Odor encoding by signals in the olfactory bulb

Supplementary Material

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The information measurement algorithm

The aim is to measure how much information is provided on average on a single trial about which stimulus was presented, using measures of the responses of a population of neurons, which in this case stand for the responses of glomeruli in the olfactory bulb. The measures of the responses of each neuron might include the firing rates, and one or more temporal measures such as the latency of the neuronal response. In the present study, three temporal measures were used for each neuron, the time on each trial for the neuron to reach 10% (t10), 50% (t50), and 90% (t90) of its maximal rate response. We wish to measure the information from the rate alone, from the temporal measures alone (to compare their magnitude), and from both the rate and the temporal measure (to show whether there is additive information, which would indicate independence of the rate and temporal measures, with the alternative being redundancy). It is noted that Shannon information theory (Shannon, 1948) provides a principled approach to this type of question, because information measures are additive if they are independent; and the amounts of information from different measures can be directly compared, including for example neuronal, fMRI, and behavioral measures (Rolls et al., 2009; Rolls and Treves, 2011; Rolls, 2016, 2021).

The direct approach is to apply the Shannon mutual information measure (Shannon, 1948; Cover and Thomas, 1991)

$$I(s,\mathrm{r}) = \sum_{s \in S} \sum_{\mathrm{r}} P(s,\mathrm{r}) \log_2 \frac{P(s,\mathrm{r})}{P(s)P(\mathrm{r})}. \qquad (1)$$

where P(*s*,**r**) is a probability table embodying a relationship between the variable *s* (here, the stimulus) and **r** (a vector that includes the response of each neuron, and might for each neuron include its firing rate and a temporal measure or measures such as latency).

However, because the probability table of the relation between the neuronal responses and the stimuli, P(*s*,r) is so large (given that there may be many stimuli, and that the response space which has to include temporal information is very large), in practice it is difficult to obtain a sufficient number of trials for every stimulus to generate the probability table accurately, at least with data from mammals in which the experiment cannot usually be continued for many hours of recording from a whole population of cells. To circumvent this undersampling problem, Rolls et al. (1997) developed a decoding procedure, in which an estimate (or guess) of which stimulus (called *s'*) was shown on a

given trial is made from a comparison of the neuronal responses on that trial with the responses made to the whole set of stimuli on other trials. One then obtains a conjoint probability table P(*s,s'*), and then the mutual information based on probability estimation (PE) decoding (I_p) between the estimated stimuli *s'* and the actual stimuli *s* that were shown can be measured:

$$\langle I_p \rangle = \sum_{s \in S} \sum_{s' \in S} P(s,s') \log_2 \frac{P(s,s')}{P(s)P(s')}, \tag{2}$$

$$= \sum_{s \in S} P(s) \sum_{s' \in S} P(s'|s) \log_2 \frac{P(s'|s)}{P(s')}. \tag{3}$$

These measurements are in the low dimensional space of the number of stimuli, and therefore the number of trials of data needed for each stimulus are of the order of the number of stimuli, which is feasible in experiments. In practice, it is found that for accurate information estimates with the decoding approach, the number of trials for each stimulus should be at least twice the number of stimuli.

Decoding procedures

The nature of the decoding procedure is illustrated in Fig. S1. The left part of the diagram shows the average firing rate (or equivalently spike count) responses of each of 3 cells (labelled as Rate Cell 1,2,3) to a set of 3 stimuli. The last row (labelled Response single trial) shows the data that might be obtained from a single trial and from which the stimulus that was shown (St. ?) must be estimated or decoded, using the average values across trials shown in the top part of the table, and the probability distribution of these values. The decoding step essentially compares the vector of responses on trial St.? with the average response vectors obtained previously to each stimulus. This decoding can be as simple as measuring the correlation, or dot (inner) product, between the test trial vector of responses and the response vectors to each of the stimuli. This procedure is very neuronally plausible, in that the dot product between an input vector of neuronal activity and the synaptic response vector on a single neuron (which might represent the average incoming activity previously to that stimulus) is the simplest operation that it is conceived that neurons might perform (Rolls and Treves, 1998; Rolls, 2021). Other decoding procedures include a Bayesian procedure based on a Gaussian or Poisson assumption of the spike count distributions as described in detail by Rolls et al. (1997). The Gaussian one is what it used throughout this paper, and it is described below. The step taken in this paper is to introduce into the Table Data(*s*,**r**) shown in the upper part of Fig. 2 new columns, shown on the right of the diagram, containing a measure (or measures) of the temporal aspects of the neuronal response, such as the response latency (averaged across trials in the upper part of the Table). (An analogous procedure was introduced by Franco et al (2004) to measure the effects of cross-correlations between the firing of pairs of neurons.) The decoding procedure can then take account of any temporal information such as latency in the response of each cell to each stimulus, and thus measure any contributions to the information from the population of cells that arise from temporal and /r rate information. This is the new concept introduced in this paper for information measurement from neuronal populations to include temporal information such as one or more latency measures.

Further details of the decoding procedures are as follows (see also Rolls et al. (1997)). The full probability table estimator (PE) algorithm uses a Bayesian approach to extract P(*s'*|**r**) for every single trial from an estimate of the probability P(**r**|*s'*) of a stimulus-response pair made from all the other trials (as shown in Bayes' rule shown in equation 4) in a cross-validation procedure described by Rolls et al. (1997).

$$P(s'|r) = \frac{P(r|s')P(s')}{P(r)}. \qquad (4)$$

where (the vector containing the firing rate of each neuron, where each element of the vector is the firing rate of one neuron) is obtained as :

$$P(r) = \sum_{s'} P(r|s')P(s'). \qquad (5)$$

This requires knowledge of the response probabilities P(**r** |*s'*) which can be estimated for this purpose from P(**r** , *s'*), which is equal to $P(s') \prod_c P(r_c|s')$, where r_c is the firing rate of cell *c* . We note that P(r_c| s') is derived from the responses of cell from all of the trials except for the current trial for which the probability estimate is being made. The probabilities P(r_c| s') are fitted with a Gaussian (or Poisson) distribution whose amplitude at r_c gives P(r_c| s')[2]. By summing over different test trial responses to the same stimulus *s* , we can extract the probability that by presenting stimulus *s* the neuronal response is interpreted as having been elicited by stimulus *s'*,

$$P(s'|s) = \sum_{r \,\in\, test} P(s'|r)P(r|s). \qquad (6)$$

After the decoding procedure, the estimated relative probabilities (normalized to 1) were averaged over all 'test' trials for all stimuli, to generate a (Regularized) table $P_N^R(s|s')$ describing the relative probability of each pair of actual stimulus *s* and posited stimulus *s'* (computed with *N* trials). From this probability Table the mutual information measure (I_p) was calculated as described above in equation 3.

We also generated a second (Frequency) table $P_N^F(s \mid s^p)$ from the fraction of times an actual stimulus *s* elicited a response that led to a predicted (single most likely) stimulus s^p . From this probability Table the mutual information (I_{ml}) measure based on maximum likelihood decoding was calculated with equation 7:

$$\langle I_{ml} \rangle = \sum_{s \in S} \sum_{s^p \in S} P(s, s^p) \log_2 \frac{P(s, s^p)}{P(s)P(s^p)}. \qquad (7)$$

The maximum likelihood decoding does give an immediate measure of the percentage correct.

A detailed comparison of maximum likelihood and probability decoding is provided by Rolls et al. (1997), but we note here that probability estimate decoding is more regularized (see below) and therefore may be safer to use when investigating the effect on the information of the number of cells. For this reason, the results described in this paper were obtained with probability estimation (PE) decoding.

We note that any decoding procedure can be used in conjunction with information estimates both from the full probability table (to produce I_p), and from the most likely estimated stimulus for each trial (to produce I_{ml}).

Because the probability tables from which the information is calculated may be unregularized with a small number of trials, a bias correction procedure to correct for the undersampling is applied, as described in detail by Rolls et al. (1997) and Panzeri & Treves (1996). In practice, the bias correction that is needed with information estimates using the decoding procedures described here and by Rolls et al. (1997) is small, typically less than 10% of the uncorrected estimate of the information, provided that the number of trials for each stimulus is in the order of twice the number of stimuli. We also note that the distortion in the information estimate from the full probability table needs less bias correction than that from the predicted stimulus table (i.e. maximum likelihood) method, as the former is more regularized because every trial makes some contribution through much of the probability table (see Rolls et al. (Rolls et al., 1997)). We further note that the bias correction term becomes very small when more than 10 cells are included in the analysis (Rolls et al., 1997).

We note that if Bayesian decoding is used an assumption is that the joint probability distribution of the spike count responses of the cells is approximated by the product of the separate probability distributions for each cell. This approximation holds if the distributions are independent, and may be less exact if there are correlations between the neurons' responses. In practice this is not a limitation of the method in that the level of correlations found in practice produce only a relatively small distortion of the probability values used to compute the information, partly because these probability values are normalized before being used, reducing the distortion especially when relatively few (e.g. 20) trials of data per stimulus are used. We also note that trying to estimate the parameters for the joint probability distribution would require a very large number of trials of data.

Response quantification

The data from the neuronal activity that was entered into the Table Data(s,$\mathbf{r}$) shown in the upper part of Fig. S1 was as follows.

From the response of each cell or glomerulus c to each stimulus, we extracted a single activity signal in a fixed time window, which was from timebin 1 when the odor delivery started until the last timebin, 15, unless otherwise stated. Each timebin was 33.3 ms long. The algorithm measured the information in the rates, and in any co-modulation of the rates of the glomeruli, from these rate counts to a given stimulus on a given trial. We also extracted the 3 temporal parameters already mentioned, the time until 10% of the maximum response (t10), until 50% (t50), and until 90% (t90), and entered these into the responses table as shown in Fig. S1.

The correlations in the mean responses of the neurons across the set of stimuli (sometimes called 'signal' correlations) v ij:
We also measured the correlations between the mean response profiles to the set of stimuli of populations of glomeruli, to provide insight into whether the populations of glomeruli could in principle encode the stimuli differently, even though the information measure might be low if there was great trial-to-trial variability of the neural responses.

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; Rolls and Treves, 2011; Rolls, 2021). It is defined by:

$$v_{ij} = \frac{\left\langle \overline{r_i}(s)\,\overline{r_j}(s) \right\rangle_s}{\left\langle \overline{r_i} \right\rangle_s \left\langle \overline{r_j} \right\rangle_s} - 1, \tag{8}$$

where $\overline{r_i}(s)$ is the mean rate of response of cell i to stimulus s over all the trials in which that stimulus was present. It can vary from -1 to ∞. ($\left\langle \cdots \right\rangle_s$ indicates the ensemble average over the s stimuli.) The similarity of the mean response profiles can also be measured by the Pearson correlation coefficient, r .
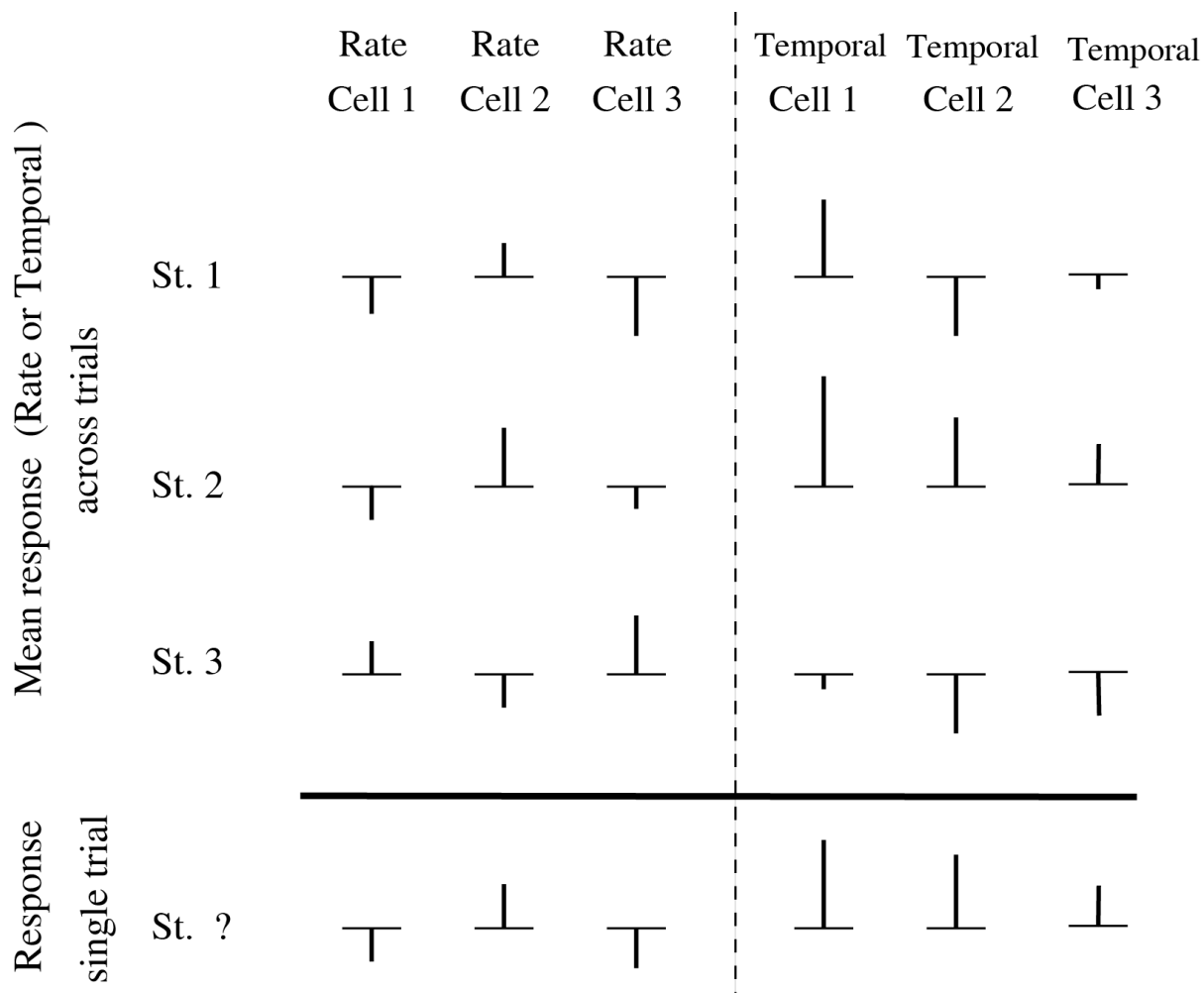
Fig. S1. Decoding rate and temporal measures of neural responses that might encode information about which stimulus had been presented on a single trial. The upper left part of the diagram shows the average firing rate (or equivalently spike count) responses of each of 3 cells (labelled as Rate Cell 1,2,3) to a set of 3 stimuli. The upper right three columns show the average across trials of a measure of temporal aspects of the neural response, for example latency for each cell. The bottom row (labelled Response single trial) shows the data that might be obtained from a single trial and from which the stimulus that was shown (St. ? or s') must be estimated or decoded, using the average values across trials shown in the top part of the table. From the responses on the single trial, the most probable decoded stimulus is stimulus 2, based on the values of both the rates and the temporal measures.

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