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Information encoding in the inferior temporal visual cortex: contributions of the firing rates and the correlations between the firing of neurons

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Abstract. The encoding of information by populations of neurons in the macaque inferior temporal cortex was analyzed using quantitative information-theoretic approaches. It was shown that almost all the information about which of 20 stimuli had been shown in a visual fixation task was present in the number of spikes emitted by each neuron, with stimulus-dependent cross-correlation effects adding for most sets of simultaneously recorded neurons almost no additional information. It was also found that the redundancy between the simultaneously recorded neurons was low, approximately 4% to 10%. Consistent with this, a decoding procedure applied to a population of neurons showed that the information increases approximately linearly with the number of cells in the population.

Introduction

A fundamental issue in understanding brain function is how information is encoded by populations of neurons (Gawne and Richmond 1993; Singer 1999, 2000; Shadlen and Movshon 1999; Rolls and Deco 2002; Treves 2000; Franco et al. 2003). In this paper we apply recently developed information-theoretic techniques to quantify the encoding of information which is contributed by the number of spikes from the different neurons in the population and by the relative timing of spikes from different cells (Panzeri et al. 1999; Rolls et al. 1997; Rolls and Deco 2002). The information-theoretic approaches used here enable these different contributions to be compared quantitatively. The approaches are applied to the encoding of information in the macaque inferior temporal visual cortex (IT), where neurons respond to objects and faces (Tanaka 1996; Rolls 2000; Rolls and Deco 2002).

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Simultaneously recorded neurons sometimes show cross correlations in their firing. One example of this is neuronal response synchronization. A significant peak or trough in the cross-correlation function of the spike trains of two neurons could reflect a synaptic connection from one cell to the other, a common input to each of the cells, or any of a considerable number of other possibilities. If the synchronization occurred for only some of the stimuli, then the presence of the significant cross correlation for only those stimuli could provide additional evidence separate from any information in the firing rate (or equivalently the number of spikes in a short time period) about which stimulus had been shown. Information theory in principle provides a way of quantitatively assessing the relative contributions from these two types of encoding by expressing what can be learned from each type of encoding in the same units, bits of information. An information-theory-based approach to this has been developed by Panzeri et al. (1999) and extended and evaluated by Rolls et al. (2003).

The purpose of the research described in this paper is to describe new simultaneous recordings from several rhesus macaque inferior temporal cortex neurons made in order to examine the neural encoding of information about visual stimuli and analyzed with an information-theoretic method developed and evaluated recently (Rolls et al. 2003). We measured the cross correlations between the spike trains of simultaneously recorded neurons and quantified the relative contributions to the total information available of the numbers of spikes emitted by each cell and the cross correlations between the spike trains. The stimuli consisted of a set of 20 images of different objects and faces, as these are known to be effective for inferior temporal cortex neurons because these neurons typically have differential neuronal firing to the members of such a set of stimuli (Rolls et al. 1997; Booth and Rolls 1998; Rolls 2000; Rolls and Deco 2002). Each object can be thought to consist of a set of features which might need to be bound together in the correct spatial configuration, and neuronal synchronization might be used to implement the correct spatial binding of different subsets of features (Singer 1999,

2000; Shadlen and Movshon 1999). The aims of the experiments described here were to measure the amount of information which might be available on a single trial from any cross-correlated firing about what stimulus was shown compared to that obtainable from the number of spikes, to measure the amount of redundancy which simultaneously recorded cells may have, and to determine how the information about the set of stimuli scales with the number of neurons in the population in this major output of the ventral (or "what") visual stream. The investigation thus addresses the encoding of information when it is passed from the visual system to other brain systems which utilize visual information for functions such as long-term memory, short-term memory, and emotion (Rolls and Deco 2002).

Methods

Neurophysiological procedures

The responses of single neurons in the temporal cortical visual areas were measured to a set of 20 visual stimuli in a rhesus macaque performing a visual fixation task using experimental procedures similar except as described below to those described in detail previously (Rolls et al. 1997). The stimuli included $S = 20$ images of objects (7), faces (8), natural scenes (3), and geometrical stimuli (2) of the type which produce differential responses from inferior temporal cortex neurons and examples of which have been illustrated previously (Rolls and Tovee 1995). The neurons were selected to show responses which differed between the different stimuli (as shown by a one-way ANOVA). Usually, 20 trials for each stimulus were available. The set of stimuli were shown once in random order, then a second time in a new random sequence, etc. Populations of 2–9 neurons were recorded simultaneously using 2–4 independently movable single neuron epoxy-insulated tungsten electrodes with uninsulated tip diameters of less than 10 μm (FHC Inc., USA) using an Alpha-Omega (Israel) recording system. Typically we were able to move the microelectrodes until 2–4 of the simultaneously recorded neurons responded differentially to the set of stimuli used. The recordings were made as part of the experimental design in one rhesus macaque, *Macaca mulatta*, so that in addition to the analysis of simultaneously recorded neurons, another analysis could be performed of nonsimultaneously recorded neurons in which the information from all the recordings made from different neurons in different sessions in the same animal could be analyzed as described by Rolls et al. (1997). The microelectrodes were stereotaxically guided, and the location of the microelectrodes was reconstructed on each track using X-rays and subsequent histological reconstruction using microlesions made on selected tracks as described by Feigenbaum and Rolls (1991). The recording system (Neuralynx Inc. USA) filtered and amplified the signal and stored spike waveforms which were later sorted to ensure that the spike waveforms from each neuron in the small number of cases when there were more than two spikes on one microelectrode were clearly separated into different waveform clusters using the Datawave (USA) Discovery software. The neurophysiological methods used here have been described in detail by Booth and Rolls (1998). All procedures, including preparative and subsequent ones, were carried out in accordance with the NIH Guide for the Care and Use of Laboratory Animals, the guidelines of The Society for Neuroscience, and licenced under the UK Animals (Scientific Procedures) Act, 1986.

The sites of the tips of the microelectrodes during the neuronal recordings included in this investigation are shown in Fig. 6 and for the majority were in the cortex in the anterior part of the ventral lip of the superior temporal sulcus (areas TEa and TEm), in area TE, or in the cortex deeper in the superior temporal sulcus (Seltzer and Pandya 1978; Baylis, Rolls and Leonard 1987).

Measuring the information available from simultaneously recorded cells in short time windows

An introduction to and overview of the information-theoretic methods used here are provided by Rolls and Deco (2002). The general approach used was developed by Panzeri et al. (1999) and extended and validated with simulated data by Rolls et al. (2003).

When applying information theory to the responses of two or more simultaneously recorded neurons, the number of possible combinations of the relative times of the spikes of the different cells becomes very large. That is, the dimensionality of the space which must be filled adequately with real neurophysiological data to obtain estimates of the information becomes so large that the information estimates become unreliable and in fact are biased upwards (i.e., are an overestimate) (Tovee et al. 1993; Rolls and Treves 1998; Rolls and Deco 2002; Panzeri and Treves 1996).

The approach taken here limits the dimensionality problem by taking short time epochs for the information analysis in which low numbers of spikes are likely to occur from each neuron. In this case, in which at most a low number of spikes are emitted from the population, the response probabilities can be calculated in terms of pairwise correlations. These response probabilities are inserted into the Shannon information formula shown in Eq. 1 to obtain expressions quantifying the impact of the pairwise correlations on the information $I(t)$ transmitted in a short time t by groups of spiking neurons:

$$I(t) = \sum_{s \in S} \sum_{\mathbf{r}} \mathrm{P}(\mathrm{s}, \mathbf{r}) \log_2 \frac{\mathrm{P}(\mathrm{s}, \mathbf{r})}{\mathrm{P}(\mathrm{s})\mathrm{P}(\mathbf{r})} \quad , \tag{1}$$

where $\mathbf{r}$ is the firing rate response vector (comprised of the number of spikes emitted by each of the simultaneously recorded cells in the population in the short time t) and $\mathrm{P}(s, \mathbf{r})$ refers to the joint probability distribution of stimuli with their respective neuronal response vectors. The firing rate response vector $\mathbf{r}$ for a single trial consists of the number of spikes n_i emitted by each cell i in a short time t.

The approach consists, then, in the short timescale limit, of using the first (I_t) and second (I_{tt}) information derivatives (in a Taylor expansion) to describe the information $I(t)$ available in the short time t

$$I(t) = t\, I_t + \frac{t^2}{2}\, I_{tt} \quad . \tag{2}$$

(The zeroth order, time-independent term is zero, as no information can be transmitted by the neurons in a time window of zero length. Higher-order terms are also excluded as they become negligible in a time window with sufficiently few spikes.)

The instantaneous information rate I_t is:

$$I_t = \sum_{i=1}^{C} \left\langle \overline{r}_i(s) \log_2 \frac{\overline{r}_i(s)}{\langle \overline{r}_i(s') \rangle_{s'}} \right\rangle_s \quad . \tag{3}$$

This term is just a simple sum across the C cells in the population of the instantaneous information rate of each single cell (Bialek et al. 1991; Skaggs et al. 1993), and thus this term does not take into account any interactions (arising from any of the correlations) between the neurons. Nor does this term reflect the trial by trial variability in the responses of each cell taken individually (which is reflected in the terms containing γ_{ii}).

The second derivative term I_{tt} breaks into three components that can be expanded in terms of two types of correlation:

The correlations in the neuronal response variability from the average to each stimulus, $\gamma_{ij}(s)$.

$$\gamma_{ij}(s) = \frac{\overline{n_i(s) n_j(s)}}{(\overline{n}_i(s)\overline{n}_j(s))} - 1 = \frac{\overline{r_i(s) r_j(s)}}{(\overline{r}_i(s)\overline{r}_j(s))} - 1 \tag{4}$$

where $\overline{r}_i(s)$ is the mean rate of response of cell i ($\overline{n}_i(s)$ is the mean number of spikes of cell i) (among C cells in total) to stimulus s over all the trials in which that stimulus was present.

This is called a "noise" correlation (Gawne and Richmond 1993; Shadlen and Newsome 1994, 1998) because it reflects the trial by trial co-variation in the responses of the neurons, and is also called the 'scaled cross-correlation density' (Aertsen et al. 1989; Panzeri et al. 1999). It can vary from -1 to ∞; negative values of $\gamma_{ij}(s)$ indicate anticorrelation, whereas positive values of $\gamma_{ij}(s)$ indicate correlation. $\gamma_{ij}(s)$ can be thought of as the amount of trial-by-trial covarying firing of the cells i and j, compared to that expected in the uncorrelated case. Although the $\gamma_{ij}(s)$ measure utilizes the numbers of spikes from the different neurons, and thus reflects rate co-modulation, this will almost always with real neurons (as contrasted with possible artificial scenarios) capture any synchronization that is present. This is because in a sufficiently short time window (and the information measures are for this reason plotted in the Figures in different time windows in the range 0 to 100 ms), in the unlikely event that cell i fires, if cell j also fires, this is likely to reflect synchronization (Rolls et al. 2003).

There is also an autocorrelation term $\gamma_{ii}(s)$, which reflects the variability of the number of spikes emitted by a cell i to a given stimulus s from trial to trial

$$\begin{aligned} \gamma_{ii}(s) &= \frac{\overline{n_i(s) n_i(s)} - \overline{n_i(s)}}{(\overline{n}_i(s)\overline{n}_i(s))} - 1 \\ &= \frac{\overline{r_i(s) r_i(s)} - \overline{r_i(s)}}{(\overline{r}_i(s)\overline{r}_i(s))} - 1 \quad . \end{aligned} \tag{5}$$

$\gamma_{ii}(s)$ is related to the probability of observing a spike emission, given that the same cell has already fired in the same time window. Its relationship with alternative cross-correlation coefficients, like the Pearson correlation, is discussed in Panzeri et al. (1999) and Rolls et al. (2003).

The second type of correlation is the correlations in the mean responses of the neurons across the set of stimuli, v, and is defined by:

$$\begin{aligned} v_{ij} &= \frac{\langle \overline{n}_i(s)\overline{n}_j(s) \rangle_s}{\langle \overline{n}_i(s) \rangle_s \langle \overline{n}_j(s) \rangle_s} - 1 \\ &= \frac{\langle \overline{r}_i(s)\overline{r}_j(s) \rangle_s}{\langle \overline{r}_i(s) \rangle_s \langle \overline{r}_j(s) \rangle_s} - 1 \quad , \end{aligned} \tag{6}$$

where $\overline{r}_i(s)$ is the mean rate of response of cell i ($\bar{n}_i(s)$ is the mean number of spikes of cell i) to stimulus s over all the trials in which that stimulus was present. It can vary from -1 to ∞. ($\langle \ldots \rangle_s$ indicates the ensemble average over the s stimuli.) v_{ij} can be thought of as the degree of similarity in the mean response profiles (averaged across trials) of the cells i and j to different stimuli. v_{ij} is sometimes called the "signal" correlation (Gawne and Richmond 1993; Shadlen and Newsome 1994, 1998).

If v_{ij} is zero, the cells have different response profiles to the stimuli, and there is no redundancy. If v_{ij} is either positive or negative, it always reflects redundancy between the cells, as both cases mean that the two cells i and j are conveying the same information about the stimuli. The autoterms, v_{ii}, reflect the degree to which a single cell i responds differently to the different stimuli.

In terms of the correlations introduced above the second derivative of the total information becomes:

$$\begin{aligned} I_{tt} = & \frac{1}{\ln 2} \sum_{i=1}^{C} \sum_{j=1}^{C} \langle \overline{r}_i(s) \rangle_s \langle \overline{r}_j(s) \rangle_s \\ & \times \left[v_{ij} + (1 + v_{ij}) \ln\left(\frac{1}{1 + v_{ij}}\right) \right] \\ & + \sum_{i=1}^{C} \sum_{j=1}^{C} \left[\langle \overline{r}_i(s)\overline{r}_j(s)\gamma_{ij}(s) \rangle_s \right] \log_2\left(\frac{1}{1 + v_{ij}}\right) \\ & + \sum_{i=1}^{C} \sum_{j=1}^{C} \left\langle \overline{r}_i(s)\overline{r}_j(s)(1 + \gamma_{ij}(s)) \right. \\ & \left. \times \log_2 \left[\frac{(1 + \gamma_{ij}(s)) \langle \overline{r}_i(s')\overline{r}_j(s') \rangle_{s'}}{\langle \overline{r}_i(s')\overline{r}_j(s')(1 + \gamma_{ij}(s')) \rangle_{s'}} \right] \right\rangle_s \quad . \end{aligned} \tag{7}$$

The first term of I_{tt} is always equal to or less than zero and expresses for the case $i \neq j$ redundancy that could arise from similar response profiles from the cells to different stimuli. The second term quantifies the amount of stimulus-independent information and depends on both types of correlation v and γ. The third term contributes only if the correlations are stimulus-dependent (Rolls et al. 2003).

To evaluate the significance of the stimulus-dependent information that may be present in the correlations of simultaneously recorded cells, a Monte Carlo procedure was applied by randomly shuffling the recorded trials and computing for these cases the value of the stimulus-dependent information obtained. If the measured information was greater than 2 times the standard deviation obtained from the different shuffled cases, the stimulus dependent-information was taken to be significant. Rolls et al. (2003) provide a more detailed explanation of the method, together with procedures for ensuring that a longer time window with too many spikes from each cell which would exceed the validity of the Taylor expansion was not used. These procedures were applied to all the analyses described in this paper, and allowed 100 ms times for all experiments in Table 1 except for experiments bj240 and bj286, for which the time windows were 60 ms. In practice, the useful heuristics are that the Taylor expansion remains valid with up to 4 simultaneously recorded cells if the time window does not exceed 2 or 3 times the average interspike interval of the fastest firing cell to its most effective stimulus; and the power of the method with respect to the accuracy of the cross-cell stimulus-dependent contributions is sufficient if there are in the order of 15–20 trials per stimulus or more (Rolls et al. 2003).

We note that the 'total information' shown on the graphs is the total information from the full expansion, that is $tI_t + 0.5t^2 I_{tt}$, and includes a stimulus-dependent auto term. The ''stimulus-dependent auto term'', is the auto part of the third term of I_{tt} in Eq. 7 for the case when $i = j$ in $\gamma_{ij}(s)$. This term is subtracted out by the Monte Carlo procedure, but it can be estimated by subtracting the sum of the other components of the information (rate, stimulus-independent, and stimulus-dependent-cross) from the total information. This term is normally close to zero, both in simulations and in real data. There is a special case in which the stimulus-dependent auto term could be positive. This would arise for example if the trial by trial variability to a given stimulus, $\gamma_{ii}(s)$, was different for different stimuli. If the brain could measure this trial by trial variability, and found that it was large, then this might give information about which stimulus was shown. However, it is not clear how such a measurement could be implemented in the brain.

Measuring the information from many recorded cells using a decoding procedure

We were also able to use these new recordings to provide an estimate of how the information increases as a function of the number of cells in a population of 21 neurons for which the same set of 20 images was used. This analysis was performed using the decoding method described by Rolls et al. (1997) to analyse the information. This method does not analyse the information that might be present in simultaneously recorded neurons due to stimulus-selective cross-correlations, and so could be applied to the data accumulated from different cells recorded in the same macaque over different days. The method measures approximately what is included in the rate and stimulus-independent terms of the information expansion described in this paper. The method can be used for very large numbers of cells, and when there are many spikes in a time window. The method uses a decoding procedure in which on each trial the

Table 1. The average contributions (in bits) of the different components (Eqs. 3 and 7) of Eq. 2 to the information available in a 100 ms time window from 20 sets of simultaneously recorded inferior temporal cortex neurons when shown 20 stimuli effective for the cells

Exper.	Total information	Rate information	Stim. dep. (cross correl.)	Stim. indep. (cross correl.)	Stim. indep. (auto correl.)
bj185	0.22	0.29	0.08	0.00	−0.27
bj207	0.24	0.24	−0.01	−0.01	−0.12
bj213	0.21	0.21	−0.01	0.00	−0.03
bj215	0.24	0.20	0.00	0.00	0.01
bj220	0.13	0.33	0.01	−0.24	−0.18
bj229	0.22	0.16	0.05	0.05	−0.09
bj240	0.00	0.17	−0.04	−0.16	−0.25
bj243	0.20	0.20	0.00	0.00	0.00
bj278	0.46	0.29	0.06	0.02	−0.07
bj280	0.43	0.40	0.01	−0.01	−0.01
bj283	0.23	0.25	0.08	−0.09	−0.11
bj285	0.125	0.125	0.00	−0.01	0.01
bj286	0.15	0.05	0.06	−0.03	−0.10
bj287	0.70	0.20	0.21	−0.10	−0.11
bj288	0.62	0.40	0.12	−0.04	0.01
bj290	0.28	0.28	−0.05	−0.06	−0.11
bj291	0.46	0.40	0.00	−0.01	0.09
bj292	0.20	0.20	−0.02	−0.02	−0.08
bj292b	0.34	0.42	−0.03	−0.22	−0.10
bj293	0.75	0.42	0.22	−0.01	0.11
Mean	0.31	0.26	0.04	−0.05	−0.07

probability that each stimulus (called s') was shown is estimated from the vector of neuronal responses. This estimate is made by comparing the vector of neuronal responses on that trial to the average response vectors to each stimulus. Then, knowing the actual stimulus shown on that trial, the mutual information $\langle I_{\mathrm{p}} \rangle$ between the estimated stimulus s' and the real stimulus s over the set of stimuli S can be calculated as

$$\langle I_{\mathrm{p}} \rangle = \sum_{s \in S} \sum_{s' \in S} \mathrm{P}(s, s') \log_2 \frac{\mathrm{P}(s, s')}{\mathrm{P}(s)\mathrm{P}(s')} \quad . \tag{8}$$

The decoding procedure used for the results presented in this work, is Bayesian probability estimate (PE) decoding using a Gaussian fit, as described by Rolls et al. (1997), Rolls and Treves (1998) and Rolls and Deco (2002), and includes a cross-validation procedure.

Results

Measurement of the information available from small numbers of simultaneously recorded neurons

The responses of 54 neurons obtained in 20 recording sessions in which it was possible to measure the responses of several simultaneously recorded inferior temporal cortex neurons to the set of 20 visual stimuli were analyzed using an information theoretic approach (Panzeri et al. 1999; Rolls et al. 2003) that separates the contribution of the firing rates and the correlations between the firing of neurons (see Experimental Procedures).

The majority of the sets of simultaneously recorded cells analysed did not show significant cross-correlations between the firing of pairs of cells. An example of these typical cross-correlation results is shown for cells 11 and 31 of a set (bj280) of 3 simultaneously recorded cells in Fig. 1a. (The first number of the cell designation indicates the electrode number.) The firing rates of these two cells (based on the number of spikes in a 100 ms window starting 100 ms post-stimulus) to the set of stimuli are shown in Fig. 1c and e respectively (with d showing the responses of the third simultaneously recorded cell). Figure 1b shows that most of that information available was available in the rates, and that there was little contribution to the information from the cross-cell stimulus-dependent term (which would have shown a positive value if for example there was stimulus-dependent co-modulation of the neuronal responses); or from cross-cell stimulus-independent terms, which might if present have reflected common input to the different neurons so that their responses tended to be correlated independently of which stimulus was shown. For these cells, the stimulus-independent auto term was approximately 0, indicating that the variability of the neuronal spike counts from trial to trial was close to that expected for a Poisson process.

In some other sets of simultaneously recorded inferior temporal cortex neurons some statistically significant cross-correlations were found between particular pairs of IT neurons. One such case is shown in Fig. 2, where the cross-correlogram in Fig. 2a shows a significant correlation between cells 01 and 04 close to a lag of 0 ms, and a smaller more broadly peaked region in addition. From the cross-correlogram, it is not possible to quantify the impact of the cross-correlation on the total information available from the pair of cells, but application of the information theoretic method described here showed that the cross-correlation reflected redundancy. The results of the information analysis are shown in Fig. 2b–e. The "rate" component was large and positive (as much as 0.33 bits in 100 ms), but the total information available from the cells was reduced to approximately 0.13 bits because there was a relatively large cross-cell stimulus independent contribution (estimated at −0.24 bits). The cross-cell stimulus-independent contribution was large and negative, because, as shown in Fig. 2d–e, both the values of v_{ij} and those from the terms $\left\langle \bar{n}_i(s)\bar{n}_j(s)\gamma_{ij}(s) \right\rangle_s$ are large and have the same sign (see the second term of Eq. 7). The positive values for v_{ij} reflect some correlation in the firing rate response profiles of the cells to the set of stimuli; while the positive values of $\left\langle \bar{n}_i(s)\bar{n}_j(s)\gamma_{ij}(s) \right\rangle_s$ indicate that there is (on average across stimuli) a trial-by-trial correlation (reflecting e.g. synchronization or co-modulation). The stimulus-dependent information is very low (Fig. 2b–c), around 0, indicating that the cross-correlation that exists is not stimulus-modulated, a fact also confirmed by fact that the cross-correlations were similar for each stimulus (not illustrated). We also note that the stimulus-independent auto terms for all 3 cells are negative as shown in Fig. 2b. This fact, also found in many of the experiments (see Table 1, column Stim. indep. (auto correl.)) indicates that the variability of the number of spikes from trial to trial (within a stimulus, then averaged across stimuli) is greater than would be expected from spike trains produced by a Poisson process.

We also found cases where the cross-correlations were associated with a cross-cell stimulus-dependent contribution to the information. A cross-correlogram from such a case is shown in Fig. 3a. The cross-correlation has a central peak, and is flanked by a region of positive cross-correlations. Figure 3b (top right) shows that a considerable proportion of the information available in a 100 ms time period was available in the rates. In addition, there was a negative value for the cross-cell stimulus-independent term, produced by a small positive value for v_{ij} (shown in Fig. 3d), together with a positive value for $\left\langle \bar{n}_i\bar{n}_j\gamma_{ij}(s) \right\rangle_s$ (as shown in Fig. 3e). Figure 3b shows that there is a small positive contribution to the information from the stimulus-dependent cross-cell term, and Fig. 3c shows that this is more than two standard deviations from what is produced by random reassortment of the trials within those available for each stimulus, and so is taken as significant (see further Rolls et al. (2003)). Overall, because these cells had some negative stimulus-independent cross-cell contribution to the total information (reflecting redundancy), the total information from the cells was close to that available in the rates (Fig. 3 top left). We note that the cells were recorded on two different electrodes, so that cells that

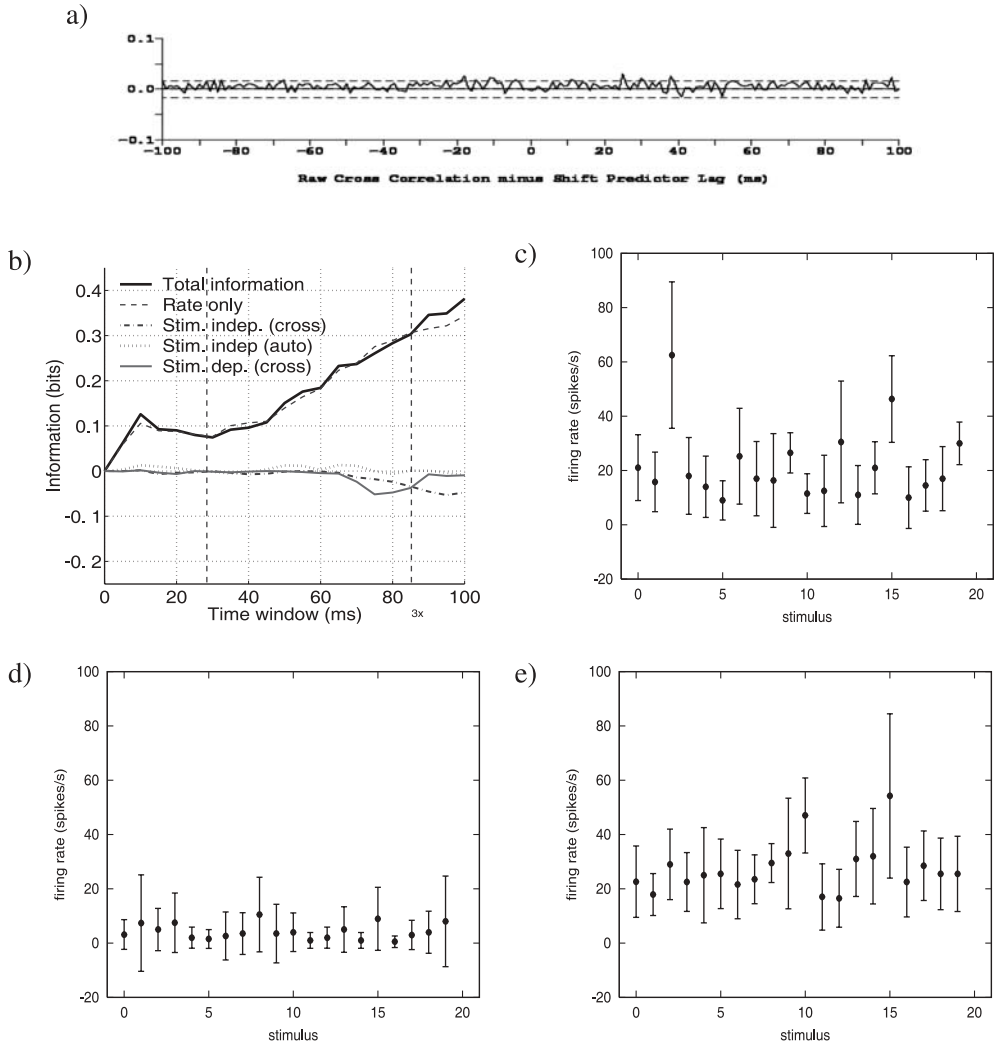

Fig. 1. a–e Information analysis on experiment bj280. **a** Cross correlogram (corrected by subtracting the shift predictor and with the $p < 0.01$ confidence limits indicated) between the responses of two simultaneously recorded neurons (11 and 31) from experiment bj280. **b** Information analysis on the set of three simultaneously recorded inferior temporal (IT) cortex neurons (in experiment 280) about which of the 20 stimuli had been shown. The graphs show the contributions to the information from the different terms in Eqs. 3 and 7, as a function of the length of the time window, which started 100 ms after stimulus onset, which is when IT neurons start to respond. The rate information reflects the term in Eq. 3 and the first term of Eq. 7, combined as in Eq. 2. The stimulus-independent contribution to the information reflects the second term of Eq. 7 and is separated into components arising from the correlations between cells (the cross component, for $i \neq j$) and from the autocorrelation within a cell (the auto component, for $i = j$). The stimulus-dependent contribution of the noise correlation to the information reflects the third term of Eq. 7, and only the cross term is shown (for $i \neq j$), as this is the term of interest. The first *vertical dashed line* shows the average interspike interval of the neuronal response to the most effective stimulus for any cell. The second *vertical dashed line* indicates three times this value. **c–e** The average firing rates and standard deviations of the neuronal spike counts in the same 100-ms time window to each of the 20 stimuli for the three cells of experiment bj280

are 1–3 mm apart can show these stimulus-dependent correlation effects.

The results for the 20 experiments completed with groups of 2–4 simultaneously recorded inferior temporal cortex neurons are shown in Table 1. The total information is the total from Eq. 2 in a 100 ms time window, and is not expected to be the sum of the contributions shown in Table 1 because the stimulus-dependent auto term is not shown in the Table. (This latter term includes contributions that arise in the Monte-Carlo correction algorithm.) The results show that the greatest contribution to the information is that from the rates, that is from the numbers of spikes from each neuron in the time window of 100 ms. On average a value of −0.07 bits was obtained for the cross-cell term of the stimulus independent 'noise' correlation, but it is worth noting that this average value mainly arises from particular cases with a large amount of redundancy (6 out of 20 experiments), while in the remaining experiments the values are closed to 0 (see the distribution in Fig. 4b). (No significant difference was found between these stimulus-independent cross-cell contributions computed for pairs of cells from the same or different electrodes.) Figure 4a shows the values of $< \bar{n}_i \bar{n}_j \gamma_{ij}(s) >_s$ and v_{ij} for all simultaneously recorded neuronal pairs. The graph is divided into sectors which show the regions within which the two

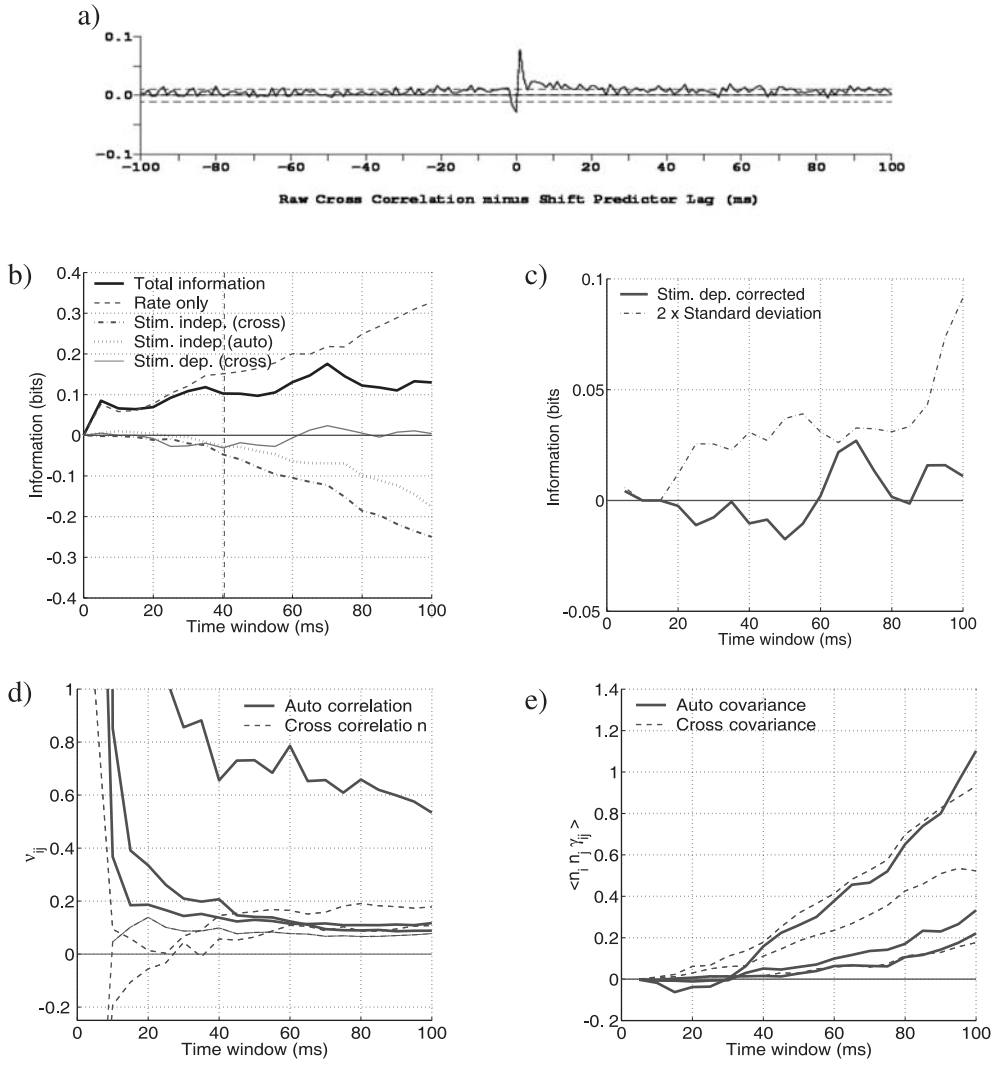

Fig. 2. a–e Information analysis on experiment bj220. **a** Cross correlogram (corrected by subtracting the shift predictor, and with the $p < 0.01$ confidence limits indicated) between the responses of two simultaneously recorded neurons from experiment bj220. **b** Results of the information analysis on a set of three simultaneously recorded inferior temporal cortex neurons in experiment bj220. The graph shows the contributions to the information from the different terms in Eqs. 3 and 7, as a function of the length of the time window, which started 100 ms after stimulus onset. The conventions are as in Fig. 1. **c** Value of the cross-cell term of the stimulus-dependent information and two standard deviations of its variation as estimated by the Monte Carlo method described in Methods. **d** Values of v_{ij}, signal correlations, measured both across cell pairs (*cross correlation, dashed lines*) and within cells (autocorrelation, i.e., $i = j$, shown by a *solid line* for each cell). **e** The time course of the terms $\langle \bar{n}_i(s)\bar{n}_j(s)\gamma_{ij}(s)\rangle_s$ (with separate "autocovariance" *solid lines* for each of the individual cells, and separate "cross covariance" *dashed lines* for each pair of cells i and j)

factors plotted lead to redundancy or synergy for a pair of cells. (The dividing lines were calculated analytically from the first two terms of Eq. 7).

Table 1 also shows that the stimulus-dependent cross-cell term of the information, expressing information transmitted through stimulus-dependent synchronization or co-modulation, has a small positive value, averaged across experiments, of 0.04 bits. However, in most experiments this contribution was so small that it was less than that which can arise by chance statistical fluctuations of the time of arrival of the spikes, as shown by Monte-Carlo control rearrangements of the same data. (These chance fluctuations account for some of the values for this term being negative in Table 1.) Indeed, for only three of the data sets (283, 288 and 293) of simultaneously recorded neurons shown in Table 1 did the cross-cell stimulus-dependent information exceed the statistical criterion of $p < 0.01$. Thus there was rarely any significant contribution to the information from stimulus-dependent cross-correlation effects, and on average their contribution was small (0.04 bits) compared to the information available in the number of spikes (0.26 bits).

Table 1 (last column) also shows the values of the stimulus-independent within-cell term, which reflects the variability of the number of spikes from trial to trial (within a stimulus, then averaged across stimuli). If this is negative, this indicates that this variability is greater than would be expected from spike trains produced by a Poisson process. On average this term was just less than 0.

Table 2 shows for each of the same sets of simultaneously recorded cells how the information available from the number of spikes to each stimulus combines across cells. The Table shows the information available from each cell separately, the sum of these single cell rate information values, and the rate information measured with the Taylor expansion approach when the cells were considered as simultaneously recorded (column labelled 'simultaneous rate inf'). The 'total information' estimated by the algorithm is also shown. (To ensure that there was information from each cell that could add, only cells in which the single cell rate information after 100 ms was 0.03 bits or more were included in this analysis.) The values obtained indicate that the information in the 20 datasets from the simultaneously measured rates (0.26 bits) was on average just a little

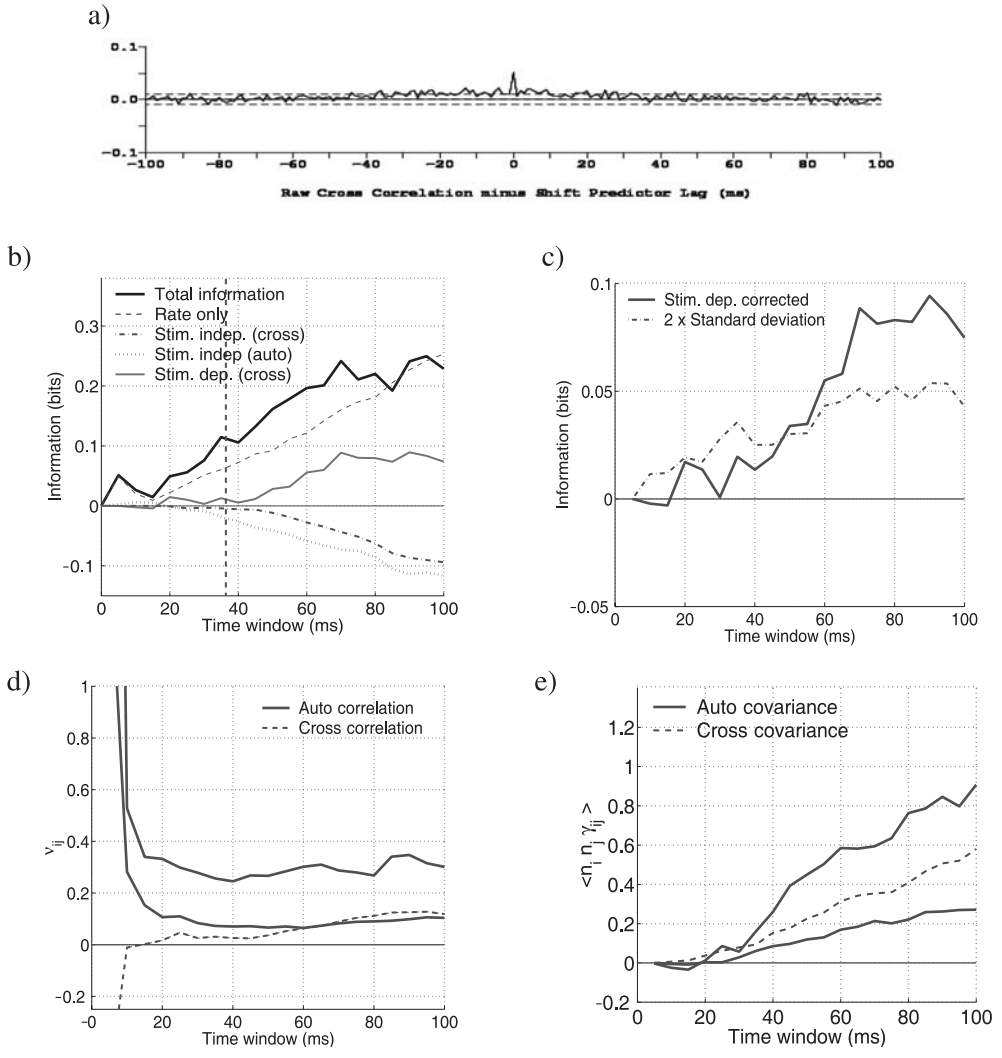

Fig. 3. a–e Information analysis on experiment bj283. **a** Cross correlogram (corrected by subtracting the shift predictor and with the $p < 0.01$ confidence limits indicated) between the responses of two simultaneously recorded neurons from experiment bj283. **b** Results of the information analysis on a set of two simultaneously recorded inferior temporal cortex neurons in experiment bj283. The graphs show the contributions to the information from the different terms in Eqs. 3 and 7 as a function of the length of the time window, which started 100 ms after stimulus onset. The conventions are as in Fig. 1. **c** Value of the cross-cell term of the stimulus-dependent information and two standard deviations of its variation as estimated by the Monte Carlo method described in Methods. **d** Values of v_{ij}, the signal correlations, measured both across the cell pair (cross correlations, *dashed line*), and within cells (autocorrelations, i.e., $i = j$, shown by a *solid line* for each cell). **e** The time course of the terms $\langle \bar{n}_i(s)\bar{n}_j(s)\gamma_{ij}(s)\rangle_s$ (with separate "autocovariance" *solid lines* for each of the individual cells and a "cross covariance" *dashed line* for the pair of cells i and j)

lower (by 10%) than might be expected by the sum of the single cell rate terms (0.29 bits). The redundancy estimated in this way was thus approximately 10% for these sets of 2–4 simultaneously recorded cells. We note that the 'simultaneous rate' information shown in Table 2 includes the first term of the second derivative of the Taylor expansion (see Eq. 7). It incorporates the redundancy that arises from the non-zero values of the v term that reflect correlated or anticorrelated response profiles of the cells to the set of stimuli. The 'total information' was as shown for some datasets a little higher or lower than that available from the 'simultaneous rate' contributions, reflecting the synergy in some cases from stimulus-dependent contributions, and the redundancy from generally stimulus-independent terms as shown in Table 1. If we calculate the total information for each single cell (which includes the stimulus-dependent and stimulus-independent auto terms), and take the sum of these for each dataset, we obtain an average value across the 20 datasets of 0.278 bits. If we compare this with the average value of the total information estimated from each simultaneously recorded dataset, which is 0.29 bits as shown in Table 1, then we see by this alternative method that there is overall a little redundancy between the cells in these small simultaneously recorded datasets of approximately 4%.

We also used a very different approach which enables the information available from a population of cells to be measured when the number of cells in the population is larger than a few cells, and when there may be many spikes present if a longer time window is used. This procedure involves a decoding step in which the stimulus that was presented on each trial is estimated by the decoding procedure from a population of cells, and then the mutual information between the estimated stimulus, and that actually used, was measured (see Experimental Procedures and Rolls et al. (1997)). This procedure enabled the information from a set of 21 cells recorded in small simultaneously recorded subsets on different days and recorded with the same set of visual stimuli to be measured. The method does not allow the possible effects of stimulus-dependent synchronization of neuronal responses to be considered, but does allow the information in the numbers of spikes on each trial and of the correlations between the average response vectors of the neurons which could introduce redundancy, to be measured. Fig. 5 shows for both 100 ms and 500 ms epochs how the information

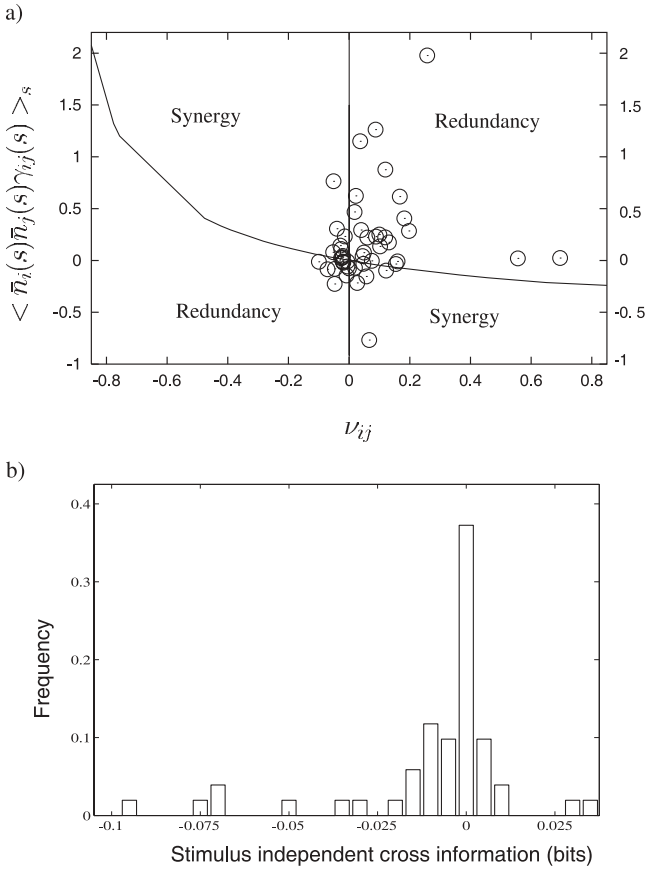

Fig. 4. a,b Synergy vs. redundancy for pairs of cells arising for different combinations of signal and noise correlations. **a** *Open circles* show actual values of $\langle \bar{n}_i(s)\bar{n}_j(s)\gamma_{ij}(s)\rangle_s$ and v_{ij} for simultaneously recorded pairs of inferior temporal cortex cells included in this paper, measured at the end of a 100-ms window using the short time expansion method for measuring the information described in Experimental Procedures. The *lines* separate the space into different regions in which the correlations between the firing of the cells could contribute with synergy or redundancy to the total information. **b** Distribution of the stimulus-independent cross-cell information for the pairs of simultaneously recorded cells. (One pair is not shown in the graph as it had a large value of −0.16 bits)

increases with the number of cells recorded. In both cases there is a linear increase in the information with the number of cells in the population. This indicates that the cells provide information that is approximately independent, that is that the redundancy is very low. Because the information does not reach the ceiling required to discriminate 20 stimuli ($\log_2 20 = 4.32$ bits), there is no asymptotic approach to this ceiling (see Rolls et al. (1997)). A similar linear increase in the information was found with dot product decoding which models how neurons may operate, though the amount of information per cell was somewhat less, as expected with this less efficient decoding procedure (Rolls et al. 1997; Robertson et al. 1999). Although the total amount of information measured with this method was lower than that measured by the Taylor expansion approach, and the decoding approach necessarily cannot be optimal in the amount of information it extracts, the decoding approach does allow demonstration that the information does increase approximately linearly with the number of cells.

Discussion

The experiments and analyses described in this paper provide evidence for considerable information available from the number of spikes that each cell produces to different stimuli, and evidence for little impact of common input leading to redundancy, or of stimulus-dependent cross-correlation, on the amount of information provided by sets of simultaneously recorded inferior temporal cortex neurons. So far, we know of no analyses which have shown with information theoretic methods that considerable amounts of information are available about the stimulus shown from the correlations between the responses of neurons in the ventral visual system. The use of such methods is needed to test quantitatively the hypothesis that synchronization contributes to the encoding of information by neurons. Moreover, the results described here provide clear evidence that the regions which receive outputs about objects and faces from the ventral visual stream, in particular from the inferior temporal visual cortex, could read almost all the information that is available in the spike trains of populations of neurons by utilizing the number of spikes from each of the population of cells. The decoding could thus be as simple as measuring the dot product between the vector of neuronal spikes provided by each cell in a short time period, and the synaptic weight vector of a receiving neuron (see Rolls and Deco (2002) and Rolls and Treves (1998)).

In this investigation we analysed how the information from simultaneously recorded cells adds, to provide quantitative evidence on independence vs redundancy in the information conveyed by simultaneously recorded neurons. The first method compared the information available using the Taylor expansion approach in the "rates" when added from single cells and when estimated from simultaneous recordings. This yielded an estimate of 10% for the redundancy for groups of 2–4 simultaneously recorded cells. This did not take into account the trial-by-trial variability in the neuronal responses to a given stimulus. The second method (also using the Taylor expansion approach) provides a better estimate by taking this variability into account, as well as any stimulus-dependent cross-correlation effects, by comparing the total information measure when added from single cells and when estimated from simultaneous recordings. This yielded an estimate of 4% for the redundancy for groups of 2–4 simultaneously recorded cells.

We note that the redundancy arising from non-zero signal correlations can in principle be compensated for by the "noise" correlations averaged across stimuli. As described above, this compensation occurs when the signs of the signal and noise correlations are opposite, and is reflected in the second term of Eq. 7, the stimulus-independent contribution to the total information which depends on the noise correlations. We illustrate how the

Table 2. The information available from 54 cells considered separately, and in small groups of 2–4 simultaneously recorded cells. The information is that available in a 100 ms time window from 20 sets of simultaneously recorded inferior temporal cortex neurons when shown 20 stimuli effective for the cells

Exper.	1^{st} cell rate info.	2^{nd} cell rate info.	3^{rd} cell rate info.	4^{th} cell rate info.	Sum of rate info.	Total Rate simultaneous	Total simultaneous
bj185	0.10	0.20	–	–	0.30	0.29	0.22
bj207	0.12	0.13	–	–	0.25	0.24	0.24
bj213	0.125	0.09	–	–	0.215	0.21	0.21
bj215	0.075	0.10	0.045	–	0.22	0.20	0.24
bj220	0.17	0.17	0.04	–	0.38	0.33	0.13
bj229	0.10	0.06	–	–	0.16	0.16	0.22
bj240	0.07	0.03	0.08	–	0.18	0.17	0.00
bj243	0.07	0.05	0.08	–	0.20	0.20	0.20
bj278	0.06	0.10	0.14	–	0.30	0.29	0.46
bj280	0.21	0.08	0.15	–	0.44	0.40	0.43
bj283	0.175	0.105	–	–	0.28	0.25	0.23
bj285	0.09	0.04	–	–	0.13	0.125	0.125
bj286	0.03	0.03	–	–	0.06	0.05	0.15
bj287	0.07	0.125	0.03	–	0.225	0.20	0.70
bj288	0.18	0.05	0.16	–	0.39	0.40	0.62
bj290	0.06	0.06	0.09	0.09	0.30	0.28	0.28
bj291	0.41	0.05	–	–	0.46	0.40	0.46
bj292	0.05	0.15	–	–	0.20	0.20	0.20
bj292b	0.13	0.17	0.13	0.21	0.64	0.42	0.34
bj293	0.24	0.10	0.09	0.05	0.48	0.42	0.75
Mean	0.13	0.095	0.095	0.12	0.29	0.26	0.31

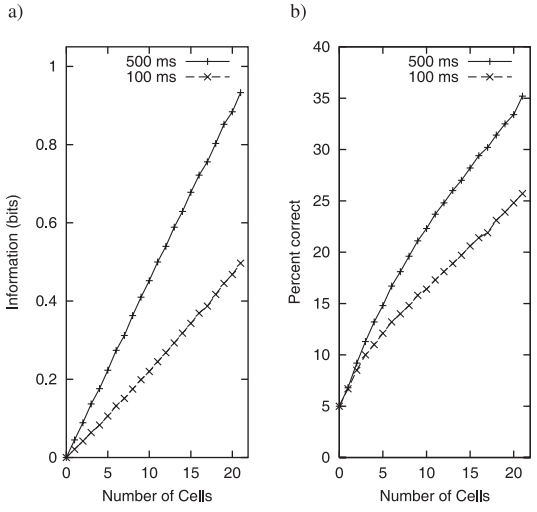

Fig. 5. a,b Information available from different numbers of inferior temporal cortex neurons measured with the decoding procedure. **a** Values for the average information available in the responses of 21 neurons about which of a set of 20 faces or objects had been shown. Separate graphs are shown for 100-ms and 500-ms time windows starting 100 ms after stimulus onset. The decoding method was probability estimation. **b** Percent correct values for the data corresponding to those shown in **a**

space divides by the lines shown in Fig. 4a. This figure shows that for the cell pairs analysed in the inferior temporal visual cortex, the signal correlations v_{ij}, and the noise correlations averaged across stimuli $\langle \bar{n}_i \bar{n}_j \gamma_{ij}(s) \rangle_s$, tend to be clustered around zero but with a bias towards positive values. As a result, most cell pairs show a small negative value for the cross-cell stimulus-independent term, which reflects a small amount of redundancy. The distribution of these values for pairs of cells is shown in Fig. 4b, and the average values for each experiment are shown in Table 1.

The analysis just described with the Taylor expansion method shows, when discussed in a different way, that with simultaneously recorded data, the information adds approximately linearly with the number of cells in the ensemble. (This linear additivity is what occurs if the cells carry independent information, which could be because there is no redundancy or synergy, or these cancel.) This finding of independence in the information encoded by simultaneously recorded neurons is an important extension from an earlier investigation in which the cells were not simultaneously recorded (Rolls et al. 1997). The evidence for this finding is shown in Table 1. Although the low measured redundancy is an interesting result, it is not straightforward to extrapolate to larger numbers of cells with this approach, because the analysis depends on the Taylor expansion shown in Eq. 2 which is valid only with limited numbers of spikes from each cell, and with limited numbers of cells. Indeed, for two experiments described (bj240 and bj286) the time window for the analysis had to be limited to 60 ms in order to prevent the signs of breakdown of the Taylor expansion noted elsewhere in this paper and by Rolls et al. (2003) becoming apparent.

In this context of how the information adds from different cells, and whether there is significant redundancy, the results of application of the decoding procedure for measuring the information encoded by large numbers of cells (Rolls et al. 1997; Franco et al. 2003) are very helpful. The analysis shown in Fig. 5 indicates that with the decoding procedure developed by Rolls et al. (1997), it is confirmed that the information available from larger populations of neurons increases approximately linearly with the number of neurons in the sample. Because the information from the population of cells did not reach near the ceiling of 4.32 bits needed to specify which of the 20 stimuli had been seen, there was no tendency of the information to asymptote at 4.32 bits (Rolls et al. 1997). As noted above, the method was applied to 10 (non-simultaneous) experi-

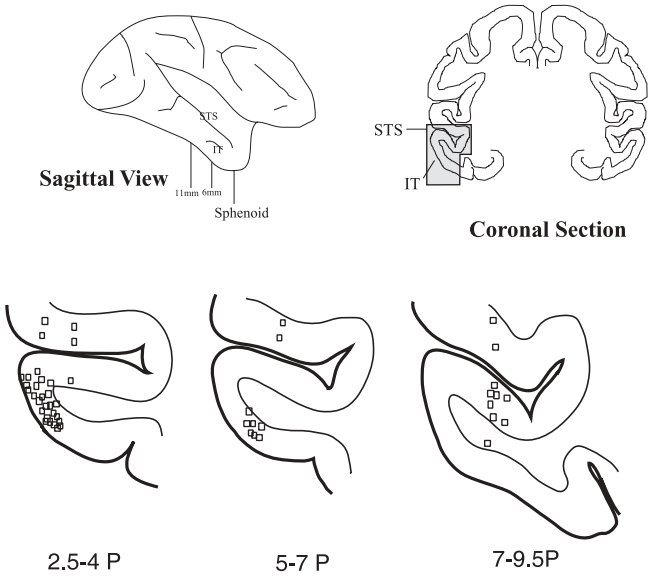

Fig. 6. The locations of the inferior temporal cortex sites at which the neurons described in this paper were recorded. The coronal (transverse) sections are at different distances behind (P, posterior to) the sphenoid bone, which is approximately at the anterior–posterior position of the optic chiasm and anterior commissure. STS – superior temporal sulcus; IT – inferior temporal visual cortex

ments in which small groups of simultaneously recorded neurons were analysed. The method does not allow the possible effects of stimulus-dependent synchronization of neuronal responses to be considered, but does allow the information in the numbers of spikes on each trial and of the correlations between the average response vectors of the neurons which could introduce redundancy, to be measured. Indeed, if all the cells had been recorded simultaneously, the decoding procedure would have allowed estimation of the "stimulus-independent cross-cell" information as described in this paper. The finding in this paper that possible effects of stimulus-dependent cross-correlation are quantitatively negligible in the responses of inferior temporal cortex neurons supports the validity of using the decoding approach for this brain area that was developed by Rolls et al. (1997).

The information values reached in this population were not as high as in a previous study (Rolls et al. 1997). Part of the reason for this may be that because in the study described here we were moving up to 4 microelectrodes during an experiment in order to try to find cells that responded to the stimulus set on as many electrodes as possible, there was less time in a recording session to search for selectively responding neurons with high peak firing rates to their most effective stimulus on every electrode. Another factor may be that we altered the stimulus set from the 20 faces used with face-selective neurons by Rolls et al. (1997) to a set which included faces, objects, and also natural scenes, which would results in less total information if for example a neuron had differential responses to the faces within the set, but no responses to any of the other stimuli.

The average redundancy we found for small groups of simultaneously recorded cells, in the order of 4%, is a little lower redundancy than that estimated by Gawne and Richmond (1993) for pairs of inferior temporal visual cortex neurons. Part of the difference may be that they used a less varied stimulus set (of Walsh patterns), which by spanning the space of the types of stimulus that are effective for IT neurons less well than natural stimuli, may have led to more correlated response tuning profiles of IT neurons. They also were able to obtain data only for cells recorded from the same microelectrode, which were accordingly likely to be very close together in the cortex. We were able to measure whether this factor affects the redundancy because some of our simultaneously recorded cells were on different electrodes. We found that this was not a factor, with similar information encoding, including similar redundancy, for cells recorded on the same electrode (for which the cells might be within 50 microns), and on different electrodes (for which the cells might be 1–3 mm apart).(The redundancy, as estimated by the stimulus-independent cross-cell term, was -0.012 ± 0.05, sem, $n = 9$ for pairs of cells recorded on the same microelectrode, -0.015 ± 0.05, $n = 42$, ns for cell pairs that were recorded on different microelectrodes.) A further advance of the approach used here is that it could be applied to more than just pairs of cells, and that the approach could separate out different contributions (including stimulus-independent and stimulus-dependent cross-cell and auto terms), as described above. We also note that Gawne and Richmond (1993) did not use correction procedure to correct for the bias introduced by having relatively small numbers of trials, and it is known that information estimates using the direct method without these correction procedures are unreliable (Tovee et al. 1993; Rolls and Treves 1998; Rolls and Deco 2002; Panzeri and Treves 1996).

Little stimulus-dependent information from the cross-correlations was available about which stimulus was shown from the neurons recorded in the inferior temporal visual cortex. Could this be because the code is so sparse that it is difficult to detect, and might require simultaneous recordings from very large numbers of neurons to be detected? Although this is certainly possible, we would argue that considerable information was available from the spike counts of the simultaneously recorded neurons about which stimulus was shown, and that this information could be easily decoded by receiving neurons, which might be more difficult if the code was very sparse. Moreover, in the population from which we recorded, there were sufficient spikes from the simultaneously recorded neurons for any stimulus-dependent cross-correlations to be measured if present, in that, as shown on the ordinate of Fig. 5, the values of $\left\langle \bar{n}_i(s)\bar{n}_j(s)\gamma_{ij}(s)\right\rangle_s$ were non-zero for many neuronal pairs. This indicates that such pairs of neurons were responding to the same stimulus, and had firing that was cross-correlated, yet, as shown in Table 1, had only small amounts of stimulus-dependent cross-correlation information compared to the information available from the spike counts. Further evidence that pairs of simultaneously recorded neurons were responding strongly to the same stimulus was obtained by analysing the firing rate responses of all the pairs of simultaneously recorded

neurons to all the stimuli. This provided 992 cases. Of these 992 cases, 73 showed large and significant responses to the same stimulus. (Large was defined for the purposes of this comparison as a response that was 25% greater than the average rate across all stimuli for each neuron. This corresponds to a p value of approximately 0.02.) This result means that each of our 20 simultaneous recording experiments would have on average 3.65 cases where a pair of neurons respond strongly to the same stimulus. (We further note that in 17 out of the 20 experiments, at least one pair of the neurons responded to the same stimulus with this strong response.) The underlying basis for this result is very close to what would be predicted given that neurons, at least in the inferior temporal visual cortex, have an approximately exponential distribution of firing rates to a large set of stimuli (Rolls and Tovee 1995; Rolls and Deco 2002). Overall, the results described here thus show that while it is possible to obtain information from the spike counts of cells that adds usefully to increase the total amount of information, the same sets of cells do not provide much information by any stimulus-dependent correlated firing that is present, which would indeed have to be very large if it were to make a significant contribution to the total information yet was present in only very sparse form across the population of neurons.

One issue is whether we would in these investigations have detected information in the stimulus-dependent cross-correlations between cells even if it were present in the underlying spike-generation process. It is just possible that it could be missed, because of the variability in the spike generation processes, which for some sets of trials might not by chance have included significant cross-correlation related information. Rolls et al. (2003) tested this possibility, and showed that a Poisson-like spike generation process does lead to information that can be detected significantly (by e.g. this algorithm) in 75% of experiments when 20 trials of data for each stimulus are available. (To ensure that these points apply to the real neurophysiological data we analysed in this paper, we performed new simulations in which we used the actual firing rate distributions of some of the neurons analysed in this paper. Part of the purpose of this was to check that low rates to some stimuli by some neurons in real datasets might have insufficient spikes for any cross-corelation to be detectable, resulting in some loss of power of the analysis. The new simulations showed that with the actual firing rate distributions of the real neurons analysed here, there were sufficient spikes for the algorithm to detect information in the cross-correlations between the neurons with the power just described. For the new simulations, the cross-correlations were present in only 4 of the 20 stimuli chosen, and the minimum amount of information that could be reliably detected was approximately 0.015 bits.) In the investigations presented here we did have 20 trials of data for each stimulus, and thus would have been able to detect any stimulus-dependent cross-correlation information that was available in 75% of the 20 experiments if it was present in all 20 experiments. The fact that such information was detected in the present series of 20 experiments in only three experiments (283, 288 and 293 in Table 1), and even in these experiments was quantitatively small with respect to the total information, provides evidence that such stimulus-dependent correlation-related information is not an important feature of encoding in the inferior temporal visual cortex. We also note that 20 experiments are needed to provide an accurate estimate of the stimulus-dependent correlation-related information (as shown by Rolls et al. (2003)), that we did have 20 experiments in the present data set, and that the average contribution was low as described above (see Table 1). In the neurophysiological experiments described here, when stimulus-dependent cross-correlation effects were found, they were found typically in one of the typically 3 possible pairs of simultaneously recorded neurons, and were detected satisfactorily by the approach we describe. However, it is possible that if stimulus-dependent cross-correlations between simultaneously recorded neurons were very infrequent, though nevertheless were still making a significant contribution to the total information, then further research with much larger numbers of recordings might be needed.

The task used involved the presentation of complex stimuli of the type known to activate inferior temporal visual cortex neurons. It is therefore of considerable interest that when this cortical area is responding to its effective stimuli, there is little evidence for stimulus-dependent cross-correlation of neurons, and for this to add substantially to the information present in the number of spikes received. Although only one stimulus was presented at a time in the experiments described, and not for example two with for example either correlated motion or not (Singer 1999, 2000), we note that inferior temporal cortex cells do generally require the stimuli to which they respond to have the features bound together in the correct spatial configuration, for if the features are jumbled, many of these cells do not respond Rolls et al. (1994). In this sense, binding of features is required for the perception of objects or faces composed of different features. If stimulus-dependent cross-correlations are not present to implement this, as the results of this paper suggest, then one possibility is that binding of features in another part of the visual system is implemented by stimulus-dependent synchronization, but is not evident in the inferior temporal visual cortex. Another possibility is that stimulus-dependent cross-correlations between neurons are not necessary for normal visual object recognition, but are called into play only when a new stimulus is being seen. A more likely possibility is that the binding of features is instead implemented by neurons that respond non-dynamically to combinations of features in the correct spatial configuration. Such a feature binding set of combination-sensitive feature encoding neurons could be set up by a self-organizing learning process, and can implement the binding needed for invariant visual object recognition (Elliffe et al. 2002; Rolls and Deco 2002; Riesenhuber and Poggio 1999).

The approach to the encoding of information by simultaneously recorded neurons used in this paper

utilizes a Taylor expansion of the basic Shannon Eq. 1. We know of very few other approaches to measuring the information that may be available in the stimulus-dependent cross-correlation of neurons, though of course many investigators have been interested in synchronization (Singer 2000); and there are approaches to how the noise correlations and the signal correlations contribute to the information available without explicitly addressing that available from stimulus-dependent synchronization (Reich et al. 2001; Sompolinsky et al. 2001; Abbott and Dayan 1999; Oram et al. 1998). Other investigators have measured the information that may be encoded within the spike train of individual neurons. For example, Brenner, Strong, Koberle and Bialek (2000), show that when moving stimuli are used, information may be evident in the relative time of firing of (single) neurons in the fly visual system. It may be that with multiple cell simultaneously recorded data in primates, information from the relative time of firing of the different neurons may be especially evident primarily when moving stimuli are used, or when the analysis depends on different arrival times for different stimuli Panzeri et al. (2001), which is a relatively simple way in which information can be reflected in the temporal variations in spike trains, as shown by Tovee et al. (1993). We also note that the investigation is an advance on some earlier investigations, in that we measured information and not just correlations (Erickson et al. 2000), in that we measured how stimulus-dependent synchronization, as well as redundancy (Gochin et al. 1994), contribute to the total information.

The overall conclusion from the results described in this paper is that inferior temporal visual cortex neurons, the major output of the ventral visual stream, convey information that is almost independent, with little redundancy; and that there is considerable information in the spike counts. In the context of finding that the spike counts are important in the encoding, we found no evidence that stimulus-dependent cross-correlations contribute significantly to the code. The encoding is thus in an appropriate form for readout by receiving areas in which the neurons compute a dot product between the numbers of spikes received from different neurons and their synaptic weight vectors (Rolls and Treves 1998; Rolls and Deco 2002). Finally, we note that to test hypotheses about the functions of the numbers of spikes vs cross-correlations between spike trains, it is appropriate to use information theoretic approaches to quantify the different contributions to neuronal encoding on the brain.

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The program used to perform the information theoretic analysis, corrinfo3, implemented the algorithm described by Panzeri et al. (1999). The original program used by Panzeri et al. (1999) was written in C, but was rewritten in Matlab by Drs. S.Panzeri (University of Newcastle, U.K.) and R.S.Petersen (SISSA, Trieste, Italy), used for research on the rat somatosensory cortex (Panzeri et al. 2001; Petersen, Panzeri, Diamond 2001), and kindly made available to us. We (Rolls et al. 2003) developed this Matlab code to separate the auto- and cross-cell terms (in a different way to that used by Panzeri et al. (2001) and Petersen et al. (2001)), and incorporated the Monte Carlo procedure which allows the statistical significance of the cross-cell stimulus-dependent term to be evaluated.

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