$$\Delta\bar{z} = \frac{\Sigma_{i=1}^{k} a_i M_{i+1}}{a_0 + \Sigma_{i=2}^{k} a_i M_i} \tag{10a}$$

$$\Delta M_2 = \frac{\Sigma_{i=1}^{k} a_i (M_{i+2} - M_i M_2)}{a_0 + \Sigma_{i=2}^{k} a_i M_i} - (\Delta\bar{z})^2 \tag{10b}$$

(compare refs 19–21). These equations are exact. If trait z is additive and linkage disequilibrium can be neglected, segregation and recombination will not change $\bar{z}$ and M_2. Thus, equations (10) will give the changes in $\bar{z}$ and M_2 between two subsequent generations. For traits with sex-limited expression (such as those considered here) the changes in $\bar{z}$ and M_2 between two subsequent generations will be equal to one-half of the values predicted by equations (10). The fitness functions for male and female traits defined in the main body of the paper belong to a class of polynomial fitness functions (9) with $k = 4$ and $k = 2$, respectively. Resulting equations for the means are given in the main body of the paper whereas the per generation changes in genetic variances are

$$\Delta V_x = 2\alpha V_x^2 \frac{s}{\theta}\left[1 - 3\frac{\alpha(\bar{y} - \bar{x})^2}{\theta}\right] + \mu_x \tag{11a}$$

$$\Delta V_y = -\alpha V_y^2 + \mu_y \tag{11b}$$

where μ_x and μ_y are genetic variances introduced by mutation. To derive these equations (see Supplementary Information for details) one identifies coefficients a_i of the polynomial expansion (9), then plugs them into equations (10), and simplifies the resulting expressions by assuming that $\alpha \ll \theta$, $s \ll 1$, and allowing the term $\alpha(\bar{x} - \bar{y})^2$ to have the same order of magnitude as θ and s. In addition, to derive the equations for changes in the means, I neglected the third moments; and to derive the equations for the variances, I neglected the third moments and assumed that $M_4 - 3M_2^2 = 0$ (zero kurtosis). Numerical results for a case of stabilizing selection with moving optimum[30] suggest that this is a satisfactory approximation. The dynamic equations (3) and (11) can be analysed by standard methods.

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Supplementary information is available on *Nature*'s World-Wide Web Site (http://www.nature.com) or as paper copy from the London editorial offices of *Nature*.

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Thermal stimulation of taste

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The first electrophysiological recordings from animal[1] and human[2] taste nerves gave clear evidence of thermal sensitivity, and studies have shown that as many as half of the neurons in mammalian taste pathways respond to temperature[3–6]. Because temperature has never been shown to induce sensations of taste, it has been assumed that thermal stimulation in the gustatory system is somehow nulled[6]. Here we show that heating or cooling small areas of the tongue can in fact cause sensations of taste: warming the anterior edge of the tongue (chorda tympani nerve) from a cold temperature can evoke sweetness, whereas cooling can evoke sourness and/or saltiness. Thermal taste also occurs on the rear of the tongue (glossopharyngeal nerve), but the relationship between temperature and taste is different there than on the front of the tongue. These observations indicate the human gustatory system contains several different types of thermally sensitive neurons that normally contribute to the sensory code for taste.

Research into thermal effects on taste has focused on modulation of sensitivity to the flavours of chemicals (see, for example, refs 7–9) rather than on the possibility that temperature itself might stimulate taste. Our attention was drawn to this possibility during preliminary experiments on the thermal sensitivity of the tongue. We noticed that warming the tongue tip from 20 to 35 °C caused a transient sensation of sweetness, and that cooling it to ⩽20 °C induced a sour taste that for one of us turned to saltiness at temperatures below 10 °C. A screening test for thermal taste conducted on 24 naive subjects yielded 21 individuals who reported at least one taste quality and 19 (5 males and 14 females) who reliably reported two or more tastes at one or more sites along the anterior edge of the tongue. Tastes were generally described as weak but expressions of surprise at their clarity and strength were not uncommon. The subjects who reported two or more taste qualities were enrolled in a study of the psychophysical properties of thermal taste.

We began by exploring the relationship between temperature and taste quality. Figure 1a shows that warming the tongue tip from 20 °C induced sweetness but not other significant tastes in 16 subjects (repeated measures analysis of variance (ANOVA) (temperature × taste quality × replicate), main effect of quality; $F(3, 45) = 40.18$, $P < 0.05$). Sweetness intensified between tem-

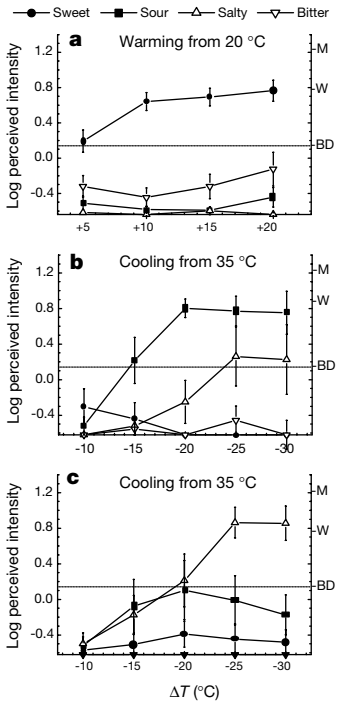

Figure 1 The perceived intensity of taste sensations reported during thermal stimulation of the midline of the tongue tip. The log of the mean perceived intensity is plotted against ΔT, the temperature change. On warming trials (**a**) temperature was increased from 20 °C; on cooling trials (**b**, **c**) temperature was decreased from 35 °C. Each graph contains the data from those subjects (**a**, $n = 16$; **b**, $n = 6$; **c**, $n = 6$) whose average rating of the dominant taste quality (sweetness, sourness, saltiness) exceeded 'barely detectable' on the labelled magnitude scale[16] (LMS). Letters along the right *y*-axis on these and subsequent graphs denote intensity descriptors on the LMS: BD, barely detectable (horizontal dotted line); W, weak; M, moderate. Vertical bars indicate standard errors of the means (s.e.m.s).

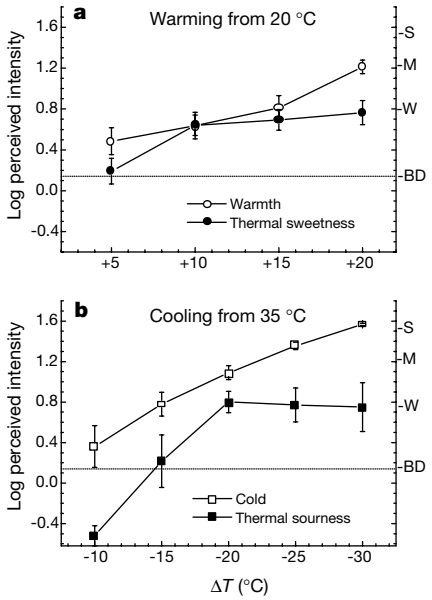

Figure 2 Temperature and thermal taste ratings as a function of temperature change at the tongue tip. **a**, During warming; **b**, During cooling. The thermal taste data are from Fig. 1a and b; the temperature data are from the same subjects.

perature changes (ΔTs) of +5 and +10 °C (temperature × taste quality interaction, $F(9, 135) = 4.96$, $P < 0.05$; Tukey HSD test, $P < 0.05$), but further warming had little additional effect. Figure 1b shows that cooling the tongue tip by 15 to 20 °C evoked sourness in 6 subjects (main effect of quality, $F(12, 60) = 4.61$, $P < 0.05$) which did not intensify with further cooling. Another 6 subjects (Fig. 1c), 3 of whom had reported sourness at ΔTs of −15 and −20 °C, rated saltiness as the dominant quality at colder temperatures (main effect of quality, $F(3, 15) = 6.31$, $P < 0.05$; interaction between temperature and quality, $F(12, 60) = 6.24$, $P < 0.05$). In contrast to thermal taste, perceived warmth and cold both continued to intensify as ΔT increased (Fig. 2).

Next we studied the sites on the edge of the tongue where the two tastes most frequently reported during the screening test, thermal sweetness (T_{SW}) and sourness (T_{SO}), were maximal. 'Best sites' for both taste qualities identified from the screening data indicated the locations of peak sensitivity to T_{SW} and T_{SO} did not coincide: the best sites for thermal sweetness ('sweet-best sites') were always near the tongue tip, whereas all but one of the 'sour-best sites' were lateral to the tip. Indeed, when testing was not restricted to the tongue tip, the number of subjects who reliably reported sourness rose from 6 to 15. Systematic measurements on sweet-best and sour-best sites showed that warming from 20 to 35 °C failed to stimulate significant T_{SW} on sour-best sites (Fig. 3a, left), and cooling from 35 to 15 °C evoked only barely detectable T_{SO} on sweet-best sites (Fig. 3b, left). Cooling to 5 °C tended to evoke T_{SO} on sour-best sites and thermal saltiness (T_{SA}) on sweet-best sites, but this difference was not significant (Fig. 3c, left). Ratings of warmth and cold revealed no difference in responsiveness to cooling between sweet- and sour-best sites, but warmth was rated significantly more intense on sweet-best sites (*t*-test for dependent samples $t_{18} = 3.15$, $P < 0.01$).

The same sites were tested with chemical stimuli to study the

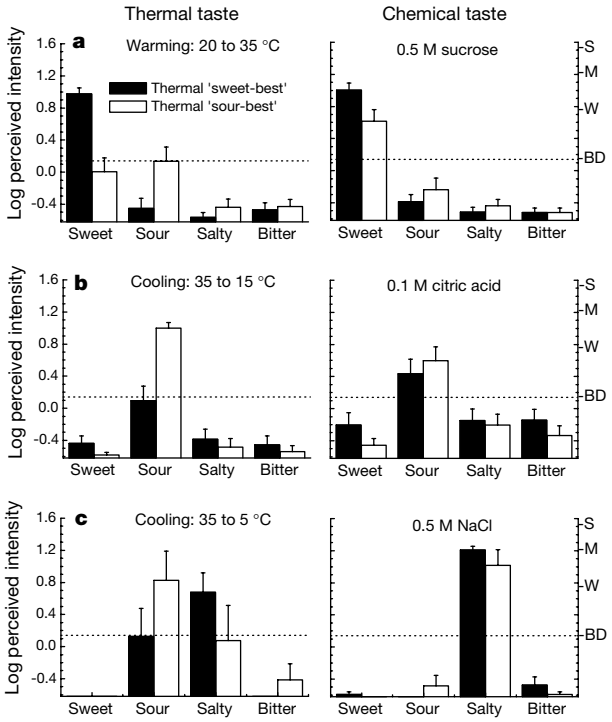

Figure 3 Perceived intensity of thermal taste (left column) and chemical taste (right column) on different sites on the tongue. Data are shown for the 'best' sites for thermal sweetness (filled bars) and thermal sourness (open bars). The data shown are again from those subjects who reported greater than 'barely detectable' sweetness (**a**, $n = 18$), sourness (**b**, $n = 15$) or saltiness (**c**, $n = 5$) during warming (20 to 35 °C), moderate cooling (35 to 15 °C), or extreme cooling (35 to 5 °C), respectively.

relationship between thermal and chemical taste. The graphs on the right side of Fig. 3 show that whereas sweet- and sour-best sites were both sensitive to sucrose, citric acid and NaCl, sweet-best sites (Fig. 3a, right) yielded higher sweetness ratings for sucrose than did sour-best sites ($t_{18} = 2.84, P < 0.02$). Tendencies for citric acid to be rated more sour on sour-best sites and NaCl to be rated saltier on sweet-best sites did not reach significance. Bitterness (quinine hydrochloride (QHCL); not shown) was perceived equally on both sites. While these results point to a spatial relationship between thermally and chemically induced sweetness, they also indicate that sensitivity to thermal taste is not distributed as uniformly as sensitivity to chemical taste.

The finding that sweet-best sites yielded higher warmth ratings than sour-best sites prompted a more detailed survey of the association between thermal taste and thermal sensitivity along the anterior edge of the tongue. Stepwise spatial testing confirmed that T_{SW} was strongest near the tip of the tongue (repeated measures ANOVA, main effect of stimulus location, $F(6, 78) = 38.1$, $P < 0.05$) and was closely associated with perception of warmth (Fig. 4a). In contrast, T_{SO} was no stronger on the tongue tip than it was more laterally (Fig. 4b), and a significant stimulus × location interaction ($F(6, 72) = 2.47$, $P < 0.05$) confirmed that its spatial pattern differed from cold. Although in Fig. 4 T_{SW} appears stronger on average than T_{SO}, five of the 13 subjects who reported sourness rated it above 'moderate' on one or more test sites. The lower T_{SO} ratings were therefore caused in part by greater variation in the location of sour-best sites compared to sweetness-best sites.

The striking spatial coincidence of warmth and T_{SW} implies that C-warm fibre receptors are among the trigeminal nerve fibres that terminate in fungiform papillae[10], and raises the question whether certain types of trigeminal and chorda tympani neurons may become spatially associated during development and innervation of these papillae[11].

We also studied thermal taste on circumvallate papillae, which are innervated by the glossopharyngeal nerve. Twelve subjects from the first experiment who could place the temperature stimulator on the back of the tongue without gagging were screened using the same thermal conditions as on the front of the tongue. Ten of these subjects reported thermal taste, but systematic tests showed that its characteristics were different than in the fungiform region: warming (Fig. 5a) failed to produce even barely detectable sweetness whereas cooling (Fig. 5b and c) elicited thermal bitterness (T_{BI}) as well as T_{SO} (but not T_{SA}), with half the subjects reporting bitterness and half reporting sourness. The appearance of T_{BI} was particularly striking in that subjects who experienced it had reported sourness under the same conditions in the fungiform region. These differences appear unrelated to possible regional differences in sensitivity to chemical taste, as intensity ratings obtained for all four taste solutions on the circumvallate papillae were comparable to those previously obtained on the front of the tongue. In particular, 0.5 M sucrose evoked approximately moderate sweetness on circumvallate papillae, just as it did on the tongue tip. Consistent with the close association between T_{SW} and warmth on the front of the tongue, warmth sensitivity was poor on circumvallate papillae, whereas cooling was rated similarly in both regions.

The most straightforward explanation of thermal taste is that temperature-sensitive neurons in the human chorda tympani[2] and glossopharyngeal nerves encode taste rather than temperature. Electrophysiological studies in animals have shown that cold-sensitive gustatory neurons tend to be sensitive to acids (sour) or salts, and that warm-sensitive neurons tend to be sensitive to sucrose (sweetness) or bitter substances[3,4]. Because sensitivity to sweet and bitter chemicals depends upon G-protein-coupled receptors (GPCRs)[12,13] and sensitivity to salts and acids depends upon specialized Na^+ and H^+ ion channels[14], it is possible some GPCR cascades can be triggered by warming and that certain Na^+ and H^+ channels[5] can be gated by cooling. If so, the large individual and spatial differences in thermal taste we observed may reflect variations

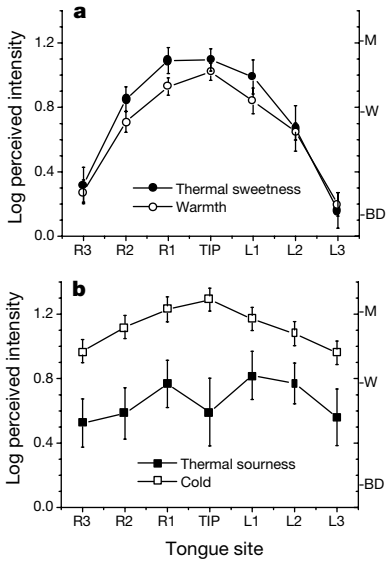

Figure 4 Thermal sweetness and warmth (**a**), and thermal sourness and cold (**b**) as a function of test site along the anterior edge of the tongue. The stimulus for warming was an increase from 20 to 35 °C; for cooling it was a decrease from 35 to 15 °C. R1–R3 and L1–L3 refer to contiguous test sites (~8 mm wide) along the right and left sides of the tongue, respectively. The data are from those subjects whose average rating of sweetness (**a**, $n = 14$) or sourness (**b**, $n = 13$) exceeded 'barely detectable' at one or more sites.

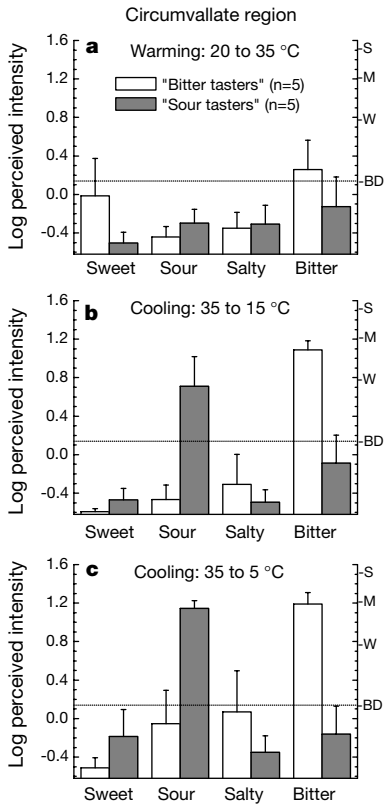

Figure 5 Thermal taste ratings from the circumvallate region of the tongue. Data are shown for 10 subjects in three temperature conditions: **a**, warming from 20 to 35 °C; **b**, cooling from 35 to 15 °C; **c**, cooling from 35 to 5 °C. Subjects were grouped according to the dominant taste quality they reported (bitter or sour) during cooling.

in the incidence and distribution of neurons whose chemosensory mechanisms are temperature-sensitive. However, the absence of significant bitterness during warming and the reports of bitterness during cooling on circumvallate papillae raise the possibility that thermal sensitivity in some gustatory neurons may arise from cellular processes that are unrelated to chemosensory transduction.

We note that thermal taste was nearly discovered 35 years ago by von Békésy. In a well-known but controversial paper, von Békésy[15] reported that taste and thermal stimuli (heated or cooled water) presented to opposite sides of the tongue merged into a single sensation when warm water was paired with sucrose or quinine, or when cold water was paired with citric acid or NaCl. This observation led him to propose the 'Duplexity Theory of Taste'[15], in which he posited that "warm and cold stimuli act similarly to the four primary taste stimuli…" Our results now suggest that von Békésy's subjects may have reported a single sensation in the middle of the tongue when bilateral thermal and chemical stimuli evoked the same taste quality. □

Methods

Thermal taste screening procedure

The incidence of thermal taste was tested in naive subjects (8 males and 16 females, most of whom were students at Yale University) using three temperature conditions that pilot tests had shown were capable of producing sweetness, sourness and saltiness, respectively: warming from 20 to 35 °C, cooling from 35 to 15 °C, and cooling from 35 to 5 °C. Temperature was varied at approximately $\pm 1.5\,^{\circ}C\,s^{-1}$ using an 8 mm × 8 mm computer-controlled Peltier thermode with thermocouple feedback. The thermode was affixed to a pencil-sized water-circulated heat sink and covered with plastic wrap for hygienic purposes. On each trial the thermode was set to the starting temperature, and with guidance from the experimenter and the aid of a mirror, subjects used the heat sink as a handle to position the thermode against the tongue. Heating or cooling began as soon as the temperature at the tongue–thermode interface stabilized at the starting temperature (5–10 s). Subjects were told to attend to the temperature change and to report if they perceived any other sensations, including tastes (defined as sweetness, sourness, saltiness or bitterness); they were assured that not everyone perceived such sensations, and that the purpose of the study was to discover how often and under what conditions they might appear. Stimulation began on the tongue tip and proceeded stepwise along the edge of the tongue to a distance ~5 cm caudal to the tip. Both sides of the tongue were tested, and each temperature condition was applied twice to each test site. When tastes were detected subjects reported their intensities verbally using a scale from 1 to 10. These ratings served to locate 'best' sites for thermal taste that were later tested more systematically.

Thermal testing on the tongue tip

The thermode was used to warm or cool the tongue tip over a series of temperature steps (ΔTs) that increased from 20 °C in steps (°C) of +5, +10, +15 and +20, or decreased from 35 °C in steps (°C) of −10, −15, −20, −25 and −30. Subjects rated the intensity of taste (sweetness, sourness, saltiness, bitterness) and thermal sensations (warmth, cold) using the labelled magnitude scale (LMS)[16], a continuous scale of sensation intensity bounded by 'no sensation' and 'strongest imaginable oral sensation'. The LMS was displayed on a computer monitor and subjects made their ratings using a mouse. Instructions were given to "attend now" as soon as heating began on warming trials and as soon as the target temperature was reached on cooling trials. Different instructions were used for heating and cooling because pilot tests had shown that sweetness occurred only while temperature rose, whereas sourness and saltiness persisted at steady temperatures. Because thermal taste was always accompanied by temperature sensations, taste and temperature ratings were obtained separately to help subjects make independent judgments. Each condition was presented twice in pseudo-random sequence.

Testing on 'best' thermal taste sites

18 subjects (one of the original 19 left the study between experiments) rated thermal tastes and temperature sensations in the same manner as on the tongue tip, except temperature was varied only as follows: from 20 to 35 °C to assess T_{SW}, from 35 to 15 °C to assess T_{SO}, and from 35 to 5 °C to assess T_{SA}. Chemical taste was assessed in a separate session on the same sites using four aqueous taste solutions (0.5 M sucrose, 0.1 M citric acid, 0.5 M NaCl and 0.01 M QHCl) found in pilot tests to produce approximately 'moderate' sweetness, saltiness, sourness or bitterness, respectively, when applied to small areas of the tongue. The experimenter used cotton-tipped applicators to carefully swab these solutions onto T_{SW} and T_{SO} 'best' sites for 3 s. Subjects used the LMS to rate intensity and rinsed between trials with distilled H_2O. Two replicates were obtained for each thermal and chemical condition.

Stepwise spatial testing

Measurements of T_{SW} and T_{SO} on the edge of the tongue were made on another group of 15 subjects (12 females and 3 males, screened as before from a sample of 22 females and 8 males). Seven sites were tested: the tongue tip and three contiguous locations on either side of the tip. Stimulation began at the tip and stepped approximately one width of the thermode (8 mm) at a time, first along one side of the tongue and then the other. At each site the thermode was warmed from 20 to 35 °C or cooled from 35 to 15 °C, with cooling and warming trials blocked. Two replicates were obtained for each temperature condition at each site.

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Postsaccadic visual references generate presaccadic compression of space

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With every rapid gaze shift (saccade), our eyes experience a different view of the world. Stable perception of visual space requires that points in the new image are associated with corresponding points in the previous image. The brain may use an extraretinal eye position signal to compensate for gaze changes[1,2], or, alternatively, exploit the image contents to determine associated locations[3,4]. Support for a uniform extraretinal signal comes from findings that the apparent position of objects briefly flashed around the time of a saccade is often shifted in the direction of the saccade[5–9]. This view is challenged, however, by observations that the magnitude[4,10] and direction[11] of the displacement varies across the visual field. Led by the observation that non-uniform displacements typically occurred in studies conducted in slightly illuminated rooms[4,7,10–13], here we determine