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Supertaster, super reactive: Oral sensitivity for bitter taste modulates emotional approach and avoidance behavior in the affective startle paradigm

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HIGHLIGHTS

- People differ in both their sensitivity for bitter taste and emotional responding.
- We investigated the relationship between these sensitivities.
- PROP-sensitive or insensitive individuals took part in an affective picture paradigm.
- PROP-tasters and PROP-insensitive subjects differed in startle reflex modulation.
- Therefore, bitter sensitivity and approach/avoidance behavior are related.

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ABSTRACT

People differ in both their sensitivity for bitter taste and their tendency to respond to emotional stimuli with approach or avoidance. The present study investigated the relationship between these sensitivities in an affective picture paradigm with startle responding. Emotion-induced changes in arousal and attention (pupil modulation), priming of approach and avoidance behavior (startle reflex modulation), and subjective evaluations (ratings) were examined. Sensitivity for bitter taste was assessed with the 6-n-propylthiouracil (PROP)-sensitivity test, which discriminated individuals who were highly sensitive to PROP compared to NaCl (PROP-tasters) and those who were less sensitive or insensitive to the bitter taste of PROP. Neither pupil responses nor picture ratings differed between the two taster groups. The startle eye blink response, however, significantly differentiated PROP-tasters from PROP-insensitive subjects. Facilitated response priming to emotional stimuli emerged in PROP-tasters but not in PROP-insensitive subjects at shorter startle lead intervals (200–300 ms between picture onset and startle stimulus onset). At longer lead intervals (3–4.5 s between picture onset and startle stimulus onset) affective startle modulation did not differ between the two taster groups. This implies that in PROP-sensitive individuals action tendencies of approach or avoidance are primed immediately after emotional stimulus exposure. These results suggest a link between PROP taste perception and biologically relevant patterns of emotional responding. Direct perception–action links have been proposed to underlie motivational priming effects of the startle reflex, and the present results extend these to the sensory dimension of taste.

1. Introduction

Sensitivity for bitter taste differs inter-individually. Phenotypically, individuals can be classified on a dimension from subjectively tasting "nothing at all" (nontasters) to reporting tasting "unpleasantly bitter" ("supertasters") while having the same concentration of a bitter chemical called PROP (6-n-propylthiouracil) in their mouth. Since the seminal findings of Blakeslee and Fox [1,2], the distribution of PTC (phenylthiocarbamide) and PROP tasting has been extensively analyzed. This phenotypical variation has led to the classification of supertasters, mediumtasters, and nontasters [1]. Due to the toxicity of PTC, the safer chemical PROP is now used in experimental research with humans to determine bitter taster status. When tested behaviorally, PROP-tasters evaluate the bitter compound PROP relative to

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probes of salt (NaCl) as more intense, whereas PROP-insensitive individuals are unable to appropriately discriminate PROP from NaCl in lower concentrations (mediumtasters) or even rate PROP solutions lower in concentration compared to solutions of NaCl (nontasters) [3,4].

There is evidence for a genetic influence on the sensitivity to taste PROP [2]. Research on the heritability of this sensitivity suggests that PROP sensitivity follows an incompletely dominant pattern [5], with three phenotypes: PROP-tasters are believed to have two dominant alleles, and perceive PROP the most. PROP-nontasters are believed to have two recessive alleles, while mediumtasters are believed to have one dominant and one recessive allele. Mediumtasters can perceive high concentrations of PROP, but do not perceive PROP at lower concentrations, as PROP-tasters do [1]. More recently, multiple genes, or multiple alleles of a single gene, have been identified to regulate taste and bitter sensitivity. Regarding PROP, the genetic determinants of this variation in bitter sensitivity are alleles of the human TAS2R38 gene [6,7]. To date, more than 25 different genes have been identified as being involved in bitter taste perception, but PROP sensitivity and the TAS2R38 gene and its receptors have been studied most frequently, although other genes have also been identified to play a role in the PROP taster phenotype [8].

Sensitivity for PROP has been related to eating behaviors, preferences for particular foods, and body weight: PROP-tasters avoid food and beverages with a strong bitter component, such as broccoli, kohlrabi, turnips, and alcohol [9–11]. Further research has revealed that PROP-tasters also dislike high caloric, fatty dishes [10–13]. However, the data on food preferences and fat intake vary across studies, with no clear association between taster status and food preferences or body weight. There are studies showing no association [14,15] or even the opposite association, that PROP-tasters do eat more fat [16] or have higher body fat [17]. Environmental factors may reduce or strengthen the influence of PROP on eating behavior across life stages [18].

It has been hypothesized that sensitivity for bitter taste could protect individuals from ingestion of potentially poisonous substances which threaten survival [19–21]. Hence, it is likely that PROP sensitivity is not related to food intake per se, but to inter-individual differences in defensive and emotional reactivity. Akin to other sensory signals, taste signals are projected via afferent nerve fibers to several brain regions, including the insula, which play a critical role in neurovisceral integration and the experience of emotions such as disgust [22–24].

Early evidence for a relationship between sensitivity for bitter taste and emotional reactivity came from animal research [25–27]. Rats selectively bred for being highly sensitive to bitter taste show elevated acoustic startle reflexes and stress-induced analgesia in the open-field test [26]. Startle reflex potentiation and stress-induced analgesia are protective responses that are typically elicited when confronted with intense fear-, threat-, or pain-inducing stimuli.

In humans, several studies have reported sensitivity towards bitter taste to vary with self-reported negative affect, depression, or anxiety, either positively [28–30] or negatively [31,32]. The relationship between mood, psychiatric disorders, and taste could be mediated by changes in neurotransmitter systems (serotonin and noradrenaline) influencing taste perception [33].

Macht and Mueller [34] screened 108 healthy individuals for PROP taster status and induced different mood states experimentally by using emotional film clips. The films induced predominately anger and tension, or sadness and depressed mood. Valence ratings were obtained before and after film viewing. PROP-tasters reported more intense emotions – increased anger, tension, and fear in particular – than individuals who were classified as PROP-insensitive (PROP-nontasters and PROP-mediumtasters). This relationship was observed for the anger inducing film clips while no differences between taster groups were found for the sad movies.

The results of Macht and Mueller [34] suggest a relationship between PROP sensitivity and emotional reactivity beyond clinical disorders. As reported by Dess and Minor [26] in rats, the enhanced emotional reactivity in the PROP-taster group appeared to be specific for negative emotions that trigger action tendencies of fight or flight, defense, and avoidance. However, in contrast to the observations in animals, the findings by Macht and Mueller [34] point towards taster-dependent differences in subjective evaluations of emotions, which are not necessarily driven by or accompanied by changes in bodily emotional responses. Similarly, taster-specific differences in negative emotions other than anger, such as fear and disgust, might exist but have not yet been investigated thoroughly. Although anger is considered a negative emotion, the motivational direction engendered by anger-eliciting stimuli could be either approach or avoidance [35]. Fear, on the contrary, has consistently been linked with defense and avoidance responses. This is also true for the emotion of disgust, which promotes avoidance and withdrawal from stimuli that could be contaminating and potential carriers of diseases, such as rotten food, death, or body products (e.g. excrements, including those from sexual practices), and violations of the outer body envelope [36]. Given that disgust originates from a food rejection impulse, typically bitter substances [37,38], one might expect a very close relationship between sensitivity towards bitter taste and individual responses to disgust.

In the present study, startle modulation, pupil responses, and subjective evaluations were measured during an emotional picture viewing paradigm to determine whether PROP-sensitivity is associated with differences in emotional reactivity for the emotional categories of fear, anger, disgust, and pleasure across different levels of emotional responding. Compared to the previous studies outlined above a multi-method approach like the present one could hold a number of advantages. Examining startle modulation during emotional picture viewing shows whether action tendencies of approach or avoidance are more readily and more intensely primed in PROP-sensitive individuals compared to individuals who are less sensitive to PROP (PROP-mediumtasters and PROP-nontasters).

Modulation of startle eye blink response amplitude has proven to reliably indicate the amount of motivational engagement during picture viewing [39]. Startle modulation has been found when exposed to in vivo foods [40,41], and while viewing food pictures [42–44] or disgusting scenes [45,46]. Moreover, converging evidence suggests that startle modulation is driven by the hedonic valence of the foreground stimuli: startle amplitude is potentiated for unpleasant stimuli in relation to pleasant or neutral stimuli and inhibited during presentation of emotionally positive stimuli (sexually arousing stimuli in particular). These response patterns are thought to be modulated by phylogenetically old motivational brain systems [39], which regulate approach and avoidance behavior across species and situations. In humans, affective startle modulation has been replicated many times by research probing startle modulation during emotional picture viewing, predominantly when the startle stimulus was presented at long lead intervals (several seconds from picture onset to startle stimulus onset: for an overview see [47,48]). Regarding affective modulation at shorter lead intervals (startle stimulus presentation in the first second after picture onset) most studies have demonstrated reflex attenuation for both positive and negative picture contents relative to neutral pictures, indicating inhibition of response priming by affectively engaging and attention capturing foregrounds prior to preparation for approach or avoidance. However, there is some evidence that response priming can occur at shorter lead intervals as well [49], particularly in highly emotionally sensitive individuals [50,51]. Investigating startle reflex modulation across lead intervals and simultaneously measuring modulation of the pupil response could help determine the extent to which startle modulation at short lead intervals is driven by the hedonic valence of the stimuli, by arousal, or by attention.