NEUROSCIENCE

Working memory freed from the past

Working memory is influenced by past experiences. An area of the rat brain has now been identified that represents recent history — silencing this area can remove biases from working memory and decision-making. SEE LETTER P.368

LAURA BUSSE

Our natural environment is characterized by statistical regularities in both space and time — for example, it does not consist of randomly distributed light, but frequently contains objects that have elongated vertical and horizontal contours[1] and predictable motion[2]. These regularities are exploited by our brains to interpret the often-ambiguous information that reaches our senses, to improve perception, decision-making and working memory. Although, in the natural world, past experiences can thus have a vital role in information processing and cognition, past experiences can impair performance in laboratory experiments that involve random structure. On page 368, Akrami *et al.*[3] take advantage of this difference to identify an area of the rat brain that holds recent sensory history, and show that temporarily silencing this area removes history-related biases in memory-guided decision-making.

More than a century ago, the cognitive psychologist Harry Hollingworth identified a phenomenon called contraction bias[4], in which the representation of a stimulus in working memory is systematically biased towards the average of recent past observations. As an example of contraction bias, consider Hollingworth's historic experiment, in which participants were asked to judge the sizes of different cards. Subjects tended to overestimate the size of memorized cards if they were smaller than others used in the experiment, and to underestimate the size of memorized cards that were relatively large.

Akrami *et al.* first set out to show that, like these findings in humans, contraction bias governs the behaviour of rats. They trained rats in an auditory working-memory task, in which the animals had to determine which of two tones, delivered several seconds apart, was louder. This task requires rats to hold the loudness of the first tone in working memory during the delay period between the two tones, to enable comparison with the second (Fig. 1).

The authors used a custom-built, high-throughput facility for automated rat training and testing, allowing them to collect data from almost half a million trials. Analysis of the rats' behaviour revealed that, in trials in which the first tone was the fainter, performance was improved if the previous trial had contained a pair of relatively faint tones, and hampered if it had contained louder tones. The group fitted powerful computational models to the rats' behaviour that captured the animals' recent sensory history. The models demonstrated that these systematic patterns of performance are predicted by contraction bias, which pulls the representation of the first tone (held in working memory) towards the recently experienced tones. In doing so, contraction bias facilitates or impedes the comparison of the two tones.

In a search for the site of working memory in the rat brain, Akrami *et al.* next made a truly exceptional observation. They temporarily silenced a brain region called the posterior parietal cortex (PPC), which has been implicated in working memory[5], and found that overall task performance was improved by this intervention, particularly when the PPC was silenced during the delay period. This observed cognitive enhancement is clearly inconsistent with the idea that the PPC maintains the working-memory trace during the delay period, because silencing the PPC would erase the trace and hence lead to performance breakdown.

What underlies this remarkable improvement in performance during PPC silencing? Akrami and colleagues fitted their computational model to the rats' behaviour during PPC silencing, and found that the improvement was due to a markedly reduced influence of past recent experience. Previous sensory information can distort working-memory representations. Therefore, in the randomized world of laboratory experiments, it makes sense that silencing a brain area that holds traces of sensory history can lead to more bias-free working-memory content and thus to behaviours more aligned with reality.

To directly test how PPC neurons encode the recent past, Akrami *et al.* recorded PPC

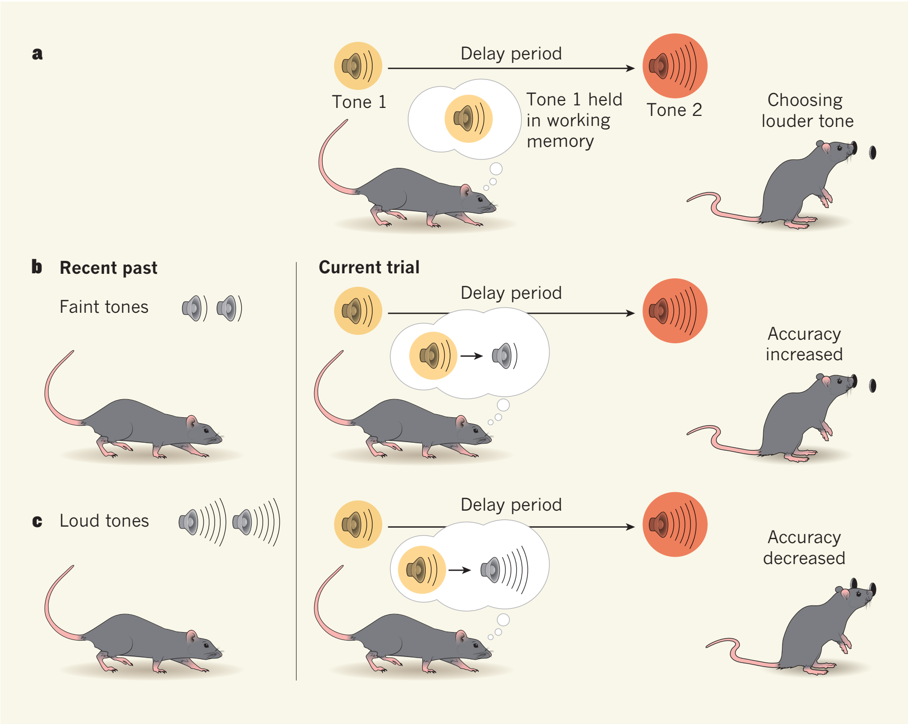

Figure 1 | Biasing the working memory of rats. **a**, Akrami *et al.*[3] trained rats in a working-memory task, in which the animals listened to two tones separated by a delay of a few seconds, and had to indicate, through a nose poke, which was the louder. The task requires the first tone to be held in working memory during the delay period. **b**, The authors investigated how recent sensory history affected trials (here, trials in which the first tone was the fainter). If the animal had recently been exposed to faint tones, it remembered the first sound as fainter than it really was, improving its ability to compare the two tones. **c**, By contrast, the animal's judgement was hampered if it had recently been exposed to loud tones, because it remembered the first tone as louder than it really was. Thus, the rat's recent sensory history impinged on how it held the first tone in working memory.

© 2018 Macmillan Publishers Limited, part of Springer Nature. All rights reserved.

activity during task performance. Consistent with their other results, the group found that, during the delay period, PPC neurons carried more information about the recent past than about the current tone held in working memory. Furthermore, across rats, the percentage of neurons holding such history-related information was tightly correlated with the level of history-induced bias in each animal's performance.

It has long been recognized that even simple perceptual decisions are not isolated, static computations — rather, they are dynamic processes embedded in a stream of past information[6]. Akrami and colleagues have taken a crucial step towards understanding these processes, by identifying a node in the brain network that influences working-memory performance by holding a representation of recent history. That their discovery was made in an animal model offers the exciting possibility that future studies could investigate, at the cellular level, precisely which neurons in the PPC represent recent history, how this representation arises, and where and how it is integrated with sensory information to guide memory-based decision-making.

Statistical regularities not only influence working memory, but can also bias motor outputs and the encoding and decoding of sensory information[7]. It is therefore likely that history-related biases are implemented across many nodes of the decision-making brain network in addition to the PPC, through various mechanisms. Long-term mechanisms, on evolutionary and developmental scales, include the adaptation of neurons in sensory areas to the statistics of the natural environment. For example, the over-representation of vertical and horizontal contours in our visual environments is paralleled by an over-representation in the brain of neurons that respond preferentially to horizontal and vertical orientations[8], and a biased ability to perceive these orientations[9]. Dynamic, short-term mechanisms occurring on a scale of milliseconds to seconds probably involve activity in long-range feedback or neuromodulatory circuits that adjust sensory areas[10], the decision-making network[11] and motor areas[12]. Elucidating the interplay between these mechanisms is just one of the remaining challenges in the quest to understand the powerful role of past experience in working memory. ■

Laura Busse *is in the Division of Neurobiology, Department Biology II, LMU Munich, Munich 82152, Germany.*
e-mail: busse@bio.lmu.de

1. Burton, G. J. & Moorhead, I. R. *Appl. Opt.* **26,** 157–170 (1987).
2. Dong, D. W. & Atick, J. J. *Netw. Comput. Neural Syst.* **6,** 345–358 (1995).
3. Akrami, A., Kopec, C. D., Diamond, M. E. & Brody, C. D. *Nature* **554,** 368–372 (2018).
4. Hollingworth, H. L. *J. Phil. Psychol. Sci. Methods* **7,** 461–469 (1910).
5. Harvey, C. D., Coen, P. & Tank, D. W. *Nature* **484,** 62–68 (2012).
6. Gold, J. I. & Stocker, A. A. *Annu. Rev. Vis. Sci.* **3,** 227–250 (2017).
7. Kiyonaga, A., Scimeca, J. M., Bliss, D. P. & Whitney, D. *Trends Cogn. Sci.* **21,** 493–497 (2017).
8. Coppola, D. M., White, L. E., Fitzpatrick, D. & Purves, D. *Proc. Natl Acad. Sci. USA* **95,** 2621–2623 (1998).
9. Girshick, A. R., Landy, M. S. & wSimoncelli, E. P. *Nature Neurosci.* **14,** 926–932 (2011).
10. St. John-Saaltink, E., Kok, P., Lau, H. C. & de Lange, F. P. *J. Neurosci.* **36,** 6186–6192 (2016).
11. Akaishi, R., Umeda, K., Nagase, A. & Sakai, K. *Neuron* **81,** 195–206 (2014).
12. Pape, A.-A. & Siegel, M. *Nature Commun.* **7,** 13098 (2016).

This article was published online on 7 February 2018.

CONDENSED-MATTER PHYSICS

The two faces of a magnetic honeycomb

Quantum spin liquids are long-sought exotic states of matter that could transform quantum computing. Signatures of such a state have now been observed in a compound comprising iridium ions on a honeycomb lattice. **See Letter p.341**

MARTIN MOURIGAL

Scientists are searching for elusive forms of magnetism in which spins — atomic-scale 'compass needles' associated with electrons — perpetually dance to an intrinsic quantum beat. On page 341, Kitagawa *et al.*[1] describe the synthesis and properties of a remarkable quantum magnet in which the ballet of spins persists down to a temperature of 0.05 kelvin. Such behaviour might be associated with exotic magnetic excitations that are of great fundamental interest and are sought for quantum-computing technologies.

Quantum magnets are often found in electrically insulating crystals. In such materials, unpaired electrons are arranged on a periodic lattice, which allows the spins of the electrons to interact with those of their neighbours. At low temperatures, these spins usually organize into symmetrical and regular patterns.

In rare cases, however, quantum fluctuations prevent the spins from becoming ordered. Instead, the spins enter a quantum superposition — a concerted and perpetual dance in which the spins are entangled, meaning that they are inseparable and share a common quantum state. Many flavours of such states, called quantum spin liquids, have been predicted[2]. At first sight, these states resemble paramagnetic materials, in which spins are disordered in the absence of an external magnetic field. However, whereas spins behave as independent entities in paramagnets, those in quantum spin liquids are entangled with one another, even if separated by long distances.

Experimental physicists have long pondered how to obtain and detect quantum spin liquids in real materials[3]. Much has been learnt from the study of one-dimensional quantum magnets — in particular, from chains of spins that exhibit antiferromagnetism[4], whereby each spin is aligned in the opposite direction to that of its neighbours. For instance, a by-product of long-range entanglement is the presence of magnetic excitations that have fractional quantum numbers (fractions of quantities such as electric charge and spin). These excitations have been shown to leave distinct fingerprints in measurements of a material's thermodynamic and magnetic properties. Furthermore, the presence or absence of an excitation gap (a lack of excitations that have particular energies) often reveals whether the underlying entanglement is short- or long-range, respectively.

However, in spite of these breakthroughs, finding two- and three-dimensional quantum spin liquids has been a daunting task[5]. One approach has been to use geometric frustration[3], in which there is an incompatibility between the spatial arrangement of spins and their interactions. This causes many spin configurations to have the same energy, which jump-starts entanglement. Kitagawa and colleagues used a different materials-science strategy, and focused on a quantum spin liquid that was proposed by the theoretical physicist Alexei Kitaev[6] in 2006.

In Kitaev's model, spins on a honeycomb lattice are forced to interact in seemingly unnatural ways. The resulting quantum spin liquid has two types of exotic magnetic excitation: Majorana fermions, which have fractional quantum numbers, lack an excitation gap and can propagate on the lattice; and other excitations that have a small excitation gap and remain localized.

In a seminal paper[7], it was demonstrated that the ingredients of Kitaev's model might exist in real materials, accompanied by more-conventional spin interactions called Heisenberg interactions. It was later suggested[8] that the model could be realized in materials that have two key properties. The first is a strong coupling between the motion of electrons and their spin — a feature present in the

© 2018 Macmillan Publishers Limited, part of Springer Nature. All rights reserved.