studies, changes in activity in these regions are observed that correlate with the subjective value of rewards in decision-making tasks[14]. This offers a hint that Mohebi and colleagues' findings might have relevance across species.

The authors found that neuronal activity in the VTA of rats was unaffected by an increase in the reward rate, however, suggesting that the motivation-related dopamine release is dissociated from the activation of dopamine neurons. To test this hypothesis, the authors examined dopamine release in the rat nucleus accumbens using a method for the rapid imaging of dopamine release[15] that enables monitoring on a subsecond timescale, rather than the timescale of minutes that is possible with microdialysis.

As expected, the authors found that cues for reward availability, as well as the reward itself, were linked to an increase in the activity of dopamine neurons in the VTA (Fig. 1). These cues were also associated with an increase in dopamine release in the nucleus accumbens (the only brain region that was examined for dopamine release in this experiment) that serves as a learning signal to influence future behaviour.

As the reward rate increased, extracellular dopamine levels ramped up progressively as the rats approached either the central port or the port where food was dispensed, which is consistent with dopamine driving the motivation, as has been proposed previously[8–13]. However, there was no ramping up of the activity of dopamine neurons in the VTA (Fig. 1). This evidence for dopamine release in the absence of an increase in activity in dopamine neurons provides further support for the authors' model that neuronal activity and dopamine release can be dissociated. Importantly, these data point to the possibility of a local regulation of dopamine release that is independent of the activity of dopamine neurons. The power of such local regulation[5] is familiar to those who study the cells and circuits of the striatum.

Unanswered by Mohebi and colleagues' study is which local factors in the nucleus accumbens might generate the ramped-up increases in dopamine release — or, in other words, what it is that motivates motivation. One possibility might be the release of the neurotransmitter acetylcholine from cells called cholinergic interneurons[16,17]. Of course, if the authors had reported evidence to support this, then the key question would have become which parts of the brain are conveying information about motivation to those neurons. Mohebi *et al.* report that there is a ramping up of activity of some non-dopamine neurons in the VTA before the animal carries out a nose poke. Perhaps those neurons have a role in facilitating dopamine release, which could be a topic for future research.

As well as providing evidence for the textbook view that a spike in the activity of dopamine neurons is accompanied by dopamine release, albeit not in all target regions, the unexpected observation of dopamine release in the absence of activity of dopamine neurons provides a new depth of understanding of dopamine signalling in the brain. Like the ramping up of dopamine, this is bound to provide the motivation for more work. ■

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1. Mohebi, A. *et al. Nature* **570**, 65–70 (2019).
2. Matsuda, W. *et al. J. Neurosci.* **29**, 444–453 (2009).
3. Schultz, W. *J. Neurophysiol.* **80**, 1–27 (1998).
4. Fiorillo, C. D., Tobler, P. N. & Schultz, W. *Science* **299**, 1898–1902 (2003).
5. Sulzer, D., Cragg, S. J., Rice, M. E. *Basal Ganglia* **6**, 123–148 (2016).
6. Howe, M. W. & Dombeck, D. A. *Nature* **535**, 505–510 (2016).
7. Brown H. D., McCutcheon, J. E., Cone, J. J., Ragozzino, M. E., Roitman, M. F. *Eur. J. Neurosci.* **34**, 1997–2006 (2011).
8. Phillips, P. E., Stuber, G. D., Heien, M. L., Wightman, R. M. & Carelli, R. M. *Nature* **422**, 614–618 (2003).
9. Roitman, M. F., Stuber, G. D., Phillips, P. E., Wightman, R. M. w& Carelli, R. M. *J. Neurosci.* **24**, 1265–1271 (2004).
10. Wassum, K. M., Ostlund, S. B. & Maidment, N. T. *Biol. Psychiatry* **71**, 846–854 (2012).
11. Howe, M. W., Tierney, P. L., Sandberg, S. G., Phillips, P. E. & Graybiel, A. M. *Nature* **500**, 575–579 (2013).
12. Hamid, A. A. *et al. Nature Neurosci.* **19**, 117–126 (2016).
13. Syed, E. C. *et al. Nature Neurosci.* **19**, 34–36 (2016).
14. Bartra, O., McGuire, J. T. & Kable, J. W. *NeuroImage* **76**, 412–427 (2013).
15. Patriarchi, T. *et al. Science* **360**, eaat4422 (2018).
16. Threlfell, S. *et al. Neuron* **75**, 58–64 (2012).
17. Cachope, R. *et al. Cell Rep.* **2**, 33–41 (2012).

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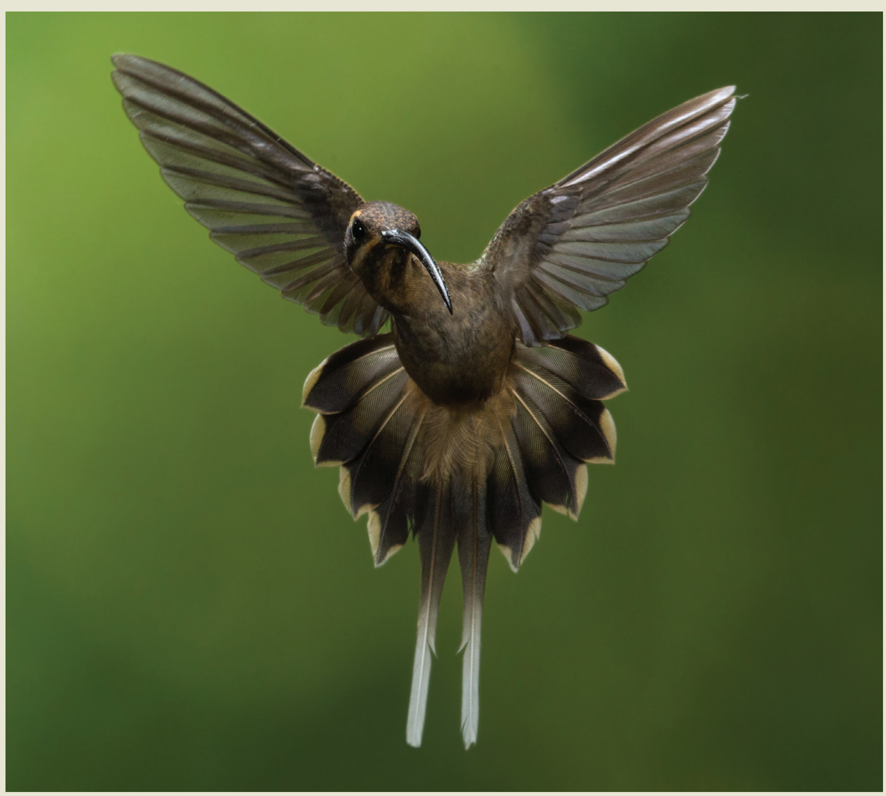
EVOLUTION

Look and learn

Like humans, hummingbirds are vocal learners: they can adapt their vocalizations by listening to others. Vocal learning might have evolved from the ability to learn movements from others. If this is true, vocal learners should also be able to learn movements by watching one another. Writing in *Proceedings of the Royal Society B*, Araya-Salas *et al.* provide evidence for social learning of complex movements in long-billed hermit hummingbirds (*Phaethornis longirostris*; M. Araya-Salas *et al. Proc. R. Soc. B* **286**, 20190666; 2019).

Male hummingbirds sing and perform elaborate visual displays to attract mates and defend their territory. The authors found that each community of hummingbirds has its own variants of the songs and displays, indicating social learning of both. These observations support the theory that vocal learning evolved from general motor learning. **Natasha Bray**



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