Effects of Noise Correlations on Information Encoding and Decoding

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Averbeck, Bruno B. and Daeyeol Lee. Effects of noise correlations on information encoding and decoding. J Neurophysiol 95: 3633–3644, 2006. First published March 22, 2006; doi:10.1152/jn.00919.2005. Response variability is often correlated across populations of neurons, and these noise correlations may play a role in information coding. In previous studies, this possibility has been examined from the encoding and decoding perspectives. Here we used d prime and related information measures to examine how studies of noise correlations from these two perspectives are related. We found that for a pair of neurons, the effect of noise correlations on information decoding can be zero when the effect of noise correlations on the information encoded obtains its largest positive or negative values. Furthermore, there can be no effect of noise correlations on the information encoded when it has an effect on information decoding. We also measured the effect of noise correlations on information encoding and decoding in simultaneously recorded neurons in the supplementary motor area to see how well d prime accounted for the information actually present in the neural responses and to see how noise correlations affected encoding and decoding in real data. These analyses showed that d prime provides an accurate measure of information encoding and decoding in our population of neurons. We also found that the effect of noise correlations on information encoding was somewhat larger than the effect of noise correlations on information decoding, but both were relatively small. Finally, as predicted theoretically, the effects of correlations were slightly greater for larger ensembles (3–8 neurons) than for pairs of neurons.

INTRODUCTION

The possibility that patterns of activity across neurons are important features of the neural code has led to their study from a number of perspectives. Many of these studies have focused on noise correlation, which is between neuron correlation in the variability of the neural response to a fixed stimulus, with the response often measured as a spike count (Gawne and Richmond 1993; Lee et al. 1998). Noise correlations should be distinguished from signal correlations, which are correlations in average spike count, and from coherent oscillations, which decompose noise correlations into multiple temporal or frequency points (Averbeck and Lee 2004). Here we examine the role of noise correlations in information encoding and decoding. Studying information encoding involves studying the mapping between the stimulus and the population neural response, and estimating the total amount of information present in the neural responses. To evaluate the effect of noise correlations on information encoding, we can determine whether neurons with correlated noise encode more or less information relative to those without correlated noise. Studying information decoding involves studying the mapping from the population neural response to a prediction of the stimulus. When we assess the effects of noise correlations on information decoding, we calculate the amount of information lost when a decoding algorithm derived by ignoring correlations is applied to the neural responses with noise correlation.

Theoretical studies using Fisher Information have examined the effect of correlations on the information encoded by populations of neurons. Fisher Information bounds the variance with which a parameter encoded by a population of neurons can be estimated (Casella and Berger 1990). These studies have found that noise correlations can increase or decrease the information encoded with respect to an uncorrelated population, depending on their relationship with signal correlation (Johnson 1980; Snippe and Koenderink 1992). They have also found that information either grows with the number of neurons in a population (Abbott and Dayan 1999; Shamir and Sompolinsky 2004; Wilke and Eeurich 2002) or saturates as the number of neurons goes to infinity (Sompolinsky et al. 2001; Zohary et al. 1994), depending on the structure of the correlations in the population. Theoretical work has also been done on the effect of noise correlations on information decoding (Shamir and Sompolinsky 2004; Wu et al. 2001). However, how the effects of noise correlation on information encoding and decoding are related has not been systematically investigated.

Empirical studies have focused on whether more or less information can be extracted from neural responses when trials are shuffled, destroying correlations, (Averbeck et al. 2003; Gawne and Richmond 1993; Gawne et al. 1996; Gollledge et al. 2003; Panzeri and Schultz 2001; Panzeri et al. 1999, 2002; Petersen et al. 2001, 2002; Pola et al. 2003; Rolls et al. 2003; Romo et al. 2003) or whether correlations could be ignored by decoding algorithms without a loss of information (Averbeck and Lee 2003; Dan et al. 1998; Maynard et al. 1999; Nirenberg et al. 2001; Oram et al. 2001). These studies have generally found that noise correlations have little impact on information coding (Averbeck and Lee 2004). However, they have only analyzed interactions at the level of pairs of neurons. Finally, a number of other studies have considered neural coding at the ensemble level, but they have not directly addressed the effects of noise correlations on encoding or decoding (Brown et al. 1998, 2004; Nicolelis et al. 1997; Truccolo et al. 2005).

The effects of noise correlations on neural coding have been assessed using information measures and decoding algorithms. In general, there are many different ways to quantify information (Arndt 2001). In this study, we measured information using the square of d prime (d²) and used d² to estimate the fraction or percent correct we obtained in corresponding decoding analyses. This allowed us to link directly the results of
using an information measure ($d^2$) and using a decoding analysis to study the effects of noise correlations. Although measures of the fraction correct are often closely correlated with Shannon information (Averbeck et al. 2003), it is theoretically possible to dissociate them (Thomson and Kristan 2005). The fraction correct is more directly related to behavior in experiments in which stimuli must be discriminated or movements must be produced. Because $d^2$ is the discrete analog of Fisher Information, the use of $d^2$ on our experimental data provides an assessment of the effect of correlations similar to that used in the theoretical studies cited above. Finally, $d^2$ is a simple measure, and therefore its interpretation is straightforward. We exploit this simplicity to examine how the effects of noise correlations on information encoding and decoding are related because both encoding and decoding have been studied in the literature, but they have not been linked.

In our results, we show extensively that $d^2$ provides an accurate measure of the amount of information in the neural activity recorded from the supplementary motor area of monkeys. In this study, information refers to the discriminability of the targets toward which the monkey reached. The analyses also showed that the decoding performance predicted by $d^2$ agreed closely with the results from actually carrying out the corresponding linear decoding analyses and that nonlinear decoding algorithms do not extract more information than a linear decoding algorithm. Thus both $d^2$ and the corresponding linear decoding algorithms provide an accurate measure of the information in the neural activity.

METHODS

General

The data set analyzed in this study has been described previously (Lee and Quessy 2003). All the procedures used in this study were approved by the University of Rochester Committee on Animal Research and conformed to the principles outlined in the Guide for the Care and Use of Laboratory Animals (National Institutes of Health Publications No. 85–23, revised 1996). Neurons analyzed in the present study were recorded from the left caudal supplementary motor area (SMA-proper or F3) in two rhesus macaques producing sequences of visually guided reaching movements.

Behavioral task

Two animals were trained on the serial reaction time task shown in Fig. 1. They sat facing a computer monitor on which a series of targets was presented in a $4 \times 4$ grid. The animals acquired each target by reaching toward the corresponding location on a touch screen placed horizontally in front of the animal. After acquisition of a target, the subsequent target was presented after a 250-ms delay. A correct trial consisted of a sequence of 10 target acquisitions after which a juice reward was given. All data analyzed in this study were obtained from the task condition in which the monkey repeated a deterministic sequence of three movements three times (i.e., a single trial was 3 repeats of a 3 target sequence, for example, ABCABCACA as shown in Fig. 1), with the first target of the sequence repeated at the end of the sequence. A new target sequence was selected randomly for each recording session. The minimum number of trials analyzed was 152, and the average was 267. Because each movement was repeated three times in each trial, 545 repetitions of each movement were available for analysis, with an average of 801.

Data preprocessing

We analyzed the responses of 193 pairs and 19 ensembles of simultaneously recorded neurons. The data for each trial were split into epochs corresponding to each of the ten movements of the sequence. Data from the first movement were not considered because they followed the inter-trial interval and varied from trial to trial. Neural activity in the period from 0 to 200 ms after target onset was used to predict the target toward which the animal was about to reach. Previously, we found that the optimal classification accuracy was obtained when we split the 200-ms epoch into 3 bins of 66-ms duration (Averbeck and Lee 2003). Thus the same three bins were used for the analyses shown in Figs. 4 and 5. For the analyses in which a single 66-ms window was considered (Figs. 7 and 8), the final 66 ms of the 200-ms epoch (i.e., from 134 to 200 ms) was used because this tended to contain the most information.

In our previous work (Averbeck and Lee 2003), the neural responses were used to predict one of the three possible movement targets (e.g., A, B, or C in Fig. 1). In this paper, we decoded targets in pairs because this is the case described by $d$ prime, as discussed in the following text. Pairwise analyses of the three targets resulted in three separate analyses for each set of neural responses considered. For most of the analyses in the present study, we averaged the results from the three different pairs of targets. For the decoding analysis carried out on ensembles of neurons (Fig. 5), we showed the results separately for each target pair because a relatively small number of ensembles were available for that analysis.

Analysis of $d$ prime, encoding, and decoding

In the present study, we used $d^2$ to measure information. Figure 2A shows the components of $d^2$, which is defined as

$$d^2 = \frac{(\mu_i - \mu_j)^2}{\sigma^2} = \frac{\Delta \mu^2}{\sigma^2}$$

where $\mu_i$ indicates the mean spike count of a neuron to target $i$ and $\sigma^2$ is the variance of spike count. This plot shows that $d^2$ is a measure of the discriminability of samples from two Gaussian response distributions, characterized by the same variance and different means. In our case, these response distributions correspond to the spike counts of a single neuron for two different movement directions. In RESULTS, because we always considered the responses of more than one neuron, we used a multivariate generalization (Poor 1994), given by

$$d^2 = \Delta \mu^T Q^{-1} \Delta \mu$$

where $\Delta \mu$ is the vector difference in mean responses to the pair of targets and $Q$ is the pooled or average covariance matrix with the
average taken across targets. The dimensionality of $\Delta \mu$ and $Q$ depends
on the specific analysis. For example, when pairs of neurons and three
time bins are analyzed, the dimensionality is 6. Multiplying by the
inverse covariance matrix is analogous to dividing by the variance in
Eq. 1. We also used two other measures that, when combined with $d^2$,
provide an estimate of the effect of noise correlations on information
encoding and decoding. The first is a measure of the information
that would be contained in the neural responses if they were uncorrelated.

We call this $d^2_{\text{shuffled}}$ because shuffling trials is often used to destroy
 correlations in neurophysiological data. It is defined as

$$d^2_{\text{shuffled}} = \Delta \mu^T Q_{\text{diag}}^{-1} \Delta \mu$$  \hspace{1cm} (3)

where $Q_{\text{diag}}$ is the diagonal covariance matrix obtained by setting the
off-diagonal elements corresponding to correlations between neurons
to 0. Finally, we defined $d^2_{\text{diag}}$ as

$$d^2_{\text{diag}} = \frac{(\Delta \mu^T Q^{-1} \Delta \mu)^2}{\Delta \mu^T Q_{\text{diag}}^{-1} Q_{\text{diag}}^{-1} \Delta \mu}$$  \hspace{1cm} (4)

This measures the amount of information that would be extracted
by using a decoding algorithm that ignored correlations on the original
unshuffled dataset. We refer to this as $d^2_{\text{diag}}$ because it amounts to
assuming a diagonal covariance matrix for the neural responses when
deriving the decoding algorithm. In this case, the decoding algorithm
is suboptimal. This quantity can be derived by computing the variance
of the linear decoder obtained by ignoring correlations with respect to
the real response distribution. It was derived for Fisher Information
by Wu et al. (2001) as a local linear approximation. In our case, the
formula is exact because the difference in the mean responses is
maximally separable because it amounts to
diagonalizing the distributions, projection onto a sub-optimal
decision boundary, for example one derived by ignoring correlations,
always results in worse classification performance, in theory. Corre-
spondingly, $d^2_{\text{diag}}$ as it would be measured in the distribution on the
left, cannot be larger than $d^2$, as it would be measured in the
distribution on the right, and decoding algorithms that ignore corre-
lations cannot lead to fewer misclassifications.

Given $d^2$, $d^2_{\text{shuffled}}$ and $d^2_{\text{diag}}$, we can estimate the effects of noise
correlations on information encoding and decoding. The effect of
noise correlations on decoding, which we will refer to as $\Delta d^2_{\text{diag}}$, is
given by

$$\Delta d^2_{\text{diag}} = d^2 - d^2_{\text{diag}}$$  \hspace{1cm} (5)

This quantity estimates the difference between the total amount of
information that could be extracted from the neural responses using an
optimal decoder, and the amount of information that would be
extracted by a decoding algorithm which ignored correlations. Be-
cause information can only be lost by a decoding algorithm that
ignores correlations, $\Delta d^2_{\text{diag}}$ is always positive. Similarly, the effect of
noise correlations on the information encoded, $\Delta d^2_{\text{shuffled}}$, is given by

$$\Delta d^2_{\text{shuffled}} = d^2 - d^2_{\text{shuffled}}$$  \hspace{1cm} (6)

This quantity measures the difference in the information between the
correlated neural responses, and the information that would be in
a fictitious dataset of uncorrelated neural responses. $\Delta d^2_{\text{shuffled}}$ can be
positive or negative.

The measures $d^2$, $d^2_{\text{shuffled}}$ and $d^2_{\text{diag}}$, can each be converted to
percent correct classification performance for the corresponding case
(Poor 1994). In Fig. 2, the portion of the distribution for target 1 to the
right of the classification boundary would be misclassified as having
come from the distribution for target 2. Therefore we can write the
probability of missclassification using the error function as

$$p(t = 2 | \hat{t} = 1) = \frac{1}{\sqrt{2\pi}} \int_{-\infty}^{\hat{t}} \exp\left(-\frac{(x - \hat{\mu})^2}{2\sigma^2}\right) dx$$  \hspace{1cm} (7)

where $\hat{\mu}$ refers to the decision boundary, $\hat{t}$ is the predicted target, and
t is the actual target. If we make the change of variables, $z = (x - \mu)/\sigma$, we get

$$p(t = 2 | \hat{t} = 1) = \frac{1}{\sqrt{2\pi}} \int_{\frac{-\hat{\mu}}{\sigma}}^{\infty} \exp\left(-\frac{z^2}{2}\right) dz$$  \hspace{1cm} (8)

FIG. 2. Illustration of $d^2$: A: $d^2$ measures the separability of 2 Gaussian distributions. The portion of the left distribution that is shaded in yellow would be
incorrectly classified using the optimal decision boundary indicated at the midpoint between the distributions. Therefore an estimate of the amount of the left
distribution lying to the right of the midpoint provides an estimate of the percentage of movements which would be misclassified. B: projection of multivariate
response distributions onto a linear discriminant line (solid line). The dotted lines represent corresponding decision boundaries. The green lines correspond to
the optimal decision boundary and the red lines to the sub-optimal decision boundary obtained by ignoring correlations. Classification is carried out by projecting
responses (example $r$) onto the discriminant line perpendicular to the decision boundary.
Finally, noting that \( \mu - \mu_2 = (\mu_2 - \mu_1)I_2 \), we can rewrite Eq. 8 as the normalized error function, with a lower integration limit of \( d/2 \)

\[
p(t|t-1) = (2\pi)^{-1/2} \exp \left( -\frac{1}{2} r^t Q^{-1} r \right)
\]

Which shows that the function correct is only a function of \( d \), where \( H \) is the complementary error function. From Eq. 9 we can calculate the percent correct performance or accuracy as

\[
A = 1 - P(t|t-1) = 1 - H(d/2)
\]

(Eq. 10)

Equation 10 shows that the percent correct is only a function of \( d \). Although Eq. 9 was derived for the univariate case, given by Eq. 1, it is the same for Eq. 2 as discussed in the preceding text. The predicted classification performance shown in the results was obtained by first calculating \( d_i \), \( d_{i+} \), and \( d_{i-} \) per Eqs. 2–4 for each pair or ensemble of neurons. Then Eq. 10 was used to convert each of these to the corresponding decoding accuracy, denoted as \( A_i \), \( A_{i+} \), and \( A_{i-} \). We then refer to the changes in accuracy related to the effect of noise correlations on encoding and decoding as \( \Delta A_{i+} \) and \( \Delta A_{i-} \), respectively, and these were calculated as follows

\[
\Delta A_{i+} = A_i - A_{i+}
\]

\[
\Delta A_{i-} = A_i - A_{i-}
\]

(Bhattacharyya distance)

We also used the Bhattacharyya distance (BD) as an information measure (Basseville 1989) because it does not make the assumption of equal covariance matrices implicit in \( d^2 \) and thus provides a measure of the information in the differential variance and covariance of the neural response to different targets. The BD is a special case of the Chernoff distance, which was recently used in the analysis of V1 responses (Kang et al. 2004). The BD is given by

\[
BD[p(r|t-1), p(r|t-2)] = -\log \int \sqrt{p(r|t-1)p(r|t-2)}dr
\]

where the integral is over all possible responses, \( r \). If we assume additive Gaussian noise, the response distributions are given by

\[
p(r|t-i) = [2\pi Q_i]^{-1/2} \exp \left[ -\frac{1}{2} (r - \mu_i)^T Q^{-1}_i (r - \mu_i) \right]
\]

(Eq. 14)

where \( r \) is a vector of spike counts for a given movement, \( \mu_i \) is the vector of mean spike counts for target \( i \), the superscript \( T \) indicates transpose, \( Q_i \) is the noise covariance matrix for target \( i \), and \( i \) indicates the determinant of the matrix. Substituting Eq. 14 into Eq. 13 leads to the BD for Gaussian distributions (Basseville 1989)

\[
BD_{0} = \frac{1}{4} \mu^T (Q_1 + Q_2)^{-1} \mu + \frac{1}{2} \log \left[ \frac{Q_1 + Q_2}{2\sqrt{Q_1 Q_2}} \right]
\]

(Eq. 15)

The first term of Eq. 15 is equal to \( d^2/8 \). Thus the second term indicates contributions due to the difference in covariance for different targets.

If covariance matrices vary between targets, the maximum likelihood estimator for the target is a quadratic Gaussian classifier (Johnson and Wichern 1998). This is referred to as a quadratic classifier because it contains terms that are products of firing rates between pairs of neurons. If the covariance matrices are the same across targets, the maximum likelihood estimator is a linear classifier, which does not contain interaction or product terms of the responses of individual neurons.

Decoding analyses

We compared the predicted percent correct classification performance based on \( d^2 \) (Eq. 10) to the results of carrying out decoding analyses and classifying the data movement by movement. Although it may seem counter-intuitive to use decoding analyses to estimate the effects of noise correlations on information encoding, an optimal decoder will extract all of the information available in the neural responses, and in our encoding analyses, we are trying to determine how much information is encoded. This was the approach adopted originally by Bialek and his colleagues (Bialek et al. 1991; Rieke et al. 1997). The effects of correlations on information decoding were examined using a sub-optimal decoder, specifically one that assumed that there were no noise correlations. In this case, the question is how much information is lost when the suboptimal decoder is used.

The Gaussian decoding analyses have been described in detail previously (Averbeck and Lee 2003). Two-fold cross validation was used whenever different decoding algorithms were being compared. In general, the target was predicted by selecting the target with the maximum probability from the conditional distribution of targets given the neural activity. This can be formalized as

\[
\hat{t} = \arg \max \frac{p(t|r)}{p(r)}
\]

where \( \hat{t} \) is the estimated target for the subsequent movement and \( p(t|r) \) is the conditional probability distribution of a target, \( t \), given the response vector, \( r \), that represents the response of one or more neurons across a given number of bins. The conditional probability of \( t \) is given by Bayes’ rule

\[
p(t|r) = \frac{p(r|t)p(t)}{p(r)}
\]

(Eq. 16)

The likelihood for the Gaussian model is given by Eq. 14. We fit linear models by estimating a single, pooled covariance matrix for both targets, and we fit quadratic models by estimating separate covariance matrices for each target. These covariance matrices were the same as those used to calculate the predicted accuracy described in the preceding text, using \( d^2 \).

The decoding analysis based on the linear Gaussian model was carried out under three conditions to derive values for the measured accuracy shown in Figs. 4 and 5. These conditions were in correspondence with the predicted accuracy, derived from \( d^2 \), \( d_{i+} \), and \( d_{i-} \), given by Eq. 10. In this study, we only analyzed the effect of noise correlations, i.e., correlations between neurons, not autocorrelations which were analyzed in a previous study (Averbeck and Lee 2003). In the first condition, which was used as an estimate of \( A \), the decoding analysis was carried out on the original dataset using a covariance matrix that used the measured values for the noise correlations. In the second condition, which was used as an estimate of \( A_{\text{shuffled}} \), the analysis was carried out on a shuffled dataset. The shuffling effectively destroyed the correlations between neurons. The shuffling analysis was carried out five times, and the average of these five analyses was used as the estimate. In the final analysis, a decoding model was used in which all off-diagonal elements of the covariance matrix that correspond to inter-neuronal correlations were set to zero. This model was then applied to the original unshuffled dataset. This was used as an estimate of \( A_{\text{diag}} \) and corresponds to the independent model from our previous work (Averbeck and Lee 2003). Thus the decoding model was essentially the same for \( A_{\text{shuffled}} \) and \( A_{\text{diag}} \) because in both cases the off-diagonal elements of the covariance matrix were zero, but the decoders were applied to the shuffled trials
function for each target. In this case, the likelihood is estimated by

\[ p(r|t=j) = \frac{n_{ij}}{N_j} \]  

(19)

where \( n_{ij} \) is the number of times response \( r \) occurred when target \( j \) was presented and \( N_j \) is the number of times target \( j \) was presented. This is the same characterization of neural responses used in the direct method of estimating mutual information between neural responses and stimuli (Strong et al. 1998). These models provide the most detailed description of responses, at a given bin size, that is possible. It is important to note, however, that each different response type that occurs is a parameter of the model, and estimating these models for several response bins or multiple neurons is not possible without an extremely large dataset because the number of parameters necessary to estimate the models grows quickly. Therefore we estimated this model using a single 66-ms response bin for a pair of neurons. When we compared this model to the linear and quadratic models, those models were also fit on the same bin.

RESULTS

Noise correlations and information coding

The impact of noise correlations on information encoding and decoding can be compared by looking at \( \Delta d_{\text{diag}}^2 \) and \( \Delta d_{\text{shuffled}}^2 \), which measure the effect of noise correlations on information encoding and decoding respectively (see METHODS). \( \Delta d_{\text{shuffled}}^2 \) is defined as

\[ \Delta d_{\text{shuffled}}^2 = d^2 - d_{\text{shuffled}}^2 \]

where \( d^2 \) is the information in the correlated neural responses, and \( d_{\text{shuffled}}^2 \) is the information in the uncorrelated (shuffled) neural responses. The effects of noise correlations on information decoding have been studied by examining how much information is lost by a decoding algorithm that ignores correlations. Therefore \( \Delta d_{\text{diag}}^2 \) is defined as

\[ \Delta d_{\text{diag}}^2 = d^2 - d_{\text{diag}}^2 \]

where \( d_{\text{diag}}^2 \) is the information that would be extracted by a decoding algorithm that ignores correlations, from the original correlated dataset. Thus \( \Delta d_{\text{diag}}^2 \) measures the amount of information lost by a decoding algorithm that ignores correlations.

The relation between \( \Delta d_{\text{shuffled}}^2 \) and \( \Delta d_{\text{diag}}^2 \) is shown in Fig. 3 (\( d^2, d_{\text{shuffled}}^2 \), and \( d_{\text{diag}}^2 \) are also shown for reference). In this figure, we used relatively large values for the correlation coefficient between neurons (0.6), so the effects of noise correlations can be clearly visualized. When noise correlations are smaller, the effects have the same periodicity, and are simply scaled down. Figure 3, B—D, shows three illustrative examples of the responses of two fictitious neurons to two different movement directions. The mean response vector for the corresponding movement direction is indicated as \( \mu_r \), and the ellipse represents the response distribution, or the variability of the responses, for each movement direction. The ellipse also indicates the covariance of the pair of neurons because the orientation of the ellipse indicates whether the covariance is positive or negative. If the covariance was zero, i.e., no noise correlation, the ellipses would be circles because these neurons have the same variance. The primary axis of each ellipse is given by the eigenvector, \( e_1 \) (shown in Fig. 3D), which corresponds to the largest eigenvalue of the covariance matrix. The covariance in each panel of Fig. 3, B—D, is the same, as is the length of \( \Delta \mu_r \), which defines the difference in the mean responses. However, \( \alpha \), the angle between \( e_1 \) and \( \Delta \mu_r \), is different. As is shown in Fig. 3A, this is the key parameter for relating \( \Delta d_{\text{shuffled}}^2 \) and \( \Delta d_{\text{diag}}^2 \).

The effects of noise correlations on information encoding and decoding are different, and depend on the value of \( \alpha \). For example, for values of \( \alpha \) near 0 or \( \pi \), \( \Delta d_{\text{diag}}^2 \) is zero, whereas \( \Delta d_{\text{shuffled}}^2 \) is negative, whereas \( \Delta d_{\text{diag}}^2 \) is zero. Thus when \( \alpha \) is near zero, assessing the effect of correlations on the information encoded would suggest that they have a negative effect, whereas assessing the effect of correlations on information decoding would suggest no effect. Between approximately \( \pi/7 \) (a value that depends on the size of the correlation) and \( \pi/2 \), both \( \Delta d_{\text{shuffled}}^2 \) and \( \Delta d_{\text{diag}}^2 \) are positive, whereas for \( \alpha = \pi/2 \), \( \Delta d_{\text{shuffled}}^2 \) takes on its largest value and \( \Delta d_{\text{diag}}^2 \) is again zero. The effect of noise correlations on \( \Delta d_{\text{shuffled}}^2 \) can be seen by looking at the overlap of the response distributions. The more the distributions overlap, the less information encoded. To gain an intuition for the effect of noise correlations on \( \Delta d_{\text{diag}}^2 \), we have plotted the optimal decision boundaries in green, and the decision boundaries
derived by a decoding algorithm that ignored correlations (a diagonal decoding algorithm) in red. In Fig. 3, B and D, the optimal and the suboptimal (i.e., derived under the assumption of no correlation) decision boundaries are the same. Because the decision boundaries are the same in these cases, no information is lost by ignoring correlations, and \( \Delta d_{\text{diag}}^2 \) is zero. In Fig. 3C, however, the optimal and suboptimal decision boundaries are not the same, and so if the suboptimal decision boundary is used for classification, information will be lost, as indicated by the positive value of \( \Delta d_{\text{diag}}^2 \) at \( \pi/4 \).

Comparison of predicted and measured information

Implicit in the use of \( d^2 \) as an information measure is the assumption that the variance and covariance of the neural responses is the same for both targets. In this case, all of the information available in the neural responses can be extracted by computing the dot-product between the vector of spike counts of individual neurons, in time bins of the appropriate size (Averbeck and Lee 2003), and an appropriate weight vector. As shown in Fig. 3C, the weight vector can be affected by the correlations, i.e., it is not the same for correlated and uncorrelated neural responses. However, explicitly taking into account correlations between neurons by computing products or interactions between neural responses will not extract more information. Thus all of the information is available in the spike counts of neurons considered individually. This is a strong assumption about how information is encoded in neural responses. In the Discussion, we consider the biophysical implications of this code.

As a first step toward examining how accurately \( d^2 \) predicts the information in neural responses, we compared the decoding accuracy predicted by \( d^2 \) to the results of actually carrying out decoding analyses and classifying individual movements. Figure 4 shows the predicted and the measured values of the decoding accuracies for pairs of simultaneously recorded neurons in the supplementary motor area for each of the information measures shown in Fig. 3A. The predicted values of the accuracy, \( A, A_{\text{shuffled}} \), and \( A_{\text{diag}} \), were calculated by estimating \( d^2, d_{\text{shuffled}}^2 \), and \( d_{\text{diag}}^2 \), based on the covariance, \( \Sigma \), and mean response vectors, \( \mu_A \), estimated for each pair of neurons, and then converting these to estimates of percent correct classification performance or accuracy (see Methods, Eqs. 9 and 10). The values plotted along the axis labeled measured accuracy were derived by explicitly classifying every movement using a linear decoding algorithm applied to the spike counts of pairs of neurons. Although \( d^2 \) is only a function of the covariance matrix and the difference in the mean response vectors, these measures predicted the outcome of actually carrying out the decoding analyses accurately (Fig. 4). The quantities \( \Delta A_{\text{shuffled}} \) and \( \Delta A_{\text{diag}} \), which measure the effects of correlations on the classification performance, were also well approximated by the predicted values.

The histograms at the top of the scatter plots (Fig. 4, bottom) show the distribution of the corresponding measured accuracies. These plots show that, on average, correlations had almost no effect on the information encoded and only a small effect on decoding performance or accuracy (see Methods, Eqs. 9 and 10). Although the distribution was centered near zero, correlations did affect the information encoded in some cases, increasing it or decreasing it by up to a few percent. The negative values of measured accuracy for \( \Delta A_{\text{diag}} \), due to finite sampling and mismatches
between the linear model and the actual distribution of the data. As shown in Fig. 3, there could be a large effect of noise correlations on information encoding, when the effect on decoding is minimal. Similarly, the outlined data points indicated by the arrows in the plots of $\Delta A_{\text{shuffled}}$ and $\Delta A_{\text{diag}}$ in Fig. 4 show a pair of neurons for which the effect of noise correlations on information encoding was relatively large and the effect on information decoding was essentially zero.

To examine the role of noise correlations in ensembles of more than two neurons, the analyses were applied to groups of three to eight simultaneously recorded neurons (Fig. 5). As with the pair-wise analyses, the predicted and measured decoding performances again agreed closely. However, the largest effects of correlations at the ensemble level were larger than the effects for pairs of neurons (see histograms in Fig. 5, bottom). To ensure that this increase in the size of the effects of correlations was not due to the fact that we were fitting more complex models, we also re-ran the analysis using only half the data. The results were essentially the same (data not shown). Overall, correlations reduced the information encoded slightly, but the effect was small and the mean of the distribution was not significantly different from zero. Again the only distribution with a mean that was significantly deviated from zero was $\Delta A_{\text{diag}}$ ($t$-test, $P < 0.01$). These analyses show that noise correlations have a relatively small effect on either information encoding or decoding. The size of the effects will depend on the size of the noise correlations in the population. On average, noise correlations in our data are almost zero, although a few pairs do have correlations $>0.2$ (Fig. 6A). The signal correlations are somewhat larger, but close to zero on average (Fig. 6B).

**Contribution of target-related changes in covariance to encoded information**

As described in the preceding text, even correlations that are the same for both targets can affect information encoding and decoding. In this case, the correlations themselves cannot be used directly to predict which target was presented. The correlations can, however, still affect information decoding by changing the optimal decision boundary used to estimate the target. For all the analyses described so far, it was assumed that the covariance of neural activity was identical for both targets. However, it is often observed that the variance of spike counts scales with the mean, and the covariances may change as well (Averbeck and Lee 2003; Tolhurst et al. 1981). This raises the possibility that additional information can be carried in the variances and the covariances of the neural responses. A classifier that explicitly computes interactions, a nonlinear operation, must be used to extract this information (Shamir and Sompolinsky 2004).
We examined the possibility that changes in the covariances for different targets might carry additional information by computing the BD, and comparing it to \( d^2 \). The BD has one term that is proportional to \( d^2 \), and a second term that measures the amount of information in the covariances (see METHODS). Thus by comparing the BD to \( d^2 \), we obtained an estimate of the additional information available in the covariances that cannot be extracted by a linear decoding algorithm. The results of this analysis suggested that there was additional information available in the covariances for many pairs of neurons (Fig. 7A). To test this further, we compared the classification performance of a nonlinear, quadratic classifier, which is a decoding model that can extract information from the target-dependent variances and covariances of the responses, to that of the linear classifier that uses only information available in the individual spike counts (Fig. 7B). In this analysis, only the accuracy in the unshuffled neural responses (A) was considered, and the analysis was applied to pairs of neurons to control model complexity. In contrast to the increase in information predicted by the BD, the performance of linear and nonlinear classifiers was essentially equivalent in most cases with the performance of the quadratic classifier being slightly worse on average than that of the linear classifier. We investigated possible reasons for the discrepancy between the information predicted by the BD and the actual performance of the decoding algorithms by looking at the decision boundaries produced by both classifiers (e.g., Fig. 7C). As expected, the classification boundaries of both classifiers separated the data equally well despite the fact that the BD predicted suboptimal performance for the linear classifier. This is due to at least two factors. The first is that neural responses are discrete quantities (i.e., spike counts), so the exact position of the decision boundary does not affect the classification performance, i.e., whether the decision boundary is at 1.2 or 1.4 spikes does not matter because the responses never take any values between 1 and 2. Second, negative firing rates may not be properly classified by the linear model (see Fig. 7C), but they do not occur. Thus the BD does not predict the actual decoding performance accurately, as does \( d^2 \).

Non-Gaussian, multinomial decoding algorithm

To further validate the results we obtained using the linear Gaussian decoding algorithm, we used a multinomial decoding algorithm. The multinomial decoding algorithm provides a general, assumption-free description of the neural responses, and as such allowed us to re-examine the effects of noise correlations on information encoding and decoding, without making the Gaussian assumption. We fit the multinomial model to the joint spike count distributions for pairs of neurons and a single 66-ms bin of neural responses. Comparison of the performance of the multinomial model to that of the linear model showed that the performance was similar, with a slight but not statistically significant advantage for the multinomial model (mean = 0.013%, paired t-test, \( P = 0.4 \); Fig. 8A). However, because the performance of these models was assessed with cross validation, the cases in which the multinomial performs better than the linear model are individually relevant. Interestingly, when the quadratic model outperformed the linear model for a given neuron pair, the multinomial model was also more likely to outperform the linear model (Fig. 8B). Thus in a small number of cases, extra information does appear to be available, beyond the spike counts of individual neurons. We also compared estimates of \( \Delta A_{\text{shuffled}} \) and \( \Delta A_{\text{diag}} \) obtained with the linear and multinomial decoding algorithms. As can be seen by the histograms in Fig. 8, C and E, the size of the effects of noise correlations on encoding and decoding assessed with the multinomial model are similar to those assessed with the linear decoding algorithm (histograms in Fig. 4). Additionally, Fig. 8D shows that there is a fairly strong correspondence, on a pair by pair basis, between the multinomial and linear decoding algorithms for \( \Delta A_{\text{shuffled}} \). However, the correspondence is poor for \( \Delta A_{\text{diag}} \). Thus the size of the effect of noise correlations on encoding and decoding is quite similar, independent of the algorithm with which it is assessed, but on a pair-by-pair basis, the estimates of the two algorithms differed somewhat for the effects on decoding.

Possibility of learning-related changes in noise correlation

The dataset used in this study was generated using a serial reaction-time task (Lee and Quesy 2003). This raises the possibility that learning-related changes in noise correlations could affect our decoding analyses. To examine this possibility, we divided each of our datasets into four parts, and compared the noise correlations in the first and last quarter of the data (Fig. 9). We found that there was a strong correlation between the noise correlations in the first and last blocks (\( r = \ldots \))

![Figure 7](image-url)
by dividing the dataset in half would be expected to broaden
than the distribution shown in Fig. 4, reducing the sample size
second halves, respectively. Although this is slightly broader
means for decoding, \(H_9004\) and linear classifiers. \(E\)
small changes, we also computed noise correlation on information coding is influenced by these
first and the last quarter of the data. To test how the effect of
confidence interval: 0.908 – 0.967). Thus there is a very small
diag assessed with the multinomial classifier. \(F\): comparison of
A: decoding accuracy for linear vs. multinomial classifier. Inset: histogram of the difference between
linear and multinomial classifiers. \(B\): comparison of differences in decoding accuracy for linear vs. quadratic and for linear vs. multinomial classifiers. \(C\): effect of noise correlations in information encoded, \(\Delta d_{\text{shuffled}}\), assessed with the
multinomial classifier. \(D\): comparison of \(\Delta d_{\text{shuffled}}\) assessed with the multinomial and linear classifiers. \(E\): effect of noise correlations on information decoding, \(\Delta d_{\text{diag}}\), assessed with the multinomial classifier. \(F\): comparison of
\(\Delta d_{\text{diag}}\) for multinomial and linear classifiers.

FIG. 8. Performance of multinomial classifier. A: decoding accuracy for linear vs. multinomial classifier. Inset: histogram of the difference between
linear and multinomial classifiers. \(B\): comparison of differences in decoding accuracy for linear vs. quadratic and for linear vs. multinomial classifiers. \(C\): effect of noise correlations in information encoded, \(\Delta d_{\text{shuffled}}\), assessed with the
multinomial classifier. \(D\): comparison of \(\Delta d_{\text{shuffled}}\) assessed with the multinomial and linear classifiers. \(E\): effect of noise correlations on information decoding, \(\Delta d_{\text{diag}}\), assessed with the multinomial classifier. \(F\): comparison of
\(\Delta d_{\text{diag}}\) for multinomial and linear classifiers.

\(0.933\) but that the slope of the best fit line was not unity (95% confidence interval: 0.908 – 0.967). Thus there is a very small
but significant difference in the noise correlations between the
first and the last quarter of the data. To test how the effect of
noise correlation on information coding is influenced by these small changes, we also computed \(\Delta d^2_{\text{shuffled}}\) and \(\Delta d^2_{\text{diag}}\) in the
first and second half of the dataset for pairs of neurons. For this
analysis, we used halves of the dataset to ensure a sufficient number of trials. The mean ± SE (\(n = 132\)) for \(\Delta d^2_{\text{shuffled}}\) were
\(0.036 ± 0.092\) and \(0.414 ± 0.086\%\) for the first and second halves of the data, respectively, and the corresponding values for \(\Delta d^2_{\text{diag}}\) were \(0.074 ± 0.021\) and \(0.094 ± 0.023\%\). The means for \(\Delta d^2_{\text{shuffled}}\) were significantly different from zero, but
the overall size of the effect was still quite small, with 95 and
93% of the distributions confined within ±2% for the first and
second halves, respectively. Although this is slightly broader
than the distribution shown in Fig. 4, reducing the sample size
by dividing the dataset in half would be expected to broaden
the distribution. To examine this quantitatively, we generated a
dataset with half as many trials by sampling randomly with
replacement from the original dataset and calculated \(\Delta d^2_{\text{shuffled}}\)
in this bootstrapped dataset. The resulting distribution was
somewhat broader with only 89% of the data between −2 and
+2%. Thus there is a slight shift in the mean of the distribution
for \(\Delta d^2_{\text{shuffled}}\) due to learning-related changes in neural activity
or to nonstationarities in the neural responses not related to
learning, but the overall width of the distribution, which is a
measure of the largest positive and negative effects, appears to
be a relatively stable feature of our dataset.

FIG. 9. Comparison of noise correlation in 1st and last block of data. The
best fit line is shown (—; slope = 0.94) as well as the line with unit slope
(——).

DISCUSSION

Noise correlations have been studied both empirically and
theoretically using a variety of methods. One approach to the
empirical study of noise correlations is to consider how much
information is lost when neural responses are decoded using
algorithms that assume that the response of individual neurons
are uncorrelated. Theoretically, decoding algorithms can only
do worse when correlations are ignored. Most of these studies
have found that little information is lost when correlations are
ignored (Averbeck and Lee 2003; Nirenberg et al. 2001; Oram
et al. 2001), although some studies have shown that the effect
of ignoring correlations can be larger (Dan et al. 1998; May-
nard et al. 1999). Empirical analyses have also assessed the
impact of noise correlations on information encoding. Romo
and his colleagues (2003) have shown that for a subpopulation
of their neurons correlations increase the amount of informa-
tion encoded. As shown in this study (Fig. 3A), this occurs when
the difference in the response vectors for different movements
is nearly orthogonal to the longest axis of the noise
covariance matrix, which was the case with the subset of the
data considered by Romo et al. (2003). Another series of
studies have examined the encoding effects of correlations
using a decomposition of the Shannon information (Panzeri et
al. 1999), which can be related to the decomposition used in
this study. Their approach also considered the total effect of
correlations, as well as splitting the correlation into two terms,
one of which is related to \(\Delta d^2_{\text{diag}}\). Similar to our finding, which
is based on neural activity recorded in the supplementary motor
area, these studies have shown that correlations in pairs of
neurons carry relatively little information in V1 (Golledge et
al. 2003), rat barrel cortex (Petersen et al. 2002), and inferior-temporal cortex (Rolls et al. 2003). Thus studies based on the analyses of pairs of neurons have consistently demonstrated that the role of correlations in information coding is limited (Averbeck and Lee 2004).

Studying correlations from both the encoding and the decoding perspectives are useful. Assessing the effects of noise correlation on information encoding is valuable for at least two reasons. The first is to check predictions for the amount of information contained in the responses of populations of neurons, based on the recording of single neurons. If neurons are indeed independent, then extrapolation from single-cell recording studies, which by definition cannot estimate the effects of noise correlations, are valid. If, however, neurons are not independent, then these extrapolations are not valid. Second, information maximization models of information coding in the cortex often ignore correlations (Bell and Sejnowski 1995; Hyvarinen et al. 2001; Olshausen and Field 1996). However, maximizing the information contained in the responses of a population of neurons is not simply a matter of optimizing the mean responses of a population of neurons. It also requires the optimization of the distribution of the noise in the neural responses. Assessing the effects of noise on information encoding in small ensembles of neurons is a first step toward assessing the effects of noise in larger populations.

Consideration of the effect of noise correlations on decoding, in addition to the effects on encoding, is also valuable for several reasons. First, understanding the impact of noise correlations on information decoding is important in the design of algorithms for driving neural prosthetic devices (Musallam et al. 2004; Taylor et al. 2002). Second, insights into the biophysical or network mechanisms that would be necessary to extract all of the information from spike trains of upstream neurons can be gained from studying $\Delta d^2_{\text{diag}}$. To carry out computation, the brain has to solve the same computational problem faced by our decoding algorithm. If $\Delta d^2_{\text{diag}}$ is small, the neural responses can be decoded reliably by assuming the upstream neurons are conditionally independent. This simplifies the computational task of defining the optimal decision boundaries, which presumably simplifies the problem to be solved by the biological system. When the decoding problem is considered from a more general, probabilistic perspective, estimation of the full joint distribution of neural responses is considerably simplified if the distribution can be factorized. This implies that the neurons can be considered conditionally independent for purposes of decoding. These simplifications are the basis for the recent success of graphical models (Jordan and Sejnowski 2001). Furthermore, if all the information in the neural responses resides in the spike counts of individual neurons, i.e., if $d^2$ describes all of the information available in the responses, they can be decoded linearly. This might obviate the need for computational machineries at the single neuron or network level that combine inputs nonlinearly. For example, if dendritic arbors combine their inputs linearly, they would not be able to extract information from differential covariances. Some results have suggested that dendritic arbors process their inputs relatively linearly (Cash and Yuste 1998, 1999), whereas others have shown that some level of nonlinearity can be found (Koch 1998; Margulis and Tang 1998; Nettleton and Spain 2000). In general, however, it is unlikely that the brain is limited to linear computations. Understanding the relation between the features of neural responses that carry information and the processing capabilities of dendritic arbors and networks will provide important converging perspectives for understanding the neural code.

When considering whether or not correlations have an effect, studying information encoding and information decoding can lead to different answers (Fig. 3). For some pairs of simultaneously recorded neurons in the supplementary motor area, we found that noise correlations affected the information encoded. However, the effects were relatively small, and averaged across the population, the mean effect was not significantly different from zero. The effect of noise correlations on information decoding was similar in magnitude to the effect on information encoding. Although the mean of the distribution of effects on decoding was significantly different from zero, this term is in principle nonnegative, so this result is not surprising. At the ensemble level, the effects of noise correlations were somewhat larger, but the average effect for information encoding was again not significantly different from zero. It is important to point out that, as we and others have shown before (Averbeck and Lee 2003; Constantinidis and Goldman-Rakic 2002; Reich et al. 2001), measured correlations, and correspondingly the size of the effect of correlations, depend on the bin size used for their estimation. This is due to the fact that cross-covariances between neurons are much stronger at low frequencies and thus larger bins show stronger correlations between neurons (Averbeck and Lee 2004). We have chosen 66 ms in this study because our previous work (Averbeck and Lee 2003) showed that this was the optimum bin size for information extraction. The correlations we observed were similar in size to those that have been observed in other studies (Constantinidis and Goldman-Rakic 2002; Reich et al. 2001). Therefore a relatively small effect of noise correlation on information coding found in the present study may generalize to other brain areas and task conditions, although this remains to be investigated in future studies.

Implicit in the use of $d^2$ is the assumption that the conditional response distributions of the neurons are Gaussian, and have the same variance for different targets. Theoretically, this is a strong limitation of using $d^2$ as an information measure because the variance of neural responses tends to scale with the mean response (Averbeck and Lee 2003; Tolhurst et al. 1981; Werner and Mountcastle 1963), and response distributions are at best truncated Gaussians unless spike rates are high (Wiener and Richmond 1999). We have shown that the predicted decoding performance derived from $d^2$ closely matched the actual decoding performance of a linear decoding model. We have also shown, through a series of analyses, that linear decoding models can generally extract almost all of the information available in the neural responses. More general decoding models that assumed that variances can change for different targets, as well as a very general multinomial decoding model, were only able to do marginally better than the linear decoding model. The major discrepancy we found was between $\Delta d^2_{\text{diag}}$ measured with the linear and the multinomial decoding algorithms. Although the relative magnitude of the effects was similar across our population, the two decoding algorithms did not agree on a pair by pair basis. Continued investigation of the limitations of the Gaussian assumption will be important because most current theoretical models of information coding in the cortex make this assumption (Abbott and Dayan 1999;
Shamir and Sompolinsky 2004; Sompolinsky et al. 2001; Wilke and Eurich 2002; Wu et al. 2001).

Another information measure often computed on the responses of pairs of neurons is synergy/redundancy (Averbeck et al. 2003; Gawne and Richmond 1993; Latham and Nirenberg 2005; Narayanan et al. 2005; Puchalla et al. 2005; Schneiderman et al. 2003). There are two important differences between this measure and our measures of the effects of noise correlations on encoding and decoding. The first is that synergy/redundancy is a function of both noise correlations and signal correlations. Specifically, even if noise correlations are zero, there can and likely will be redundancy in neural responses. Given that noise correlations play a relatively small role in information coding for pairs of neurons, and measured redundancy is normally large, signal correlations are presumably responsible for the reported redundancy effects. It has been shown that \( d^2_{\text{buffered}} \) can be small when there are large redundancies (Averbeck et al. 2003). Furthermore, the redundancy is largely a function of the finite entropy of discrete Shannon information, since discrete Shannon information saturates. We would get a similar effect if we calculated a synergy/redundancy statistic on the percent correct classification, which of course saturates at 100%. For example if we computed the statistic

\[
\Delta A_{\text{synergy}} = A_{1,2} - (A_1 + A_2)
\]

where \( A_1 \) is the percent correct classification for neuron 1, \( A_2 \) is the percent correct classification for neuron 2, and \( A_{1,2} \) is the joint percent correct classification. If \( A_1 \) and \( A_2 \) individually perform at a 90% classification rate, but \( A_{1,2} \) is only at 98%, the responses would be considered redundant. This could be true even if there were no noise correlations. However, if there are no noise correlations, a statistic based on \( d^2 \), for example

\[
\Delta d_{\text{ synergy}} = d^2_{1,2} - (d^2_1 + d^2_2)
\]

will be zero. Thus it seems to us that if synergy/redundancy is being calculated, the separate effects of signal and noise correlations should be examined, as has been done in some studies (Gawne and Richmond 1993; Gawne et al. 1996; Panzeri et al. 1999; Petersen et al. 2001; Pola et al. 2003).

In conclusion, noise correlations can differentially affect information encoding and decoding. Both perspectives are useful, and they address different questions about the nature of the neural code. We found that in general, the effects of noise correlations were relatively small in our population of SMA neurons. However, we have only considered analyses in small ensemble of neurons, and theoretical work (Shamir and Sompolinsky 2004) suggests that small effects of noise correlations in pairs of neurons can become substantial in large populations. Furthermore, because the output of a system cannot contain more information than the input, correlations must ultimately limit information, if the number of neurons becomes sufficiently large (Narayanan et al. 2005; Seriès et al. 2004). Consistent with this, the effects of correlations in our study were slightly larger in ensembles than in pairs of neurons. Perhaps this is also an explanation for the saturation effects seen in studies related to neural prosthetics that have attempted to use relatively small ensembles to decode hand kinematics (Averbeck et al. 2005; Paninski et al. 2004; Wessberg et al. 2000). Future studies with larger populations of neurons will help to answer these questions empirically.

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