Sparse Representation in the Human Medial Temporal Lobe: Supplementary Methods

S. Waydo, A. Kraskov, R. Quian Quiroga, I. Fried, C. Koch

Derivation of the Joint Probability of N_r and S_r

Here we calculate the joint probability of measuring N_r responsive neurons and S_r evocative stimuli given that we are recording from N neurons and presenting S stimuli. This distribution is then used to generate Figure 2 in the main text. We will first derive a recursive relation for the conditional distribution of S_r given N_r, then solve the recurrence in closed form and apply Bayes' rule to obtain the joint distribution.

In what follows we assume the sparseness a is known, that is all probability distributions are conditioned on a. First, let M be the number of stimuli among the S presented that a particular neuron responds to. The value of M follows a binomial distribution,

$$P[M = m] = \binom{S}{m} a^m (1-a)^{S-m}.$$

If we assume that the neuron in question is responsive (i.e. $M \geq 1$), this distribution becomes (using Bayes' rule)

$$P[M = m | M \geq 1] = \frac{P[M = m]}{P[M \geq 1]} = \binom{S}{m} \frac{a^m (1-a)^{S-m}}{1-(1-a)^S}. \quad (1)$$

To begin our recursive definition, note that $P[S_r = s_r | N_r = 1] = P[M = s_r | M \geq 1]$. Now assume the first $n_r - 1$ responsive neurons are excited by R stimuli. Let Q be the number of stimuli *not* in the set of size R that excite the next neuron (neuron n_r). The distribution of Q is given by

$$P[Q = q | R = r] = \sum_{m=q}^{r+q} P[M = m | M \geq 1] \frac{\binom{r}{m-q}\binom{S-r}{q}}{\binom{S}{m}}, \quad (2)$$

where $q \in \{0, \ldots, S-m\}$. The first term in the sum is simply the probability that the neuron in question responds to m stimuli total. The second term is the number of ways these m stimuli could be split such that q of them are not in the set of size r divided by the total number of ways these m stimuli could be chosen, so it is the probability that the m stimuli include exactly q stimuli not already in the set responded to by the first $n_r - 1$ neurons.

With a little effort we can find a closed-form expression for Equation 2. If $q > 0$, we can combine equations 1 and 2 and pull out terms unrelated to the sum to obtain

$$P[Q=q|R=r] = \begin{pmatrix} S-r \\ q \end{pmatrix} \frac{(1-a)^S}{1-(1-a)^S} \sum_{m=q}^{r+q} \begin{pmatrix} r \\ m-q \end{pmatrix} \left(\frac{a}{1-a}\right)^m .$$

Substituting $m' = m - q$ this becomes

$$P[Q=q|R=r] = \begin{pmatrix} S-r \\ q \end{pmatrix} \frac{(1-a)^S}{1-(1-a)^S} \left(\frac{a}{1-a}\right)^q \sum_{m'=0}^{r} \begin{pmatrix} r \\ m' \end{pmatrix} \left(\frac{a}{1-a}\right)^{m'} .$$

Applying the binomial theorem to the sum we have

$$P[Q=q|R=r] = \begin{pmatrix} S-r \\ q \end{pmatrix} \frac{(1-a)^S}{1-(1-a)^S} \left(\frac{a}{1-a}\right)^q \left(\frac{1}{1-a}\right)^r \qquad (q>0) \tag{3}$$

If $q = 0$, the first term in the sum vanishes and we have instead

$$P[Q=0|R=r] = \frac{(1-a)^S}{1-(1-a)^S} \sum_{m=1}^{r} \begin{pmatrix} r \\ m \end{pmatrix} \left(\frac{a}{1-a}\right)^m .$$

Again applying the binomial theorem this becomes

$$P[Q=0|R=r] = \frac{(1-a)^S}{1-(1-a)^S} \left[\left(\frac{1}{1-a}\right)^r - 1\right] . \tag{4}$$

We can combine Equations 3 and 4 to obtain the final result,

$$P[Q=q|R=r] = \begin{pmatrix} S-r \\ q \end{pmatrix} \frac{(1-a)^S}{1-(1-a)^S} \left(\frac{a}{1-a}\right)^q \left[\left(\frac{1}{1-a}\right)^r - \delta(q)\right] , \tag{5}$$

where $\delta(q) = 1$ if $q = 0$ and $\delta(q) = 0$ otherwise.

The relationship in Equation 5 now lets us complete the recursive definition of the conditional distribution of S_r given N_r:

$$P[S_r = s_r|N_r = n_r] = \sum_{y=1}^{s_r} P[S_r = y|N_r = n_r - 1]P[Q = s_r - y|M = y]. \tag{6}$$

Simply put, this is the probability that neuron n_r adds just enough new stimuli to the set responded to by the first $n_r - 1$ neurons to total s_r. Since we calculated the base case $P[S_r = s_r|N_r = 1]$ above, this probability can be calculated for any n_r and s_r by starting at $N_r = 1$ and working upward. Next we solve the recurrence to find a simpler expression for this probability and eliminate the need to calculate the needed probability recursively.

Proposition 1. *The recurrence given in Equation 6 has solution*

$$P[S_r = s_r | N_r = n_r] = \left(\begin{array}{c} S \\ s_r \end{array} \right) \left[\frac{(1-a)^S}{1-(1-a)^S} \right]^{n_r} (-1)^{n_r} \sum_{k=1}^{n_r} \left(\begin{array}{c} n_r \\ k \end{array} \right) (-1)^k \left[(1-a)^{-k} - 1 \right]^{s_r}. \tag{7}$$

Proof. For convenience, define

$$\begin{aligned} G &\equiv \frac{(1-a)^S}{1-(1-a)^S}, \\ H &\equiv \frac{a}{1-a}. \end{aligned}$$

Then the recurrence we are trying to solve is

$$\begin{aligned} P[S_r = s_r | N_r = n_r] &= \sum_{y=1}^{s_r} P[S_r = y | N_r = n_r - 1] P[Q = s_r - y | R = y] \qquad (8) \\ &= G \left\{ H^{s_r} \sum_{y=1}^{s_r} P[S_r = y | N_r = n_r - 1] \left(\begin{array}{c} S-y \\ s_r - y \end{array} \right) a^{-y} - P[S_r = y | N_r = n_r - 1] \right\} \\ P[S_r = s_r | N_r = 1] &= \left(\begin{array}{c} S \\ s_r \end{array} \right) H^{s_r} G, \end{aligned}$$

and the proposed solution is

$$P[S_r = s_r | N_r = n_r] = \left(\begin{array}{c} S \\ s_r \end{array} \right) G^{n_r} (-1)^{n_r} \sum_{k=1}^{n_r} \left(\begin{array}{c} n_r \\ k \end{array} \right) (-1)^k \left[\left(\frac{H}{a} \right)^k - 1 \right]^{s_r}. \tag{9}$$

We will prove the result using induction. For the base case, let $n_r = 1$. Then

$$\begin{aligned} P[S_r = s_r | N_r = 1] &= \left(\begin{array}{c} S \\ s_r \end{array} \right) G(-1)(-1) \left[\frac{H}{a} - 1 \right]^{s_r} \\ &= \left(\begin{array}{c} S \\ s_r \end{array} \right) G H^{s_r}, \end{aligned}$$

the desired result. For the inductive step, assume the result holds for $n_r - 1$. Then substituting into

Equation 8 we have

$$\begin{aligned}
P[S_r = s_r | N_r = n_r] &= G \Bigg\{ H^{s_r} \sum_{y=1}^{s_r} \binom{S}{y} G^{n_r - 1} (-1)^{n_r - 1} \sum_{k=1}^{n_r - 1} \binom{n_r - 1}{k} (-1)^k \left[\left(\frac{H}{a} \right)^k - 1 \right]^y \\
&\quad \binom{S - y}{s_r - y} a^{-y} - \binom{S}{s_r} G^{n_r - 1} (-1)^{n_r - 1} \sum_{k=1}^{n_r - 1} \binom{n_r - 1}{k} (-1)^k \left[\left(\frac{H}{a} \right)^k - 1 \right]^{s_r} \Bigg\} \\
&= G^{n_r} (-1)^{n_r} \binom{S}{s_r} \sum_{k=1}^{n_r} \binom{n_r}{k} (-1)^k \left[\left(\frac{H}{a} \right)^k - 1 \right]^{s_r},
\end{aligned}$$

where the simplification results from extensive algebraic manipulation and applications of the binomial theorem. This is exactly the proposed solution from Equation 9 and the proof is complete. □

To obtain the joint probability of measuring N_r responsive neurons *and* S_r stimuli to which they respond from Bayes' rule, we will need the probability of measuring N_r responsive neurons independent of S_r. The probability that a neuron responds to *some* stimulus, which we denote p_r, is 1 minus the probability that it responds to no stimuli, or

$$p_r = 1 - (1 - a)^S.$$

The number of responsive neurons then follows a binomial distribution,

$$\begin{aligned}
P[N_r = n_r] &= \binom{N}{n_r} p_r^{n_r} (1 - p_r)^{N - n_r} \\
&= \binom{N}{n_r} \left[1 - (1 - a)^S \right]^{n_r} (1 - a)^{S(N - n_r)}.
\end{aligned}$$

We are now ready to apply Bayes' rule to obtain the desired probability,

$$\begin{aligned}
P[N_r = n_r \wedge S_r = s_r] &= P[S_r = s_r | N_r = n_r] P[N_r = n_r] \\
&= \binom{S}{s_r} \left[\frac{(1 - a)^S}{1 - (1 - a)^S} \right]^{n_r} (-1)^{n_r} \sum_{k=1}^{n_r} \binom{n_r}{k} (-1)^k \left[(1 - a)^{-k} - 1 \right]^{s_r} \\
&\quad \binom{N}{n_r} \left(1 - (1 - a)^S \right)^{n_r} (1 - a)^{S(N - n_r)} \\
&= \binom{S}{s_r} \binom{N}{n_r} (1 - a)^{NS} (-1)^{n_r} \\
&\quad \sum_{k=1}^{n_r} \binom{n_r}{k} (-1)^k \left[(1 - a)^{-k} - 1 \right]^{s_r}. \qquad (10)
\end{aligned}$$

Equation 10 has been verified to match Monte Carlo results within 5% for all cases in which the number of trials (10^8 simulated sessions) was statistically significant (10^8 trials is sufficient to measure a probability of 0.01 to within 5% with 99% confidence) for select values of a. Note also that it can be shown that if the roles of N and S and those of n_r and s_r are reversed Equation 9 does not change, an expected result due to the symmetry of the problem. Furthermore, summing Equation 9 over all s_r or n_r yields the expected marginal distributions. We should also note that Equation 9 is numerically very poorly conditioned, as the binomial coefficients can easily produce numbers much larger than machine precision allows. Hence care is needed when evaluating these probabilities numerically. In some cases wildly inaccurate results were obtained using MATLAB, and it was necessary to make use of Mathematica's arbitrary-precision capabilities to generate meaningful results.

Note that all of the above assumed a was known, so replacing a by α in the derived distribution we obtain the conditional distribution $P[N_r = n_r \wedge S_r = s_r | a = \alpha]$. As in the single-neuron example from the main text, we can invert this relationship using Bayes' rule to obtain the probability distribution of a given N_r and S_r:

$$f_a(\alpha | N_r = n_r \wedge S_r = s_r) = \frac{P[N_r = n_r \wedge S_r = s_r | a = \alpha] f_a(\alpha)}{\int_0^1 P[N_r = n_r \wedge S_r = s_r | a = \alpha] f_a(\alpha) d\alpha}. \tag{11}$$

Equation 11 was calculated by numerical integration in Mathematica on a session-by-session basis and averaged to produce Figure 2 in the main text.