chy of visual processing. Adapting rapidly and strongly to low-level features such as spatial frequency or orientation too early in the processing stream would filter out important information, as many different objects share common low-level features.

Increased adaptation with attention is easily implemented in the brain. Qualitatively, the results from Murray and Wojciulik[8] might be expected even with a simple multiplicative gain mechanism of attention. This is because the enhancement of a neuronal response should also cause greater adaptation of those neurons that are selective to the adapting stimulus. Murray and Wojciulik acknowledge this, but argue that under reasonable assumptions, their effects are greater than would be expected without additional sharpening of selectivity with attention. But perhaps this simple explanation should not be dismissed, because it demonstrates how a simple gain change with attention can result in more adaptation and thus greater sensitivity to changes in an attended stimulus.

Clearly the mechanisms serving both attention and adaptation are complex. But from the results of Murray and Wojciulik, it does appear that attention leads to a larger effect of orientation on the population response of neurons in area LOC. It remains to be seen whether attention causes a sharpening of the tuning of underlying neurons, an enhancement of the response of a more selective subset of neurons, changes in the adaptability of neurons, or a combination thereof. Future single-unit neurophysiological studies should help to distinguish among these hypotheses.

1. Murray, S.O. & Wojciulik, E. *Nat. Neurosci.* **7**, 70–74 (2004).
2. Hillyard, S.A., Vogel, E.K. & Luck, S.J. *Phil. Trans. R. Soc. Lond. B Biol. Sci.* **353**, 1257–1270 (1998).
3. McAdams, C.J. & Maunsell, J.H.R. *J. Neurosci.* **19**, 431–441 (1999).
4. Reynolds, J.H., Pasternak, T. & Desimone, R. *Neuron* **26**, 703–714 (2000).
5. Spitzer, H., Desimone, R. & Moran, J. *Science* **240**, 338–340 (1988).
6. Haenny, P.E. & Schiller, P.H. *Exp. Brain Res.* **69**, 225–244 (1988).
7. Treue, S. & Martinez Trujillo, J.C. *Nature* **399**, 575–579 (1999).
8. Schoups, A., Vogels, R., Qian, N. & Orban, G. *Nature* **412**, 549–553 (2001).
9. Grill-Spector, K. & Malach, R. *Acta Psychol. (Amst.)* **107**, 293–321 (2001).
10. Buckner, R.L. *et al. Neuron* **20**, 285–296 (1998).
11. George, N. *et al. Nat. Neurosci.* **2**, 574–580 (1999).
12. Li, L., Miller, E.K. & Desimone, R. *J. Neurophysiol.* **69**, 1918–1929 (1993).
13. Miller, E.K., Li, L. & Desimone, R. *Science* **254**, 1377–1379 (1991).
14. Boynton, G.M. & Finney, E.M. *J. Neurosci.* **23**, 8781–8787 (2003).
15. Tootell, R.B. *et al. Proc. Natl. Acad. Sci. USA* **95**, 811–817 (1998).

How does practice makes perfect?

John Jonides

Studies of nonhuman animals have taught us a great deal about how the brain changes during learning. An imaging study in this issue investigates how behavioral strategies interact with brain activation in humans during learning of a working memory task.

What happens when we learn? One possibility is that we acquire greater skill at applying our initial strategy to the problem at hand, making it more efficient. Another possibility is that we acquire a new, more efficient strategy. In this issue, Olesen, Westerberg and Klingberg[1] investigate the brain mechanisms that accompany learning a simple task. They find a set of brain regions that increase activation with practice and another set of regions that decrease activation. These results may bear on which of the two learning possibilities occurs in this case.

To see how learning might proceed along two different paths, consider a simple example. Suppose you practice the mental arithmetic problem of multiplying two-digit numbers, for example, 23 × 18. As you work on more of these problems, your time to solve them decreases and your accuracy increases. On the one hand, with practice you may acquire greater skill at applying elementary arithmetic facts to each problem because you can retrieve them from memory faster[2]. Thus, if you continue to use the strategy you learned in school, you might remember more quickly that 3 × 8 = 24. On the other hand, practice might lead you to a new and faster strategy to apply to the problem. For example, you might come to realize that the problem can be solved by multiplying 20 × 18 followed by 3 × 18, and then adding these two sums. We can often characterize learning as a function of either increased automaticity in the application of one strategy or development of some new strategy.

John Jonides is in the Department of Psychology, University of Michigan, 525 E. University, Ann Arbor, Michigan 48109-1109, USA.
e-mail: jjonides@umich.edu

These alternative accounts can be difficult to distinguish using behavioral data alone. However, brain imaging offers the opportunity to see whether patterns of brain activation change as a function of learning, thereby suggesting the acquisition of new strategies. Olesen and colleagues[1] took advantage of this opportunity. They trained participants in tasks that required working memory, the system used to store small amounts of information for several seconds in the service of more complex tasks such as mental arithmetic. In one task (**Fig. 1**), participants had to memorize a series of spatial locations on a screen so that they could reproduce this series in the correct order. 0A sequence of 4 × 4 target matrices was presented, each blank except for one cell colored in red. After the last target matrix, participants saw a sequence of blank matrices, and they had to mark one cell in each to reproduce the sequence of locations that had been marked in the target matrices. Participants were trained on this task (and two others) for 18 days, during which they improved both their accuracy and speed. Before, during and after the training, they were scanned using functional MRI to assess the effect of training on brain activations.

Let's examine some predictions before considering the results. On the one hand, if learning results from a change in strategy, then one might expect that the brain regions activated early in training might be different from those activated later in training—assuming that the new strategy and the old strategy involve some different brain regions. For example, in the mental arithmetic example above, the canonical strategy of working with one digit at a time may rely on retrieval of arithmetic facts from memory, whereas the strategy that treats each number as a whole may require more complex calculation. If memory retrieval and calculation are mediated by different mechanisms, this would

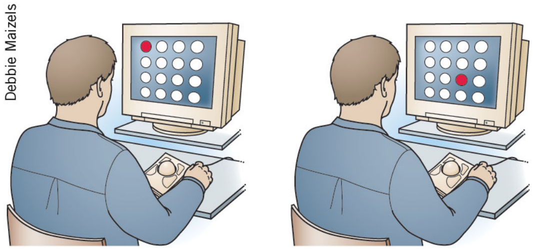

Figure 1 Working memory task in which participants were shown a series of 4 × 4 matrices, each with a single cell marked in red. They had to remember the locations that were marked, as well as the order of presentation.

show up as different patterns of brain activation. On the other hand, if learning results from increased efficiency in applying a single strategy, no new brain regions should be recruited, but the activity in the original brain regions should change. Should activation go up or down, though? At first glance, it might seem sensible that it should go down, as improved automaticity should require less and less neural activity. By analogy, imagine a set of inexperienced mail clerks in a corporate mailroom sorting incoming correspondence with pressure to increase performance. As the clerks get more familiar with the recipients, perhaps fewer clerks would be needed to sort the same volume of mail faster and more accurately. Another possibility, however, is that mail-sorting performance is optimized by adding more clerks even as each one gets faster. Motor skill learning in humans and other animals is accompanied by expansion of the neural resources applied to a task[3].

Olesen and colleagues[1] report two outcomes of learning. Activation increased with training in one set of regions, including parietal and frontal cortex and nuclei in the basal ganglia and thalamus (see their Fig. 3d), while activation decreased in another set of regions, including anterior cingulate cortex, postcentral gyrus and inferior frontal sulcus.

What do we make of these results? Based on what we know about the functions of these regions, we can make some educated guesses. The increased activations in lateral frontal and parietal cortices may reflect increased recruitment of neurons or increases in synaptic connectivity that accompany improved encoding, storage or retrieval of information in working memory. We know from other research[4] that these two regions are critical to the functioning of working memory for processing spatial information. Also, superior parietal cortex and the pulvinar nucleus of the thalamus are important for selective attention and possibly the control of rehearsal in spatial working memory[5]. Thus, increased activation in these sites may reflect recruitment of working memory.

The decreased activations are more of a mystery. The decrease in anterior cingulate may be a signal of reduced effort in the task, as anterior cingulate activation is often suggested to reflect task difficulty[6]. Although Olesen and colleagues[1] do not say so, the participants very likely found the task less taxing with practice. The remaining sites of decreased activation are not typically associated with spatial working memory, and so it is not at all clear how these regions might contribute to changed performance on this task.

The overall pattern of activations in the new study[1] suggests the following: during learning, the same mechanisms used by inexperienced participants are also active after practice, but with increased or decreased magnitude. Indeed, the authors debriefed their participants, most of whom claimed to have used the same strategies throughout. An analysis of some behavioral results confirms this. However, the debriefing came only after training, and it would be difficult for participants to have a detailed enough memory of all the sessions to have good insight into the evolution of their strategies. The analysis of behavior is of some interest in this regard, but these variables may not be the most sensitive assays of participants' strategic choices. So, although we have a hint that learning involves an incremental change in the same mechanisms, more detailed analysis of this issue is still needed.

Now we might inquire about what, exactly, improves with practice. Processes of working memory are often categorized as encoding of information, its storage during a delay, and then its retrieval. The experiments of Olesen and colleagues[1] do not permit us to single out a particular process to see what might be changing as performance changes. That is, we have no way to know whether the brain changes reflect changes in the encoding of the information to be recalled, the efficiency of its storage, or the ease of retrieval. These experiments inspire a need to delve into these specific processes.

Another issue is raised by some additional analyses in the new paper[1]. A frequent strategy to assess what is learned is to examine how the learning transfers to other tasks. The authors thus tested participants on a set of standard neuropsychological instruments. The outcome was limited: practice reliably improved performance on the Stroop task (a test of the ability to inhibit irrelevant information), with only marginal effects on other tasks compared to a control group. The Stroop task improvement may tie in to the increased activation in middle frontal gyrus, as dorsolateral prefrontal cortex is frequently activated by this task. So, there may be a mechanism in common between improved performance in spatial working memory and interference resolution. What we need now is much more such testing of transfer tasks. One would like more behavioral data on other tasks to determine how broadly the training transfers, along with neuroimaging data on these tasks in the same participants to see just what brain mechanisms are shared in common.

One could quickly expand this list of to-do's, largely because studies of the brain mechanisms of learning in humans are few in number. The greatest leaps forward in understanding learning have come from invasive studies of other animals[7]. Many of these studies have detailed the expansion of synaptic connections that accompanies learning and interaction with complex environments even over short time intervals. From these studies, we have acquired a fundamental base of knowledge about the plastic changes in neural structure that accompany acquired skill. The stage is now set for much more research that tests humans, of the sort initiated by Olesen and colleagues[1]. We can now learn a good deal about why it is that 'practice makes perfect'.

1. Olesen, P.J., Westerberg, H. & Klingberg, T. *Nat. Neurosci.* **7**, 75–79 (2004).
2. Ashcraft, M.H. & Christy, K.S. *J. Res. Math. Education* **26**, 396–421 (1995).
3. Ungerleider, L.G., Doyon, J. & Karni, A. *Neurobiol. Learn. Mem.* **78**, 553–564 (2002).
4. Smith, E.E. & Jonides, J. *Science* **283**, 1657–1661 (1999).
5. Kastner, S. & Ungerleider, L.G. *Annu. Rev. Neurosci.* **23**, 315–341 (2000).
6. Barch, D.M. *et al. Neuropsychologia* **35**, 1373–1380 (1997).
7. Greenough, W.T., Withers, G.S. & Wallace, C.S. in *The Biology of Memory, Symposia Medica Hoechst* Vol. 23 (eds. Squire, L.R. & Lindenlaub, E.) 159–185 (F.K. Schattauder, New York, 1990).