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Medial Orbitofrontal Cortex: Its Role in Mediating Satiety in the Macaque

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Introduction

Taste serves three basic functions: (i) to mediate somatic and autonomic reflexes for the acceptance or rejection of potential foods; (ii) to perform a cognitive evaluation of the quality and intensity of gustatory stimuli; and (iii) to mediate hedonic responses to tastants based on the perceived desirability of consuming them at the moment.

In primates, direct and circumstantial evidence implies that the reflexive functions are mediated by brain stem nuclei, that the cognitive evaluation is performed in insular/opercular cortex, and that hedonics are managed in the ventral forebrain and orbitofrontal cortex. In this paper, we will focus on these last functions: the hedonic value of foods.

Edmund Rolls and his colleagues made the initial gustatory foray into the caudolateral orbitofrontal cortex (CLOFC) of macaques. They discovered a subset of neurons narrowly tuned for taste, with particular sensitivity for sweet stimuli. Anatomical tracings (Baylis *et al.*, 1995) suggested that the CLOFC received projections from the insula, and since the latter was the primary taste cortex, the CLOFC was dubbed secondary taste cortex. Whereas taste cells in the insula were unaffected by changes in the hedonic appeal of tastants as macques were fed to satiety (Yaxley *et al.*, 1988), those in the CLOFC treated hedonics as the most salient variable. The prevailing view during the intervening 15 years has been of an abrupt functional transition between the appraisal of stimulus quality, performed in the insula, and the assessment of hedonic value in the CLOFC.

Detailed anatomical studies by Carmichael and Price (1996) have since revealed that projections from the insula to the orbitofrontal cortex (OFC) are more complex and distributed than the canonical view would suggest. Primary taste cortex projects only sparsely to any division of the OFC, but rather to more ventral regions of the insula, from which axons are sent to multiple OFC targets.

Based on these results, we recorded from medial OFC in five macaques and have revealed an area more densely populated with taste cells than any other known in the macaque's forebrain. Moreover, these cells expressed properties intermediate between those of the insula and the CLOFC, implying a more gradual functional transition between assessments of quality and hedonics mediated by a multisynaptic pathway.

Taste in the medial orbitofrontal cortex (MOFC)

Within its 12 mm^2 core, 20% of MOFC neurons responded to gustatory stimuli, as did 10% of cells in the 1-mm-wide perimeter surrounding it—triple the density recorded from the insula or the CLOFC.

The mean spontaneous discharge rate of taste cells in MOFC was 3.1 ± 5.6 spikes/s, the same as in the insula (Scott and Plata-Salamán, 1999) and double that of the CLOFC (Rolls *et al.*, 1990). Excitation represented 96% of the evoked activity; inhibition, 4%.

The mean breadth-of-tuning coefficient, based on the proportion of responses to each of the four basic stimuli, was 0.79, similar to the value of 0.70 in the insula, but much broader than the 0.39 reported in the CLOFC.

There was no evidence that gustatory cells were clustered according to their sensitivities, i.e. there was no apparent relationship between a neuron's location and its function. This same conclusion was reached both in the insula and the CLOFC.

Among taste cells, 20% also responded to another modality: 10% to olfaction and 10% divided among touch, temperature and vision. Multimodality in the MOFC is slightly more common than in the insula, but only one-fifth of that reported in the CLOFC.

Satiety has little impact on taste cells in the insula (Yaxley *et al.*, 1988). Conversely, in the CLOFC, nearly every cell that responds to the satiety solution at the beginning of the experiment has been reduced to unreponsiveness at its end (Rolls *et al.*, 1989). We tested 14 MOFC neurons through a full satiety sequence. Six showed a decline in responsiveness as satiety was induced, but seven others did not, and one gave increased responses.

These results call for a reexamination of the canonical view that taste quality in the macaque is analyzed independently of a hedonic appraisal through the level of the primary taste cortex (insula), then imbued with hedonic tone in the secondary taste cortex (CLOFC). Rather, it would appear that there are one or more gustatory relays between these two areas, and that the functional progression from a cognitive to hedonic assessment may be incremental.

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