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Dissociating Intensity from Valence as Sensory Inputs to Emotion

In this issue of *Neuron*, Small and colleagues used fMRI to find evidence for a neural segregation of two dimensions underlying human gustatory experience: intensity and valence. These results join several recent reports that challenge long-held notions regarding amygdaloid representation of negatively valenced events.

A salad of perfectly grilled woodsy-flavored calamari paired with subtly bitter pale green leaves of curly endive and succulent petals of tomato flesh in a deep, rich balsamic dressing. Delicate slices of pan-roasted duck breast saturated with an assertive, tart-sweet tamarind-infused marinade. A big, vibrant Pinot Noir with ripe, sun-dried cherry fruit and smoky, wood-spiced notes. Hungry? The above descriptions serve to illustrate how the subjective complexity and infinite variety of gustatory experience may rest upon only a few primary dimensions such as quality (e.g., sweet, bitter, sour), intensity (subtle or robust), and hedonic tone or valence (pleasant or unpleasant). Such a coarse coding scheme may be likened to the retinal decomposition into short, medium, and long wavelengths underlying the experience of color, but in fact, it deviates in a critical regard. Unlike vision, reward value appears to be a fundamental dimension of gustatory sensation, without need for higher-order stimulus associations. This characteristic may infuse chemosensory experience with an acute emotional primacy (Schiffman, 1974).

In humans' present ecological niche, many eat for pleasure. The origins of taste preference, however, are utilitarian, not esthetic. For example, sweetness is common to safely edible foods, whereas bitterness may signify poison or spoilage. Therefore, humans do not enter the world with a *tabula rasa* palate, as evidenced by aversive responses to bitter taste in neonates (Steiner et al., 2001). That said, food preference is also dynamic and follows a developmental course that is modulated by the powerful influence of culture (Rozin and Fallon, 1987). For example, although highly aversive to adults, for young children excrement is not excluded from the list of appropriate things to place in one's mouth (despite other neonatal taste aversions). Less appallingly, the appropriateness of foods for different times of day and restrictions for their complimentariness have a developmental time course as well. For instance, the idea of

ketchup-drizzled ice cream delicately perched on top of a succulently juicy hot dog may seem a quite sensible breakfast during childhood.

Recent work has significantly advanced understanding of neural building blocks underlying hedonics of chemosensory experience (Zald et al., 1998; Gottfried et al., 2002; Anderson et al., 2003; Small et al., 2003 [this issue of *Neuron*]). In this issue of *Neuron*, Small and colleagues used fMRI to examine the neural basis of why things taste good or bad and how the neural coding of these hedonic dimensions is related to the intensity of taste. Low and high concentrations of sucrose and quinine sulfate were administered such that the subjective intensity and hedonic quality could be examined independently. These two dimensions are normally strongly positively correlated in everyday life. For example, the bitterness of vinegar may be pleasing at low concentrations, but strongly aversive at high concentrations. Through careful manipulation, Small et al. found that the often-correlated dimensions of valence and intensity are supported by dissociable neural substrates. In particular, responses in the pons, mid-insular cortex, and the amygdala responded commensurately with the intensity of taste irrespective of its hedonic quality. In contrast, the anteroventral insular cortex and secondary taste areas in orbitofrontal cortex, *inter alia*, were responsive to hedonic value irrespective of intensity. Furthermore, the right caudolateral orbitofrontal cortex was more responsive to the pleasant experience of sucrose, and the anterior left orbitofrontal cortex and dorsal insular cortex were more responsive to the unpleasant experience of quinine.

The results of Small's study of taste bear remarkable similarity to our recent results in olfaction (Anderson et al., 2003). In a similar design, we found that the amygdala and adjacent primary olfactory cortex were driven by the intensity of odorants independent of their judged valence, and conversely, distinct right and left orbitofrontal regions responded to pleasant and unpleasant valence, independent of judged intensity. The striking convergence of these two studies provides firm ground for two notions regarding the neural representation of affective responses.

First, electrophysiological, lesion, and imaging studies have in the past pointed to an essential role of the amygdala in the processing of threatening, fearful, and highly aversive events (Aggleton, 2000). This view has been challenged by findings demonstrating amygdala involvement in processing positively valenced events (Cahill and McGaugh, 1990). Such indeterminacy of what characterizes amygdala responsiveness is likely related to the multidimensional nature of affective space. Intensity and valence are often asymmetrically correlated between valences. Viewing negative stimuli (e.g., a picture of a vicious dog) typically results in a more intense and arousing subjective and physiological response than viewing positive stimuli (e.g., a puppy). The Small study demonstrated that when this inequity in experiential intensity is eliminated, the amygdala responds robustly and equally both to events evoking positive and to events evoking negative hedonic experience. Such a pattern of response could reflect that the amygdala codes the intensity of experience irrespective of valence, or rather, that it codes variations in both pleasant

and unpleasant valence. Results from Small et al. (2003) and Anderson et al. (2003) were consistent with the former: when valence was held constant, the amygdala was vigorously responsive to manipulations of intensity, and when intensity was held constant, the amygdala was quiescent to manipulations of valence.

Second, despite strong phenomenal correlation, the above results suggest that there is a fundamental segregation in the neural representations of the intensity and valence of sensory experience. This finding is consistent with psychological theories of the underlying structure of emotion, which propose that unified affective experience is the result of activation along separate dimensions of experiential intensity (also referred to as arousal) and valence.

All that said, a word of caution is merited in that much of the evidence in support of this newly emerging view of amygdaloid encoding is the result of human imaging studies. All methods of measuring neural activity have particular strengths and weaknesses that predispose them to better measure particular patterns of neural activity, while they fail to discern others. For example, functional imaging (PET and fMRI) is a strong method for measuring activity in relatively large regions of brain simultaneously. This enables questions on whole-brain intact processing that are far beyond the scope of recording electrodes. By contrast, the temporal (seconds) and spatial (millimeters) resolution of functional imaging is poor in relation to many of the underlying processes of interest. For example, the amygdala may still be encoding sensory valence, but using a temporal rather than rate-encoding scheme. In other words, stimulus valence may be reflected in the temporal order of amygdaloid activity rather than in its overall activity rate. Such encoding is undetectable using current functional imaging methods. Furthermore, the spatial resolution of functional imaging may also prevent measuring amygdaloid valence coding with fMRI. Specifically, if a very small proportion of amygdaloid neurons encode for valence while the majority encode for intensity, this limited spatial representation may be obscured. Thus, for the newly emerging view of amygdaloid processing to take firm root, the studies of both Small et al. (2003) and Anderson et al. (2003) await replication with additional methods of measuring neural activity.

If hedonic quality is not encoded in the amygdala, where in the brain is this dimension encoded? Many studies point to the orbitofrontal cortices (OFC) (Zald et al., 1998). The results of Small et al. suggest that a constellation of discrete OFC and anterior insular cortical regions code for gustatory preferences. Consistent with this proposed extra-amygdala locus of hedonic tone, the underlying structure of positive and negative affectivity has been shown to remain intact following amygdala lesions (Anderson and Phelps, 2002) but to be damaged following stroke affecting prefrontal cortices and in particular the OFC (Davidson and Irwin, 1999). Such critical prefrontal contributions to hedonicity dovetail nicely with appraisal theories of human emotion that emphasize how affective responses are not simply a reflection of the intrinsic quality (positive versus negative) of a stimulus, but result from interactions among the person, the situational context, and the stimulus. For example, the smell and taste of rotting shark meat

is foul by American standards, but may be appetizing to a hungry Icelander, to whom fermented shark is a traditional culinary delicacy (hákarl). Even to an Icelander such appeal would diminish after having sated one's appetite. Such flexibility of hedonic response is the hallmark of OFC representations, which are modulated by changes in behavioral relevance, such as the hunger state of the perceiver (O'Doherty et al., 2000). This individual and situational variability in hedonic responsiveness is integral to any account of the neural representation of affectivity and reflects the malleability of human hedonic experience that is characteristic of the flexible and integrative functions often ascribed to the prefrontal cortices.

Small et al.'s findings also illuminate the proposed hedonic primacy of chemical sensation. The first stages of taste processing, from pontine taste relay nuclei to mid-insular primary taste cortex, were shown to be insensitive to the hedonic quality of taste input. Rather, these regions were modulated by the quantity and not the quality of stimulation. By contrast, adjacent secondary taste cortex in the OFC was modulated by the pleasant and unpleasant quality and not the amount of stimulation. This evidence suggests a hierarchical neural coding scheme, whereby early intensity coding is further elaborated into differentiable responses to pleasant and unpleasant taste. Compared to other sensory systems such as vision, the hedonic differentiation undertaken by the OFC occurs relatively early in the neural hierarchy. Although the OFC has been shown to critically participate in the anticipation and receipt of reward across a variety of sensory systems, in the case of gustatory and olfactory sensation, the OFC does double duty, also being the region where basic analysis of stimulus input occurs. This sharing of common neural resources may subject chemical senses to a degree of inseparability from hedonic response. Although not discriminated at the earliest stages of processing, hedonic quality may nevertheless be dominant in organizing the character of chemosensory perception, effectively coloring the brain's chemical interface with the world (Schiffman, 1974).

The neural evidence from gustatory and olfactory responses may have a lot to say about higher-order forms of emotional responsiveness. In humans, it has been argued that gustatory sensation is the origin of the basic emotion of disgust (literally meaning "bad taste"), and more abstractly, moral offensiveness (Rozin and Fallon, 1987). Such neural processing of taste not only serves as the basis for food rejection but may provide the neural substrates for such lofty emotional responses as repulsion toward acts against humanity. Evidence consistent with this neural elevation of more primitive distaste processing is shown in how identification of social signals of disgust depend upon the same anteroventral insular cortical region involved in hedonic valuation of taste (Phillips et al., 1997). The degree to which such primitive hedonic processing is integrated with cognition will be an important subject for future study.

Unraveling the neural substrates underlying human emotional competence will surely further reveal its dependence on an intricate balance of neural activity in regions representing different sensory dimensions. Elucidating these mechanisms may finally allow an appreci-

ation of various oddities of human nature, such as why a charcoal-grilled filet mignon just tastes so good with a full-bodied Australian Cabernet Sauvignon. Hungry yet?

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