CHAPTER 5

Neuronal Population Coding: Multielectrode Recordings in Primate Cerebral Cortex

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The central nervous system can be described in terms of its ability to detect and categorize various spatiotemporal patterns in the sensory receptor arrays and to produce coordinated behavior by providing appropriate control signals to the individual effectors. This task is achieved by a vast network of neurons, and, therefore, it may be difficult to fully understand the functional significance of the activity of individual neurons outside the context of the network. Direct information concerning the role of individual neurons in a network can be obtained by simultaneously recording the activity of several neurons. For that purpose, we have been using a seven-electrode system to examine neuronal activity in the primate cortex while the animal performs various behavioral tasks.

This chapter first describes our recording system and software/hardware for spike isolation and then reports some results from our analysis on the activity of neurons recorded simultaneously during a simple visuomotor task. Specifically, we sought to evaluate ensemble measures computed post hoc from a number of trials by comparing them to the same measures computed from a single trial. We were interested in the neuronal population vector (Georgopoulos et al., 1983), which is a measure of the directional tendency in a neuronal ensemble.

The population vector has been used extensively in various applications (see Georgopoulos, 1990, for a review), and in all cases, the calculation of the population vector was based on neuronal activity recorded in different trials. The results, however, were interpreted as if the recordings had been done simultaneously. Our current multielectrode recording system allowed the testing of this crucial assumption: namely, whether the population vector computed from simultaneously recorded trials would differ systematically from that computed from trials recorded at different times. Finally, we used the original method as well as a recent one (Salinas and Abbott, 1994) for calculating the population vector. This latter method, which relies on an optimization technique, is called the optimal linear estimator

(OLE). We found that with the OLE method, movement direction can be estimated with reasonable accuracy for individual trials from about 30 directionally tuned neurons that are simultaneously recorded. Data from a similar number of neurons can be also used to construct time-varying population vectors.

METHODS

Recording System

We recorded extracellularly the impulse activity of individual neurons in the primary motor cortex and in parietal areas 2 and 5, using a seven-electrode system (Uwe Thomas Recording, Marburg, Germany). This recording system, which has been described in detail by Mountcastle et al. (1991), is briefly summarized here. The microdrive consisted of two mated platforms, one fixed to a base and the second driven along the base by a screw linked to a separately mounted stepping motor. Seven stainless steel guide tubes were mounted on the platform. A fiber electrode was passed through each tube across the gap between the movable and stationary platforms, and into the implant thimble. At one position on each of the two platforms, the electrodes were exposed by hemicylindrical holes in the tubes. Small rubber-shod feet attached to miniature solenoids were poised over the electrodes through these holes. Any combination of the seven electrodes could be moved by a microprocessor controlling the activation/deactivation sequence of the solenoids in a brake–clutch action. The distal ends of the tubes could be arranged in any x-y pattern, constrained by the 300 μ tube o.d. We used a linear or circular array of tubes spaced at 330 or 660 μm.

The entire assembly of the microdrive was mounted on a three-dimensional translation stage, which was placed on a heavy professional video camera monocolumn. The electrodes were flexible quartz fibers approximately 80 μm in outer diameter whose 30 μm cores were filled with a platinum–tungsten alloy (Reitboeck, 1983). The filaments were drawn in a high temperature chamber (~2100°C) of nitrogen gas and ground to a conical tip (12–14 μm). The impedance ranged from 1 to 4 MΩ, measured at 1000 Hz.

Spike Data Collection

Each electrode was connected to a head stage, as well as to low-pass and 60 Hz notch filters, a gain amplifier, an equalizing bandpass filter, and a dual-amplitude window discriminator (Bak Electronics, Germantown, MD). The output of the amplifier was connected to a display oscilloscope (Tektronix 2232) and an audio monitor. The output of the discriminator was also connected to a different audio monitor station as well as to a selected bit in the input register of the data collection computer. A multiple spike discriminator (MSD, Alpha-Omega Engineering, Nazareth, Israel) is currently being used in addition to the window discriminators.

Behavioral Task

Two adult male rhesus monkeys were trained to move the handle of a two-dimensional articulated manipulandum described in Georgopoulos et al. (1981).

The visual stimuli were presented on a computer screen, located 57 cm from the animal. The position of the handle was shown on the screen as a feedback cursor (6 mm in diameter) in a one-to-one scale, and the *x-y* position of the handle was sampled at 100 Hz, and with a spatial resolution of 0.125 mm. In the beginning of each trial, a circle appeared in the center of the screen, and the monkey was required to move the handle to align the feedback cursor over the circle. After a random interval between 1 and 3 seconds, one of eight radially arranged stimuli was presented, and the animal was required to move the feedback cursor, capture the stimulus, and hold there for 0.5 second. Correct performance was rewarded by a drop of juice.

Data Analysis

Directional Tuning of Cortical Neurons The activity of most neurons in the primate motor cortex has been successfully described by a cosine tuning function (Georgopoulos et al., 1982, 1988). The mean discharge rate of a neuron for a movement at an angle θ_i can be described by the following regression equation:

$$f(\theta_i) = B_0 + B_1 \sin \theta_i + B_2 \cos \theta_i \tag{5.1}$$

This equation can be reexpressed in terms of the preferred direction,

$$f(\theta_i) = B_0 + A\, cos(\theta_i - \theta_0) \tag{5.2}$$

where θ_0 is the neuron's preferred direction and A is the amplitude of activity modulation. The preferred direction and the amplitude of modulation can be computed from the coefficients from equation (5.1) by the following expressions.

$$\theta_0 = \text{atan}\left(\frac{B_1}{B_2}\right), \tag{5.3}$$

$$A = (B_1^2 + B_2^2)^{1/2} \tag{5.4}$$

In the present report, the preferred direction θ_0 was calculated using trigonometric moments (Mardia, 1972), and this is equivalent to the value obtained using equation 5.3. The statistical significance of directional tuning was determined by a bootstrap (Lurito et al., 1991), using $p < 0.05$ as the level of statistical significance.

Population Vectors Since individual neurons are broadly tuned, the precise direction of movement cannot be inferred from the activity of any single individual neuron; instead the activity of multiple neurons must be observed. The population vector hypothesis (Georgopoulos et al., 1983, 1986) demonstrated how a movement direction can be determined unequivocally from a population of neurons with broad directional tuning. According to this hypothesis, the direction of a movement is determined by a vector sum of the preferred directions weighted by the activity of individual neurons. That is, for a specific direction,

$$\boldsymbol{V}_{\text{vector}} = \sum_{i=1}^{N} w_i \boldsymbol{C}_i \tag{5.5}$$

where $\boldsymbol{V}_{\text{vector}}$ is the estimated movement direction according to the population vector hypothesis, w_i and $\boldsymbol{C}_i$ are the normalized activity and the preferred direction of a neuron i, and N is the number of neurons. The normalized activity was obtained by the following equation:

$$w_i = \frac{R_i - B_i}{R_i^{\max} - B_i} \tag{5.6}$$

where R_i is the average firing rate during the interval between the target onset and the end of the movement, B_i is the background firing rate (same as B_0 in eq. 5.1), and $R_i^{\max}$ is the maximum firing rate. In the following description, this original population vector approach is referred to as the vector method, to distinguish it from the OLE method, described next.

Optimal Linear Estimator Method If the preferred direction is uniformly distributed among the neurons, the vector method as described above provides relatively accurate estimates for the movement direction. When this assumption is not satisfied, however, or when the number of neurons is relatively small, the results can be biased. Recently, a new method was developed that mitigates this problem (Salinas and Abbott, 1994). Known as the OLE, this method minimizes $(\boldsymbol{V}_{\text{est}} - \boldsymbol{V})^2$ averaged over all trials and all movement directions, where $\boldsymbol{V}$ and $\boldsymbol{V}_{\text{est}}$ are the movement vector and its estimate. We denote this estimate as $\boldsymbol{V}_{\text{OLE}}$ to distinguish it from the original population vector, $\boldsymbol{V}_{\text{vector}}$. Similarly to the vector method, $\boldsymbol{V}_{\text{OLE}}$ is also obtained by an average of a series of vectors weighted by the neuronal activities,

$$\boldsymbol{V}_{\text{OLE}} = \sum_{i=1}^{N} w_i \boldsymbol{D}_i \tag{5.7}$$

where w_i is the same as before, and the vector $\boldsymbol{D}$ is determined by

$$\boldsymbol{D}_i = \sum_{j=1}^{N} Q_{ij}^{-1} \boldsymbol{L}_j \tag{5.8}$$

where the vectors $\boldsymbol{L}$ represent the "center of mass" of the tuning curves, determined by the vector average of movement directions weighted by the average activity of a neuron in the same direction over all movement directions, and Q is the correlation matrix of firing rates (Salinas and Abbott, 1994). This correlation matrix Q is obtained by

$$Q_{ij} = \sigma_i^2 \delta_{ij} + \sum_{k=1}^{8} f_i(\theta_k) f_j(\theta_k) \tag{5.9}$$

where σ_i is the standard deviation of the neuronal activity around the mean in each movement direction for the ith neuron, δ_{ij} is the Kronecker delta (i.e., $\delta_{ij} = 1$, if $i = j$, and 0 otherwise), and $f_i(\theta_k)$ is the average neuronal activity for the movement direction θ_k [$\theta_k = 0, 45, 90, \ldots, 315$ degrees, for $k = 1, 2, 3, \ldots, 8$). To obtain the estimated movement direction for individual trials, we used the neuronal activity of individual trials in equation 5.5 with the same D vectors (**D** in eq. 5.8) computed from the average activity.

Calculation of Circular Standard Deviation

Special treatment is required to describe the variability of a directional measure such as movement direction, (Mardia, 1972). In this work, we used the circular standard deviation (CSD) given by

$$S_0 = \{-2 \, 1\text{n}(\overline{R})\}^{1/2} \tag{5.10}$$

where $\overline{R}$ is the length of the mean resultant of the unit length vectors.

RESULTS

Database

The data on which the present analysis is based were obtained from two rhesus monkeys. In one animal, neuronal activity was recorded from 482 cells in the primary motor cortex, whereas in the other animal, recordings were made from 508 neurons located in parietal areas 2 and 5. Among them, 265 in the motor cortex and 293 in the parietal cortex were directionally tuned. Figure 5.1 gives the number of simultaneously recorded neurons for both cortices, along with those that exhibited significant directional tuning.

Comparison of the Online and Post Hoc Methods

In the past, movement direction was estimated from a pool of neurons whose activities were recorded in separate trials. We refer to such a procedure as a *post hoc estimation.* Although we are still limited to relatively small number of neurons that were recorded simultaneously(Fig. 5.1), these data provided an opportunity to compare a post hoc reconstruction of movement direction with an online estimation based on the neuronal activities from a single trial. For the online estimation, we used the activity of simultaneously recorded neurons for individual trials to calculate the circular standard deviations of the estimated movement directions. For the post hoc estimation, we relied on the same data used in the online estimation, but the activity of each neuron was drawn from a randomly selected trial in the same condition. This post hoc estimation was repeated as many times as there were trials (five for each movement direction).

In general, the accuracy in estimation of movement direction improved as the number of simultaneously recorded neurons was increased (Fig. 5.2). In addition, for both the motor (Fig. 5.3) and the parietal (Fig. 5.4) cortices, the results showed

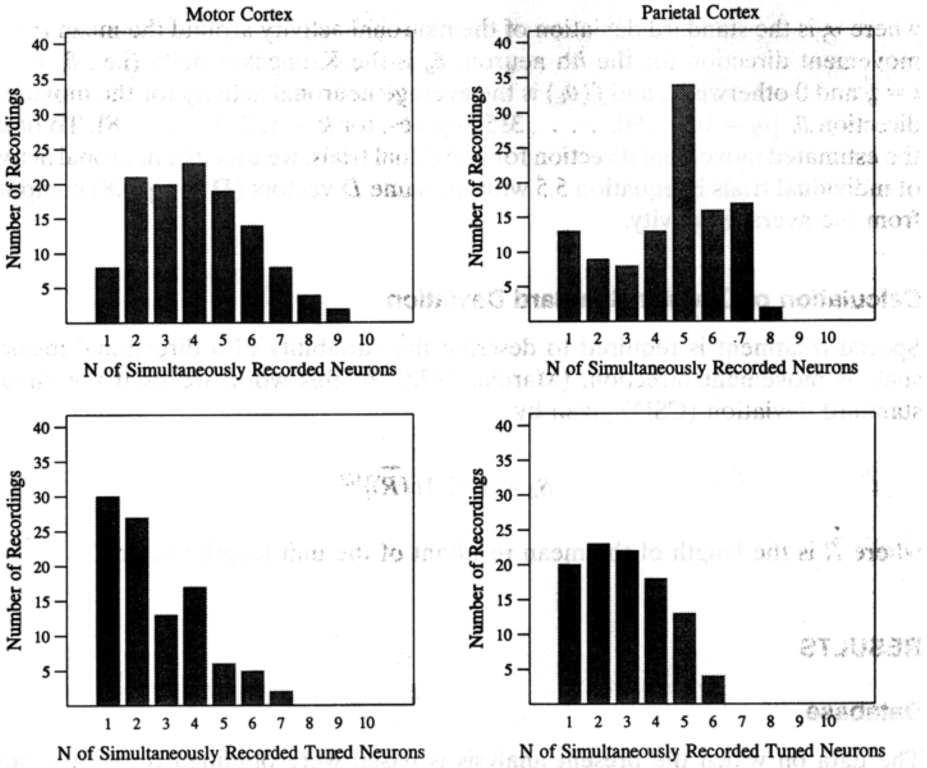

Figure 5.1 Frequency histograms showing the number of neurons (*top:* all cells, *bottom:* directionally tuned neurons) simultaneously recorded in the motor cortex and in the parietal cortex.

that for accuracy of the estimated movement direction, the online and post hoc methods were indistinguishable, irrespective of whether the movement direction was estimated using the conventional vector method or the OLE method. For both areas, the 95% confidence intervals for the slope and the intercept from the linear regression analysis applied between the circular standard deviations for the online and the post hoc methods included one and zero, respectively. In addition, the paired t test showed no significant difference in the circular standard deviations between these two methods.

Significance of Correlated Noise

Theoretically, any difference between the online and the post hoc estimations must be due to the correlation of the trial-to-trial variability in the activity of neurons recorded simultaneously, because such correlation is eliminated in any procedures based on the post hoc reconstruction. For example, if every neuron in a pool displayed identical activity for repeated trials in each direction of movement (i.e., no trial-to-trial variability), we would have to conclude that there was no difference between the post hoc and online methods. Similarly, the variability of movement direction estimated from a pool of neurons increases with the magnitude of trial-to-trial variability (Fig. 5.5).

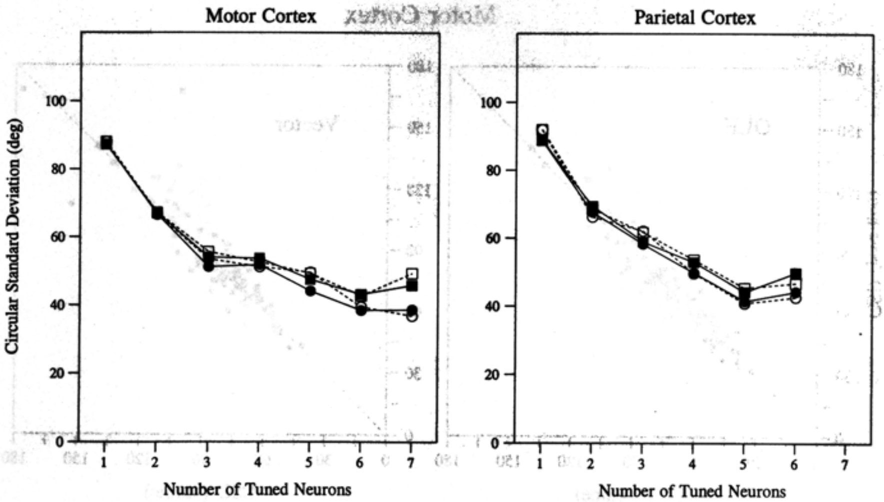

Figure 5.2 Comparison of online (solid symbols) and the post hoc (open symbols) estimations of movement direction for motor cortex and parietal cortex obtained by means of the conventional vector method (squares; Georgopoulos et al., 1983) and the OLE method (circles; Salinas and Abbott, 1994). For all cases in which there were any directionally tuned neurons (see Fig. 5.1, bottom), online estimations were performed using activities of the neurons in a single trial, whereas post hoc estimations were done by drawing activity of each neuron from a randomly selected trial in the same movement direction.

Another important factor is whether such trial-to-trial variability is correlated across different neurons. Since a movement direction is estimated from an array of directionally tuned neurons, if the same noise is introduced into all neurons simultaneously on any given trial, such noise would be canceled out between pairs of neurons with opposite preferred directions and thus would have no effect on the direction estimation. Therefore, for a given level of trial-to-trial variability in the activity of individual neurons, the variability of movement directions estimated in a neuronal population would decrease as the magnitude of correlated trial-to-trial variability among different neurons increased. A brief mathematical explanation for this relationship is presented in the Appendix 5.1.

It is reasonable to assume that in the post hoc estimation of movement direction, trial-to-trial variability in neuronal activity is not correlated across different neurons, since these activities were drawn from randomly selected trials. Thus, the finding that the online method and the post hoc method have virtually identical accuracy (see above) implies that the trial-to-trial variability is not correlated even for the neurons that are recorded simultaneously. To test this hypothesis, we analyzed the correlation of the trial-to-trial variability between all the pairs of simultaneously recorded neurons in our database. Trial-to-trial variability was computed as the difference between the activity of a neuron on a given trial and the average activity of the same neuron for the same direction of movement. Even though the range of correlation coefficients was substantial, the median correlation coefficient of neuronal noise was close to zero; it was 0.0130 and 0.0039, for the motor and parietal cortices, respectively (Fig. 5.6).

At least two different sources of trial-to-trial variability are possible in neuronal activity: One source may be related to the trial-to-trial variability in the kinematics

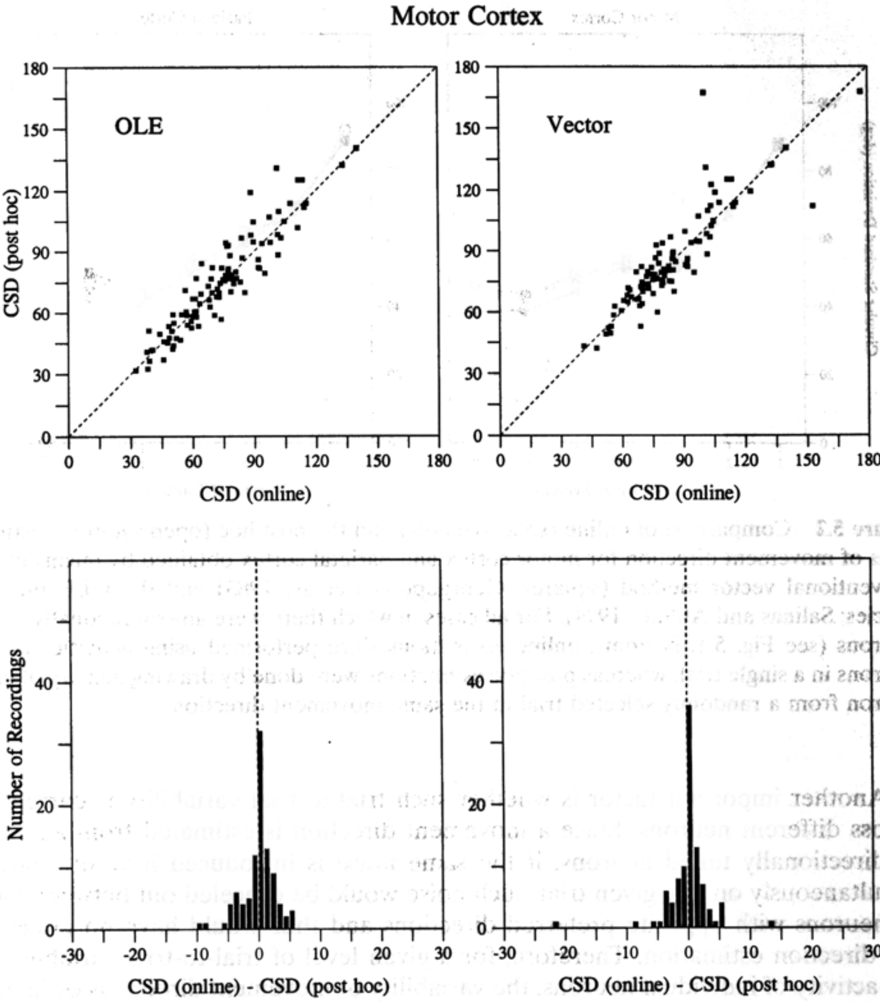

Figure 5.3 Comparison of online and the post hoc estimations of movement directions for the motor cortex. Circular standard deviation (CSD) for the post hoc estimation of movement direction (ordinate) is plotted against the CSD for the online estimation (abscissa). Movement direction was estimated using either the OLE (left) or the vector (right) method. Individual squares represent the values obtained from a group of neurons recorded in the same experimental session; the number of neurons ranged from 1 to 7 (Fig. 5.1). For the online estimation, the data from the same trials were used, whereas for the the post hoc estimation, the same data were reshuffled to eliminate any possible correlation in the trial-to-trial variability among the activity of the neurons. Frequency histograms show the difference in the CSD between the online and the post hoc methods.

of hand movements or, the variability may be pure noise. If the variability of neuronal activity is related to the kinematic variability, it would be correlated among the simultaneously recorded neurons, because they all share the same motor responses. In our data, the trial-to-trial variability was not correlated, and therefore it is unlikely to be related to the variability in the movements.

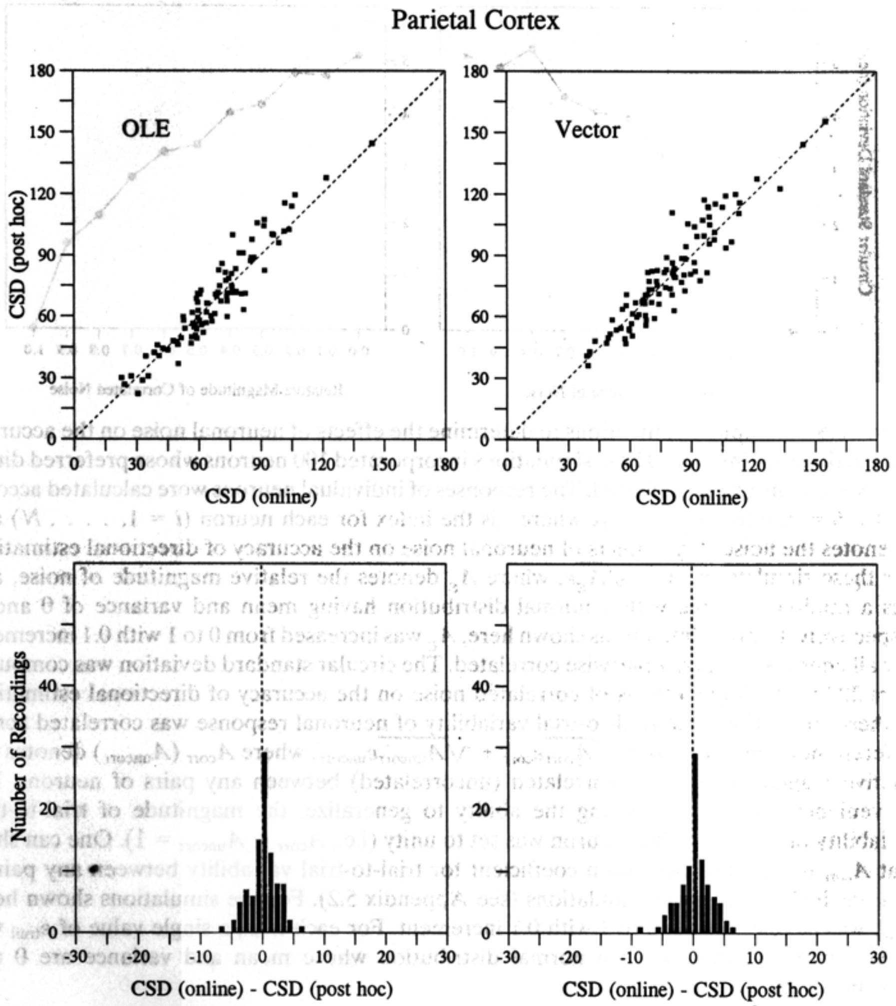

Figure 5.4 Comparison of online and the post hoc estimations of movement directions for the parietal cortex. Conventions as for Figure 5.3.

Size of the Neuronal Population

It has been already demonstrated that the OLE method provides more accurate estimates of movement directions than the original vector method (Salinas and Abbott, 1994, their Fig. 6). That analysis, however, was based on average activities computed over several repetitions for each of eight movement directions. Since activities of individual neurons include larger trial-to-trial variability than their average values, we wanted to find out the number of neurons needed to provide reasonably accurate online estimates of movement directions for individual trials. Although the maximum number of directionally tuned neurons recorded simultaneously in our database was too small to provide a direct answer to this question (Fig. 5.1), we had already shown that the post hoc estimation of movement direction provides equally accurate results. Therefore, we drew variable numbers of neurons

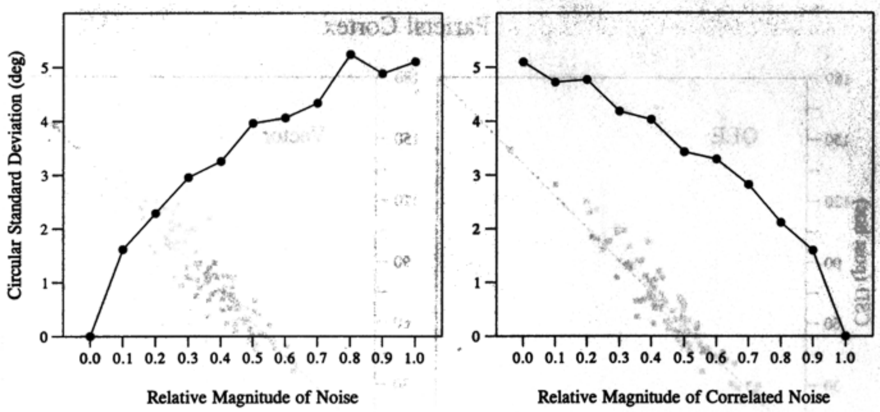

Figure 5.5 Computer simulations to determine the effects of neuronal noise on the accuracy of directional estimation. These simulations incorporated 100 neurons whose preferred directions were uniformly distributed. The responses of individual neurons were calculated according to: $f_i = \cos(360 \times i/\mathrm{N}) + \rho$, where i is the index for each neuron ($i = 1, \ldots, N$) and ρ denotes the noise. *Left:* effects of neuronal noise on the accuracy of directional estimation. For these simulations, $\rho = \sqrt{A_\varepsilon}\varepsilon$, where A_ε denotes the relative magnitude of noise, and ε is a random variable with a normal distribution having mean and variance of 0 and 1, respectively. For the simulations shown here, A_ε was increased from 0 to 1 with 0.1 increment. For all neurons, ε was not pairwise correlated. The circular standard deviation was computed from 200 trials. *Right:* effects of correlated noise on the accuracy of directional estimation. In these simulations, the trial-to-trial variability of neuronal response was correlated across different neurons. Thus, $\rho = \sqrt{A_{\mathrm{corr}}\varepsilon_{\mathrm{corr}}} + \sqrt{A_{\mathrm{uncorr}}\varepsilon_{\mathrm{uncorr}}}$, where A_{corr} (A_{uncorr}) denotes the relative magnitude of noise correlated (uncorrelated) between any pairs of neurons. For convenience, but without losing the ability to generalize, the magnitude of trial-to-trial variability on any individual neuron was set to unity (i.e., $A_{\mathrm{corr}} + A_{\mathrm{uncorr}} = 1$). One can show that A_{corr} is also the correlation coefficient for trial-to-trial variability between any pair of neurons included in these simulations (see Appendix 5.2). For the simulations shown here, A_{corr} was increased from 0 to 1 with 0.1 increment. For each trial, a single value of $\varepsilon_{\mathrm{trail}}$ was drawn for all neurons from a normal distribution whose mean and variance are 0 and 1, respectively.

from our database to simulate a larger number of simultaneously recorded neurons. By applying the post hoc method to such sets of data, we found that about 30 directionally neurons provided reasonably accurate estimates of static movement directions in both motor and parietal cortices (circular standard deviation or mean error <10 degrees; Figs. 5.7 and 5.8).

Time-Varying Movement Vectors and Time Variance of Neural Computation

Critical in any post hoc directional estimation is the assumption that the relevant motor output and underlying neural computation are relatively invariant. This is an especially important issue when movement vectors are estimated in a time-varying fashion (e.g., Georgopoulos et al., 1989; Schwartz, 1994). In the past, the post hoc method was used for such analyses, and therefore the behavioral responses had to be relatively time-invariant. For more complex behaviors, however, it may

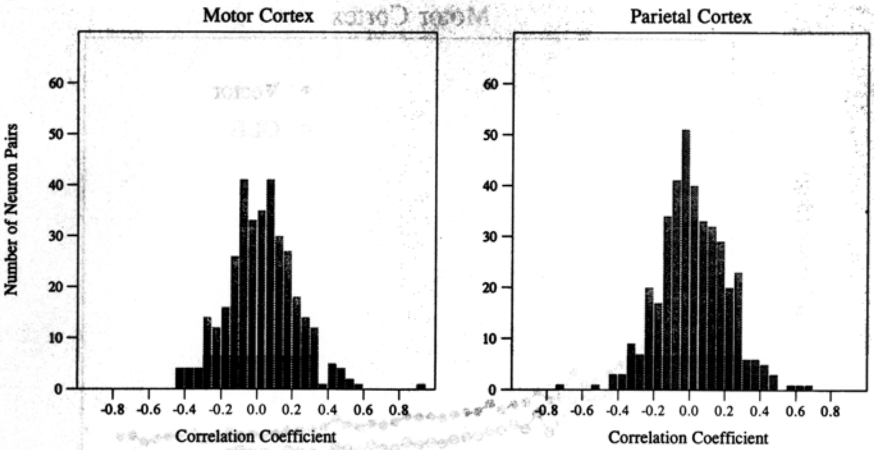

Figure 5.6 Frequency histogram showing the distribution of correlation coefficients for trial-to-trial variability in the neuronal activity (or noise) between a pair of neurons that were recorded simultaneously in the motor cortex and the parietal cortex. Trial-to-trial variability was obtained by subtracting the mean activity in each condition (same movement direction) from the activity in each trial. The median correlation coefficient was 0.0130 and 0.0039, for the motor cortex and the parietal cortex, respectively.

not be practical to meet this assumption of time invariance (e.g., Pellizzer et al., 1995; Lee et al., 1997; Port et al., 1997). In such cases, an online method should be used. Therefore, we wanted to find out roughly how many neurons would be required to construct reliable time-varying movement vectors for a single trial using the OLE method. For the movement we examined (i.e., reaching toward stationary targets), we found that about 40 neurons, thus roughly the same number of neurons needed for the static vectors, gave rise to reasonably consistent time-varying movement vectors (Fig. 5.9). These results were obtained using the post hoc method.

DISCUSSION

Online Estimation of a Directional Signal in the Primate Cortex

The increasing availability of various multichannel, single cell recording techniques is leading to many new experiments and data analyses. This chapter focuses on the possibility of online estimation of a directional signal, that is, observing directional signals from activities of neurons that are simultaneously recorded during a single trial. The most common method for estimating a directional signal has been the population vector (Georgopoulos et al., 1983, 1986), but the recently developed OLE method is more sensitive (Salinas and Abbott, 1994). Using both methods, we compared the results of online estimation with those of post hoc estimation where any correlated trial-to-trial variability among different neurons was eliminated. We found that there was no systematic difference in the accuracy of directional signals estimated by the two methods. Through mathematical analysis and computer simulation, we also showed that given the same level of noise, the presence of correlated noise could in principle ameliorate the reduction in the accuracy of the estimated directional signal. These results

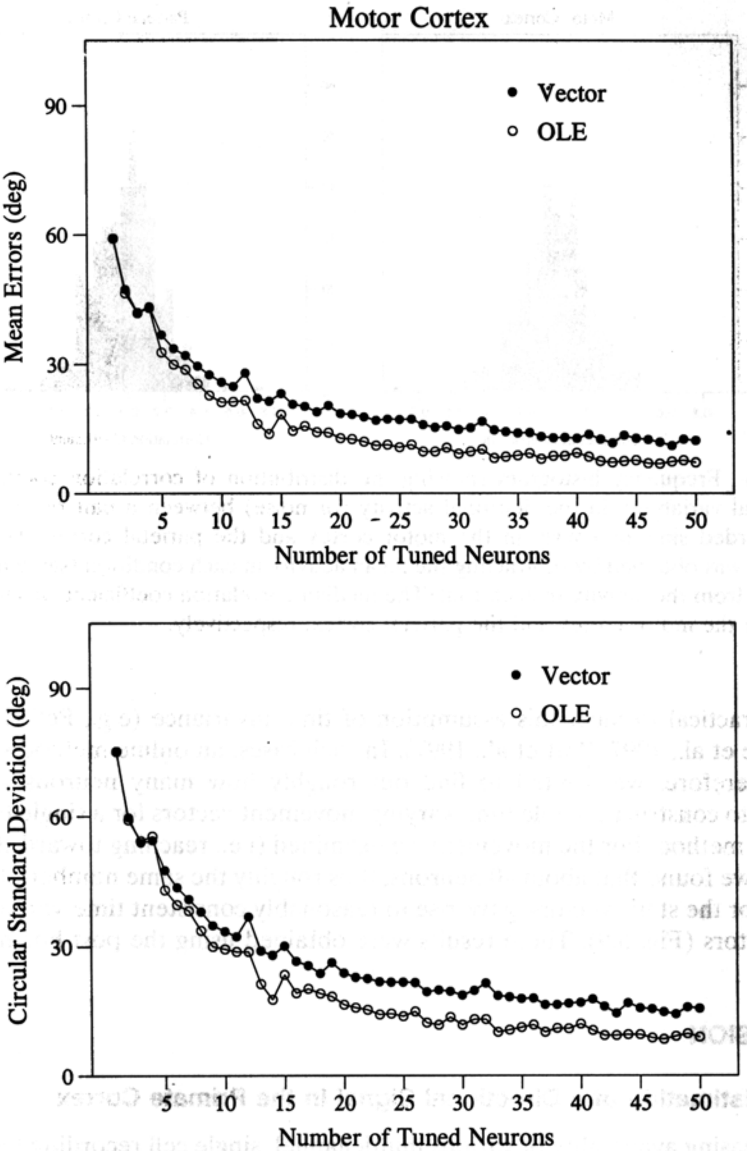

Figure 5.7 Effects of the number of neurons on the accuracy of directional estimation in the motor cortex. Accuracy of estimation is expressed as the mean of the angle between the direction of the target and the estimated population vector or the circular standard deviation for the same angle. Results from both the conventional vector method and the OLE method are shown.

suggest that the trial-to-trial variability in the activity of simultaneously recorded neurons is not correlated between pairs of cells. When correlations of trial-to-trial variability between all pairs of simultaneously recorded neurons were computed to test this hypothesis, the distributions of the correlation coefficients for such neuronal noise were found to be centered around zero.

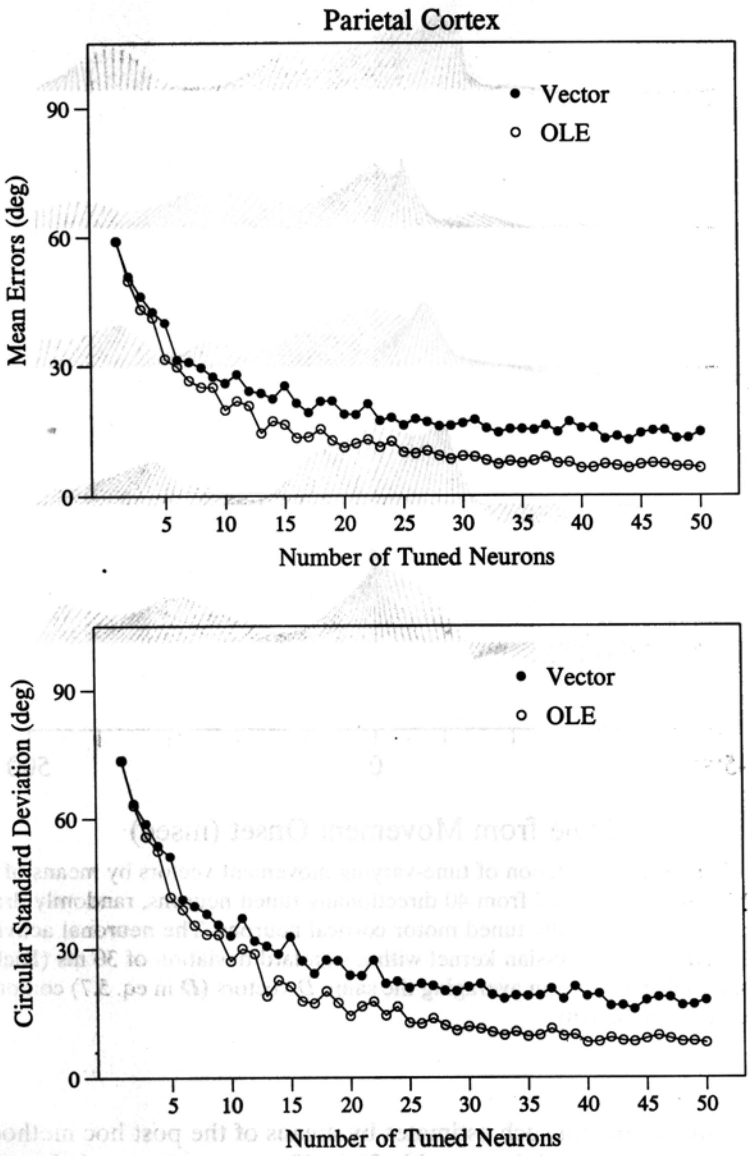

Figure 5.8 Effects of the number of neurons on the accuracy of directional estimation in the parietal cortex. Conventions as for Fig. 5.7.

For both the original vector method and the OLE method, more accurate directional estimation can be obtained as the size of the neuronal pool increases. On the other hand, the OLE method can provide more accurate estimation than the vector method for the same number of neurons (Salinas and Abbott, 1994). Even for the OLE method, however, the largest number of simultaneously recorded neurons in our database was still too small to permit us to estimate the minimum number of simultaneously recorded neurons necessary to obtain a relatively accurate online estimation. Nevertheless, similar accuracy of online and post hoc estimations

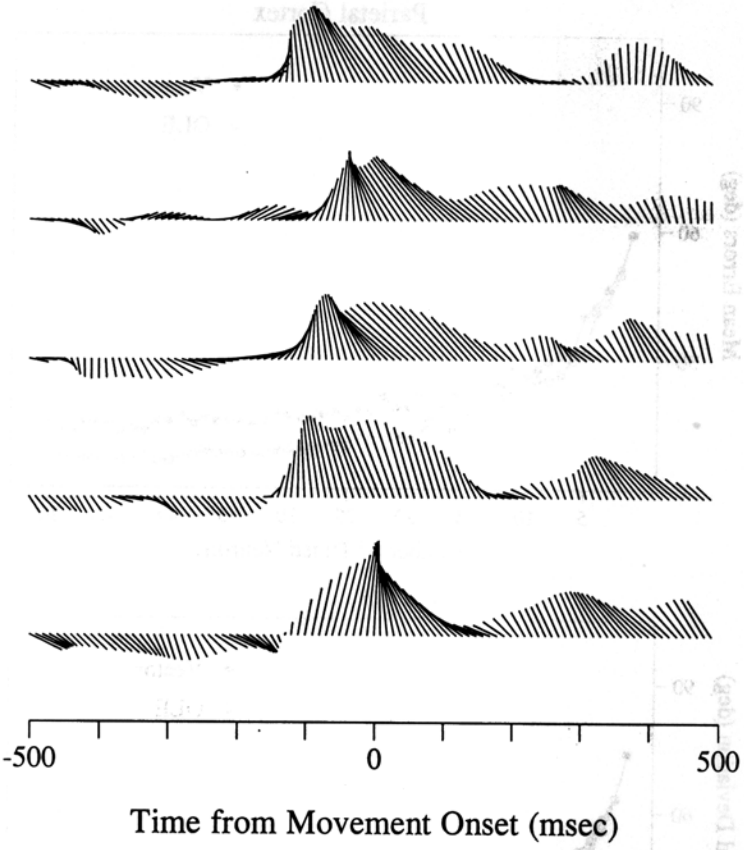

Figure 5.9 Post hoc construction of time-varying movement vectors by means of the OLE method. These were computed from 40 directionally tuned neurons, randomly drawn from our sample of 265 directionally tuned motor cortical neurons. The neuronal activities were low-pass-filtered using a Gaussian kernel with a standard deviation of 30 ms (Richmond et al., 1987) and used as weights in averaging the same D vectors ($\boldsymbol{D}$ in eq. 5.7) computed from the average neuronal activity.

made it possible to obtain such estimates by means of the post hoc method. Using the OLE method, we found that roughly 30 to 40 neurons are needed to obtain an estimation with a standard deviation of less than 10 degrees.

Although these two different methods of directional estimation produced similar results for a simple movement directed straight toward the target, online estimation may be more appropriate for estimating the time course of a directional signal, since trial-to-trial variability in the time course of the process itself can degrade the signal. To apply post hoc estimation of a directional signal in the time domain, it is essential that the time course of relevant overt/covert behavioral responses remain invariant (e.g., Georgopoulos et al., 1989; Schwartz, 1994). In online estimation, this problem is avoided because only the activities of neurons that are recorded simultaneously with the same behavioral response are used to estimate the directional signal. Since the type of movement chosen for the work reported here is highly stereotyped, we simulated the online estimation of a time-varying directional signal by the same randomization technique used for the static directional estimation. From this analysis, we predict that about 40 neurons, which is roughly the same number needed to estimate static movement direction, would also yield a consistent online estimate of a time-varying directional signal.

Significance of Correlated Neuronal Noise in Directional Coding

To relate activities of individual neurons to an animal's behavior, it is not sufficient to know the average (or signal) and the variability (or noise) of individual neurons. It is also necessary to know how noise is correlated among the neurons in a pool and to have a quantitative model attempting to explain how neuronal activities are combined. The work of Newsome and his colleagues (Britten et al., 1992, 1996; Zohary et al., 1994; Shadlen et al., 1996) offers an excellent example. The goal of these investigators was to explain the following major findings from their experiments involving a direction discrimination task:

1. Sensitivities of individual neurons in the middle temporal area (MT) are similar to psychophysical sensitivity of the animal (Britten et al., 1992).
2. For subthreshold stimuli, there is a weak correlation between the responses of individual MT neurons and the animal's decision.

In the model developed to reconcile these empirical findings (Shadlen et al., 1996), it was assumed that the psychophysical decision is based on the comparison of average responses between two groups of neurons that signal two alternative directions of visual motion. The investigators showed that the animal's decision could be best modeled by pools of about 100 neurons with weakly correlated noise, the inclusion of a broad range of sensitivities, and the introduction of a central source of noise in the pooling stage (Britten et al., 1996). It was also necessary to assume that the noise is less correlated between the two opposing pools than among the neurons in the same pool. An average correlation coefficient between 0.1 and 0.3 was required to establish correspondence between the model and the empirical data, and the average correlation coefficient of neuronal noise among the neurons in the macaque middle temporal cortex that were simultaneously recorded through the same electrode was within this range (Zohary et al., 1994).

In the population vector hypothesis, it is assumed that the pooling occurs not just via two pools of neurons with opposite preferred directions, but across all neurons whose preferred directions are more or less uniformly distributed. Just as adding pooling noise increases the psychophysical threshold in the preceding model (see Fig. 5 in Shadlen et al., 1996), larger noise resulted in more variability in the estimated direction in the vector averaging (Fig. 5.5). On the other hand, the effects of correlated noise were quite different. In the preceding model for direction discrimination (Britten et al., 1992; Shadlen et al., 1996), the responses of individual neurons were averaged before the responses of the two opposing pools were compared, and it was assumed that the noise is not correlated between these two pools, thus confining effects of correlated noise within the pool of neurons with similar preferred directions. In such a case, correlated noise will result in increased variability in the pooled signal, since variance of any linear combination of two variables can be expressed as the weighted sum of variance of these two variables and the covariance between these two variables as follows:

$$\text{var}\,(aX + bY) = a^2\,\text{var}\,(X) + b^2\,\text{var}\,(Y) + 2ab\,\text{cov}(X, Y) \qquad (5.11)$$

From this equation, we can also see that if we subtract one variable from another ($a = 1$, $b = -1$, for eq. 5.11), as with the responses of two neurons with opposite preferred directions, the variability of the pooled signal will be less when these two variables are positively correlated. This simple mathematical consideration demonstrates that the effects of correlated noise depend on the model that specifies how activities of individual neurons are combined. In the case of vector averaging, such as the original vector method and the OLE method for estimating movement direction, the effects of correlated noise on the directional estimation are eliminated because the noise is canceled between any two neurons with opposite preferred directions. This would be true as long as the pattern of correlation remained symmetrical around zero in terms of the preferred directions of the two neurons.

We found that on average, the correlation coefficient for neuronal noise was very small, virtually zero. For both motor cortex and parietal cortex, the median correlation coefficient was smaller than 0.02. These values appear to be similar to those found in the inferior temporal cortex (Gawne and Richmond, 1993). The mean R^2 for the correlated noise in that study was 0.055, and the corresponding values for our data are 0.0403 and 0.0341, for the motor and parietal cortices, respectively. Without knowing the distribution of individual data points from the earlier study, however, it is difficult to determine whether these small differences are statistically significant. The average correlation coefficients in our study, nevertheless, are substantially smaller than the average correlation coefficient found between pairs of neurons in MT (Zohary et al., 1994). On the other hand, it is important to realize that in our study simultaneous recordings of multiple neurons were made through multiple electrodes whose spacing was varied from 0 to about 4 mm, whereas in the other studies such recordings were made through the same electrode. As pointed out elsewhere (Zohary et al., 1994; Shadlen et al., 1996), it is likely that adjacent neurons share more common inputs and thus display stronger correlation in their noise than others with larger interneuronal distance. Results of our preliminary analysis indicated that, in fact, correlation in the neuronal noise increases for the pairs of neurons with similar preferred directions that were recorded through the same electrode (Lee et al., 1998).

ACKNOWLEDGMENTS

We thank Adam Carpenter, Giuseppe Pellizzer, and Kenneth Whang for their helpful comments on the manuscript. This study was supported by U.S. Public Health Service grant no. 1-PSMH48185-01, the Department of Veterans Affairs, and the American Legion Chair in Brain Sciences.

APPENDIX 5.1

Effects of Correlated Noise in Directional Estimation

The activity of the *i*th neuron in the *j*th trial can be denoted as follows

$$w_i^j = w_i + \sqrt{\lambda_i}\,\varepsilon_i^j \tag{A5.1}$$

where w_i is the average activity of the same neuron for a given movement direction, $\sqrt{\lambda_i}$ is the standard deviation of the trial-to-trial variability, and ε_i^j is a random variable whose mean and the variance are 0 and 1, respectively. Then, the equation for the OLE-estimated movement direction (eq. 5.7) can be rewritten as follows:

$$\boldsymbol{V}_{\mathrm{OLE}}^j = \sum_{i=1}^{N} w_i^j \boldsymbol{D}_i = \sum_{i=1}^{N}\left(w_i + \sqrt{\lambda_i}\varepsilon_i^j\right)\boldsymbol{D}_i = \sum_{i=1}^{N} w_i \boldsymbol{D}_i + \sum_{i=1}^{N}\sqrt{\lambda_i}\varepsilon_i^j \boldsymbol{D}_i \tag{A5.2}$$

Since w_i is constant across different trials, the trial-to-trial variability of $\boldsymbol{V}_{\mathrm{OLE}}^j$ is identical to that of $\Sigma_{\mathrm{i}=1}^{\mathrm{N}}\sqrt{\lambda_i}\varepsilon_i^j\,\boldsymbol{D}_i$. Now, if such noise ($\varepsilon_i^j$) is correlated among any number of neurons, it can be further decomposed into a part that is common to these neurons and the second part that is uncorrelated among them:

$$\begin{aligned}\sqrt{\lambda_i}\varepsilon_i^j &= \sqrt{\lambda_{\mathrm{corr}}}\varepsilon_{\mathrm{corr}}^j + \sqrt{\lambda_{\mathrm{uncorr}}}\varepsilon_{\mathrm{uncorr}}^j \\ \sqrt{\lambda_i} &= \sqrt{\lambda_{\mathrm{corr}}} + \sqrt{\lambda_{\mathrm{uncorr}}}\end{aligned} \tag{A5.3}$$

where relative values of λ_{corr} and $\lambda_{\mathrm{uncorr}}$ determine how strongly noise is corrleated, $\varepsilon_{\mathrm{corr}}^{\mathrm{j}}$ is a constant for all neurons but varies from trial to trial, $\varepsilon_{\mathrm{uncorr}}^j$ varies for each neuron and each trial, and both are random variables whose mean and variance are 0 and 1, respectively. Thus, equation 5A.2 can be now written as

$$\boldsymbol{V}_{\mathrm{OLE}}^j = \sum_{i=1}^{N} w_i \boldsymbol{D}_i + \sum_{i=1}^{N}\sqrt{\lambda_{\mathrm{corr}}}\varepsilon_{\mathrm{corr}}^{\mathrm{j}}\boldsymbol{D}_i + \sum_{i=1}^{N}\sqrt{\lambda_{\mathrm{uncorr}}}\varepsilon_{\mathrm{uncorr}}^j\boldsymbol{D}_i \tag{A5.4}$$

If the vector $\boldsymbol{D}$ were uniformly distributed in all directions, $\Sigma_{i=1}^{N}\sqrt{\lambda_{\mathrm{corr}}}\varepsilon_{\mathrm{corr}}\boldsymbol{D}_i$ would be close to zero, because $\varepsilon_{\mathrm{corr}}$ is constant for all neurons in any given trial.

Therefore, for a given level of trial-to-trial variability in the activity of individual neurons (i.e., λ_i = constant), trial-to-trial variability in V^j_{OLE} would decrease with stronger correlation of noise across neurons in a population. In other words, what is detrimental to the estimation of the directional signal is the proportion of noise that is not correlated among different neurons, not the absolute magnitude of trial-to-trial variability.

APPENDIX 5.2

The Correlation Coefficient for Neuronal Noise

This appendix presents the calculation of the correlation coefficient for the neuronal noise between a pair of neurons included in the simulations shown in Figure 5.5. If we assume that a part of the noise is correlated among all neurons, the neuronal noise can be expressed as follows:

$$\rho = \sqrt{\mathrm{A}_{\mathrm{corr}}\varepsilon_{\mathrm{corr}}} + \sqrt{\mathrm{A}_{\mathrm{uncorr}}\varepsilon_{\mathrm{uncorr}}}$$

where A_{corr} (A_{uncorr}) denotes relative magnitude of noise correlated (uncorrelated) between any pairs of neurons, and $\varepsilon_{\mathrm{uncorr}}$ and $\varepsilon_{\mathrm{corr}}$ are the random variables with the zero mean and the unit variance. If we assume, for convenience, but without losing the ability to generalize, that the neuronal noise has a variance of unity, then *r*, the correlation coefficient of the neuronal noise between any pair of neurons, is identical to its covariance and can be obtained as follows:

$$\begin{aligned} r &= E[\rho^2] \\ &= E[(\sqrt{A_{\mathrm{corr}}\varepsilon_{\mathrm{corr}}} + \sqrt{A_{\mathrm{uncorr}}\varepsilon_{\mathrm{uncorr}}})^2] \\ &= A_{\mathrm{corr}}E[\varepsilon^2_{\mathrm{corr}}] + A_{\mathrm{uncorr}}E[\varepsilon^2_{\mathrm{uncorr}}] + 2\sqrt{A_{\mathrm{corr}}}\sqrt{A_{\mathrm{uncorr}}}E[\varepsilon_{\mathrm{corr}}\varepsilon_{\mathrm{uncorr}}] \\ &= A_{\mathrm{corr}} \end{aligned}$$

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