

The urgency signal (denoted $u(t)$) in Equation 9 was estimated directly from neural responses as described in Churchland et al. (2008) and was parameterized by a hyperbolic function

$$u(t) = u_{\infty} \frac{t}{t + \tau_{1/2}}$$

In the simulations of the two-choice experiment, we used $u_{\infty} = 34.7$ spike s^{-1} and $\tau_{1/2} = 133.3$ ms, and in the four-choice experiment, we used $u_{\infty} = 39$ spike s^{-1} and $\tau_{1/2} = 343.2$ ms. These values were directly obtained from in vivo recordings in LIP as described in Churchland et al. (2008).

Stopping Bound and Action Selection

The psychometric and chronometric curves shown in Figure 6 were obtained by stopping the accumulation of evidence when the firing rate of any of the neurons in LIP, determined from the probability of firing (Equation 10), reached 55 spikes/s for the four-choice experiment and 66 spikes/s for the two-choice experiment. In the two-choice experiment, we determine the action selected by the network using the preferred direction of the neuron that reached the bound first. If this preferred direction was within the interval $[-90^{\circ}, 90^{\circ}]$, the network decision was set to 0° ; otherwise, it was set to 180° . A similar strategy was used for the four-choice experiment, except that we used four quadrants.

Note that the implementation of the bound (as well as saccade selection) is not based on the output spike trains of individual neurons. Indeed, this would not be a robust way to proceed: estimating the rate of a single neuron on a single trial is subject to a very large variability. A more robust approach consists of using spike counts filtered across direction and time. This is effectively what we have done here, since we are using the probability of firing. That probability, which is m_i in Equation 10, is a filtered version of the spike trains both from MT and LIP.

Decoding Probability Distributions from Population Activity

To generate Figures 2B and 4B, we need to compute the posterior, $p(s|r^{LIP}(t_n))$ where here t_n is shorthand for spike count between times t_n and $t_n - \Delta t$ (where $\Delta t = 50$ ms). For this we use Bayes' rule (assuming a flat prior), which gives us

$$p(s|r^{LIP}(t_n)) \propto p(r^{LIP}(t_n)|s). \quad (11)$$

To model the likelihood in LIP, $p(r^{LIP}(t_n)|s)$, we use a distribution that lies in the exponential family with linear sufficient statistics,

$$p(r^{LIP}(t_n)|s) = \Phi(r^{LIP}(t_n), \mathbf{c}(t_n)) \exp(\mathbf{h}^{LIP}(s) \cdot \mathbf{r}^{LIP}(t_n)). \quad (12)$$

Note that this is an approximation: as discussed in the main text, the true distribution in LIP does not lie in this class. However, the approximation appears to be a good one, since we fail to find any significant Fisher information in LIP spike count beyond what can be recovered with a local optimal linear estimator, even when that estimator is independent of both coherence and time (see section Estimating Fisher Information).

To estimate $\mathbf{h}^{LIP}(s)$, we took advantage of the fact that $\mathbf{h}^{LIP}(s)$ must satisfy Equation 5 (Ma et al., 2006). Importantly, the right hand-side of Equation 5 is the local optimal linear estimator (LOLE) of LIP activity (Series et al., 2004). Therefore, we can approximate $\mathbf{h}^{LIP}(s)$ by estimating the LOLE of LIP activity and integrating it as a function of s . To obtain the LOLE, we ran the network for 10,000 trials at 51.2% coherence, with each trial lasting 200 ms. We divided each trial into four time windows of 50 ms each and extracted the spike count over each time window. We then trained four LOLEs over each of the four time windows (see Series et al. [2004] for details). This gave us four sets of weights, $\mathbf{W}_i^{LOLE}(s)$, with $i = \{1, 2, 3, 4\}$ referring to the 50 ms time interval. We then integrated the $\mathbf{W}_i^{LOLE}(s)$ with respect to s to obtain an estimate of the kernels, $\mathbf{h}^{LIP}(s, t_i)$, at the four time intervals. The resulting kernels were then averaged to obtain the overall kernel, $\mathbf{h}^{LIP}(s)$. This kernel was used in Equation 12 and 11 to obtain posterior distributions at all times and across all coherences, as illustrated in Figures 2B and 4B.

Estimating Fisher Information

To estimate the Fisher information, we used the kernels computed in the previous section to obtain the maximum-likelihood estimate of the stimulus on 5000 trials, and then computed the variance of those estimates. The Fisher

information is the inverse of the variance. The maximum likelihood estimates were given by

$$\hat{s} = \underset{s}{\operatorname{argmax}} (\exp(\mathbf{h}^{LIP}(s) \cdot \mathbf{r}^{LIP}(t_n))).$$

The activity, $\mathbf{r}^{LIP}(t_n)$, is the spike count in a 50 ms bins between times t_n and $t_n - 50$ ms. We computed the Fisher information both for $\mathbf{h}^{LIP}(s)$, the average kernel, and for $\mathbf{h}_i^{LIP}(s)$, the individual kernels (see previous section). The results are shown in Figure 3B.

We also tried a variety of nonlinear methods to estimate Fisher information (see Series et al. [2004] for details), but we found no significant information beyond what is recovered by the method described above.

Slopes of Integration In Vivo and in Simulations

Figure 7 shows the slope of integration of LIP neurons in vivo (from Churchland et al., 2008) and in the model as a function of coherence for the two-choice and four-choice experiments. The slopes of integration in the model were obtained by fitting a line in the average probability of firing $m_i(t_{n+1})$ of LIP neurons (Equation 10) over the first 50 ms of the integration period (i.e., 50 ms after the start of the response to the moving dots).

In both the model and in vivo, the slope of the integration for T_{in} (the neuron whose response field corresponds to the chosen target) increases linearly with coherence. Conversely, the slope of integration for T_{out} (the neuron whose response field corresponds to a saccade 180° away from the chosen target) decreases linearly with coherence. In addition, in the four-choice experiment, the slope of integration for T_{90} (the neuron whose response field is 90° away from the chosen target) decreases but less so than for the T_{out} neuron. Finally, for a given coherence, the slope of integration for two choices is always larger than the slope for four choices.

In the case of the model, the slope of integration for T_{90} neurons is determined by the shape of the tuning curves to saccade direction. For very narrow tuning curves, the slope of integration for T_{90} and T_{out} neurons are very similar, while for wide tuning curves, the slope of integration for T_{90} can in fact increase with coherence although always less so than for the T_{in} neurons (not shown). This is a noteworthy result because some LIP neurons show an increase in integration slope as a function of coherence (see for instance Figure 4E in Churchland et al., 2008).

SUPPLEMENTAL DATA

The Supplemental Data include two figures and a Supplemental Note and can be found with this article online at [http://www.neuron.org/supplemental/S0896-6273\(08\)00803-9](http://www.neuron.org/supplemental/S0896-6273(08)00803-9).

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