

9. Zipser, D. & Andersen, R. A back-propagation programmed network that stimulates response properties of a subset of posterior parietal neurons. *Nature* 331, 679–684 (1988).
10. Andersen, R., Essick, G. & Siegel, R. Encoding of spatial location by posterior parietal neurons. *Science* 230, 456–458 (1985).
11. Trotter, Y., Celebrini, S., Striccanne, B., Thorpe, S. & Imbert, M. Neural processing of stereopsis as a function of viewing distance in primate visual area V1. *J. Neurophysiol.* 76, 2872–2885 (1997).
12. Trotter, Y. & Celebrini, S. Gaze direction controls response gain in primary visual-cortex neurons. *Nature* 398, 239–242 (1999).
13. Galletti, C. & Battaglini, P. Gaze-dependent visual neurons in area {V3a} of monkey prefrontal cortex. *J. Neurosci.* 9, 1112–1125 (1989).
14. Bremner, F., Ilg, U., Thiele, A., Distler, C. & Hoffman, K. Eye position effects in monkey cortex. I: Visual and pursuit-related activity in extrastriate areas MT and MST. *J. Neurophysiol.* 77, 944–961 (1997).
15. Cumming, B. & Parker, A. Binocular neurons in V1 of awake monkeys are selective for absolute, not relative, disparity. *J. Neurosci.* 19, 5602–5618 (1999).
16. Boussaoud, D., Barth, T. & Wise, S. Effects of gaze on apparent visual responses of frontal cortex neurons. *Exp. Brain Res.* 93, 423–434 (1993).
17. Squatrito, S. & Maioli, M. Gaze field properties of eye position neurons in areas MST and 7a of macaque monkey. *Vis. Neurosci.* 13, 385–398 (1996).
18. Vallar, G. Spatial hemineglect in humans. *Trends Cogn. Sci.* 2, 87–97 (1998).
19. Pouget, A., Deneve, S. & Sejnowski, T. Frames of reference in hemineglect: a computational approach. *Prog. Brain Res.* 121, 81–97 (1999).
20. Piaget, J. *The Origins of Intelligence in Children* (The Norton Library, New York, 1952).
21. Kuperstein, M. Neural model of adaptive hand-eye coordination for single postures. *Science* 239, 1308–1311 (1988).
22. Widrow, B. & Hoff, M. E. in *Conference proceedings of WESCON*, 96–104 (1960).
23. Moody, J. & Darken, C. Fast learning in networks of locally-tuned processing units. *Neural Comput.* 1, 281–294 (1989).
24. Hinton, G. & Brown, A. in *Neural Information Processing Systems* vol. 12, 122–128 (MIT Press, Cambridge Massachusetts, 2000).
25. Olshausen, B. A. & Field, D. J. Sparse coding with an overcomplete basis set: a strategy employed by V1? *Vision Res.* 37, 3311–3325 (1997).
26. Jordan, M. & Rumelhart, D. Forward models: supervised learning with a distal teacher. *Cognit. Sci.* 16, 307–354 (1990).
27. Rumelhart, D., Hinton, G. & Williams, R. in *Parallel Distributed Processing* (eds Rumelhart, D., McClelland, J. & Group, P. R.) 318–362 (MIT Press, Cambridge, Massachusetts, 1986).
28. Desmurget, M. *et al.* Role of the posterior parietal cortex in updating reaching movements to a visual target. *Nat. Neurosci.* 2, 563–567 (1999).
29. Wolpert, D. M., Goodbody, S. J. & Husain, M. Maintaining internal representations: the role of the human superior parietal lobe. *Nat. Neurosci.* 1, 529–533 (1998).
30. Amit, D. The hebbian paradigm reintegrated — local reverberations as internal representations. *Behav. Brain Sci.* 18, 617–626 (1995).
31. Fuster, J. *Memory in the Cerebral Cortex: An Empirical Approach to Neural Networks in the Human and Nonhuman Primate* (MIT Press, Cambridge, Massachusetts, 1995).
32. Goldberg, M. & Bruce, C. Primate frontal eye fields. III. Maintenance of a spatially accurate saccade signal. *J. Neurophysiol.* 64, 489–508 (1990).
33. Gnadt, J. & Mays, L. Neurons in monkey parietal area LIP are tuned for eye-movement parameters in three-dimensional space. *J. Neurophysiol.* 73, 280–297 (1995).
34. Funahashi, S., Bruce, C. & Goldman-Rakic, P. Dorsolateral prefrontal lesions and oculomotor delayed response performance: evidence for mnemonic “scotomas”. *J. Neurosci.* 13, 1479–1497 (1993).
35. Zhang, K. Representation of spatial orientation by the intrinsic dynamics of the head-direction cell ensemble: a theory. *J. Neurosci.* 16, 2112–2126 (1996).
36. Somers, D. C., Nelson, S. B. & Sur, M. An emergent model of orientation selectivity in cat visual cortical simple cells. *J. Neurosci.* 15, 5448–5465 (1995).
37. Salinas, E. & Abbott, L. F. A model of multiplicative neural responses in parietal cortex. *Proc. Natl. Acad. Sci. USA* 93, 11956–11961 (1996).
38. Deneve, S., Latham, P. & Pouget, A. Reading population codes: A neural implementation of ideal observers. *Nat. Neurosci.* 2, 740–745 (1999).
39. Walker, M., Fitzgibbon, E. & Goldberg, M. Neurons in the monkey superior colliculus predict the visual result of impending saccadic eye movements. *J. Neurophysiol.* 73, 1988–2003 (1995).
40. Mazzoni, P., Bracewell, R., Barash, S. & Andersen, R. Motor intention activity in the macaque’s lateral intraparietal area. I. Dissociation of motor plan from sensory memory. *J. Neurophysiol.* 76, 1439–1456 (1996).
41. Graziano, M., Hu, X. & Gross, C. Coding the locations of objects in the dark. *Science* 277, 239–241 (1997).
42. Duhamel, J. R., Colby, C. L. & Goldberg, M. E. The updating of the representation of visual space in parietal cortex by intended eye movements. *Science* 255, 90–92 (1992).
43. Droulez, J. & Berthoz, A. A neural model of sensoritopic maps with predictive short-term memory properties. *Proc. Natl. Acad. Sci. USA* 88, 9653–9657 (1991).
44. Dominey, P. & Arbib, M. A cortico-subcortical model for the generation of spatially accurate sequential saccades. *Cereb. Cortex* 2, 153–175 (1992).
45. Seung, H. How the brain keeps the eyes still. *Proc. Natl. Acad. Sci. USA* 93, 13339–13344 (1996).
46. Snyder, L., Batista, A. & Andersen, R. Coding of intention in the posterior parietal cortex. *Nature* 386, 167–170 (1997).
47. Snyder, L., Grieve, K., Brotchie, P. & Andersen, R. Separate body- and world-referenced representations of visual space in parietal cortex. *Nature* 394, 887–891 (1998).

## Viewpoint • Models identify hidden assumptions

It is not only theorists who make models. All biologists work with explicit or implicit ‘word models’ that describe their vision of how a system works. One of the most important functions of theoretical and computational neuroscience is to translate these word models into more rigorous statements that can be checked for consistency, robustness and generalization through calculations and/or numerical simulations.

The process of turning a word model into a formal mathematical model invariably forces the experimentalist to confront his or her hidden assumptions. I have often found that I have ‘skipped steps’ in my thinking that were only revealed when we sat down to construct a formal model. It is easy to tell ‘just so stories’ about cells, circuits and behavior, and discussion sections of journal articles are filled with them, but the exercise of trying to instantiate the assertions in those stories makes the missing links in all of our data and understanding pop into view.

Models offer a solution to one of the hardest problems in experimental biology: how far to generalize from the data one has collected. Neuroscientists work on an array of cells and circuits in lobsters, flies, fish, birds, rats, mice, monkeys and humans. Many of the ‘mistakes’ in neuroscience come from inappropriate generalizations from observations made in one system, or under a given set of conditions. Experimental work I did with Scott Hooper showed that when an oscillatory neuron was electrically coupled to a non-oscillatory cell, the two-cell network had a lower frequency than the isolated oscillator. We initially assumed that this was a general statement, but later learned from theoretical work that, depending on the properties of the oscillator, either an increase or decrease in frequency could be obtained. We had correctly understood our data, but we were unaware that the other case was possible because it did not occur in the particular system we were studying. This is at the core of the usefulness of theory for an experimentalist: it helps us know when we have found only a piece of the answer, and when we have understood the full set of possible outcomes from a given set of conditions.

Finally, theory is legitimized dreaming. We all became neuroscientists out of a deep desire to explore the mysteries of how the brain works. Most of us who do experimental work spend our days preoccupied with the myriad and mundane details that are so crucial to doing experiments and analyzing data. I came of age as a scientist believing that my career would be over if I were ever wrong. For me, participating in the development of highly speculative models was akin to learning to drive as a teenager. In both cases, I remember the thrill of the freedom of the open road (and some of the trepidation of getting lost or getting a flat tire). Speculative models suggest possibilities beyond those found in one’s laboratory, and can produce just that altered outlook that can send one on a new and exciting path.

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