



Figure 1. Task and Network Architecture

(A) Binary decision making. The subject must decide whether the dots are moving to the right or to the left. Only a fraction of the dots are moving to the right or the left coherently (black arrows). The other dots move in random directions. The animal indicates its response by moving its eyes in the perceived direction (green arrow).

(B) Continuous decision making, for which the dots can move in any direction. The animal responds by making a saccade to the outside circle in the perceived direction.

(C) Network architecture. The network consists of three interconnected layers of neurons with Gaussian tuning curves. In MT, the tuning curves are for direction of motion, while in LIP and SCb, the tuning curves are for saccade direction. The layers differ by their connectivity and dynamics. The LIP neurons have a long time constant (1 s), allowing them to integrate their input, and lateral connections, allowing them to implement short-range excitation and long-range inhibition. The SCb layer forms an attractor network, for which smooth hills of activity are stable regardless of their position. The blue dots indicate representative patterns of activity 200 ms into a trial for the MT and LIP layer and at the end of the trial for the SCb layer.

When accompanied by a termination rule, our model, like a number of others (Ditterich et al., 2003; Gold and Shadlen, 2007; Laming, 1968; Link, 1992; Link and Heath, 1975; Mazurek et al., 2003; Ratcliff and Rouder, 1998; Reddi and Carpenter, 2000; Smith and Ratcliff, 2004; Stone, 1960; Usher and McClelland, 2001; Wald, 1947; Wald and Wolfowitz, 1948) accounts for the speed-accuracy tradeoff reported in humans and monkeys for binary choices. However, it goes beyond previous neural models in three ways. First, it captures the speed-accuracy trade-off and the physiology of LIP cells in experiments involving four choices. Second, as previously indicated, it predicts that neural activity in LIP encodes a probability distribution over actions. This is a new prediction about the response of LIP neurons, which we have tested and verified using data from area LIP recorded while monkeys engaged in a decision among two or four alternatives. Third, it makes predictions for the responses of cells in LIP and SC when there are multiple choices, a continuum of choices, and when the reliability of the cue varies over time.

RESULTS

Task and Model Architecture

For concreteness, we consider a motion direction task that has been extensively used to study decision making in humans and animals. In this task, an observer sees a random-dot kinematogram in which a fraction of the dots move coherently in a particular direction while all the other dots move randomly (Figure 1A). The task of the observer is to report the direction of motion with a saccadic eye movement to a choice target that is associated with that direction of motion. The reliability of the sensory evidence can be controlled by changing the percentage of dots moving coherently. In most experiments, this task is

restricted to binary decision making (right versus left) and constant coherence over the course of a trial. We also consider a more general setting in which the mean direction of moving dots and the direction of the saccade can take any value (Figure 1B) and the reliability of the motion information (the coherence) can vary not only across trials, but also during a trial.

A minimal model of this task (and, in fact, any decision-making task that involves integrating evidence over time) requires three distinct populations of neurons: an input layer, an evidence accumulation layer, and a readout layer where motor output is generated (Figure 1C). Here, we label these MT (middle temporal), LIP (lateral intraparietal), and SCb (superior colliculus, in particular those cells that exhibit a motor burst; hence the index “b”), based on what is known about the functions of these regions. These labels are used for convenience only: it is quite likely that the sensory integration involves many other cells beside the ones in LIP, and that the motor burst is not generated solely in the SC.

Bayesian Formulation

We denote the population activity of M neurons in area MT at time t_n by a vector $\mathbf{r}^{\text{MT}}(t_n)$ (see Figure 1C for an example), where $\mathbf{r}^{\text{MT}} \equiv \{r_1^{\text{MT}}, \dots, r_M^{\text{MT}}\}$ and $r_i^{\text{MT}}(t_n)$ is the spike count of neuron i in the time interval $[(n-1)\delta t, n\delta t]$. In our simulations we set δt to 50ms, although our results are insensitive to that choice.

The stimulus is characterized by a direction of motion, s , and task-irrelevant variables such as contrast and motion coherence, which we refer to as nuisance parameters and collectively denote \mathbf{c} (where $\mathbf{c} = \{c(t_1), c(t_2), \dots, c(t_N)\}$). When a stimulus (s, \mathbf{c}) is presented, MT generates a series of patterns of activity over time, denoted $\mathbf{r}^{\text{MT}}(t_1:t_N) \equiv \{\mathbf{r}^{\text{MT}}(t_1), \dots, \mathbf{r}^{\text{MT}}(t_N)\}$. Because of neural variability, $\mathbf{r}^{\text{MT}}(t_1:t_N)$ is not the same on every presentation of