

to the receiver, but they are shut down by default; the relevant connection is activated locally, at the receiver end, without the need to alter the sender's activity. It is possible that real circuits exploit both strategies, depending on the current behavior, the circuit's function or its connectivity constraints. These mechanisms could be tested by recording from suspected sender and receiver neurons in tasks in which the relationship between multiple sensory signals and motor effectors can change, as in our keyboard example. In addition, the mechanism put forth by Vogels and Abbott¹ should have a distinct microanatomical substrate reflecting the convergence of excitation and inhibition driven by the same input.

The model by Vogels and Abbott¹ may solve part of the neuronal switchboard puzzle, but many questions still remain. How is the detailed balanced between excitation and inhibition maintained? How are the connection pathways established and kept

separate? Perhaps the most pressing issue is the nature of the control signal that disrupts the local balance of excitation and inhibition to open each gate. The authors showed that it may work by acting on very few interneurons (<50) per receiver net. Therefore, this control needs to be both highly selective, to alter each interneuron by the right proportion, and fairly strong, to be able to nearly silence some interneurons. It is not clear how this can be implemented and the solution will probably require complementary new modeling and new experimental approaches. This may be the next dot that needs to be connected in the study of signal transmission.

These new results suggest that the neural circuits that give rise to flexible, nonreflexive behavior may be both highly complex and exquisitely specific. More generally, they should spur further investigations into the neural basis of such flexibility, which remains a fundamental neuroscientific challenge.

1. Vogels, T.P. & Abbott, L.F. *Nat. Neurosci.* **12**, 483–491 (2009).
2. Shadlen, M.N. & Newsome, W.T. *Curr. Opin. Neurobiol.* **4**, 569–579 (1994).
3. Troyer, T.W. & Miller, K.D. *Neural Comput.* **9**, 971–983 (1997).
4. Salinas, E. & Sejnowski, T.J. *J. Neurosci.* **20**, 6193–6209 (2000).
5. van Vreeswijk, C. & Sompolinsky, H. *Science* **274**, 1724–1726 (1996).
6. Shu, Y., Hasenstaub, A. & McCormick, D.A. *Nature* **423**, 288–293 (2003).
7. Haider, B., Duque, A., Hasenstaub, A.R. & McCormick, D.A. *J. Neurosci.* **26**, 4535–4545 (2006).
8. Abeles, M. *Corticonics: Neural Circuits of the Cerebral Cortex* (Cambridge University Press, New York, 1991).
9. Diesmann, M., Gewaltig, M.-O. & Aertsen, A. *Nature* **402**, 529–533 (1999).
10. van Rossum, M.C.W., Turrigiano, G.G. & Nelson, S.B. *J. Neurosci.* **22**, 1956–1966 (2002).
11. Felleman, D.J. & Van Essen, D.C. *Cereb. Cortex* **1**, 1–47 (1991).
12. Kumar, A., Rotter, S. & Aertsen, A. *J. Neurosci.* **28**, 5268–5280 (2008).
13. Vogels, T.P. & Abbott, L.F. *J. Neurosci.* **25**, 10786–10795 (2005).
14. Olshausen, B.A., Anderson, C.H. & Van Essen, D.C. *J. Neurosci.* **13**, 4700–4719 (1993).
15. Salinas, E. *BMC Neurosci.* **5**, 47 (2004).

It's not you, it's me. Really.

Garrett B Stanley

A subset of neurons in rat barrel cortex integrate information about the object a whisker contacts with the motion of the whisker at the time of contact, setting the stage for a highly specialized object localization system.

The information flow entering the sensory pathways of the brain is shaped by our interactions with the environment^{1,2}. For example, when we look around the room, we move our eyes, head and body to control the images that fall on our retinas. When we want to feel a texture, we actively move our fingertips across the surface to gather information. When we want to locate an object in the dark, we reach out and move our arms until our hand comes into contact with the object. The signals that the brain has access to are therefore determined by both the features of the outside world and how we use our muscles to move our sensors (retina, fingertips, etc.) to meet the outside world. How do we interpret the outside world when the information that we receive is tangled up with the manner in which we gather it?

Feeling around in the dark with one's hand to determine the location of an object requires

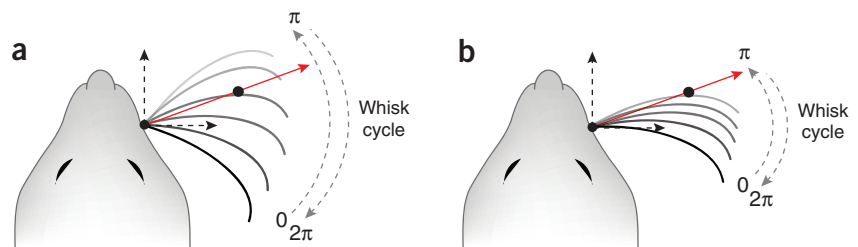


Figure 1 Object localization in a head-centered coordinate system. (a) A single vibrissa on the right side of the face and the different positions of the vibrissa during the whisker cycle are shown. Contact with an object (black dot) occurs at a particular phase of the whisker cycle, given as a fraction of the entire cycle from 0 to 2π . For the example shown, assuming contact in the forward sweep, the phase is approximately $\frac{3}{4}\pi$ at the point of contact. The phase of the contact is the same, regardless of the whisking frequency. (b) Whisking over a different amplitude leads to a different phase at the point of contact for the same object shown in a. Now the phase is closer to π , resulting in an ambiguity in object localization relative to the face.

some implicit knowledge of the motion and position of our arms. The physical contact (hard object meets soft skin) may be the same regardless of position, but when placed in the context of the position and trajectory of the arm, we unambiguously identify the location of the object. In this issue, Curtiss and Kleinfeld³ investigate sensory signals in the primary sensory cortex that reflect

the combination of elements originating strictly from objects in the environment and elements associated with active, motor-driven inputs to the sensory pathway. They utilized the rat vibrissa system in which the rats actively bring their facial whiskers (vibrissae) in contact with objects during exploratory behavior, a model system that has previously been shown to be capable of

The author is in the Coulter Department of Biomedical Engineering, Georgia Institute of Technology and Emory University, Atlanta, Georgia, USA.
e-mail: garrett.stanley@bme.gatech.edu

various forms of distance discrimination^{4–7}. They report that the neural activity measured in the corresponding primary cortical representation of each whisker (the barrel cortex) depends on vibrissa contact with an object and on the moment at which the whisker contacts the object during rhythmic movement of the vibrissae (whisking). This activity represents a combination of afferent (contact) and reafferent (self-motion) signals that could be used for perception of the correct position of the object relative to the face of the rat.

In an elegant set of experiments, Curtis and Kleinfeld³ implanted arrays of micro-electrodes in the barrel cortex of awake rats that were trained to palpate a sensor that reports whisker contacts. The spiking activity of single neurons in the barrel cortex was studied in relation to these contacts, as well as in relation to the whisking cycle (assessed by electromyogram recording of the facial musculature responsible for the active movement of the whiskers). The goal of the study was to understand how afferent touch signals are integrated with reafferent signals that are associated with the rat's own generated motion of the follicles during active sensing. The assertion is that the mixture of afferent and self-generated reafferent signals allows the rat to unambiguously identify object position in head-centered coordinate space. Given that the active whisking is approximately sinusoidal in the rostral-caudal (nose-to-tail) plane, with frequencies between 6 and 12 Hz (sweeping front to back 6 to 12 times per s), the contact of the whisker with an object occurs at a particular phase of the cyclic back-and-forth motion of the whisker (Fig. 1a). The phase is reported as a number in radians, ranging from 0 to 2π , to indicate whether the contact occurs at the beginning or at the end of the cycle, respectively. The main finding is that cortical neurons are tuned such that the touch response is greatest at a particular phase of the whisk cycle, suggesting that the reafferent signal associated with the active movement of the whiskers gates the cortical activity. The implication is that this could lead to a representation of the object in head-centered coordinates. The influence of motor signals in a primary sensory area supports the growing feeling in the sensory and motor communities that the artificial lines between historically designated sensory and motor areas of the brain are starting to blur.

Although these data suggest a potential mechanism for integrating afferent signals

with internal representations of our own motion, we maintain the ability to recognize an object independent of its location in space. This presents a paradox in the influence of our own actions in acquiring sensory information that might be best summed up as we can't live with it and we can't live without it. On the one hand, we have the perception of an invariant world whose stability seems unthreatened no matter how erratic our behavior. When asking the question 'What is that object?', an apple is still an apple, regardless of how much our eyes, head and body move while we take in the visual information. The sandpaper still has the same feeling of roughness, as long as we are moving our fingertip across it in some reasonable way. The elements of our own part of the gathering of information are thus removed from our sensory experience. On the other hand, when we are locating an object relative to ourselves, the active element of the sensing becomes important for answering the question 'Where is the object?'. The position of my center of gaze or hand, or how far I have moved my eyes or hand, suddenly become relevant for answering the question, and thus we no longer wish to remove this from our experience, but instead to somehow incorporate this information for context, as has been pursued in the study of the preparation and guidance of movement⁸. The vibrissa pathway has been implicated in a rich continuum of behaviors, from inferring distance during locomotion⁹ to generating representations for texture discrimination^{10,11}. The various behaviors are often framed simplistically in terms of questions of 'what' and 'where', although the convenience of such an artificial dichotomy probably breaks down outside of the laboratory setting, as things often do.

For the vibrissa system, how might this all work when the rubber hits the road? If the cortical neurons are tuned to respond preferentially to contact at a particular phase of the whisk cycle, independent of the frequency of a particular whisking bout, as is shown for a subset of the neurons in the Curtis and Kleinfeld study³, then the relative activity of a population of cortical neurons tuned for different phases would unambiguously identify the position of the object in face-centered coordinates. The contact with the object would occur at the same phase of the whisk cycle, just at different absolute times. However, the study³ also suggests that the representation is invariant to the amplitude of the whisk cycle,

an observation that makes the framework for the neural coding more complicated. For two situations with the same whisking frequency, but of different amplitudes (Fig. 1a,b), the contact would occur at different phases of the whisk cycle, thus recruiting a different subpopulation of cortical cells. In this case, the position can still be unambiguously identified, but not from the observation of these cortical units alone. They would need to be judged in the context of an internal representation of the actual whisking motion (amplitude and frequency). As previous studies have reported, however, and Curtis and Kleinfeld³ confirm, cortical activity is modulated in a way to reflect the nature of the whisking even in the absence of contact, thus potentially providing just such a contextual signal.

As with any ambitious study, Curtis and Kleinfeld's³ findings inspire a whole range of further questions. From a circuitry perspective, given the observation that the phase-dependent cortical units predominately reside in cortical layer 4 (the input layer to primary cortices), but less so in other layers that form projections back to subcortical areas, what is the role of cortical feedback in establishing this neural code? How do we connect this finding, which relates to active whisking, to other aspects of active sensing, such as head and body movement? How might this coding operate during more continuous contact with objects during navigation? The vibrissa system is an enormously rich model system in which to pursue these types of questions, which are central to the way in which we, as organisms, interact with the external world. Continued exploration in this area may help us begin to identify the mechanisms by which we create representations of the environment in the context of our own movements within it.

1. Gibson, J.J. *Psychol. Rev.* **61**, 304–314 (1954).
2. Gibson, J.J. *Psychol. Rev.* **69**, 477–491 (1962).
3. Curtis, J. & Kleinfeld, D. *Nat. Neurosci.* **12**, 492–501 (2009).
4. Krupa, D.J., Matell, M.S., Brisben, A.J., Oliveira, L.M. & Nicolelis, M.A. *J. Neurosci.* **21**, 5752–5763 (2001).
5. Knutsen, P.M., Pietr, M. & Ahissar, E. *J. Neurosci.* **26**, 8451–8464 (2006).
6. Hentschke, H., Haiss, F. & Schwarz, C. *Cereb. Cortex* **16**, 1142–1156 (2006).
7. Mehta, S.B., Whitmer, D., Figueroa, R., Williams, B.A. & Kleinfeld, D. *PLoS Biol.* **5**, e15 (2007).
8. Graziano, M.S.A., Yap, G.S. & Gross, C.G. *Science* **266**, 1054–1057 (1994).
9. Vincent, S.B. *Behav. Monographs* **1**, 7–85 (1912).
10. Guic-Robles, E., Valdivieso, C. & Guajardo, G. *Behav. Brain Res.* **31**, 285–289 (1989).
11. Carvell, G.E. & Simons, D.J. *J. Neurosci.* **10**, 2638–2648 (1990).