A Price to Pay for Adult Neurogenesis

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some techno-environmental conditions, only intensely cooperative social groups can endure, prosper, and spread. Although potentially applicable to many situations, including territorial defense and whale hunting, Talhelm *et al.* focus on the different labor requirements of paddy rice and wheat cultivation. By demanding intense cooperation, paddy rice cultivation fosters and reinforces the social norms that govern patrilineal clans. Growing up in strong clans creates a particular kind of collectivistic psychology. In contrast, wheat cultivation permits independent nuclear households and fosters more individualistic psychologies.

To test these ideas, Talhelm *et al.* used standard psychological tools (see the figure) to measure analytical thinking and individualism among university students sampled from Chinese provinces that vary in wheat versus rice cultivation. Focusing on China removes many of the confounding variables such as religion, heritage, and government that would bedevil any direct comparison between Europe and East Asia. The prediction is straightforward: Han Chinese from provinces cultivating relatively more wheat should tend to be more individualistic and analytically oriented.

Sure enough, participants from provinces more dependent on paddy rice cultivation were less analytically minded. The effects were big: The average number of analytical matches increased by about 56% in going from all-rice to no-rice cultivation. The results hold both nationwide and for the counties in the central provinces along the rice-wheat (north-south) border, where other differences are minimized.

Participants from rice-growing provinces were also less individualistic, drawing themselves roughly the same size as their friends, whereas those from wheat provinces drew themselves 1.5 mm larger. [This moves them only part of the way toward WEIRD people: Americans draw themselves 6 mm bigger than they draw others, and Europeans draw themselves 3.5 mm bigger (*6*).] People from rice provinces were also more likely to reward their friends and less likely to punish them, showing the in-group favoritism characteristic of collectivistic populations.

So, patterns of crop cultivation appear linked to psychological differences, but can these patterns really explain differences in innovation? Talhelm *et al.* provide some evidence for this by showing that less dependence on rice is associated with more successful patents for new inventions. This doesn't nail it, but is consistent with the broader idea and will no doubt drive much future inquiry. For example, these insights may help explain why the embers of an 11th century industrial revolution in China were smothered as northern invasions and climate change drove people into the southern rice paddy regions, where clans had an ecological edge, and by the emergence of state-level political and legal institutions that reinforced the power of clans (*7*).

Cultural evolution arises from a rich interplay of ecology, social learning, institutions, and psychology. Environmental factors favor some types of family structures or forms of social organization over others. Honed and refined over generations, these institutions create the conditions to which children adapt developmentally, shaping their psychologies and brains. Long after their ecological causes have become irrelevant, these cultural psychologies and institutions continue to influence rates of innovation, the formation of new institutions, and the success of immigrants in new lands. As such, wheat farming may contribute to explaining the origins of WEIRD psychology and the industrial revolution.

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NEUROSCIENCE

A Price to Pay for Adult Neurogenesis

Newly formed hippocampal neurons participate in the encoding of new memories in adult rodents, but too much neurogenesis may jeopardize memory retention.

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We tend to believe that plasticity is what makes brain circuits adaptable to continuous changes in environmental demands and that greater brain plasticity should result in a better ability to cope with the surrounding world. To adapt to everyday life, animals explore, learn, and remember, and these tasks make use of various cortical structures, including the hippocampus. The dentate gyrus, part of the hippocampus, is a remarkable structure in that it is one of two areas of the adult mammalian brain, including the human brain, that continue to generate new neurons throughout postnatal life (*1*). It is well established that adult-born neurons integrate into preexisting neuronal networks and participate in information processing (*2*). Much evidence accumulated over the past decade supports the hypothesis that adult neurogenesis itself is a type of circuit plasticity required for hippocampus-dependent learning and memory recall. The work by Akers *et al.* on page 598 of this issue (*3*) now shows that adult hippocampal neurogenesis may also promote forgetting.

In the adult hippocampus, new-born granule neurons develop and establish synaptic connections within preexisting neuronal networks very slowly. Input and output connections are refined during several weeks as neurons acquire a meaningful functional integration. The specific functional role of these new cells is not clear. Nor is it clear why the dentate gyrus requires freshly assembled neurons to perform its function. It has been proposed, based on its architecture, that the dentate gyrus may play a critical role in performing "pattern separation" of incoming inputs. Pattern separation is the process whereby similar pieces of information are represented by distinct (orthogonal) sets of neurons in the output network. It has been proposed that in a behavioral context pattern separation underlies the capacity to extract the subtle differences among environments or cues that are otherwise

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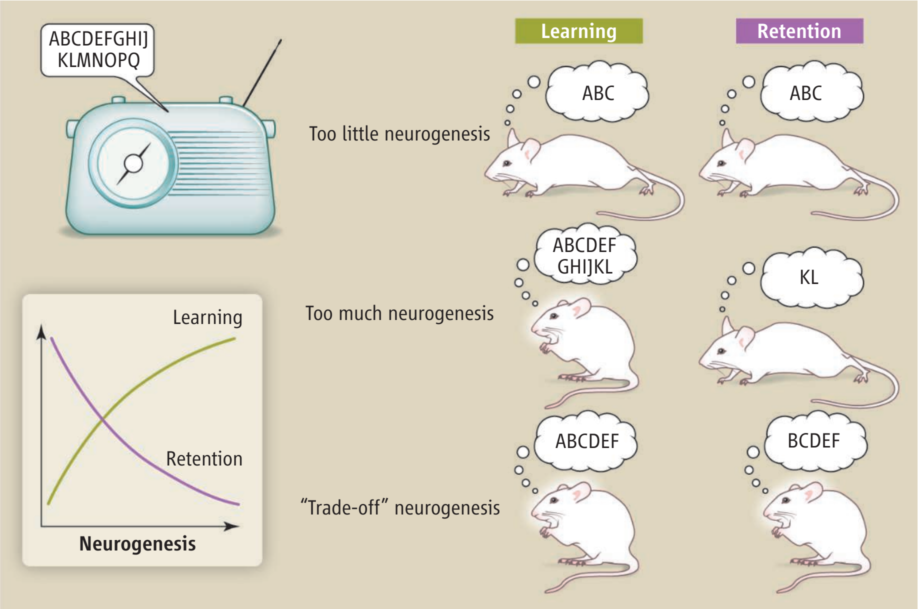

Making new neurons, but not too many. In the cartoon, the mouse must encode environmental cues depicted as characters coming out of the radio. A mouse with little hippocampal neurogenesis exhibits difficulties in learning the task, but information can be stored entirely (left on the graph). A mouse with too much neurogenesis displays excellent learning performance but poor retention due to ongoing circuit remodeling that labilizes memories (right on the graph). A "trade-off" level of neurogenesis allows good performance for both memory acquisition and retention (point of intersection on the graph).

very similar. Hence, much effort has been devoted recently to test the hypothesis that adult neurogenesis may be required for what is now called behavioral pattern separation, with experiments that have been primarily centered on the acquisition of new contextual memories.

An experiment that typifies the approach is the contextual fear discrimination paradigm. Following a randomized order, mice are placed in two very similar but not identical contexts, A or B; in A, they receive brief foot shocks, whereas in B, they receive no stimulus. This scenario is repeated once a day over a period of several days. Because they learn to associate the context with the shock, mice freeze when placed in either context, but with time they learn to identify the small differences that discriminate the safe place from the dangerous one (behavioral pattern separation) and make that learning explicit by keeping calm in the nonshock (B) context. It has shown that manipulations that decrease the number of functional adult-born neurons impair behavioral pattern separation (*4*, *5*). Consistent with those data, increasing the number of adult-born neurons seems to improve memory encoding (*6*, *7*). In light of these results, one could infer that more adult neurogenesis improves hippocampus-dependent memory. However, theoretical models have led to the suggestion that the network remodeling required to encode new information could also contribute to loss of previously stored memories (*8*), much like palimpsests from the middle ages—manuscripts written on top of older washed-off texts. Indeed, morphological studies have shown that when adult-born neurons integrate into the local dentate networks, they compete for established synapses, thus altering preexisting connections (*9*, *10*).

Akers *et al.* tested the idea that hippocampal neurogenesis will lead to competitive circuit modification and thus contribute to forgetting. The authors approached this problem from different angles using various behavioral paradigms. In an attempt to correlate the rate of neurogenesis with the extent of forgetting, they took advantage of the natural ontogenic decline in postnatal neurogenesis to compare memory retention in early postnatal (17-day-old) pups versus adult mice. Mice were exposed to a novel context where they received brief foot shocks and were tested in the same context at different times (up to 6 weeks) without the foot shocks. Whereas adult mice displayed good memory retention throughout the experimental time span, pups forgot the association within a week. Remarkably, increasing neurogenesis after contextual learning accelerated forgetting in adult mice, whereas reducing neurogenesis after learning improved memory retention in pups. To determine whether the correlation between neurogenesis and forgetting can be generalized, the authors tested memory retention in guinea pigs and degus (brush-tailed rodents), both of which species have extended gestation periods and thus lower levels of postnatal neurogenesis compared with mice. They found that guinea pig pups and degu pups display high levels of retention that are worsened by manipulations that increase neurogenesis. Altogether, the results clearly demonstrated that a substantial correlation exists between neurogenesis and forgetting.

The most straightforward explanation of these experimental observations is that enhanced neurogenesis results in more neurons actively integrating into the neuronal circuitry of the dentate gyrus. If newly generated neurons incorporate in a manner that destabilizes preexisting synaptic connections, neurogenesis would labilize previously encoded memories, as proposed by theoretical models (*11*). A prediction emerging from this mechanistic interpretation is that increasing neurogenesis should not result in an immediate change in memory retention. Instead, forgetting should develop after a certain delay, as the new neurons begin to interconnect within the existing dentate network.

Finally, if encoding novel memories involves remodeling of preexistent synaptic connections with the concomitant loss of stored information, adding new neurons does seem like an efficient strategy for minimizing interference with the preexisting network, where the alternative scenario would require modifying synaptic weights within such networks. Certainly, adult hippocampal neurogenesis does contribute to memory encoding in situations where fine discrimination is needed, such as contextual discrimination. But adding new neurons will still impose a cost to network stability. Therefore, encoding novel memories requires just the right amount of dentate gyrus neurogenesis—neither too little nor too much.

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