nonredundancy in these retinal ganglion cell signals arises from diverse intrinsic properties versus diverse circuit connections. Another caveat in this particular experimental preparation is that the definition of a ganglion cell type is somewhat subjective. One might argue that low shared information between two neurons should mean that, by definition, these cells belong to different types. Indeed, the largest information gain comes from pooling signals from different types (for example, ON versus OFF cells), rather than from cells from the same type[11,12].

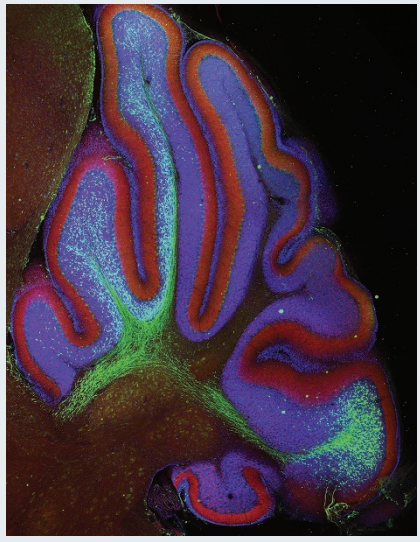
Notably, the broader implications of Padmanabhan and Urban's study[5] do not rely on any particular definition of a neuronal type. First, this study illustrates why it can be inappropriate to model populations of neurons as replicates of the same neuron with fixed intrinsic properties. Instead, it might be more realistic (in some contexts) to model populations of neurons by drawing from distributions of parameters specifying their intrinsic properties[13].

Second, this study suggests that diversity in the intrinsic properties of neurons can be a virtue. Given this, it is tempting to speculate that there might be mechanisms in place to increase diversity. These mechanisms appear to exist at the level of genetic variation. Because mechanisms of genetic replication and repair are variable and heritable, they are themselves subject to natural selection, and variants that increase mutation rates can actually enjoy an advantage[14]. Similarly, it has been postulated that there are mechanisms in place that reduce the lethality associated with genetic variation, thereby increasing the amount of variation that is retained during natural selection[15]. It will be interesting to learn whether analogous mechanisms exist to promote variation in a neural population.

COMPETING FINANCIAL INTERESTS
The authors declare no competing financial interests.

1. Rakic, P. *Nat. Rev. Neurosci.* **10**, 724–735 (2009).
2. Ryan, T.J. & Grant, S.G. *Nat. Rev. Neurosci.* **10**, 701–712 (2009).
3. Luo, L. & Flanagan, J.G. *Neuron* **56**, 284–300 (2007).
4. Prinz, A.A., Bucher, D. & Marder, E. *Nat. Neurosci.* **7**, 1345–1352 (2004).
5. Padmanabhan, K. & Urban, N. *Nat. Neurosci.* **13**, 1276–1282 (2010).
6. Ressler, K.J., Sullivan, S.L. & Buck, L.B. *Cell* **79**, 1245–1255 (1994).
7. Vassar, R. *et al. Cell* **79**, 981–991 (1994).
8. Shepherd, G.M. & Greer, C.A. in *The Synaptic Organization of the Brain* (ed. Shepherd, G.M.) 159–203 (Oxford University Press, Oxford, 1998).
9. Chen, T.W., Lin, B.J. & Schild, D. *Proc. Natl. Acad. Sci. USA* **106**, 2401–2406 (2009).
10. Kazama, H. & Wilson, R.I. *Nat. Neurosci.* **12**, 1136–1144 (2009).
11. Segev, R., Puchalla, J. & Berry, M.J. II. *J. Neurophysiol.* **95**, 2277–2292 (2006).
12. Warland, D.K., Reinagel, P. & Meister, M. *J. Neurophysiol.* **78**, 2336–2350 (1997).
13. Goldman, M.S., Golowasch, J., Marder, E. & Abbott, L.F. *J. Neurosci.* **21**, 5229–5238 (2001).
14. Drake, J.W., Charlesworth, B., Charlesworth, D. & Crow, J.F. *Genetics* **148**, 1667–1686 (1998).
15. Gerhart, J. & Kirschner, M. *Proc. Natl. Acad. Sci. USA* **104** Suppl 1, 8582–8589 (2007).

Spinal convergence of motor and sensory pathways



Effective motor execution needs to accurately integrate proprioceptive sensory feedback to update the motor command centers about the outcome of the movements. The motor system can also generate an internal prediction of the planned actions to reduce delay. Previous studies have suggested that several cerebellar and cortical sites act as integration centers, where internal motor predictions can be made by converging sensory feedback and cortical corollary pathways. On page 1232 of this issue, Hantman and Jessell find that the convergence of the cortical command pathway and the proprioceptive sensory feedback pathway occurs even earlier, at Clarke's column in the spinal cord.

Clarke's column comprises dorsal spinocerebellar (dSC) tract neurons, which form a nucleus spanning thoracic and lumbar spinal cord and that relay proprioceptive sensory information from the hindlimb. Although dSC tract neurons are known to be active upon electrical stimulation of descending corticospinal tracts, the exact nature of corticospinal input and the interaction between corticospinal efferent activity and spinocerebellar afferent activity were unclear. Hantman and Jessell used genetic and anatomical tracers to map out dSC neurons and their inputs and outputs in the mouse and found that dSC tract neurons in Clarke's column receive both proprioceptive axonal projections from the dorsal root ganglion and descending corticospinal projections. To do this, they identified Clarke's column dSC neurons by their expression of *glial cell-derived neurotrophic factor* (*Gdnf*); this expression pattern distinguishes them from other spinocerebellar projections neurons. The authors then used the *Gdnf* promoter to create inducible mice that selectively expressed the fluorescent protein mGFP in their dSC neurons. Using this elegant genetic technique, the authors found that dSC spinocerebellar projections reach cerebellar lobules I, II, III and VIII (see image; mGFP-positive dSC projections terminating at the cerebellum are shown in green, vGlut1 immunostaining is shown in red and Neurotrace Nissl staining is shown in blue). The authors also measured the electrophysiological responses of dSC neurons on corticospinal or dorsal root ganglion stimulation and found that these neurons receive excitatory inputs from proprioceptive dorsal root ganglion projections and direct excitatory inputs from corticospinal axons and/or indirect cortically-evoked inhibitory inputs.

These findings suggest that dSC neurons in Clarke's column represent a spinal cord–level convergence site where descending motor corollary signals and ascending sensory feedback may be integrated, perhaps serving to fine-tune ascending proprioceptive feedback to the locomotor command center.

Min Cho