

Model structure

Here we provide a detailed description of the model used in this study (Fig. 3). The main flow of the model consists of three stages: (1) representation of random dot motion by two pools of direction selective neurons, (2) representation of a decision signal by two pools of LIP neurons, (3) comparison of the decision signal to a threshold. The responses of individual neurons in MT and LIP are simulated by generating sequences of spikes. The instantaneous, smoothed, averaged spike rates from an ensemble of neurons is taken as the signal output and used in the subsequent computation. The model does not specify how neurons achieve the key computations: difference, integration, comparison to threshold. Nor does it address the synaptic mechanisms leading to spikes. Rather, it facilitates a comparison of spike discharge from single neurons to macroscopic behavioral parameters, choice and reaction time.

We have extended a technique introduced by Oram et al (1996) for generating random spike sequences from ensembles of noisy neurons with weak coupling (i.e., cross-correlation; see Mazurek and Shadlen 2002), consistent with properties measured in area MT (Zohary et al. 1994; Bair et al. 2001) and presumed to hold in area LIP (Pezaris et al. 1999; Pezaris et al. 2000). Each ensemble consists of 100 neurons. Each neuron in the ensemble exhibits some tendency to spike in concert with any other member of the pool, giving rise to a small correlation coefficient between spike counts ($r = 0.15 - 0.21$) and a narrow peak in the cross-correlogram (width at half-height=9ms) (Bair et al. 2001). It should be noted that such correlation implies that larger ensembles would not confer a signaling advantage or change the relationship between single neuron responses and behavior (Zohary et al. 1994; Shadlen et al. 1996; Shadlen and Newsome 1998).

The expected firing rates for neurons in the MT ensembles are determined by the motion coherence. The average spike rate on the 0% coherent motion stimulus, r_0^{MT} , is 20 spikes/s. For motion in the preferred direction,

$$\langle r_{right}^{MT}(t, C | dir = right) \rangle = \langle r_{left}^{MT}(t, C | dir = left) \rangle = \begin{cases} r_0^{MT} + b_{pref}C & t \geq \delta_{MT}, \\ r_{spont}^{MT} & t < \delta_{MT}, \end{cases} \quad (A1)$$

while for null-direction motion,

$$\langle r_{right}^{MT}(t, C | dir = left) \rangle = \langle r_{left}^{MT}(t, C | dir = right) \rangle = \begin{cases} r_0^{MT} + b_{null}C & t \geq \delta_{MT}, \\ r_{spont}^{MT} & t < \delta_{MT}, \end{cases} \quad (A2)$$

where C is the % coherence of the random dot motion, r_{spont}^{MT} is the spontaneous firing rate of MT, b_{pref} and b_{null} control the increase and decrease in expected spike rate as a function of motion strength in the neuron's preferred and null direction, respectively, and δ_{MT} is the time from onset of motion until the beginning of the steady state response in MT. Table S1 specifies the values used for these parameters and the reports from which they were obtained.

The LIP firing rates are determined by integrating the output from the MT ensembles as follows:

$$\langle r_{right}^{LIP}(t) \rangle = \begin{cases} r_{baseline}^{LIP} + k \int_{\delta_{MT}}^{t-\delta_{LIP}} r_{right}^{MT}(\psi) - r_{left}^{MT}(\psi) d\psi & t \geq \delta_{MT} + \delta_{LIP}, \\ \text{undefined} & t < \delta_{MT} + \delta_{LIP}, \end{cases} \quad (A3)$$

and

$$\langle r_{left}^{LIP}(t) \rangle = \begin{cases} r_{baseline}^{LIP} + k \int_{\delta_{MT}}^{t-\delta_{LIP}} r_{left}^{MT}(\psi) - r_{right}^{MT}(\psi) d\psi & t \geq \delta_{MT} + \delta_{LIP}, \\ \text{undefined} & t < \delta_{MT} + \delta_{LIP}, \end{cases} \quad (A4)$$

where $r_{baseline}^{LIP}$ is the baseline LIP spike rate, k scales the integrated MT difference signal for achieving proper dynamic ranges in LIP, δ_{LIP} is the delay between MT and LIP, and $r_{right}^{MT}(t)$ and $r_{left}^{MT}(t)$ are the smoothed average spike rates across the MT ensembles.

For simulations of the RT task, a random time is then added before saccade initiation. We chose a reciprocal normal distribution patterned after the latencies obtained with simple targeting saccades (Fuchs 1967; Carpenter 1988; Fisher and Weber 1993) and subtracted 100 ms to discount visual latencies and other preparatory steps, which are less likely to intercede between commitment and saccade initiation.

Model parameters

Table A1 gives the values of all parameters used in the model described above. Although numerous, there are very few model parameters that we would regard as “free” in the usual sense. Many values are set to match experimental measurements or known properties of the visual and oculomotor systems. This is a strategic decision that allows us the best chance of comparing analyses on model and real neurons. The variability and correlation of spiking in the simulated neurons are based on estimates from cortical neurons, as described above. The mean firing rates of direction selective neurons are based on values obtained from MT neurons recorded during random dot motion viewing (Britten et al. 1993). The integrated output from MT, which constitutes the decision signal, is scaled and offset to approximate the firing rates obtained from LIP neurons recorded during performance of the random dots task (Shadlen and Newsome 2001; Roitman and Shadlen 2002). δ_{MT} and δ_{LIP} , which determine the delay before visual information arrives in MT and LIP, respectively, are based on estimates from neural

recordings in these areas. These scaling factors and delays are mainly aesthetic. They allow us to compare real data to the response trajectories predicted by the model. They do not affect the model predictions in a substantial way.

Only three parameters remain unconstrained by our knowledge of neurophysiology. The first two, τ_{MT} and τ_{LIP} , determine how much the ensemble spike rates from MT and LIP are smoothed during read-out to reduce temporal fluctuations. We set these parameters by assuming that the read-out mechanisms would smooth just enough to minimize errors due to instantaneous fluctuations, thereby preserving as much temporal information as possible. The third unconstrained parameter is the height of the decision threshold, θ , which determines how much of the MT signal must be accumulated before a decision is made. The threshold height determines both the accuracy and the speed of the decision: a high threshold allows more averaging away of the temporal variance in MT, thus leading to accurate but slow decisions, and vice-versa (Link 1992; Gold and Shadlen 2002). We set θ to approximate the performance seen in the monkey; it is the only model parameter that was adjusted to fit the behavioral data.

Assumptions

A major assumption of the model is that the sensory evidence in the random dots task is provided by the difference in activity between two pools of MT neurons with opposed direction preferences. Evidence from microstimulation studies in area MT indicates that rightward preferring MT neurons contribute positive support for rightward decisions as well as negative support against leftward decisions (Ditterich et al. 2003). From a theoretical perspective, the difference in spike rate between leftward and

rightward preferring MT neurons (or ensembles) is proportional to the log of the likelihood ratio favoring one direction over the alternative (Gold and Shadlen 2001). This is just the kind of quantity a statistician would accumulate to make decisions based on a sequence of measurements (Wald 1947; Good 1979; Gold and Shadlen 2002). Indeed the integration model we propose is related to a large family of random walk and diffusion models for decision making that relate to analysis of sequential probability (Laming 1969; Vickers 1970; Link and Heath 1975; Luce 1986; Link 1992; Ratcliff and Rouder 1998; Usher and McClelland 2001).

Another fundamental assumption of the model is that the signals used for the decision are represented in the average spike rate from ensembles of neurons with similar response properties and weak coupling. The rationale for using such ensembles to represent neural signals is largely based on empirical evidence. In MT, many nearby neurons respond to a given motion stimulus (Albright et al. 1984). The variable responses of these neurons exhibit weak statistical correlation (Zohary et al. 1994; Bair et al. 2001), and the variable response of individual neurons covaries weakly with the choices that the monkey makes (i.e., the CP is greater than 0.5; see Fig. 8B). The size of this covariation is too weak to support the notion that decisions are based on the activity of a small number of neurons, but about right if the ensemble of neurons were to govern an animal's choice (Britten et al. 1996; Shadlen et al. 1996; Parker and Newsome 1998). Similar observations hold for LIP: neurons with similar response properties tend to cluster near each other; levels of neuronal variability are similar to that in MT (unpublished observations; see also Leon and Shadlen 2003); pairs of nearby neurons exhibit weak coupling (Pezaris et al. 1999; Pezaris et al. 2000). An important insight is that weak

interneuronal correlations limits the improvement in signal fidelity that would be expected to accrue in an ensemble of neurons with independent noise (Zohary et al. 1994; Mazurek and Shadlen 2002). The simulated ensemble of 100 neurons is nearly optimal given the degree of correlation (Shadlen and Newsome 1994; Shadlen and Newsome 1998).

Averaging from an ensemble of similar neurons may also be necessary from a theoretical perspective for maintaining a continuous estimate of sensory evidence. For example, using single neurons to subtract 10 spikes/s from 50 spikes/s would require waiting on the order of every 100 ms and every 20 ms, respectively, to update the calculation. Averaging allows the brain to neglect the erratic timing of particular spikes in favor of continuous estimates of important quantities.

One consequence of employing neural ensembles is that the instantaneous rate from the ensemble must be smoothed in order to be useful for reliable decision-making. Weak covariance among neurons in the ensemble induces large random fluctuations in the instantaneous rate (Mazurek and Shadlen 2002). Without smoothing, these fluctuations would dominate the ensemble spike rate. For the MT ensemble we smoothed the output of the ensemble just enough to prevent extreme fluctuations in the instantaneous rate ($\tau_{MT} = 0.02$ s). For LIP we smoothed enough to minimize the occurrence of noise-induced threshold crossings while minimizing the delay in the decision time ($\tau_{LIP} = 100$ ms).

We note that the simulated spike sequences from our model neurons exhibit less variability than those recorded from real neurons. Our method for producing spike trains yields a variance-to-mean ratio of ~ 1 for spike counts, whereas cortical neurons tend to

exhibit ratios closer to 1.5 (Tolhurst et al. 1983; Softky and Koch 1993; Geisler and Albrecht 1997; Shadlen and Newsome 1998). This property causes the model to exaggerate the sensitivity of MT neurons to weak motion signals (Fig. 8). A more realistic level of neuronal variability would necessitate a higher decision threshold to account for accuracy, which would lead to longer predicted reaction time. Our calculations indicate that this discrepancy is likely to be modest, but further analysis will be required to sort this out. Similarly, altering the variability of spike trains in MT and LIP is unlikely to significantly affect the predictions for choice probability and the trial-to-trial correlation between response and RT.

Predictions

A virtue of the kind of model developed in this paper is that it makes explicit the relationship between behavioral measurements of choice and RT on the one hand and the activity of single neurons in areas MT and LIP on the other. The model makes three straightforward predictions, which are illustrated in Figure A1. The three predictions can be tested by recording from single neurons in area MT while the monkey performs the RT direction-discrimination task.

First, it predicts that single MT neurons measured during the RT version of the direction discrimination task should be about half as sensitive as the monkey in discriminating the direction of random dot motion (Fig. A1A). This is because the decision is derived from an entire ensemble of MT neurons. The ensemble confers greater sensitivity than a single neuron, although this improvement is limited by correlated variability among neurons in the ensemble (see main text). Second, because most of the MT spikes recorded during the RT task contribute to the decision, we would expect to

observe a stronger relationship between the trial-to-trial variability of single MT neurons and the monkey's choices than what has been reported in the FD version of the task (Fig. A1B). A quantitative description of this relationship, termed the choice probability (see main text), was 0.54-0.59 in the FD experiments employing a 2 second viewing duration (Britten et al. 1993). Using the parameters in Table S1, our model predicts $CP=0.61$ for MT neurons recorded during the RT task. Interestingly, Cook and Maunsell (2002) demonstrated a relatively large MT choice probability in a motion detection experiment that is closely related to our RT experiments. Third, the model predicts that the responses from single neurons in MT should covary weakly with RT on a trial-by-trial basis. To predict this relationship quantitatively, we simulated MT responses and reaction times for one motion strength and calculated the correlation coefficient between RT and average spike rate during motion viewing. The model predicts an inverse correlation ($r=-0.11$) between MT activity and RT on preferred direction choices (Fig. A1C). This degree of correlation should be detectable with data sets of realistic size.

Alternatives

Here we consider two alternative computations that might account for the results presented in the paper. The first employs accumulation of evidence through a “leaky” integration process (Usher and McClelland 2001). Our model assumes that the integrator underlying the decision in this task can maintain its level of discharge indefinitely, without decaying (leaking) back to the starting point. Suppose, however, that the accumulated evidence were to decay as a function of time. Such leaky integration provides an alternative to the explanation we proffered to account for two observations: (1) the similarity in the monkey's accuracy in RT and FD experiments (Fig. 6) and (2) the

appearance of saturation in the LIP average response curves in FD experiments (Fig. 7). Recall that our explanation posits an accumulation to a boundary (θ) in both RT and FD tasks. However, with leaky integration, we need not imagine any boundary crossings in the FD task. According to this idea, the decision in FD experiments would not involve a comparison to threshold but would be based on a comparison of the state of the evidence at the end of stimulus viewing.

However, leaky integration is inconsistent with other important features of the data. First, it predicts that the average response of LIP neurons at low motion strengths do not diverge until shortly before the decision (the divergence time is determined by the time constant of the leak; simulations not shown) because LIP spikes in the early portion of the trial have little impact on the final decision. This is clearly not the case for the LIP data (Fig. 7A and B). Second, the leaky integrator predicts that the psychometric function relating accuracy to motion strength will be significantly shallower than that observed for the monkey, exacerbating a problem that is already present in the model without leak (Fig. 4A). Finally, the leaky integrator model makes incorrect predictions for RT. In particular, a model that successfully explains accuracy predicts decision times that are ~250 ms longer than observed at low motion strengths and ~100 ms longer than observed at high motion strengths. This is because the leak is more “effective” at low coherences, when the decision process takes longer to reach threshold. These inconsistencies suggest that it is reasonable to characterize the integration process as effectively “non-leaky” on the time scale of decision formation in the random dots task.

A second alternative to our model would incorporate interactions between LIP neurons that signal the two choices. Recall that our model contains no mechanism

allowing the two LIP ensembles (corresponding to the two alternatives) to interact during the trial; their divergent responses are solely a result of inverting the sign of the inputs from MT. A recent theoretical study by Wang (2002) suggests that the process causing the LIP responses to diverge may instead result from inhibitory interactions between competing regions of LIP. The proposed mechanism behaves in many respects like integration, making several predictions similar to those we have presented here. It will be important to extend our model to incorporate the kind of biological realism in Wang's model.

Legend to Appendix Figure

Figure A1. Predicted relationships between single MT neurons and behavior in the RT experiment. *A.* Predicted psychometric and neurometric functions. The filled symbols and solid curve are the same as in Figure 4A. The monkey is expected to exhibit higher accuracy than the average single MT neuron. *B.* Predicted choice probability. The CP is expected to be slightly greater in RT experiments than in 2 second FD experiments. *C.* Correlation between RT and MT spike rate on single trials. The scatter plot shows predicted RT and the simulated spike rate of an MT neuron during motion viewing. Motion strength is 12.8% coherence in the neuron's preferred direction. Each point represents a single simulated trial ending in a correct preferred direction choice. The model predicts a weak inverse correlation between MT spike rate and RT on preferred direction choices.

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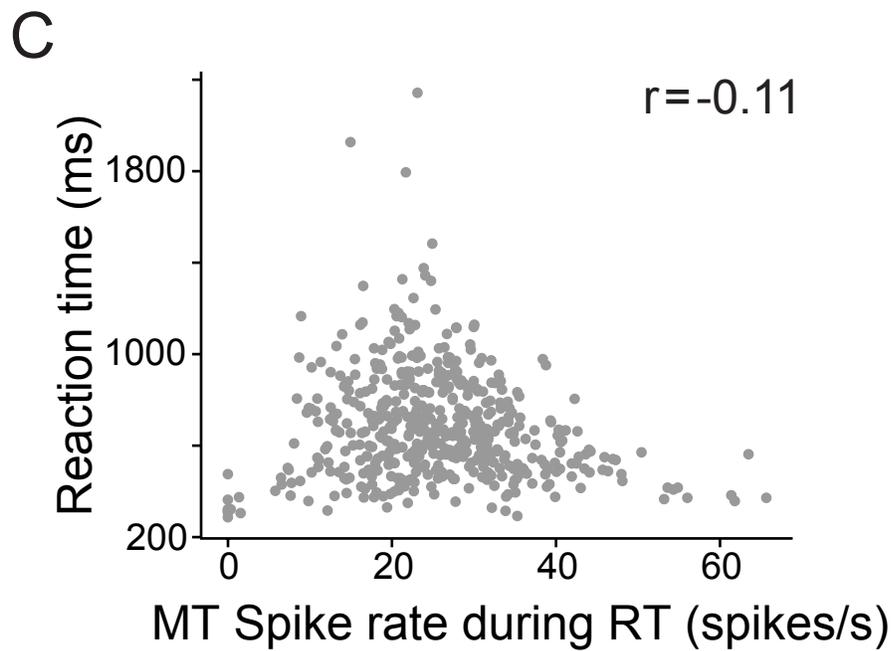
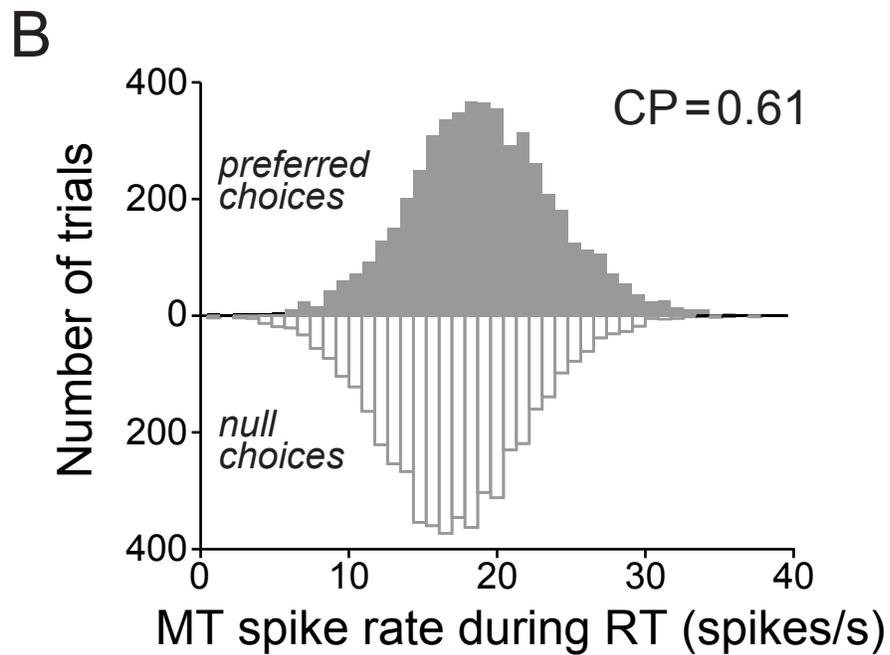
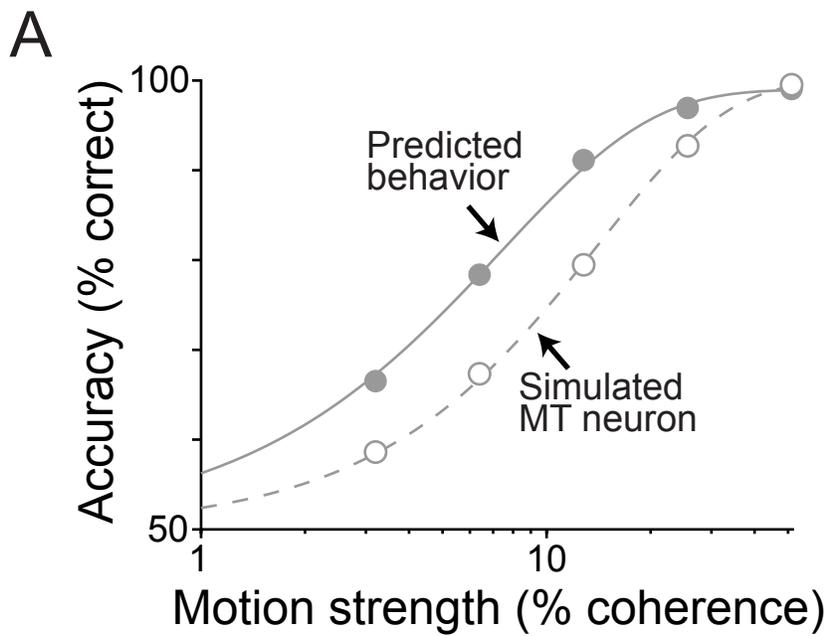
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<i>Parameter</i>	<i>Value</i>	<i>Constraint</i>
$r_{\text{spont}}^{\text{MT}}$	8 spikes/s	Britten et al 1992
r_0^{MT}	20 spikes/s	ibid.
b_{pref}	0.4 spikes/s/% coh	ibid.
b_{null}	-0.2 spikes/s/% coh	ibid.
δ_{MT}	100 ms	ibid.
Magnitude of inter-neuronal correlation	$r=0.21$	Bair et al 2000, Mazurek and Shadlen 2001
Time scale of inter-neuronal correlation	width of CCG at half-height=9 ms	ibid.
k	5	Roitman and Shadlen 2002
$r_{\text{baseline}}^{\text{LIP}}$	40 spikes/s	ibid.
δ_{LIP}	100 ms	ibid.
Post-decision time	randomly-distributed, average=100 ms	Fuchs 1976, Carpenter 1988, Fisher 1993
τ_{MT}	20 ms	
τ_{LIP}	100 ms	
θ	(various)	Mazurek and Shadlen Table A1