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Olfactory influences on appetite and satiety in humans.

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ABSTRACT

YEOMANS, M. R. *Olfactory influences on appetite and satiety in humans*. PHYSIOL BEHAV. 200X; 00(X): 000-000. Odor stimuli play a major role in perception of food flavor. Food-related odors have also been shown to increase rated appetite, and induce salivation and release of gastric acid and insulin. However, our ability to identify an odor as food-related, and our liking for food-related odors, are both learned responses. In conditioning studies, repeated experience of odors with sweet and sour tastes result in enhanced ratings of sensory quality of the paired taste for the odor on its own. More recent studies also report increased pleasantness ratings for odors paired with sucrose for participants who like sweet tastes, and conversely decreased liking and increased bitterness for quinine-paired odors. When odors were experienced in combination with sucrose when hungry, liking was not increased if tested sated, suggesting that expression of acquired liking for odors depends on current motivational state. Other studies report sensory-specific satiety is seen with food-related odors. Overall, these studies suggest that once an odor is experienced in a food-related context, that odor acquires the ability to modify both preparatory and satiety-related components of ingestion.

Our experience of flavor arises from integration of multiple sensory cues, including odor, taste, temperature, appearance, etc. [1-3]. Thus, flavor perception can be seen to be a higher-cortical function, a conclusion reinforced by recent studies using brain-imaging techniques [4]. However, while any generalization about the degree to which any one sense contributes to food flavor is to some extent meaningless, since foods engage unique combinations of the key sensory systems, it is generally recognized that olfactory stimuli contribute a significant proportion of the experience of flavors for the majority of foods. Thus the sensory and hedonic evaluations of most food-related flavors are dependent on olfactory perception, as evidenced by the large distortions in flavor perception seen in patients with anosmia [5]. However, whereas there is compelling evidence for innate preferences for sweet tastes and aversions to bitter tastes [6], there is no evidence of any innate preference or aversion for any food-related odors. Given the importance of odor in determination of food flavor, this may seem surprising. However, whereas taste perception is based on a limited range of classes of chemical which each bind onto single receptors, humans can recognize an estimated 10000 odors, and over 900 genes encode the structure of olfactory receptors [7]. Odor molecules bind to multiple receptors, thereby generating complex sensory signals. While there is still uncertainty about how the brain converts these signals into our experience of odors, the most widely cited models suggest that it is the pattern of receptors stimulated by each odor which allows the brain to discriminate different odor molecules. Evolution could favor the development of specific innate taste preferences since bitter tastes frequently relate to poisons, and thus an individual with superior bitter taste perception will have a survival advantage, while a more acute sweet preference could help direct an individual to a reliable and safe source of energy. However, because odor perception is based on a complex relationship between molecules and olfactory receptors, the opportunity for evolution to favor specific patterns of receptor relating to specific odor molecules is limited. Thus the apparent lack of innate preferences for food-related odors may be a direct consequence of the complexity of the system underlying odor perception. An alternative way of looking at this would be to suggest that the evolutionary benefit of having a flexible olfactory system which can detect a very wide range of odors outweighs the disadvantages of not being able to classify certain odor classes as safe or dangerous.

Since odors are critical to our experience of food flavor, and there is no evidence for any innate odor preferences, most of our food preferences must be acquired by learning [8, 9]. However, until recently the role of learning in food-related olfactory-perception in humans had received scant attention. The two most influential learning models of flavor-preference development are based on associations between either food flavor and the consequences of ingestion (flavor-consequence learning: e.g. the association of a flavor and energy) or associations between new flavors and existing liked or disliked flavors (flavor-flavor learning: e.g. liking developed by associating the flavor of coffee with sweetness). Both types of learning would be predicted to later how we classify and respond to food-related odors.

As well as being critical to flavor perception, food-related odors impact on appetite. For example, food odors which were rated as pleasant, which must have been an acquired response, acquire the ability to stimulate appetite, as evidenced by increased ratings of hunger following exposure to food-related odors [10]. Food-related odors reliably stimulate salivation [10-14], and recent data from our laboratory suggest that food-related odors such as odors from bacon can stimulate salivation even when presented at concentrations below those needed to be able to identify the odor (unpublished data). Studies also confirm the ability of food-related odors to stimulate other cephalic phase responses such as insulin release [15, 16] and gastric acid secretion [17]. Furthermore, a recent study using an ingenious method to explore the importance of pre-oral cues on ingestion of custard [18], where there was a discrepancy between the orthonasal odor and actual food flavor experienced while eating, found that orthonasal odor was the best predictor of how much was ingested when the product was first sampled. In this study, the custard was served in a specially designed cup with two compartments, the upper compartment containing the version that the consumer could sense but did not consume and a lower compartment containing the version to be consumed. The versions in the two compartments were either the same, or different. The finding that odor predicted intake better than the flavor of the ingested custard shows that orthonasal odor perception can have a major impact on short-term intake. Thus once we have acquired a preference or aversion for a food-related odor, that odor is able to influence both the expression of appetite and cephalic phase responses in preparation for food consumption. Thus food-related odor acts as one of the complex environmental influences on appetite [19], and may be a factor in short-term over-eating.

The worldwide increase in incidence of obesity is often attributed to the increased availability of highly palatable energy-dense foods [20-24]. However, since olfactory perception represents an important component of flavor perception, the palatability of the food we consume (defined as the hedonic evaluation of food flavor: [25]) must in turn be heavily influenced by olfactory perception during ingestion. Thus, understanding the role of olfactory perception in appetite is an important component of our broader understanding of the effects of food-related hedonic influences, and so will contribute to our broader understanding of how sensory qualities of foods may lead to over-consumption.

Critical to our understanding of the importance of food-related olfactory-perception to the control of appetite is an understanding of how we acquire odor preferences, yet until recently few studies had explored learning based on food-related odors, concentrating instead on stimuli which combined odor and taste elements. Ground-breaking work by Stevenson and colleagues [26-28] established a model for exploring olfactory-based learning in humans by examining how repeated pairing of novel food odors with sweet and sour tastes altered the subsequent experience of the odor presented alone. The surprising finding from these studies was that odors trained in this way acquired the sensory qualities of the paired tastant: odors experienced retronasally in combination with sucrose were experienced as smelling sweeter when tested in a subsequent orthonasal test [26-28], while odors paired with citric acid were rated as smelling more sour [26, 27]. However, despite strong evidence of sensory changes, hedonic evaluations of the paired odors did not change significantly in any of these studies. This is particularly surprising with sweet tastes, since there is strong evidence for an innate sweet-taste preference in humans [6]. The repeated pairing of a novel odor stimulus (acting as conditioned stimulus: CS) with a hedonically-significant taste (unconditioned stimulus: UCS) should have resulted in a change in hedonic evaluation of the CS evaluative conditioning [29]. However, liking for sweet tastes in adults is quite variable [30, 31], and since no evaluation of liking for the trained sweet stimulus was made in the studies of human olfactory conditioning [26-28], it was unclear whether participants in these studies truly liked sweet tastes. Other studies of evaluative changes in humans using sweet tastes have also generally failed to find enhanced liking for flavors paired with sweet tastes ([32] but see [33]). Subsequent studies of olfactory conditioning with sweet taste UCS which either assessed liking for the sweet taste during training, or which pre-selected participants as sweet-likers, has since confirmed that liking for sweet-paired odors can increase (Figure 1), but that this change only occurs in participants who rated the trained sweet taste UCS as pleasant at the time of testing [34]. These recent studies also confirmed that retronasal pairing of an odor CS with sucrose UCS enhanced the subsequent experience of sweetness for the odor alone, and extended that finding to acquired odor-bitterness for odors paired with a quinine UCS. Thus, the olfactory conditioning paradigm affords a robust laboratory model through which acquired sensory and hedonic characteristics of food-paired odors can be evaluated further.

A critical question in understanding the role of sensory hedonics in control of appetite is the extent to which expression of liking for food flavors is modulated by the current appetitive state of the consumer. According to the classic concept of negative gustatory alliesthesia, liking for sweet tastes is a reflection of current energetic needs: when hungry, sweet tastes are strongly liked but this liking decreases markedly once the consumer is sated [35]. Hedonic evaluation could thus be seen to have evolved as an effective means of directing attention to stimuli which can help meet current nutritional requirements. Attractive though this idea is, the clearest examples of alliesthesic-like responses in the literature relate to evaluation of sweet tastes, where liking reflects an innate preference. For alliesthesia to be relevant to food preferences in general, there would need to be a clear demonstration that acquired liking is equally sensitive to current motivational state. There is some evidence to support this suggestion: when children acquired a preference for a novel yogurt flavor which had been paired with a high energy (fat) intake relative to a second flavor paired with low-fat yoghurt, the subsequent increase in preference for the high-fat relative to low-fat paired flavor was stronger when tested hungry then when tested sated [36]. Likewise, expression of an acquired preference for a protein-paired flavor was stronger when tested at lunch after a low-protein breakfast than when tested following a high protein breakfast [37]. Both these studies provide evidence that acquired food preferences show acute sensitivity to current appetitive needs. However, in both cases the conditioned flavors were complex, and so whether learning occurred for the integrated flavor CS or occurred for components of the trained flavor, such as the component of flavor generated by odor perception, is unclear. Both studies also examined flavor preferences based on associations of flavors with post-ingestive consequences. However, not all flavor preferences are acquired in this way. The olfactory preferences described earlier [34] were based on associations of odors and tastes, which can be interpreted within the broader concept of flavor-flavor learning. In this form of learning, hedonic change is by transfer of liking or disliking for a known flavor or flavor element to the second, novel flavor. In humans, this form of learning is seen most readily where novel flavors are paired with disliked flavors such as the aversive taste of tween [32, 38]. Until recently, no study of flavor-flavor learning in humans had examined sensitivity to current appetitive state since no study had been able to reliably establish a robust acquired flavor preference. However, the recent finding that pairing novel odors with sweet tastes can generate acquired odor preferences [34] offered an opportunity to explore how acquired odor preferences relate to current hunger state .

To test sensitivity of acquired liking for a sucrose-paired odor to current hunger state, hungry volunteers who rated 10% sucrose as a pleasant taste evaluated the sweetness, bitterness and pleasantness of three novel odors before and after a series of exposure trials where odors were paired with either 10% sucrose, 0.001% quinine or water [39]. To manipulate need state post-exposure, they consumed 200ml of either water (control), a low-energy (60kCal) tomato soup or the same soup with added maltodextrin (360kcal). The extra energy in the maltodextrin-enriched soup preload had previously been shown to reduce subsequent rated appetite and food intake relative to the low-energy soup [40]. In the sucrose condition, the rated sweetness of the sucrose-paired odor had increased, and this increase was unaffected by the energy manipulation (Figure 2a). Likewise, the bitterness of the quinine-paired odor increased in all three conditions (Figure 2c). However, the rated pleasantness of the sucrose-paired odor increased in the control and low-energy preload conditions, but not following the maltodextrin-enriched preload (Figure 2c). The same dependence on motivational state was not seen for the acquired dislike of an odor by association with bitterness (Figure 2d). These findings imply that liking acquired by association between an odor and sweetness when trained in a hungry state was not expressed when tested in a sated state, consistent with the idea that the short-term expression of flavor-liking is a reflection of underlying physiological needs [35].

Sensory-specific satiety refers to the differential reduction in pleasantness of a consumed food relative to other foods [41], and this hedonic change may contribute to the normal decision to end eating. Sensory-specific satiety has been shown to occur not only for the flavor of food, but also for orthonasally-presented odors which contribute to the flavor of the consumed food [42]. Olfactory sensory-specific satiety has been shown to relate to activation of the orbitofrontal cortex in humans [43], based on the observation that activation of the orbitofrontal area by banana odor was greatly reduced after consumption of banana to satiety. Thus olfactory cues may play an important part in satiation as well as in initial appetite stimulation.

Overall, odors clearly play an important role in flavor perception, but the experienced quality of food-related odors can be affected by associated taste sensations. There is also increasing understanding of the neural basis of this odor-taste integration [4]. While odors only form a component of food flavor, liking for odors acquired by learning while experienced as flavor components generalizes to the odor on its own, so allowing the odor to develop the ability to modulate short-term appetite and prepare the body for the ingestion of food. Further research is needed to further clarify the neural basis of the acquired sensory and hedonic characteristics of odors in relation to flavor, to determine the extent to which appetite-stimulation by odor molecules before and during a meal might contribute to over-consumption and to assess whether differential sensitivity to odor-based learning might contribute to individual differences in susceptibility to sensory-stimulation of appetite.

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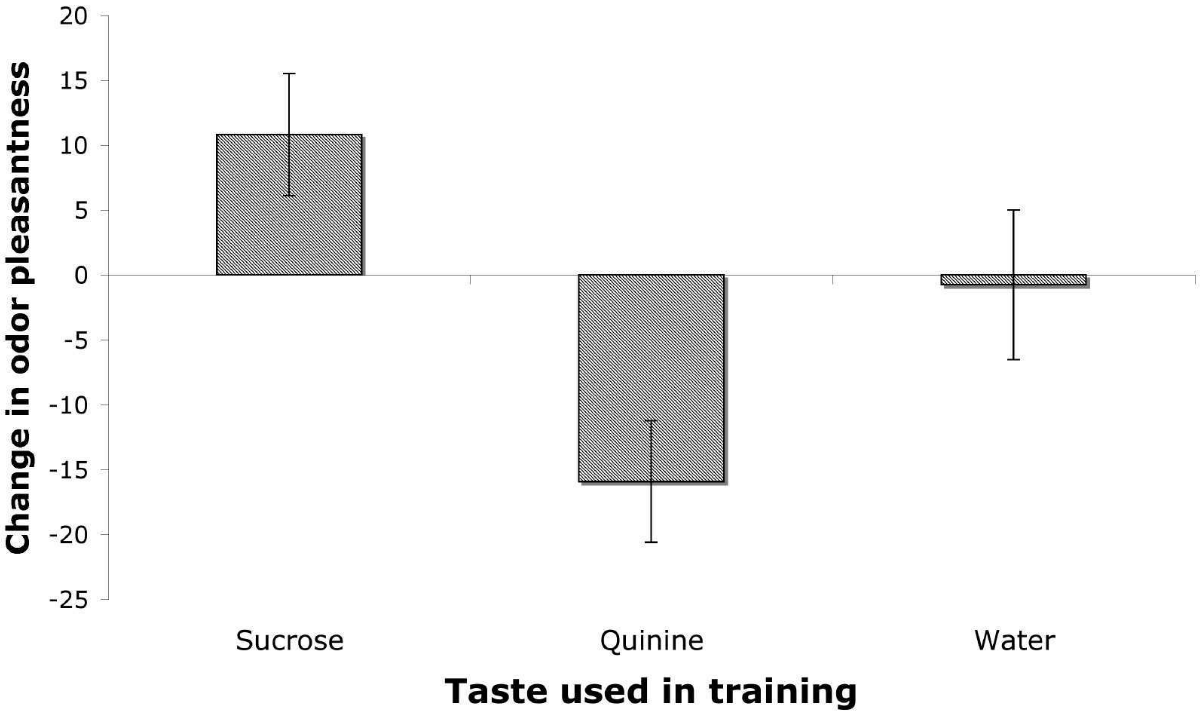
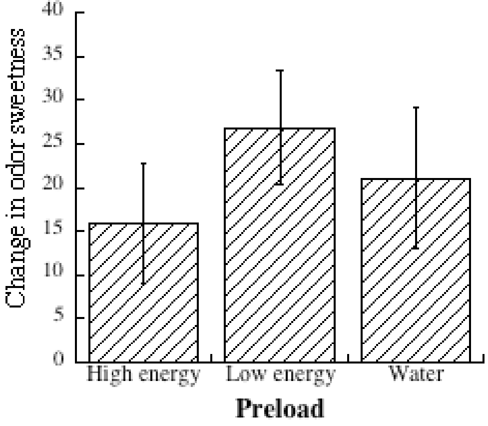
Figure legends

Figure 1. Acquired liking for odors evaluated orthonasally following repeated retronasal experience of these odors paired with either 10% sucrose, 0.01% quinine hydrochloride or water. Adapted from [34].

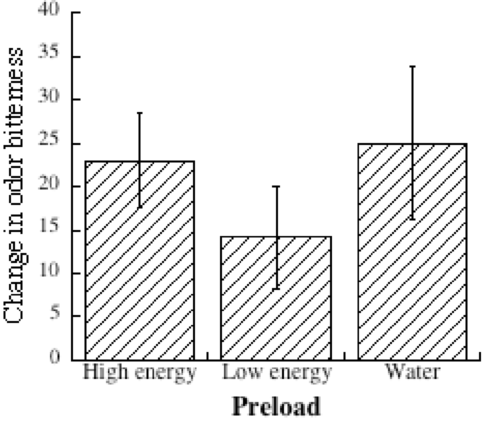
Figure 2. The effects of high and low energy soup or water preloads on expression of acquired sensory and hedonic orthonasal evaluations of odors following repeated retronasal experience of the same odors paired with either 10% sucrose, 0.01% quinine hydrochloride or water. (a) sweetness of the sucrose-paired odors (b) bitterness of the quinine-paired odor (c) pleasantness of the sucrose-paired odor and (d) pleasantness of the quinine-paired odor. Adapted from [39].


Change in odor pleasantness
20
15
10
5
0
-5
-10
-15
-20
-25
Sucrose
Quinine
Water
Taste used in training

(a)


Change in odor sweetness
40
35
30
25
20
15
10
5
0
High energy
Low energy
Water
Preload

(b)


Change in odor bitterness
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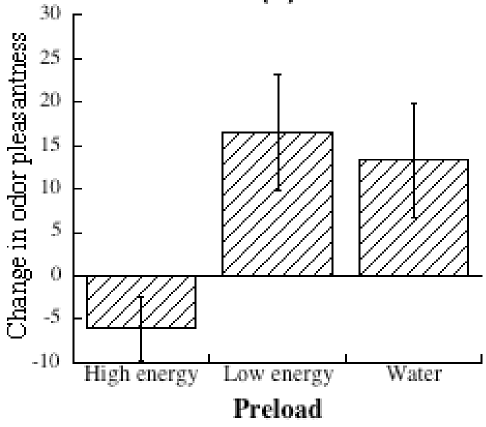
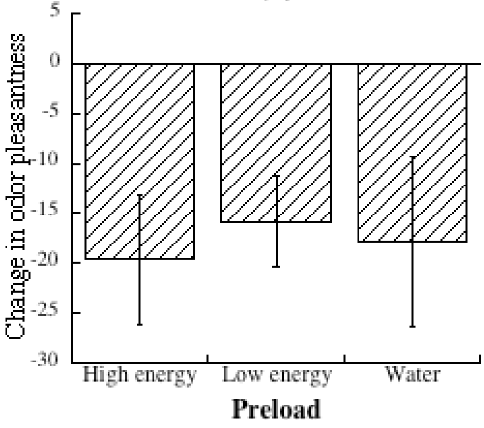
35
30
25
20
15
10
5
0
High energy
Low energy
Water
Preload

(c)


Change in odor pleasantness
30
25
20
15
10
5
0
-5
-10
High energy
Low energy
Water
Preload

(d)


Change in odor pleasantness
5
0
-5
-10
-15
-20
-25
-30
High energy
Low energy
Water
Preload