

20 to 30 minutes to reach a stable state.

What do these findings suggest about spatial processing within the hippocampus? One possibility is that CA3 encodes the animal's location with reference to the current environmental context. This would be a useful extension to the coding scheme in the entorhinal cortex, where "place cells" appear to be relatively immune to changes in the environment (8). The context-dependent representation in CA3 might allow spatial memory to differentiate between different environments and so, for example, allow me to locate my car in the supermarket parking lot without interference from occasions when I parked it at the mall. But what about CA1? Leutgeb *et al.*'s finding that the pattern of activity in CA3

can change without affecting CA1 activity suggests that the CA1 region responds to direct inputs from the entorhinal cortex rather than to information routed through CA3 (9, 10). But why would CA1 echo the entorhinal representation? One possibility is that CA1 melds information that was not explicitly examined by Leutgeb *et al.* into the spatial representation. Such information could include nongeometric features of the environment, such as odor or behavioral contingencies, or internal states such as hunger, thirst, or motivation. Alternatively, because remapping is known to take place in this region following manipulations of the spatial relationship between local and distal cues (10), CA1 may help to represent intercue associations. With

these questions still waiting to be answered, it will be interesting to see how future studies gradually tease apart the components of the entorhinal-hippocampal memory system. This process will lead to a clearer picture of how neural networks in these regions interact during memory storage and retrieval. Now, where did I leave my keys?

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BEHAVIOR

Sweet Revenge?

Brian Knutson

You've been waiting in line in traffic for what seems like hours, when a red sports car whips past on the shoulder. Eventually, the sports car creeps back into view—the driver has run out of shoulder and signals to be let in. Instead of giving way, you stare ahead and accelerate, inching dangerously close to the bumper in front of you. After squeezing back the intruder, you can't help but notice a smile creep onto your face.

Judges worry, whereas filmmakers delight, in the fact that revenge feels good. Evolutionary theorists argue that such an "eye-for-an-eye" strategy makes sense, preventing future damage to one's self or kin (1, 2). Yet, in cases ranging from inconsiderate drivers to Nazi war criminals, even unrelated onlookers seem highly motivated to seek revenge, often in spite of personal cost. From the standpoint of self-interest, punishing those who violate the interests of strangers—a form of revenge called altruistic punishment—seems irrational. Enter de Quervain and colleagues (3) on page 1254 of this issue, who offer an alternative explanation—instead of cold calculated reason, it is passion that may plant the seeds of revenge.

Using an elegant laboratory task designed to elicit acts of revenge among human volunteers, de Quervain and colleagues appear to have captured this complex emotional dynamic of schadenfreude with a positron emission tomography (PET) camera. During the task, subjects played games involving real money with a series of different partners.

In each interaction, subjects chose to give their partners money, which was then quadrupled. Next, partners who received the money had a chance to reciprocate, or to pay back half to the subject. If partners decided not to reciprocate, or defected, subjects could choose to administer punishment. At this point, their brains were scanned.

De Quervain and co-workers first asked whether choosing to punish a defector would recruit brain circuits implicated in reward processing. They found that when subjects administered a monetary punishment to defectors, a subcortical region of the brain called the striatum increased its consumption of oxygen (that is, was "activated"). The investigators interpreted this to indicate that punishing a defector activates brain regions related to feeling good about revenge rather than brain regions related to feeling bad about having been violated. Indeed, these striatal foci lie near brain areas that rats will work furiously to stimulate electrically (4). The investigators then asked whether the striatum would be activated even when administering the punishment carried a personal cost. They found that the striatum was still activated when subjects chose to administer punishment at a personal cost, as was a region in the medial prefrontal cortex (MPFC) that has been implicated in balancing costs and benefits (5). Although these findings



"Go ahead, make my day." Dirty Harry succinctly informs a norm violator that he anticipates deriving satisfaction from inflicting altruistic punishment.

suggested a connection between striatal activation and the satisfaction one might derive from punishing a defector, they do not establish a directional relationship between the two. Thus, in a clever internal analysis, the investigators observed that the degree of striatal activation during no-cost punishment predicted the extent to which subjects chose to punish at a personal cost (that is, under less satisfying conditions). This find-

ing suggested to the investigators that striatal activation indexed subjects' anticipation of satisfaction, rather than satisfaction per se.

These findings fit a fresh piece into the rapidly expanding puzzle of reward processing as revealed by brain imaging. Ironically, punishment of defectors in this study activated the same regions (that is, striatum and MPFC) that were activated when people rewarded cooperators in a recent functional magnetic resonance imaging (fMRI) study (6). These seemingly diametrically opposite social behaviors are united by a common psychological experience—both involve the anticipation of a satisfying social outcome. As presaged by comparative research (7), humans also show increased striatal activity during anticipation of nonsocial rewards such as monetary gains (8) and pleasant tastes (9). Together, these findings imply that for certain parts of the striatum, it's the feeling that counts.

As with any compelling study, the findings raise additional questions for future research. Although PET measures absolute metabolism (and can even provide neurochemical information), its spatial and temporal resolution are limited (in this case, to

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15 mm³/min). Thus, although they were able to visualize activation at the head of the caudate, the investigators may not have been able to track activity in the smaller ventral part of the striatum—the part most directly implicated in motivation (10). Fortunately, event-related fMRI can resolve activity in smaller regions (~4 mm³) on a second-to-second basis (11). Techniques like this may enable future investigators to make even more specific observations regarding when and where activation occurs during altruistic punishment. Second, while the present PET study of defectors included male subjects, the aforementioned fMRI study of cooperators included females. Future research will undoubtedly need to explore which social interactions most powerfully motivate men compared with women (as well as members of different social groups). Regardless, the findings do powerfully illustrate the importance of considering proximal emotional mechanisms in brain

imaging studies of social behavior (12). The new results also suggest that, depending on social learning, some of the same emotions that bring us together can also break us apart.

The findings of de Quervain *et al.* also chip yet another sliver from the rational model of economic man. In fact, their subjects illustrated at least two types of irrationality: reacting on the basis of emotional considerations and spending costly personal resources to ensure that defectors got their due. Beyond providing a compelling justification for adding social justice concerns to existing economic models, the findings serve as a harbinger of future “neuroeconomic” studies that strive to descriptively reconstruct these models using neurobehavioral data. One can imagine the new models accommodating both “passionate” and “rational” forces, as well as specifying when and how they come together to influence individual choice.

Back in traffic, brake lights flare ahead. You realize that your smile was short-sighted. Your car skids to a halt. Fortunately, the smile didn't cost a pile-up. This time.

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GEOSCIENCE

What Caused the Great Lisbon Earthquake?

Marc-André Gutscher

On 1 November 1755, as worshippers in Portugal and southwestern Spain were gathered for mass on All Saint's Day, a tremendous earthquake struck, toppling many churches and killing about 60,000 people (1, 2). Many churchgoers were killed, sparking a lively debate among philosophers about divine justice. Recent studies have shed light on what caused the earthquake and what the seismic future of the region may be.

The Great Lisbon earthquake had an estimated magnitude (*M*) 8.7. It triggered a 5- to 10-m-high tsunami and caused many casualties in Europe and northwestern Morocco (2). In this region, the African plate pushes toward the northwest against southern Iberia at a rate of 4 mm/year (see the figure, left panel). But the plate boundary off southern Iberia is not well defined (3), and the source of the Great Lisbon earthquake has remained elusive (2). Indeed, it has been difficult to find a simple plate-tectonic model that explains all geological observations in the region (4, 5).

During the past 15 million years, crustal thinning and extension have produced a

deep marine basin in the West Alboran Sea (western Mediterranean), while shortening and thrusting continued in the horseshoe-shaped Betic and Rif mountain belts (see the figure, left panel) (4, 5). A popular model concluded that this region was a prime example of “delamination” (breaking off of a deep mantle root following continental collision) (4). However, new data increasingly support eastward subduction beneath the Straits of Gibraltar (see the figure, right panel) (5, 6). Tomographic cross sections of the Earth show cold, dense material—a slab of oceanic lithosphere—descending from the surface to depths of nearly 700 km (6). The chemistry of 15- to 5-million-year-old volcanoes in the Alboran Sea shows that they were formed in an arc setting (like that of arcuate island chains in the West Pacific landward of the subduction zone) (7).

Overall, the movement of tectonic blocks in the southern Iberia region is best explained by a model of slab retreat (roll-back) during subduction, causing extension in the region behind the subduction zone (5, 6, 8). The southeastern limit of deformation in this back-arc region appears to be a major north-east trending strike-slip fault across the West Alboran Sea (9). This fault emerges on land in northeast Morocco, right where the Al Hoceima earthquake (*M* = 6.3) struck on 24 Feb-

ruary 2004, causing nearly 600 deaths.

One big question remains. Is the subduction system still active, and does it pose a seismic risk? New evidence supports continued activity. Numerous active mud volcanoes have been identified and sampled in the Gulf of Cadiz (10). These features indicate ongoing dewatering processes, which are widespread in accretionary wedges (compressed sediment piles formed at subduction zones, like piles of dirt in front of a bulldozer). Marine seismic data indicate active folding and thrusting of the youngest sediments (which are a few thousand years old) at the outermost edge of this accretionary wedge (11). Marine heat flow data are also indicative of active subduction (12).

An active subduction zone off southern Iberia poses a long-term seismic risk and is a likely candidate for having produced the Great Lisbon earthquake in 1755. However, no instrumentally recorded subduction interface earthquakes have been recorded in the Gulf of Cadiz. Hence, subduction has either ceased, is active and aseismic, or is active but the seismogenic fault zone is locked. The latter interpretation seems most likely. In this case, the Gibraltar subduction would resemble the Nankai and Cascadia subduction zones, which are characterized by a large locked zone and have a recurrence time of 100 to 1000 years for great earthquakes.

Additional clues can help to pinpoint the likely location of the Great Lisbon earthquake. The generation of a strong tsunami implies a source region mostly at sea. The tsunami wave can be modeled and compared to historical observations (2). A record of past great earthquakes exists in the abyssal plains off southwest Iberia in

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