Journal of Neuroscience Methods 197 (2011) 109–117

Contents lists available at ScienceDirect

Journal of Neuroscience Methods

journal homepage: www.elsevier.com/locate/jneumeth

Analyzing neural responses with vector fields

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ARTICLE INFO

Article history:
Received 8 November 2010
Received in revised form 23 January 2011
Accepted 15 February 2011

Keywords:
Reference frames
Vector correlation
Gradients
Receptive field
Movement field
Separability

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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0165-0270/$ – see front matter
doi:10.1016/j.jneumeth.2011.02.008

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.

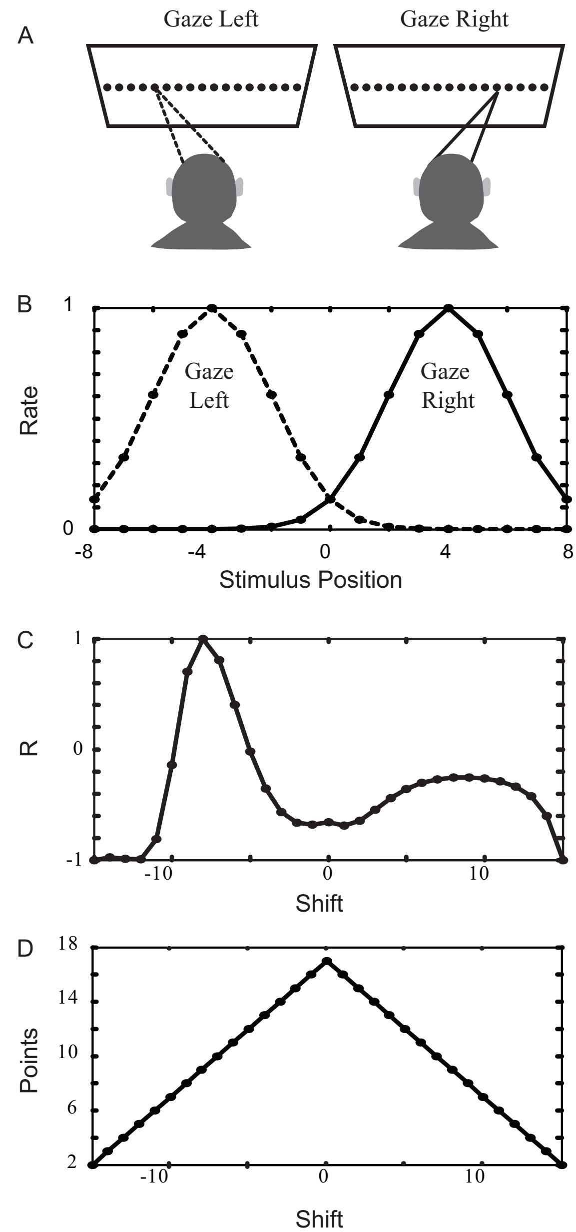

Fig. 1. Cross-correlation of one-dimensional response fields. (A) Illustration of an experiment involving visual receptive field mapping at two gaze positions. (B) Response fields corresponding to the two gaze positions in (A), plotted in world/screen coordinates (arbitrary units). (C) Correlation coefficient (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 is demonstrated using idealized and real response fields in the context of reference frame experiments though the method can be used to quantify 2D field changes in virtually any context. In addition, an extension of the method is discussed in the context of the 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:

$$f(X, Y) = Ae^{-(X^2/2\sigma_X^2+Y^2/2\sigma_Y^2)} \tag{1}$$

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 and which describes the degree of relatedness between two sets of two-dimensional vectors. In addition, the method quantifies the degree of rotational or reflectional dependence and the scaling relationship between the vector fields. Vector fields illustrate rotational dependence when the pairwise difference of the angular components of the vectors is constant. One can then identify the angle of rotation (clockwise or counterclockwise) that best aligns the sets of vectors with respect to one another. Fig. 2A and B show vector fields exhibiting perfect rotational dependence. The field in B can be reproduced by rotating each of the vectors in A counterclockwise by exactly 45°. In contrast, reflectional dependence is implied when the pairwise *sum* of the angular components is constant. Here it is possible to identify the reflectional axis that best aligns the vector fields. The vector fields in Fig. 2A and C demonstrate perfect reflectional dependence: the field in C can be reproduced exactly by reflecting each of the vectors in A about the 45°/225° axis.

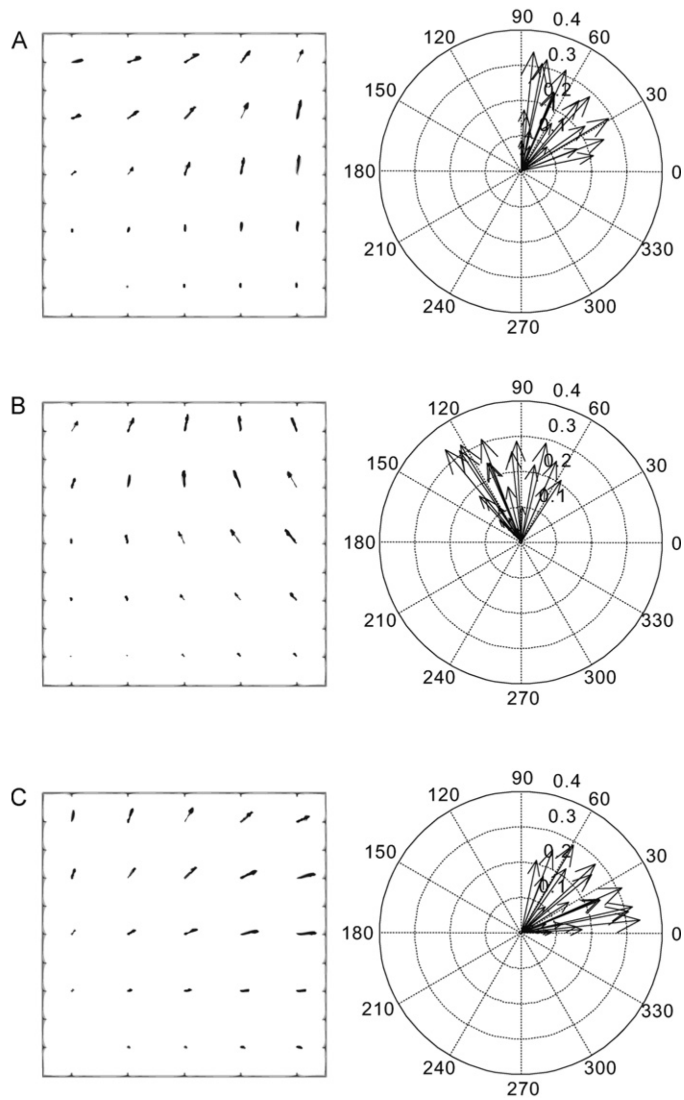

Fig. 2. Illustration of vector field rotation and reflection. (A) Gradient plotted as a two-dimensional vector field (left) and in polar form (right). (B) Vector field obtained by rotating the vectors in A counter clockwise by 45°. (C) Vector field obtained by reflecting the vectors in A about the 45/225° axis.

Derivations of the following equations are given in Hanson et al. (1992) and will not be repeated here. If x and y refer to the components of one set of vectors and u and v the components of the second set, the vector correlation (ρ) can be computed as follows:

$$\rho = s\sqrt{\frac{\sigma_{xu}^2+\sigma_{yv}^2+\sigma_{xv}^2+\sigma_{yu}^2+2s\xi}{(\sigma_x^2+\sigma_y^2)(\sigma_u^2+\sigma_v^2)}} \tag{2}$$

where

$$\xi = \sigma_{xu}\sigma_{yv} - \sigma_{xv}\sigma_{yu}, \tag{3}$$

$$s = \frac{\xi}{|\xi|} \tag{4}$$

and σ_x, σ_y, σ_v, and σ_u represent the variances of x, y, u and v and σ_{xu}, σ_{yv}, σ_{xv}, and σ_{yu} represent the four component covariances. The vector correlation p 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 variances. The quantity ξ is a rotation/reflection index; if ξ is positive it implies that the relationship between the two sets of vectors is better explained by rotational dependence and if ξ 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

$$\beta = s\rho\sqrt{\frac{\sigma_u^2+\sigma_v^2}{\sigma_x^2+\sigma_y^2}} \quad (5)$$

and a phase angle

$$\theta = a\tan\left(\frac{\sigma_{xv}-s\sigma_{yu}}{\sigma_{xu}-s\sigma_{yv}}\right). \quad (6)$$

β 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 θ represents the angle of reflection or rotation required to best align the two sets of vectors.

The correlation coefficient ρ ranges from −1 to 1, with 1 representing a perfect rotational relationship, −1 representing a perfect reflectional relationship and 0 representing no relationship (Hanson et al., 1992). Thus, correlating a field with itself would be expected to give a ρ of 1, a phase angle (θ) of 0° and a scale factor (β) of 1. It is important to note that ρ quantifies the degree of relatedness of the two sets of vectors *after* accounting for the rotational (or reflectional) dependence. Thus, it is possible to have large phase angles between two vector fields while still having correlation coefficients that are close to 1 or −1.

2.2. Field orientations

In some situations it is useful to quantify the orientation of a response field and gradients can be used for this purpose (Buneo et al., 2002). The "field orientation" is essentially the magnitude normalized resultant of the individual vectors in a given field, which provides a concise description of the variable or variables that most strongly determine the firing rate of the cell. Field orientations have previously been used to quantify the manner in which reach and saccade related variables such as target, hand and eye position are represented in single neurons (Buneo et al., 2002; Pesaran et al., 2006, 2010). Although to date these analyses have been used exclusively in the sensorimotor domain they can potentially be used in any circumstance where quantification of field orientations is desirable, for example in the investigation of the space-time separability of visual responses (Deangelis et al., 1995).

Idealized responses were also used to illustrate the field orientation analysis. Here responses were assumed to be obtained in experiments involving independent manipulation of two experimental variables, e.g. space and time (Deangelis et al., 1995), target position and hand position (Buneo et al., 2002), etc. Responses were simulated using either Eq. (1) or the following equation, where X and Y were assumed to be encoded as a single variable:

$$f(X,Y) = e^{-((X-Y)^2/2\sigma_{(X-Y)}^2)} \quad (7)$$

Field orientations were determined by (1) computing the two-dimensional gradient of the scalar response field, (2) doubling the angles of the individual vectors, (3) summing these vectors, and (4) normalizing the result by its magnitude. Angling doubling is commonly used in circular statistics when estimating mean vectors, and prevents cancellation of diametrically opposed groups of vectors (Zar, 1996). Here the angle doubling procedure prevents cancellation of the vectors in cases where the neural response fields are centered and symmetrically shaped. As a byproduct, the procedure transforms the data in such a way that the responses of a neuron can be expressed in terms of their dependence on each of the experimental variables, as well as their sum and difference. This has been shown to be useful for determining the relevant parameters encoded by reach-related and saccade-related cortical neurons (Buneo et al., 2002; Pesaran et al., 2006, 2010).

3. Results

3.1. Vector correlation

As indicated above, vector correlation can be used to quantify changes in two-dimensional response fields arising from virtually any experimental manipulation. Here the technique is illustrated in the context of a reference frame experiment. Fig. 3 shows idealized neural responses plotted on a 5 × 5 grid; this grid could represent horizontal and vertical position on a vertical tangent screen, touch screen, etc. As a result, the choice of axis labels is arbitrary and as a result 'X position' and 'Y position' were used here and throughout. The leftmost columns depict grayscale maps of scalar firing rates, simulated as two-dimensional Gaussian functions of X and Y position (Eq. (1)). The peak response (white square) shifts from left to right in panels 3A–C. These responses could represent the behavior of a retinotopic receptive field in an experiment where gaze is varied from left to right along the X axis. The middle column shows vector field representations derived from the scalar responses. These field vectors clearly converge toward the peak response in all three panels; thus vector fields provide information not only about the location of the peak response but also how rapidly responses changes from location to location within a given response field.

The right column of Fig. 3 shows polar plots of the same field vectors; these plots are useful for visualizing the rotational and reflectional relations between vector fields. Vector correlation of the fields in A and C gave a correlation coefficient (ρ) of −0.24. This negative correlation indicates that reflection (rather than uniform rotation) best described the relationship between these two sets of vectors. Indeed, close inspection of the compass plots suggests the field vectors in C have the same spatial distribution as those in A, reflected about the Y (±90°) axis. This was partially supported by the vector correlation analysis which returned a phase coefficient (θ) of 90°. However, the low correlation coefficient indicates that even after accounting for this reflection the two vector fields were not well correlated. This is due to the fact that in the vector correlation procedure, the 2D structure of each field is preserved. As a result, examination of the compass plots alone (which ignore this structure), can lead to erroneous interpretation of the degree of correlation between fields. To appreciate the latter one has to compare the 2D fields at each position. Doing so reveals that even after each of the vectors in C is reflected, the magnitudes of the two vectors differ at nearly every position, which results in the relatively low degree of correlation.

Vector correlation and scalar correlations can result in markedly different impressions of the degree of relatedness of two response fields. This can again be appreciated from the data in Fig. 3. When the scalar fields in Fig. 3A and C were each compared with the one in 3B using the Pearson product–moment correlation coefficient, the degree of correlation was quite low in both cases (r = 0.18). Note however that the vector fields in A and C illustrate some similarity with the one B in the sense that at least half of the vectors have a similar orientation; this can be best appreciated in the polar plots. In contrast to scalar correlation, vector correlation was sensitive to these similarities: correlation of the fields in A and C with the one if B resulted in a negative correlation, again indicating a reflectional relation, with a phase angle of 90°. The magnitude of this correlation however (0.59) indicated that after accounting for this reflection, the two fields were better related than simple scalar correlation would suggest.

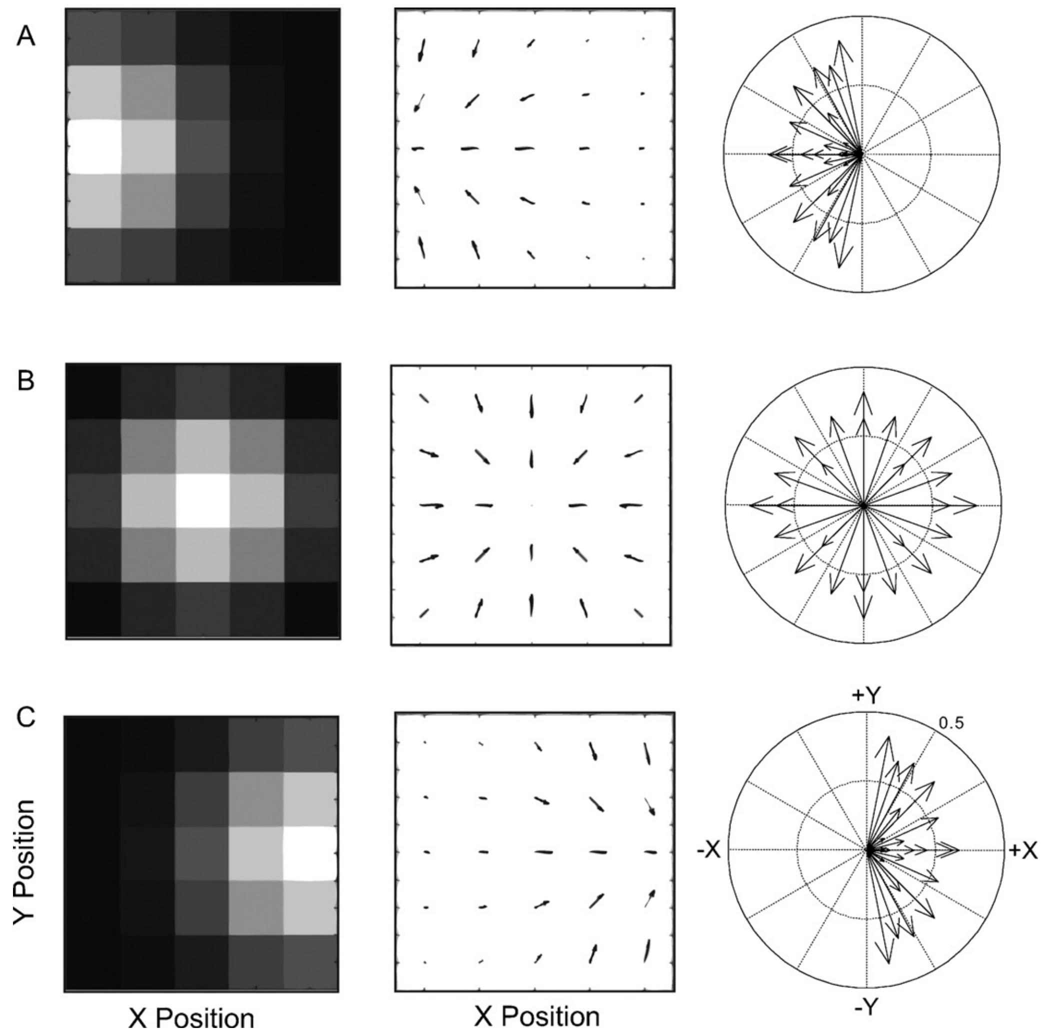

Fig. 3. Idealized scalar response fields and vector fields. (A) Left: Idealized response field with a peak response (white square) at the left middle region of the workspace (top). Middle: Vector field representation of the scalar data. Gradient converges toward the peak response. Right: Vector field 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 a ρ, θ, and β of −0.59, 90°, 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 (ρ), 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 (θ), 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 (β) 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 (ρ) and scale factors (β) 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 ρ 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

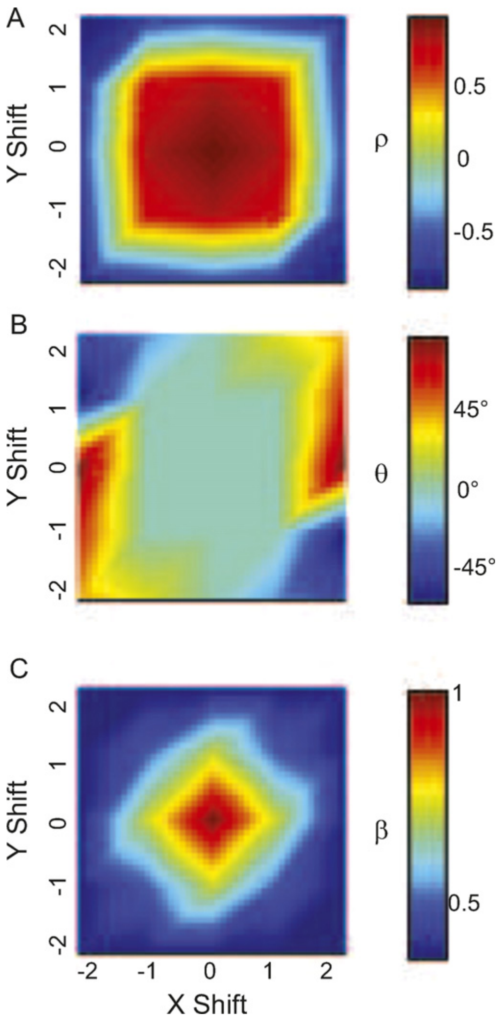

Fig. 4. Variation in vector correlation parameters with response field shifts along the *X* and/or *Y* axes. (A) Vector correlation coefficients (ρ), plotted as a pseudocolor map, with redder hues indicating stronger (positive) correlations. (B) Phase (θ): redder hues indicate positive (counterclockwise) 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.)

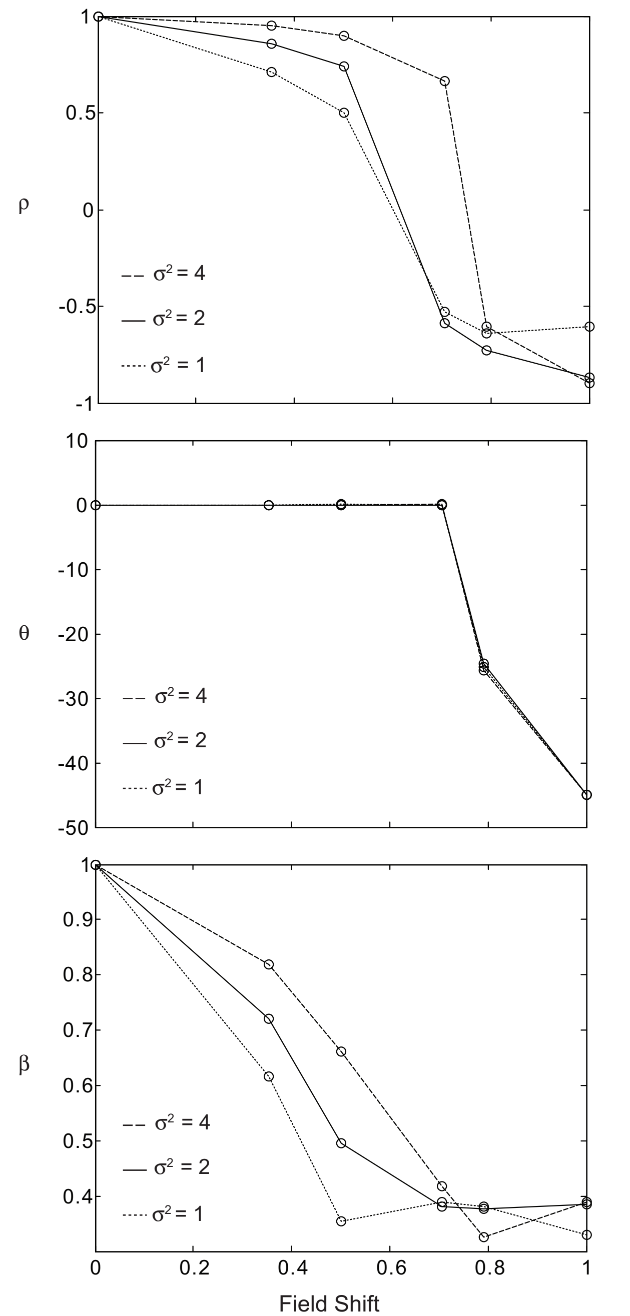

Fig. 5. Variation in vector correlation parameters with response field shift. Data for 2D Gaussian response fields of various widths are shown. Field shift is defined as the norm of the vector joining the peak of a shifted 2D Gaussian with an identical 2D Gaussian located at the center of the workspace.

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 (reflectional) 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 patterns 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. 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

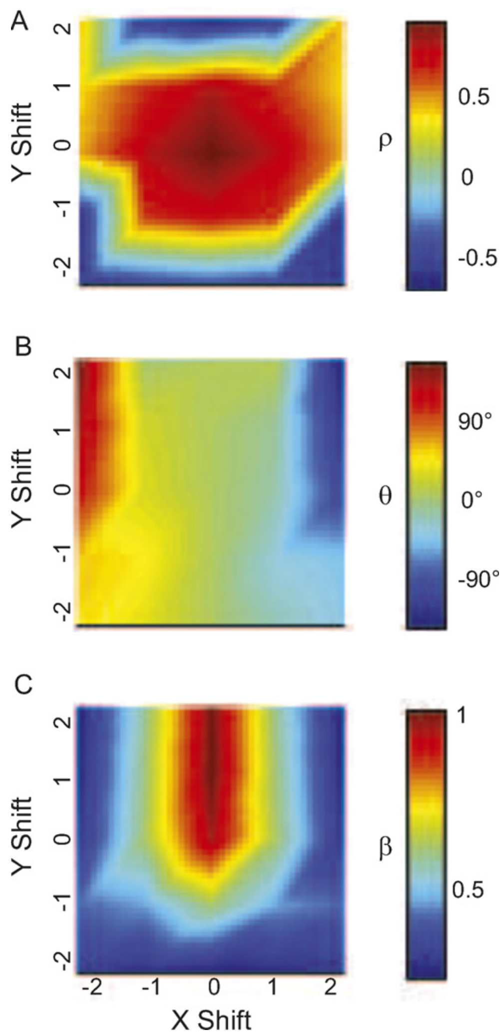

Fig. 6. Variation in vector correlation parameters with response field shifts along the *X* and/or *Y* axes. Figure conventions as in Fig. 4. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

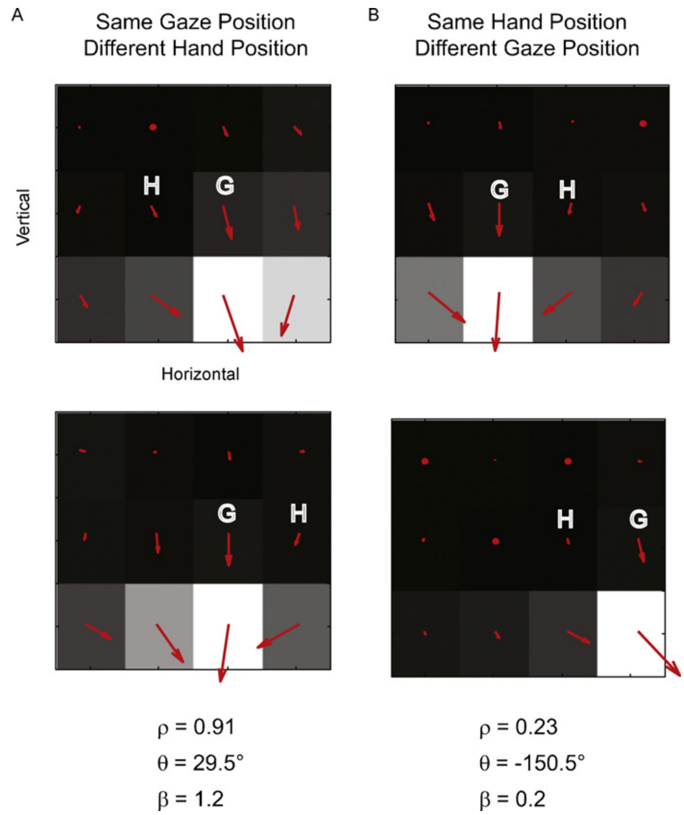

Fig. 7. Vector correlation analysis applied to real neural responses. (A) Response fields and vector fields under conditions where reaching movements were made from two different starting hand positions (H) to 12 target locations (squares) on a vertically oriented board of pushbuttons (top and bottom) while gaze (G) was held fixed. Vector fields were well correlated with a low phase angle, suggesting the same reference frame was used to encode spatial information in the two conditions. (B) Response fields and vector fields under conditions where the same initial hand position was used but gaze was varied. Vector fields were weakly correlated with a high phase angle, which suggests different reference frames were used under these conditions.

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 ρ, θ, and β of 0.91, 29.5°, and 1.2, respectively while correlation of the fields in B gave a ρ, θ, and β 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. $\sigma_Y^2 > \sigma_X^2$). 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 that 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.

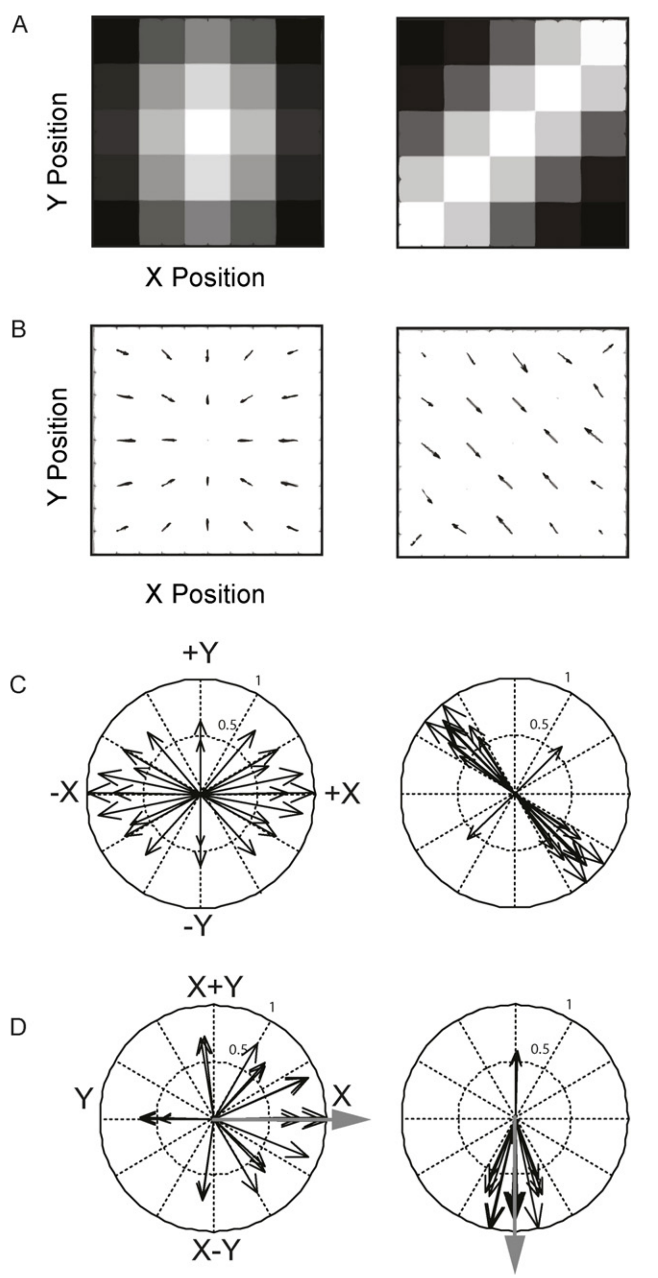

Fig. 8. Illustration of the field orientation analysis. (A) Two idealized scalar response fields. (B) Vector field representations of the scalar data. As in Fig. 3, gradients converge toward the peak response(s). (C) Vector fields plotted in polar format. Lengths of the vectors have been normalized to 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.

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 assymetric (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

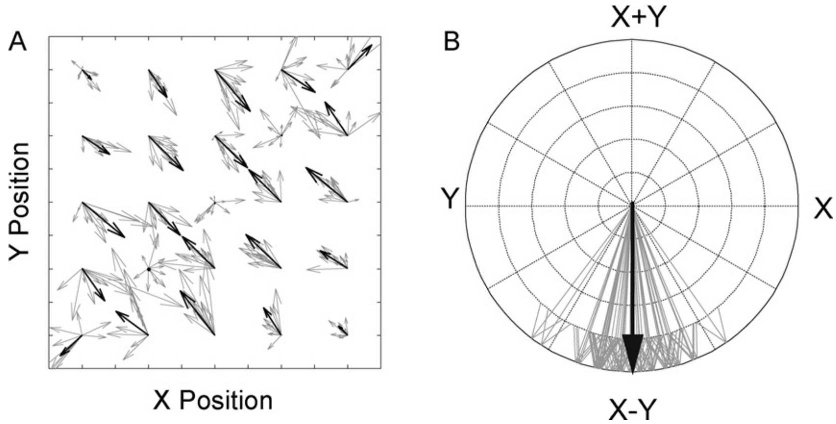

Fig. 9. Bootstrapping of vector fields. (A) Vector field described by Eq. (7) (black vectors) with simulated bootstrap-resampled versions of the same field superimposed (grey vectors). (B) Field orientations for the 'mean' field in A (black) and the bootstrapped fields (grey).

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.

Acknowledgments

This work was supported by National Science Foundation grant IOS-0746398 and Arizona Biomedical Research Commission grant 0813.

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