Dynamic decision making in the brain

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How do we make decisions? A study uses MEG to provide the spatial as well as the temporal resolution needed to answer this question, together with computational modeling, which allows for complex non-linear decision models. This work helps resolve some of the seemingly contradictory results from previous work.

What happens when we decide between two different routes on our morning commute or two different meals at lunch? How do we weigh costs and benefits against one another and do so in a way that minimizes mental effort and regret? For economists, psychologists and others who study decision making, these questions form the heart of the science of choice. For neuroscientists, such concerns inform the study of neural circuit dynamics that translate sensory inputs into behavior. What we refer to as the decision occurs between these inputs and behavioral outputs, and any neurobiologically complete account of this process must explain the flow of information from one set of neurons to the next, from retina to eye movement or cochlear hair cell to button press.

Intuitively, the richness and flexibility of such transformations must depend on the multiplexed connections and feedback among neurons in the brain, which result in a highly interactive nonlinear system. In theory, different types of decision algorithms should give rise to distinct patterns of network activity, thus yielding clues to the underlying neural computations. In practice, most current experimental techniques are severely limited in their ability to examine network dynamics, sacrificing whole-brain information for direct access (as in individual neuron recordings) or focusing on either temporal (electroencephalograms) or spatial information (functional magnetic resonance imaging, fMRI). In this issue of *Nature Neuroscience*, Hunt *et al.*[1] set out to address this gap via a new, model-based approach to studying whole-brain network dynamics using magneto-encephalography (MEG), which measures magnetic fields generated by electrical currents in the brain. Although typical experiments use theoretical models to supply putative correlates of hemodynamic response or neuronal firing, Hunt *et al.*[1] simulate a well-known decision algorithm to predict the measured neural signal itself (**Fig. 1**). That is, by identifying correspondences between their model's total synaptic input and the physiological MEG signal, Hunt *et al.*[1] were able to look for correspondences between measured data and their simulated brain.

This study makes several key advances over previous studies. First, the high temporal resolution of MEG, in combination with source reconstruction, provides a whole-brain picture of the unfolding decision process with millisecond precision. Task-related activations begin in visual cortex, spread to fronto-polar and ventromedial prefrontal regions, pass to medial and lateral parietal cortex, and conclude in motor areas at the time participants press the response button, all in a matter of a few seconds.

Second, by modeling measured neural responses directly, Hunt *et al.*[1] were able to use standard linear methods to study highly nonlinear decision models. That is, rather than attempt to correlate model-based variables with MEG responses, the authors produced two parallel datasets—real and simulated MEG, broken into distinct frequency bands—and subjected both to the same (linear) correlation analyses (**Fig. 1**). By looking for correspondences between the two sets of results, the authors were able to search for telltale signs of the decision algorithm without needing to invert the complex relationship between model inputs and MEG.

Finally, by using a model-based prediction for the time course of MEG data, Hunt *et al.*[1] were able to make compelling inferences about the underlying decision algorithm. Typical studies only detect correlates of specific model-inspired variables, but temporal patterns of activation are, in principle, much more distinct, implying greater power to compare models. In fact, the authors were able to compare several alternative decision models and found only one among their set that adequately reproduced task-dependent activity in the brain.

In the authors' experiment, participants chose between pairs of options (rewarded with points that were eventually exchanged for money). For each option, participants were shown both the number of points they might get and the probability with which they would get them. Thus, subjects had to consider both pieces of information before making a decision: a higher point-value option with low probability may well be the worse of the two options. Hunt *et al.*[1] measured the time it took participants' to make their decisions, which depended on both the sum and difference in the values of the two options.

To model the network dynamics underlying the decision, Hunt *et al.*[1] employed a simplified version of previously described reverberating networks[2–5]. In these models, mutually inhibitory pools of neurons represent each option and implement a winner-take-all competition that represents the outcome of the decision process. As a result, higher overall values across all options lead to higher neuronal activation, and thus to more total inhibition, reducing decision times, whereas small differences in option values lead to more difficult decisions, less inhibition and longer reaction times[6,7]. Most model parameters are constrained biophysically, leaving a few parameters, such as the speed-accuracy tradeoff, to be fit to individual participant's choices. By identifying total synaptic activity in the model with the measured MEG signal,

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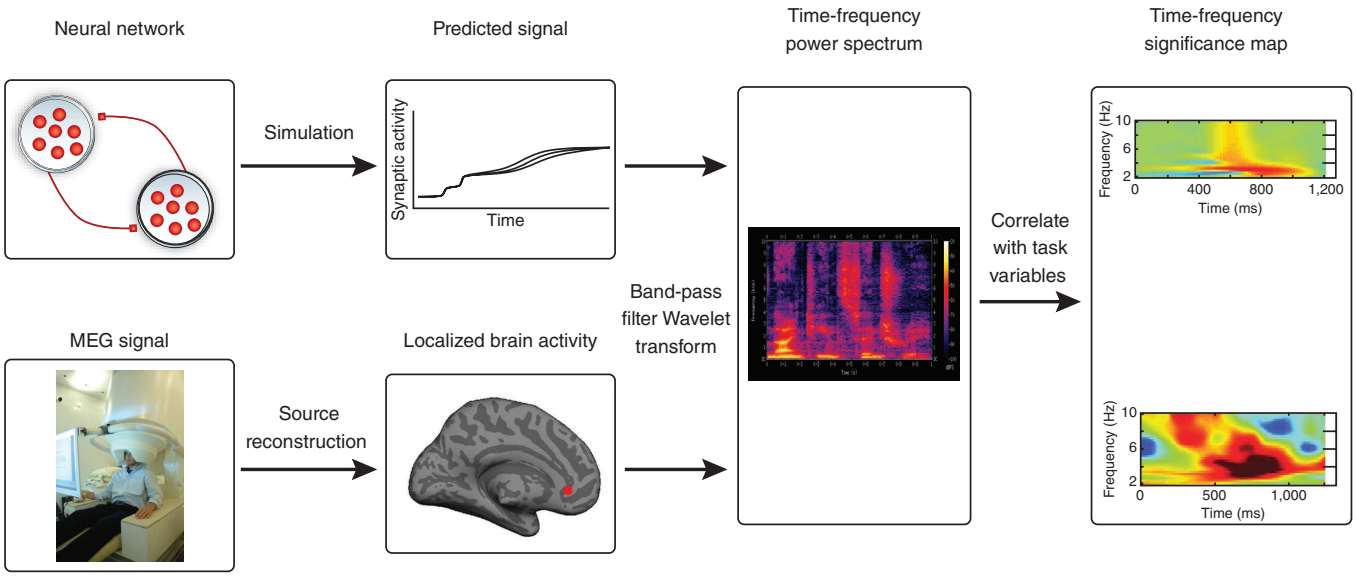

Figure 1 Schematic for analysis of decision-making dynamics in the brain. Simulated data from a winner-take-all neural network model are used to produce predictions of synaptic activity to be compared to responses of individual brain regions measured with source-reconstructed MEG. Both real and predicted signals are then filtered and wavelet transformed to plot brain activity across time and frequency. Finally, activity in regions of interest is correlated with task-specific variables to produce maps of statistical significance. Warmer colors indicate a more significant effect of task variables at a given time in a given frequency band.

Hunt *et al.*[1] were then able to make telltale predictions for the neural signature of the winner-take-all decision.

The authors found that activity in the ventromedial prefrontal cortex (vmPFC) and the posterior superior parietal lobule (pSPL) strongly followed the predictions of the model. In both areas, overall value exerted a strong effect in the 2–10-Hz frequency range early in the trial, whereas value difference dominated later on, with a response confined to lower frequencies (2–4 Hz). Although the particular locations of these effects might have been anticipated on the basis of previous studies, in this case, the observed pattern provides evidence for a particular computation underlying the decision process[8–12]. Moreover, these results may help to resolve a dispute over whether vmPFC encodes overall value or value difference[13,14]. Hunt *et al.*[1] found representations of both quantities, each with a distinct time course, in a duration that was too short to be distinguishable by fMRI. Moreover, these patterns are consistent with previous recordings from single neurons in monkeys[15].

In addition, activity in these areas bore out two key predictions of the decision model. First, although correct trials showed an effect of overall value early in the trial and of value difference later in the trial, this value difference signal was blunted on error trials, as would be expected if the information were poorly encoded or weakly transmitted to these areas. Second, participants' individual speed-accuracy tradeoffs, as reflected in median reaction time, predicted variability in the coupling of their MEG signals to the overall value of both options. Together, these results lend additional weight to the finding that vmPFC and pSPL contribute to the implementation of a winner-take-all decision.

Despite these findings, several questions remain to be answered. Although Hunt *et al.*[1] were able to show that their results both were robust to parameter changes in the biophysical model and provided a better account of the observed MEG data than other commonly used models, they were not able to rule out alternative networks that might also receive value-related information and interact with the vmPFC and pSPL. That is, other brain areas may be involved in the decision process in ways that are difficult to describe with simple models. Moreover, it may be possible that, for other tasks, very different single-unit computations give rise to similar large-scale signals, rendering it difficult to distinguish between some classes of models. Finally, MEG has limited utility in measuring activation in subcortical brain areas that are thought to substantially contribute to decision making[3].

The model-based approach of Hunt *et al.*[1] opens new possibilities for investigating behavior as the output of the brain's highly dynamic networks. By allowing models to motivate not only the analysis, but also the design, of experiments, it also generates new opportunities for theoretical neuroscience. As such, it stands not only to enhance the quality of our collected data, but the power and realism of our models.

COMPETING FINANCIAL INTERESTS
The authors declare no competing financial interests.

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