levels after whisker stimulation. This suggests that axons carrying information about the principal whisker were indeed wired specifically to those dendritic segments. Such clustering of coactive inputs would be the expected outcome of clustered plasticity acting over long periods of time[7,9]. As Zhang *et al.*[2] did not reconstruct entire neurons, we cannot be sure about the connectivity of the imaged segments. If non-potentiated and potentiated dendrites indeed coexist at individual neurons (**Fig. 1c**), this would strongly support the hypothesis that dendritic branches serve as independent information storage units[10]. Experiments to directly test this hypothesis are now within reach.

Direct observation of AMPA receptor insertion allowed Zhang *et al.*[2] to assess synaptic potentiation independently of spine volume changes. The volume of the spines carrying the most strongly potentiated synapses did not in fact increase particularly. AMPA receptor enrichment in spines was stable during the 48 h following stimulation, but this functional strengthening did not affect spine morphology in an obvious way. Whether this sensory-evoked plasticity also increased the long-term stability of synapses remains to be seen. More dramatic manipulations, such as whisker trimming[11] or monocular deprivation[12], have been shown to affect spine turnover. However, the time lag between plasticity induction and spine loss can be considerable[13], suggesting that potential effects on synaptic stability might not manifest in the 2-d observation window of the current study[2].

Although direct imaging of AMPA receptor insertion *in vivo* is an attractive strategy for measuring the spatiotemporal dynamics of plasticity events at the level of single synapses, Zhang *et al.*'s results[2] must be taken with a grain of salt. All of the observations were made by overexpressing the two AMPA receptor subunits GluA1 and GluA2, of which GluA1 contained the fluorescent label. The authors thoroughly characterized expression levels of those subunits and found no overexpression artifacts. Still, we cannot know for sure whether all labeled GluA1 molecules at the surface were indeed assembled into functional AMPA receptors, or whether increased fluorescence merely indicated elevated rates of local exocytosis. Fluorescent labeling of endogenous GluA subunits—for example, using gene editing[14]—would reduce the risk of disturbing expression levels and subunit composition.

In the future, the elegant approach of following the complement of receptors at individual synapses *in vivo*[2] could be combined with sophisticated learning experiments. Perhaps the rodent barrel cortex will indeed be the first system in which the potentiated synapses that constitute a new memory can be identified. The search for the memory trace, or engram, has come a long way from Lashley's original lesion experiments[15], and the current study marks an important step toward this ultimate goal.

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1. Margolis, D.J. *et al. Nat. Neurosci.* **15**, 1539–1546 (2012).
2. Zhang, Y., Cudmore, R.H., Lin, D.T., Linden, D.J. & Huganir, R.L. *Nat. Neurosci.* **18**, 402–407 (2015).
3. Ashby, M.C. *et al. J. Neurosci.* **24**, 5172–5176 (2004).
4. Shi, S.H. *et al. Science* **284,** 1811–1816 (1999).
5. Makino, H. & Malinow, R. *Neuron* **72**, 1001–1011 (2011).
6. Gambino, F. *et al. Nature* **515**, 116–119 (2014).
7. Takahashi, N. *et al. Science* **335**, 353–356 (2012).
8. Harvey, C.D. & Svoboda, K. *Nature* **450**, 1195–1200 (2007).
9. Iannella, N.L., Launey, T. & Tanaka, S. *Front. Comput. Neurosci.* **4**, 21 (2010).
10. Branco, T. & Häusser, M. *Curr. Opin. Neurobiol.* **20**, 494–502 (2010).
11. Holtmaat, A., Wilbrecht, L., Knott, G.W., Welker, E. & Svoboda, K. *Nature* **441**, 979–983 (2006).
12. Hofer, S.B., Mrsic-Flogel, T.D., Bonhoeffer, T. & Hubener, M. *Nature* **457**, 313–317 (2009).
13. Wiegert, J.S. & Oertner, T.G. *Proc. Natl. Acad. Sci. USA* **110**, E4510–E4519 (2013).
14. Hsu, P.D., Lander, E.S. & Zhang, F. *Cell* **157**, 1262–1278 (2014).
15. Lashley, K.S. *Science* **73**, 245–254 (1931).

Attention: feedback focuses a wandering mind

Edward Awh & Edward K Vogel

Neurofeedback that tracks attentional focus in real time using fMRI and alerts subjects to impending lapses by modulating the difficulty of the task itself has been demonstrated to improve behavioral performance.

Brief lapses of attention while performing daily tasks are ubiquitous. Whether it's adding salt instead of sugar to your coffee or missing a stop sign, these attentional lapses can result in unintended consequences ranging from minor nuisances to outright catastrophes[1]. A challenge for controlling such lapses is that humans often are not very good at immediately noticing when their mind has drifted off from the task at hand[2]. However, deBettencourt *et al.*[3] have now developed an approach that uses fMRI in real time to detect when the subject's brain is no longer in an attentive state and provides them with continuous feedback to get them back on track. This neurofeedback approach yielded reliable increases in behavioral performance relative to a sham feedback condition, demonstrating the value of online feedback for optimizing performance in attention-demanding situations.

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The authors required subjects to attend to either the face or scene aspect of a composite stimulus (**Fig. 1**) while tracking the strength of task-relevant information in each subject's brain. The task required them to make a response on 90% of trials, but to withhold that response on the rare trials in which non-target stimuli were presented; this task is well known to tax one's ability to sustain attention over time and to inhibit prepotent responses. As the subjects performed this attentionally demanding task, the authors used the ongoing neural signals from each subject's brain to provide moment-to-moment feedback using a clever and direct method: the weight of each image in the composite stimulus started out equal, but when ongoing neural activity indicated that attention to the relevant stimulus was waning, the percentage of the task-relevant aspect (face or scene) in the composite mixture was reduced. Conversely, when neural activity indicated increasing attentional focus, the relevant face or scene aspect of the physical stimulus was amplified (**Fig. 1**). Thus, the feedback signal that informed subjects of their current attentional state was integrated into the very stimulus subjects were attempting to attend. deBettencourt *et al.*[3] suggest that this feedback scheme served to reward subjects with an easier stimulus display when

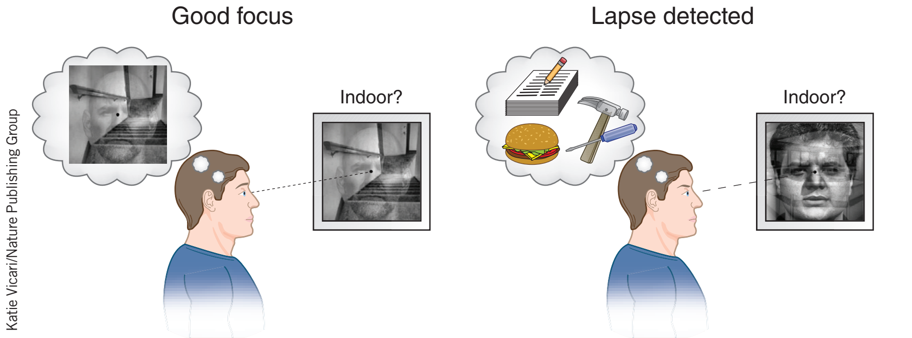

Figure 1 Real-time neurofeedback. Ongoing neural activity was used to monitor attentional focus. During moments of good focus, the weight of the salient stimulus (here, the scene) was amplified in the physical display, making the task easier. By contrast, if attention toward the salient stimulus waned, its weight in the physical display was reduced. Stimuli reprinted from ref. 3 with permission.

they were on task and punish them when their attention began to stray.

Remarkably, this neurofeedback procedure produced reliable improvements in behavioral performance after a single training session. Other participants who spent an equivalent amount of time practicing the task with sham feedback did not show reliable improvement, suggesting that accurate feedback based on ongoing neural activity was responsible for the improvement in behavioral sensitivity. Indeed, those subjects whose neurofeedback signal improved the most over time were the ones who showed the greatest improvement from the pre-training to the post-training assessment of attentional function. deBettencourt *et al.*[3] also found that neural activity discriminating between the two attentional states (face versus scene) was sharpened by neurofeedback, such that distinct attentional states evoked more differentiated patterns of activity following neurofeedback training. This effect was most pronounced in a distributed network of brain regions that included ones, such as frontoparietal cortex, outside of the traditional sensory areas, suggesting that neurofeedback may have influenced processing in attentional control regions that extend beyond category-selective visual regions. These findings suggest that individually tailored neurofeedback can be an effective approach for helping individuals to avoid lapses of attention and take full advantage of their existing ability to engage in goal-driven selection of relevant information.

The focus of deBettencourt *et al.*[3] on attentional lapses may also provide a productive perspective for understanding individual differences in attentional ability. It has long been known that an individual's ability to voluntarily select the relevant over the irrelevant aspects of an environment predicts broad measures of intellectual function, such as fluid intelligence[4,5] and scholastic aptitude[6]. These links with success in a wide variety of contexts motivate a search for explanations of why attentional efficiency varies across individuals. An intuitive idea is that individuals vary in the maximal efficiency of attention, leading to consistent differences in their ability to voluntarily select the most relevant aspects of a stimulus. It is also possible, however, that individual differences in attentional control reflect the probability that an individual will avoid lapses and make full use of their attentional ability. In this case, the frequency of attentional lapses could have a powerful effect on performance in attentionally demanding tasks even if there are no differences in the maximal efficiency of attention. Indeed, both the frequency of 'mind wandering'[1,7] and attentional lapses[8] predict individual differences in executive control and fluid intelligence, showing that broad measures of cognitive function are shaped by the prevalence of inattentive episodes. Thus, a fuller appreciation of how ability varies from moment to moment may sharpen our understanding of individual differences in cognitive control.

Finally, the findings of deBettencourt *et al.*[3] may have implications for 'brain training' approaches that seek to improve general cognitive function in humans. Because attentional control is a core facet of cognitive ability, there has been a longstanding interest in whether it is possible to enhance attentional ability via training exercises. Most of these attention training interventions involve attempts at boosting the native capacity of the attentional system through extensive attentional control practice[9]. However, after over 100 years of attempts, this approach has yielded only minimal success and much controversy[10–14], with some arguing that it is unrealistic to expect permanent changes in native cognitive ability following relatively short-lived exposure to a behavioral intervention[14]. Consistent with other recent work[15], the findings of deBettencourt *et al.*[3] highlight a qualitatively different approach. Instead of attempting to boost the maximal efficiency of attention, this strategy seeks to optimize the individual's existing attentional capacity through the detection and correction of lapses. Thus, rather than trying to make the individual 'smarter', the more tractable training goal may be to make the individual 'stupid less often'.

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1. Kane, M.J. *et al. Psychol. Sci.* **18**, 614–621 (2007).
2. Schooler, J.W. *et al. Trends Cogn. Sci.* **15**, 319–326 (2011).
3. deBettencourt, M.T., Cohen, J.D., Lee, R.F., Norman, K.A. & Turk-Browne, N.B. *Nat. Neurosci.* **18**, 470–475 (2015).
4. Kane, M.J. & Engle, R.W. *Psychon. Bull. Rev.* **9**, 637–671 (2002).
5. Unsworth, N., Fukuda, K., Awh, E. & Vogel, E.K. *Cogn. Psychol.* **71**, 1–26 (2014).
6. Turner, M.L. & Engle, R.W. *J. Mem. Lang.* **28**, 127–154 (1989).
7. Mrazek, M.D. *et al. J. Exp. Psychol. Gen.* **141**, 788–798 (2012).
8. Unsworth, N., Redick, T.S., Lakey, C.E. & Young, D.L. *Intelligence* **38**, 111–122 (2010).
9. Morrison, A.B. & Chein, J.M. *Psychon. Bull. Rev.* **18**, 46–60 (2011).
10. Thorndike, E.L. & Woodworth, R.S. *Psychol. Rev.* **8**, 247–261 (1901).
11. Jaeggi, S.M., Buschkuehl, M., Jonides, J. & Perrig, W.J. *Proc. Natl. Acad. Sci. USA* **105**, 6829–6833 (2008).
12. Klingberg, T., Forssber, H. & Westerberg, H. *J. Clin. Exp. Neuropsychol.* **24**, 781–791 (2002).
13. Caroll, J.B. *Human Cognitive Abilities: a Survey of Factor-Analytic Studies* (Cambridge University Press, 1993).
14. Redick, T.S. *et al. J. Exp. Psychol. Gen.* **142**, 359–379 (2013).
15. Mrazek, M.D., Franklin, M.S., Phillips, D.T., Baird, B. & Schooler, J.W. *Psychol. Sci.* **24**, 776–781 (2012).