameters with response field shifts along the X and/or Y axes. Figure conventions as in Fig. 4. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

experiment; in two conditions a monkey fixated the same location on the board while their starting hand position was varied to the left or right of this fixation point (Fig. 7A) and in the other conditions their starting hand position on the board was the same and gaze was varied (Fig. 7B). Mean firing rate is represented by shades of grey on these 2D grids and is scaled to the maximum across the four conditions. The scalar fields appear very similar for the conditions where the same gaze position was used (A) but appear to shift in the conditions where gaze was varied. For this neuron the vector correlation analysis gave a result that was very much in line with the analysis of idealized responses shown in Figs. 3 and 4. Correlation of the fields in A gave a $\rho$, $\theta$, and $\beta$ of 0.91, 29.5°, and 1.2, respectively while correlation of the fields in B gave a $\rho$, $\theta$, and $\beta$ of 0.23, −150.5°, and 0.2. Thus the fields were better correlated in A, where the same gaze position was used, than in B, where the same initial hand positions (and thus movement vectors) were used. This suggests the neuron was encoding target location in a gaze fixed reference frame.

3.2. Field orientations

Quantifying the orientation of a response field can provide valuable insight into the manner in which experimental variables are encoded. Gradients can be used to quantify this important parameter of response field shape (Buneo et al., 2002; Pesaran et al., 2006, 2010). Fig. 8 shows this analysis applied to two different response fields. The left column shows a two-dimensional Gaussian field defined by Eq. (1), but with widths differing slightly along each axis (i.e. $\sigma^2_X \neq \sigma^2_Y$). The right column shows the response field defined by Eq. (7). Panel A shows the scalar response fields, panel B the corresponding 2D vector fields and panel C the vector fields in polar form. As described in Section 2, the field orientations in both cases were obtained by first doubling the angles of the individual field vectors; this has the effect of reflecting half of the vectors in a given field (cf. 8C and D). The vectors in D were then summed to obtain resultants (longer grey vectors) which were then normalized by their respective lengths. The orientation of these vectors indicates the field orientation. For the idealized neuron in the left column, activity changed more rapidly along the X axis due to the inequality of widths (A), thus the field vectors are more strongly biased along this axis (B, C) and the resultant points in the X direction (D). For the neuron in the right column, the response was a function of the difference between $X$ and $Y$. As a result the response of the neuron is tuned along an axis which is orthogonal to the main diagonal (A). The corresponding field vectors (B, C) illustrate this trend clearly. Due to the angle doubling procedure the resultant for this neuron points downward, which is consistent with an encoding of $X−Y$. If $X$ and $Y$ were target and initial hand position respectively, this would indicate that the neuron encoded the difference vector or movement vector, rather than simply the target or initial hand position.
Resampling methods can be used to assess the significance of the vector correlation analyses discussed here. This is illustrated for the field orientation analysis in Fig. 9. Panel A depicts the vector field described by Eq. (7) as a set of black vectors. The grey vectors represent simulated bootstrap-resampled versions of the same field. These were obtained by creating multiple 'noisy' samples of the scalar field and then recalculating the corresponding gradients for each sample. Thus, the black vectors can be thought of as a 'mean' field and the grey vectors as an indication of the field's variance. If one calculates the field orientation for each of the bootstrap samples one can obtain an estimate of its variance as well, illustrated in Fig. 9B as the grey unit vectors. The non-parametric permutation or randomization tests can then be used to determine statistically significant differences in orientation (Efron and Tibshirani, 1993; Good, 2005).

4. Discussion

Vector fields are discussed here as a tool for quantifying changes in receptive and movement fields that result from temporal, attentional, experiential, and task-related phenomena. Vector correlation, a method conceptually analogous to scalar correlation, is shown to substantially augment the latter when quantifying changes in response field shape. Moreover, this additional information is gained without having to shift response fields with respect to one another, which can be problematic for data analysis and interpretation. We also illustrate a variation of this approach in the quantification of one particular aspect of response field shape, i.e. orientation. The relevant merits and drawbacks of these approaches are discussed below, as well as some instances where vector field analyses have been used to successfully analyze neural responses.

Vector correlation possesses distinct advantages over other methods used to quantify changes in response fields. As discussed above, cross-correlation is often used to quantify the degree of relatedness between two response fields. This method necessarily results in loss of data as the fields or tuning curves are systematically slid past each other. In addition, cross-correlation also fails to account for the fact that many response fields are skewed, i.e. asymmetric in shape on each side of the peak response. The vector correlation method however does not require shifting and can provide more information than scalar correlation about the relatedness of two fields as it distinguishes changes in shape from changes in scale. In addition, vector correlation is nonparametric and naturally accounts for asymmetric (skewed) response fields.

The vector correlation method will clearly work best for response fields that can be represented as a 2D grid. As a result the method is not well suited to data sampled on a circle, such as that generated in a center-out task. In addition, although the method accounts for asymmetries in response field shape, our simulations show that the results of vector correlation are most easily interpretable when fields are relatively symmetric. Therefore, for cell populations involving more complex fields or where an assortment of responses exist, it would likely be beneficial to augment the analysis with Monte Carlo simulations.

The field orientation method illustrated here represents an important additional application of vector fields to the analysis of neural responses. This method is designed for tasks where two experimental variables are independently varied; under these conditions field orientations can provide important insights into the manner in which these variables are encoded. For example, Andersen and colleagues have used this method to characterize the responses of reach-related parietal and premotor neurons to independent variations of target position and initial hand position (Buneo et al., 2008; Pesaran et al., 2006). In the premotor cortex, field orientations indicated that these variables were encoded largely as the difference between the position of the hand and target while parietal neurons encoded these variables in a more complex manner. Pesaran et al. (2006) combined the field orientation analysis with singular value decomposition to determine whether response fields encoded these variables separably (implying a 'gain field' representation) or inseparably. These analyses provide a level of insight which...

![Fig. 8. Illustration of the field orientation analysis. (A) Two idealized scalar response fields. (B) Vector field representations of the scalar data. As in Fig. 3, gradients converge toward the peak response(s). (C) Vector fields plotted in polar format. Lengths of the vectors have been normalized to the length of the longest vector. (D) Vector fields after doubling the angles of each of the vectors. Grey vector represents the resultant of the vector field (shortened for illustrative purposes). Note that the angle doubling transforms the space such that orientation is expressed in terms of its dependence on X and Y as well as their sum and difference.](image-url)
could not be obtained through other approaches; thus vector field and related analyses represent an important addition to the repertoire of the neurophysiologists data analysis techniques.

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