

of a rose can be appreciated through a more direct chemosensory route. The rose's fragrance may trigger additional emotional reactions through associations, but these are not essential for an emotional response to occur. Given their differential origins, it seems reasonable to suppose that the organization of the brain's response in these two cases might also differ substantially.

The amygdala has often been portrayed as the center of fear and loathing in the brain, specialized to respond to highly aversive emotional stimuli. Indeed, considerable evidence supports this view. For example, direct electrical stimulation of the amygdala in humans can induce intense fear reactions, and intracranial recording of field potentials from patients with implanted amygdala electrodes shows increased activity while viewing unpleasant scenes but not pleasant or neutral scenes<sup>9</sup>. In addition, the amygdala has a well-established role in innate and learned fear responses, such as the classical conditioning of fear associations<sup>10,11</sup>. Against this background, it is surprising that in the present study the amygdala responded solely to the emotional intensity of odors, regardless of valence. There has been a growing recognition, however, that the amygdala has a more general role in adaptive reactions to a wide range of behaviorally salient stimuli, includ-

ing pleasant and emotionally arousing visual stimuli such as erotica and appetizing food<sup>6,12,13</sup>. The work of Anderson *et al.*<sup>1</sup> supports this more general role for the amygdala by clearly showing that in the case of olfaction, the amygdala is not specialized for response to unpleasant emotion.

Overall, the evidence so far suggests that although the amygdala can respond to both pleasant and unpleasant emotional stimuli, it often is more responsive to unpleasant stimuli, for reasons that have yet to be determined. The current findings suggest that this greater role in negative emotion may be partly an illusion, however, induced by the correlation between unpleasantness and arousal. That is, even if the amygdala always responded solely on the basis of arousal (regardless of valence), its observed role in negative emotion would seem to be more prominent, simply by virtue of the higher emotional arousal triggered by unpleasant stimuli<sup>14</sup>. A more fundamental question concerns the degree to which the amygdala is intrinsically specialized or tuned toward negative emotion, after the greater arousal associated with negative emotion stimuli has been accounted for. The current study has shown that for olfaction, the amygdala has no intrinsic preference for negative emotion after the effects of arousal have

been controlled. It will be intriguing to discover whether other domains of emotional stimuli will follow the lead of the nose.

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## The master clock becomes a servant

In mammals, a specialized 'clock' or pacemaker in the hypothalamus called the suprachiasmatic nucleus (SCN) regulates daily rhythms in behavior and body function, such as sleeping and body temperature. Rhythms in the SCN are driven intrinsically, without external inputs, leading the SCN to be considered a master clock controlling other clocks within the body. However, this idea may be incomplete, report Michael Lehman and colleagues on page 111 of this issue. The researchers found that a rhythm in the phosphorylation state of the mitogen-activated protein kinase (MAPK) within a specific region of the SCN depended on external input from the eye. Therefore, at least in one case, the SCN may not be as in control as once believed.

The authors examined the SCN of hamsters with an antibody to the phosphorylated form of MAPK and found two rhythms: one located within the outer or shell region of the SCN, which peaked during the day, and another located within its core, which peaked during the night. The image shows phosphorylated MAPK expression (red) in the core partially overlapping with another SCN core marker, calbindin (green). In animals with both eyes removed, which leaves behavioral and physiological rhythms like locomotor activity and body temperature intact, the core pattern of phosphorylated MAPK was missing, whereas the shell pattern remained. Similar results were seen when both SCNs were removed and replaced by fetal SCN transplants, presumably because the transplants had not fully re-established afferent connections. Labeling the eye with an anterograde tracer revealed eye-specific terminals in close proximity to the core SCN cells that express phosphorylated MAPK, further supporting the hypothesis that these cells receive direct input from the eye. The loss in phosphorylated MAPK expression was also not a result of deafferentation-induced cell loss, because eye removal had no effect on cell density in the SCN core region. Now that it is apparent that at least one rhythm in the SCN depends on external input, the next step is to determine the functional significance of this eye-driven rhythm.

Brian Fiske

