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The genetics of phenylthiocarbamide perception

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Abstract

Summary—The ability to taste the bitter compound phenylthiocarbamide (PTC) and related chemicals is bimodal, and all human populations tested to date contain some people who can and some people who cannot taste PTC. Why this trait has been maintained in the population is uncertain but this polymorphism may influence food selection, nutritional status or thyroid metabolism. The gene product that gives rise to this phenotype is unknown, and its characterization would provide insight into the mechanism of bitter taste perception. Although this trait is often considered a simple Mendelian trait, i.e. one gene-two alleles, a recent linkage study found a major locus on chromosome 5p15 and evidence for an additional locus on chromosome 7. The development of methods to identify these genes will provide a good stepping-stone between single-gene disorders and polygenic traits.

1. Introduction

About 66 years ago, A. L. Fox, a Du Pont chemist, reported a startling accidental discovery (Anonymous 1931, Fox 1932). Boyd (1950) describes the event:

> Dr A. L. Fox had occasion to prepare a quantity of phenyl-thio-carbamide… As he was placing this compound in a bottle some of it was dispersed into the air as dust. Thereupon another occupant of the laboratory complained of the bitter taste of the dust. This surprised Fox, who being much closer to the scene of operations had of course inhaled more of the dust, but had perceived no taste. He was so positive that the stuff was tasteless that he went so far as to taste some of the crystals directly, finding them as tasteless as chalk. Nevertheless the other chemist was convinced the substance was bitter and was confirmed in this impression when he in turn tasted the crystals and found them to be intensely bitter. Naturally a lively argument arose. In an attempt to settle it, the two chemists called in various other laboratory workers, friends and other people with whom they could establish contact. Some people declared the substance was tasteless and some again found it bitter.

The threshold at which people can taste phenylthiocarbamide (PTC) is bimodal, and some people are tasters and others are nontasters (Hartmann 1939, Riddell and Wybar 1944, Kalmus 1952). Family and twin studies suggest this trait is inherited as a Mendelian recessive, with two alleles typically represented as **T** and **t**, with **T** representing the ‘tasting’ allele and **t** the ‘non-tasting’ allele (Blakeslee 1931, Snyder 1931, Blakeslee 1932, Levit and Soboleva 1935, Lee 1937, Rife 1938, Hogben 1946, Matsunaga and Tsuji 1957, Merton 1958, Pons 1960, Kaplan and Fischer 1965, Martin 1975, Rao and Morton 1977, Forrai and

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Bankovi 1984, Whissell-Buechy 1990b). The evidence for a genetic component underlying the PTC tasting ability is so strong that it was once used in paternity tests before DNA markers were available (Cardullo and Holt 1951). The ability to taste PTC is listed as a genetic trait (McKusick 1995), (MIM No. 171200) and has been referred to as an 'honorary blood group'.

Opening any genetics or anthropology journal published after 1930, one can hardly find an issue without a paper on the genetics of PTC. Indeed, the taste-blindness of PTC is perhaps the most studied trait in human genetics, second only to the ABO blood group system. However, almost 70 years after Fox's discovery, the genetic study of PTC ability has not advanced at the same rate as the genetics of other inherited phenotypes. The gene has not been characterized.

PTC tasting ability is not just one of many seemingly innocuous human traits (such as tongue-rolling or arm-folding) that are interesting but not worth pursuing the underlying genetic variability. PTC blindness is reportedly associated with food preferences and several diseases, especially disorders of thyroid metabolism. Characterization of the PTC gene would provide a powerful tool to further examine and delineate each of these associations. The exact mechanism of taste transduction is still poorly understood and has lagged behind the biology of other sensory modalities such as auditory, olfactory, mechanioreception and photoreception. The characterization of the PTC gene would provide an opportunity to investigate gustatory function, an interface where 'physiology and psychology meet' (Adrian 1963). In this paper, we will review genetic studies of PTC blindness and the evidence for the pleiotropic effects of this gene, strategies for gene identification and recent linkage results.

The ability to taste PTC and PROP are correlated and reflect the same polymorphism. 6-*n*-Propylthiouracil (PROP) and PTC are chemically related compounds (figure 1) and the taste responses to both are correlated in humans (Barnicot, Harris and Kalmus 1951, Lawless 1980, Hooper and Bartoshuk 1983). Electrophysiological evidence in primates suggested PTC and PROP produce nearly identical responses (Scott *et al.* 1998). Earlier studies used PTC, but most investigators have switched to PROP because it lacks the sulphurous odour of PTC and, because PROP is used as a medication to treat Graves' Disease, safety limits can be set for its use (Fischer and Griffin 1964, Wheatcroft and Thornburn 1972, Lawless 1980). To preserve the history of this locus, however, we will refer the major gene that confers the bitter taste polymorphism as the PTC locus, and assume that PROP is a surrogate for PTC.

Is individual variability in PTC sensitivity due to the presence or absence of a receptor contained in the taste cells? Fox (1932) first suggested that the taste of PTC and other related compounds was closely connected with the presence of the C=S group. Further investigations suggested the N—C=S group might be more critical (Hopkins 1942, Harris and Kalmus 1949–1951) (see figure 1). Nontasters may lack a receptor for PTC on the tongue that recognizes this N—C=S group (Fischer and Griffin 1964).

A family was identified that appeared to have an interesting mutation of the PTC locus, and the data collected from that family is consistent with the PTC gene being a taste receptor (Skude 1959, Skude 1960, Skude 1963). The people in the family perceived the taste of PTC to be sweet rather than bitter. This observation is interesting because PTC is structurally similar to a compound called Dulcin, which is very sweet (Cook 1933, Cohen and Ogdon 1949a). These families may harbour a mutation of the PTC receptor, such that they respond to PTC as sweet rather than bitter.

Although appealing, a simple receptor hypothesis may be incorrect. The perception of bitter compounds not containing the N—C=S group and other non-bitter oral stimuli are

influenced by PTC genotype (Falconer 1946–47, Kalmus 1958, Fischer and Griffin 1964, Dawson and West 1967, Hall *et al.* 1975, Gent and Bartoshuk 1983, Leach and Noble 1986, Mela 1989, Karrer and Bartoshuk 1991, Looy, Callaghan and Weingarten *et al.* 1992, Looy and Weingarten 1992, Bartoshuk 1993, Bartoshuk, Duffy and Miller 1994, Lucchina, Bartoshuk, Duffey *et al.* 1995, Drewnowski, Henderson and Shore 1997a, Tepper and Nurse 1997, Bartoshuk, Duffey, Lucchina *et al.* 1998, Drewnowski, Henderson, Shore *et al.* 1998b) but see Boughter and Whitney (1993). Furthermore, taste-bud distribution is anatomically different between people who experience the taste of PROP as intensely bitter compared with those who do not (Miller and Reedy 1990, Bartoshuk *et al.* 1994). Taken together, these observations are difficult to reconcile with the hypothesis that nontasters lack a membrane-bound receptor in the taste cell sensitive specifically to PTC and structurally similar compounds.

The origins of the PTC polymorphism might not be the lack of a taste cell receptor, but rather the lack of a compound in saliva that allows people to taste PTC. The clearest demonstration of the validity of this hypothesis would be if *nontasters* could taste PTC, mixed in *taster* saliva. The results of these types of experiments are negative, however (Hartmann 1939, Cohen and Ogdon 1949b). Furthermore, when saliva is removed from the tongue, tasters remain tasters (Salmon and Blakeslee 1935). There is one report of a taster who could not taste a PTC related compound when his own saliva was removed and replaced with the saliva of a nontaster (Fischer and Griffin 1964), but nonspecific effects of the testing condition could have led to this result. It is therefore unlikely that PTC nontasters lack a salivary protein that permits PTC to be tasted.

1.1. Modifiers of the genotype–phenotype relationship

Although the PTC polymorphism has been regarded as a single locus trait, most investigators have pointed out its complex features, and have proposed that certain subject characteristics and environmental factors may alter the phenotype. The most robust modifier of the genotype± phenotype relationship is sex. Women are more likely to be tasters and can taste PTC at lower concentrations than can men (Fernberger 1932, Boyd and Boyd 1936, Hartmann 1939, Falconer 1946–47, Barnicot 1950, Beach 1953, Matsunaga, Suzuki, Itoh *et al.* 1954, Buchi 1955, Buchi and Roy 1955, Kumar 1955, Pons 1955, Simmons, Graydon, Semple *et al.* 1956, Kalmus 1958, Vyas, Bhatia, Banker *et al.* 1958, Leguebe 1960, Kumar and Sastry 1961, Sheba 1962, Bhattacharya 1964, Das and Mukherjee 1964, Kaplan and Fischer 1965, Khullar 1965, Romanus 1965, Say, Kiran, Altay *et al.* 1966, Boobphanirojana, Chetanasilpin, Saengudom *et al.* 1970, Patel 1971, Scott-Emuakpor, Uviovo and Warren 1975, Mitchell, Cook and Sunderland 1977, Ranganayaki and Injeti 1979, Babu, Jaikishan and Veerraju 1984, Parveen, Goni and Shah 1990, Sengupta and Dutta 1991, Balakrishna, Ramesh and Veerraju 1992, Sudhakar, Babu and Padma 1992, Bartoshuk *et al.* 1994, Devi, Lakshmi and Veerraju 1995, Sato, Okada, Miyamoto *et al.* 1997). Not all investigators measuring male and female subjects found statistically reliable differences. Of these, however, it is striking that almost all studies show this tendency for women to be sensitive tasters compared with men (Rikimaru 1936b, Boyd and Boyd 1937, Kalmus 1952, Das and Ghosh 1954, Bhattacharjee 1956, Saldanha 1958, Soltan and Bracken 1958, Akesson 1959a, Saldanha and Becak 1959, Freire-Maia, Freire-Maia and Quelce-Salgado 1960, Beiguelman 1962, Saldanha 1962, Sharma 1962, Vyas, Bhatia, Sukumaran *et al.* 1962, Das, Mukherjee and Bhattacharjee 1963, Pullin and Sunderland 1963, Kalmus, De Garay, Rodart *et al.* 1964, Tiwari 1966, Dawson and West 1967, Sharma 1967, Srivastava and Tyagi 1967, Tiwari and Bhasin 1967, Parmar 1968, Eriksson, Fellman, Forsius *et al.* 1970, Alsbirk and Alsbirk 1972, Akcasu, Kameswaran, Sanyal *et al.* 1974, Than-Sint and Mya-Tu 1974, Rastogi and Tyagi 1975, Akcasu and Ozalp 1977, Ibraimov and Mirrakhimov 1979, Mathur, Mather and Bahadur 1983, Reddy 1983, Bokesoy and Togan 1987, Ramana and Naidu 1992, Kranzler,

Moore and Hesselbrock 1996, DiCarlo and Powers 1998). Only in a handful of cases, have investigators found marginal evidence that males are more sensitive than females (Thambipillai 1955–56, Kumar 1957, Sheba 1962, Saldanha and Nacrur 1963, Jenkins 1965, Agrawal 1966, Cartwright and Sunderland 1967, Kalmus 1967, Hashem and Khalifa 1968, Chattopadhyay 1971, Chandraiah and Bahadur 1975, Shah and Sattar 1981, Panayotou, Kritsikis and Bartsocas 1983, Babu *et al.* 1984, Yanagida 1988, Odeigah 1994, Rao and Jaikishan 1995), and in many of these studies, the subjects were children or adolescents. This observation, taken together with evidence that PTC sensitivity fluxes over the menstrual cycle (Kaplan and Fischer 1965, Bhatia, Sharma and Mehta 1981) suggest sex hormones may influence PTC sensitivity.

Although women can taste PTC at lower concentrations and are more likely to be tasters than are men, the mode of transmission for PTC taster status does not follow an X-linked inheritance pattern. Furthermore, with the exception of one study (McDonald 1979), the ability to taste PTC does not cosegregate with X-linked forms of colour blindness (Buchi and Roy 1955, Bhattacharjee 1956, Fernandes, Junqueira, Kalmus *et al.* 1957, Junqueira *et al.* 1957, Kalmus 1957, Freire-Maia *et al.* 1960, Pullin and Sunderland 1963, Kalmus, Kalmus, Wishart *et al.* 1964, Agrawal 1968, Sunderland and Ryman 1968, Lightman, Carr-Locke and Pickles 1970, Bonne, Ashbel, Berlin *et al.* 1972, Set 1973, Seth and Seth 1973, Barnicot and Woodburn 1975, Sirajuddin 1977, Bhattacharjee, Chowdhuri and Chatterjee 1978, Goud and Rao 1979a, b, Ranganayaki and Injeti 1979, Bhalla, Bhatia, Sood *et al.* 1980, Ramesh, Kumar and Murty 1981, Sharma and Bhalla 1981, Chowdhury 1988, Bagga and Seth 1992, Balakrishna *et al.* 1992, Ramana and Naidu 1992, Sudhakar *et al.* 1992, Singh and Bagga 1994, Devi *et al.* 1995). Modifier loci that increase PTC taste sensitivity, however, may lie on the X chromosome or may be autosomal genes regulated by sex hormones.

In addition to gender, smoking and ageing have been suggested as other modifiers of the PTC phenotype± genotype relationship. Either the chronic or acute effects of smoking might alter the perception of PTC (Hall and Blakeslee 1945, Srivastava 1959, Kaplan and Glanville 1964, Kaplan, Glanville and Fischer 1965) but not all studies are consistent with this hypothesis (Salmon and Blakeslee 1935, Falconer 1946–47, Pons 1955, Freire-Maia 1960, Leguebe 1960, Sharma 1962). Smoking may somehow interfere with or desensitize the function of some taste receptors. Likewise, the ability to taste PTC has been suggested to decline with age (Kalmus and Trotter 1962, Kaplan and Fischer 1965, Dass 1976, Whissell-Buechy 1990a, Schiffman, Gatlin, Frey, *et al.* 1994, Reed, Bartoshuk, Duffey *et al.* 1995), but some investigators do not observe such effects (Leguebe 1960, Sharma 1967, Koertvelyessy, Crawford and Hutchinson 1982, Koertvelyessy and Crawford 1990). The majority of these studies suggest that PTC acuity does decline with age, but the effects are modest.

Occasionally, identical twins are discordant for tasting ability and therefore environmental influences, such as illness, may change taster status (Ardashnikov, Lichtenstein, Martynova *et al.* 1936, Rife 1938). For instance, head injury and otitis media (ear infection) may influence the taster phenotype (Bartoshuk, Duffey, Reed *et al.* 1996). Overall, subjects with otitis media find the bitter taste of PTC-related compounds more intense compared with subjects without a history of otitis media; the reverse is true for subjects with and without a history of head trauma. Both of these events (ear infections and head trauma) may influence taste by damaging gustatory nerves, and the specific alterations in taste depend on the location and extent of the damage.

2. Population genetics

The population genetics of PTC has received extensive investigation. The ability to taste PTC has been tested extensively in various populations around the world (table 1) and has been partially reviewed (Cohen and Ogdon 1949a, Boyd 1950, Das 1966, Mourant, Kopec and Domaniewska-Sobczak 1976, Tills, Kopec and Hills 1983, Nasidze 1995, Mattes and Beauchamp 2000). The populations tested have varied from outbred groups such as University students in large cities (e.g. Fernberger 1932) to small, genetically isolated groups such as the Samaritans (e.g. Bonne 1966). Geographic proximity is a poor predictor of allele frequency because groups that live nearby but do not intermarry can have large differences in the proportion of tasters and nontasters (e.g. Babu *et al.* 1996). Several trends are apparent, however. The nontaster frequency is much higher than the prevalence of typical Mendelian genetic disease. With the exception of one small group of Brazilian Indians (Kalmus 1957), nontasters exist in all populations studied. In some subgroups, the frequency of nontasters is higher than the frequency of tasters (e.g. some tribes and castes in India, table 1). These observations, taken in conjunction with the presence of polymorphism in other mammalian species such as primates (Fisher 1939, Chiarelli 1963, Eaton and Gavan 1965, Smith, Lorey and Small 1981), cats (Bolekhan, Semenov, Gerasimova *et al.* 1997) and perhaps pigs (Braude 1949), suggests the creation of this polymorphism occurred before the dispersion of humans throughout the continents.

2.1. PTC heterozygotes: selectively advantageous?

Based on the ubiquitous variation in PTC-tasting ability in various populations and chimpanzees, Fisher, Ford and Huxley (1939) speculated that heterozygotes have a selective advantage over homozygotes. Otherwise, in the time elapsed since the creation of these alleles, selection, or genetic drift, or both, would have eliminated one of the alleles from the population (Fisher 1939). The nature of the proposed selective advantage is unknown. One hypothesis, however, is that genotype at the PTC locus may influence food selection through its effects on bitter taste sensitivity. Given that bitterness is associated with toxic compounds, PTC tasters may be more likely to avoid such toxic compounds while PTC nontasters might be willing to eat a broader variety of foods (Drewnowski and Rock 1995, Tepper 1998). These differences in food selection of bitter tasting foods may, in turn, influence metabolism and physiology (Greene 1974, Davis 1978). There is no single food category or food type, however, that is always preferred or avoided by PTC tasters (Fischer and Griffin 1961, Fischer, Griffin, England *et al.* 1961, Fischer, Griffin, and Kaplan 1963, Glanville and Kaplan 1965, Forrai and Bankovi 1984, Niewind, Krondl and Shrott 1988, Mattes and Labov 1989, Jerzsa-Latta, Krondl and Coleman 1990, Anliker, Bartoshuk, Ferris *et al.* 1991, Frank and van der Klaauw 1994, Noble 1994, Akella 1997, Drewnowski, Henderson and Shore 1997b, Drewnowski *et al.* 1998a, Drewnowski *et al.* 1998b), reviewed in (Reed 1999, Mattes and Beauchamp 2000) and therefore further research is needed to understand how PTC genotype influences food selection.

2.2. PTC taster status and alcoholism

Alcoholism or drinking behaviour is associated with PTC insensitivity in some (Peeples 1962, Pelchat and Danowski 1992, DiCarlo and Powers 1998, Intranuovo and Powers 1998) but not all studies (Sharma 1962, Kang, Cho and Yurn 1967, Reid, Brunt and Bias 1968, Smith 1972, Swinson 1973, Swinson 1983, Kranzler *et al.* 1996). Interestingly, PROP retards alcohol-induced liver disease (Orrego, Blake, Blendis *et al.* 1994). Perhaps PTC taster status may be related to the individual differences in the consequences of chronic alcohol consumption.

2.3. PTC taster status and diseases

There have been reports of associations or lack of associations between PTC taste status and diseases and traits not directly related to taste. These include diabetes (Terry and Segall 1947, Terry 1950, Akesson 1959b, Bayani-Sioson 1964, Schelling, Tetreault, Lasagna *et al.* 1965, Rao and Sisodia 1970, Ali, Azad Khan, Mahtab *et al.* 1994), dental caries (Chung, Witkop and Henry 1962), eye disease (Becker and Morton 1964, Suzuki, Takeuchi and Kitazawa 1966, Alsbirk and Alsbirk 1972, Kalmus and Lewkonia 1973), thyroid disorders (Harris, Kallmus and Trotter 1949, Kitchin, Howel-Evans, Clarke *et al.* 1959, Shepard and Gartler 1960, Fraser 1961, Shepard 1961, Brand 1963, Hollingsworth 1963, Bayani-Sioson 1964, Azevedo, Krieger, Mi *et al.* 1965a, Covarrubias, Barzelatto, Stevenson *et al.* 1965, De Luca and Cramarossa 1965, Paolucci, Ferro-Luzzi, Modiano *et al.* 1971, Mendez de Araujo, Salzano and Wolff 1972, Persson, Kolendorf and Kolendorf 1972, Facchini, Abbati and Campagnoni 1990, Haque 1990, Koertvelyessy and Crawford 1990, Facchini, Pettener, Rimondi *et al.* 1997), schizophrenia (Freire-Maia, Karam, Mehl *et al.* 1968, Schlosberg and Baruch 1992), gastrointestinal ulcers (Kaplan, Fischer, Glanville *et al.* 1964, Stanchev, Tsonev and Minchev 1985, Li, McIntosh, Byth *et al.* 1990), depression (Whittemore 1986, 1990), personality characteristics (Very and Iacono 1968, Mascie-Taylor, McManus, MacLarnon *et al.* 1983, Kimmel and Lester 1987), mental function (Azevedo, Snyder and Krieger 1965b, Karam and Freire-Maia 1967, Greene 1974), growth variation (Johnson, Hertzog and Malina 1966, Whissell-Buechy and Wills 1989), malignant tumours (Milunicova, Jandova and Skoda 1969, Ahnja, Reddy and Reddy 1977) and susceptibility to infectious disease (Saldanha 1956, Akesson 1959b, Bayani-Sioson 1964, Beiguelman 1964, Brand 1964, Rao 1972, Ghei and Vaidya 1977). The reports of association between diseases and taster status may be due to chance associations; there are several instances of an initial report and one or more subsequent failures to replicate. In these cases, differences between studies in the characteristics of subjects or low statistical power may explain discordant results. Also, genetic association studies are prone to false positive results due to population stratification, which may be present in some but not all study populations. Finally, the associations may be genuine, and could occur either because the taster locus is in linkage disequilibrium with other loci that predispose to a disease, or because the PTC locus has pleiotropic effects, or because the disease process changes PTC taster status.

2.4. Mode of inheritance, segregation analysis and heritability estimations

Although the inability to taste PTC, or PTC taste blindness, has often been cited as a classical textbook example of a Mendelian trait, there are controversies surrounding its exact mode of inheritance. Incomplete dominance (Falconer 1946–47, Martin 1975, Jones and McLachlan 1991, Bartoshuk *et al.* 1994, 1996, Reed *et al.* 1995), multiple alleles (Rychkov and Borodina 1969, Rychkov and Borodina 1973, Ibraimov and Mirrakhimov 1979) and multigenic inheritance have all been suggested (Boyd and Boyd 1937, Boyd 1950, Babu *et al.* 1984, Olson, Boehnke, Neiswanger *et al.* 1989). Distributions of the rating of concentrated PROP solutions demonstrate bimodallity, but there is a broad range of intensity ratings within the taster group (figure 2).

Reddy and Rao (1989) reexamined the genetics of PTC taste thresholds by studying 100 nuclear families (Reddy and Rao 1989). They concluded that variability in thresholds is controlled by a major locus with incomplete dominance as well as by a multifactorial component. Olson *et al.* (1989) studied 120 families and concluded that the data fitted best a two-locus model in which one locus controls PTC tasting and the other locus controls general taste ability (Olson *et al.* 1989). Results of studies that identify two types of nontasters, those with a specific inability to taste PTC and those with more generalized deficits in gustatory abilities, appear to be consistent with this hypothesis (Frank and Korchmar 1985). However, it is important to bear in mind that possible measurement error,

misclassifications, or hidden non-paternity might reduce support for a single-locus hypothesis, making multilocus hypothesis more acceptable. Additional segregation analysis of genotyped individuals (to exclude non-paternity) would make analysis and conclusions about heritability and mode of inheritance more robust.

When measured as a quantitative trait, it is evident that not all of the phenotypic variance in PTC taste perception is heritable. Morton, Cantor, Corey *et al.* (1981) reported a broad heritability of 55% for taste threshold for PTC (Morton *et al.*1981). The modifiers of the genotype–phenotype relationship such as gender, age, smoking, history of otitis media and head trauma may partially account for the nonheritable fraction of the phenotypic variance.

In the last decade, genetic analysis has advanced to such a degree that mapping and characterizing rare disease genes is straightforward, and significant progress has been made toward mapping multigenic traits and diseases. The PTC polymorphism, because it combines both bimodal and continuous variation, is an appealing model to develop methods and strategies for complex traits. Also, since the phenotyping is relatively stable, inexpensive, can be measured accurately, and the gene frequency is high, it is an ideal complex trait to test out current gene mapping methodology, given that the detection of genes for other complex traits has been difficult. Issues pertinent to the eventual characterization of this trait are discussed below.

Rodent models are undesirable to map the PTC locus. Because the mouse's genome is well characterized and shares many phenotypic characteristics with humans, it has gained widespread use as an experimental model in genetics. However, it is generally accepted that the mouse is not a good model system for PTC genetics. Genetic variation does account for individual and strain differences in rodents' perception of PTC (Richter and Clisby 1941, Hoshishima, Yokoyama and Seto 1962, Klein and DeFries 1970a, b, Tobach, Bellin and Das 1974, Lush 1986). However, none of the loci that influence the perception of propylthiouracil in mice are likely to be the human PTC locus (Whitney and Harder 1986, Harder, Boughter and Whitney 1996, Boughter and Whitney 1998, Harder and Whitney 1998). Moreover, the chorda tympani and glossopharyngel taste nerves are not more variable in response to PTC than to other bitter compounds (Dahl, Erikson and Simon 1997), suggesting that mice lack the extreme bimodality of the response compared with humans. Therefore, the species differences between mice and humans in PTC taste perception make the mouse of limited use for genetic investigation.

Other models might be suitable to map the PTC trait. A mutant strain of fruit flies (*Drosophila melanogaster*) displays bimodal sensitivity to PTC (Ogita 1958, Davring and Sunner 1971). Primates display the polymorphism (Fisher 1939, Chiarelli 1963, Eaton and Gavan 1965, Smith *et al.* 1981) as do cats (Bolekhan *et al.* 1997) and perhaps pigs (Braude 1949). The two best-characterized mammalian genomes are the human and the mouse and, because a well-characterized genome is essential for gene mapping and characterization, humans are the experimental species of choice.

2.5. Phenotypic considerations in gene mapping experiments

To conduct a mapping study for any trait, an accurate measure of the phenotype is essential. Two methods have been used to phenotype subjects for PTC status. One method is to determine the lowest concentration of PTC or related compound that a subject can identify or detect (threshold methods). Harris and Kalmus devised a popular threshold method widely used by other investigators (Harris and Kalmus 1949). In this test, subjects sip increasing concentrations of PTC until they detect a taste. Then four cups of PTC at that concentration, as well as four cups of water are offered to the subject, and the subject is asked to sort the cups into two groups, based upon the taste. There are other less popular

variations of threshold methods, but the results obtained from all such methods are in reasonably good agreement (Lawless 1980). Refinements, such as the choice of solvent, may improve the discrimination between tasters and nontasters (Masuoka, Lee, Hatjopoulos *et al.* 1995, Lee and O'Mahony 1998). Several investigators attempted to further subdivide subjects by their PTC ability and by other taste abilities, such as sensitivity to quinine or perception of sodium benzoate (Hoover 1956, Fischer and Griffin 1964). Testing subjects for their ability to detect other types of chemicals at low concentrations is helpful to find nontasters that have nonspecific taste loss.

The other method is for subjects to rate the intensity of a concentration of PTC well above that which a taster can taste (suprathreshold methods). Suprathreshold methods have been recently refined (Bartoshuk *et al.* 1996). Using a scale that reduces ceiling effects increases the sensitivity of suprathreshold intensity measures (Lucchina, Curtis, Putnam *et al.* 1998). It is unclear whether the threshold or suprathreshold phenotype is the most direct reflection of the genotype, and therefore both methods of phenotyping will be useful in gene mapping studies.

2.6. Statistical methods and strategies for gene identification

Traditional parametric linkage methods may have low power to detect linkage for the PTC gene because of its high allele frequency. A significant fraction of the variation of PTC tasting in humans appears to be polygenic, and therefore parametric methods are a less desirable choice to map this trait. Affected sibling pair methods may be better suited to mapping the PTC locus. These methods do not rely on models that specify mode of inheritance, can detect multiple loci, and are capable of analysing quantitative phenotypes such as threshold or suprathreshold measures of PTC status. Strictly speaking, however, these methods are unproven, because no gene has been cloned based solely on these methods alone.

Because this taste polymorphism is found in primates (Fisher 1939, Chiarelli 1963, Eaton and Gavan 1965), PTC tasting ability may be an ancient polymorphism, not a relatively new human mutation. Consequently, linkage methods such as homozygosity mapping, which is very powerful for mapping rare recessive diseases (Guo 1997), will have little power to map this trait.

2.7. Fine-scale mapping based on linkage disequilibrium and association studies

Once the gene is mapped by linkage methods, fine mapping will facilitate gene identification. Recently developed methods for fine-scale mapping based on linkage disequilibrium may be useful, provided linkage disequilibrium is present in the region containing the PTC locus (Xiong and Guo 1997a, b).

An association study compares DNA samples from populations of individuals with and without a particular trait, in our case PTC blindness, to determine which alleles are associated with the trait. An allele is said to be associated with this trait when carriers of this allele are more frequent among PTC nontasters than tasters. Association studies can be more powerful than traditional linkage studies to detect genes responsible for a given trait (Risch and Merikangas 1996, see also Xiong and Guo 1998). This approach may be a promising way to identify candidate genes responsible for PTC blindness.

2.8. Results of gene mapping experiments

Early studies investigated linkage between the PTC locus and blood groups or other genetic traits (Hogben and Pollack 1935, Burks and Wyandt 1941, Kloepfer 1946, Sanger and Race 1951, Holt, Thompson, Sanger *et al.* 1952, Umansky, Reid, Corcoran *et al.* 1966, Gedde-

Dahl and Monn 1967, Fu, Azevedo and Moreton 1968, Gedde-Dahl and Monn 1968, Blondheim and Reznik 1971, Chautard-Freire-Maia 1974, Conneally, Nance and Huntzinger 1974, Crandall and Spence 1974, Conneally, Dumont-Driscoll, Huntzinger *et al.* 1976, Keats, Morton and Rao 1978, Spence, Falk, Neiswanger *et al.* 1984, O'Hanlon, Weissbecker, Cortessis *et al.* 1988, Bhatkar, Nallulwar and Katti 1989). While some investigators detected linkage between the PTC and a polymorphism in a blood group antigen (KELL) on chromosome 7 (Umansky *et al.* 1966, Chautard-Freire-Maia 1974, Conneally *et al.* 1974, 1976, Keats *et al.* 1978), other investigators did not (Holt *et al.* 1952, Crandall and Spence 1974, Spence *et al.* 1984).

A recent linkage study using sibling pair methods has indicated that the primary PTC locus maps to chromosome 5p15, with at least one additional locus on chromosome 7 (Reed, Nanthakumar , North *et al.* 1999). The initial linkages to chromosome 7 and the subsequent non-replication described in the preceding paragraph appears to have occurred because the chromosome 7 linkage accounts for less variance than the locus on chromosome 5 and may be more important in threshold rather than suprathreshold sensitivity. Polymorphic markers near the PTC locus identified within 5p15 are differentially transmitted to taster children by heterozygous parents, suggested linkage disequilibrium (Reed *et al.* 1999). These preliminary results suggested fine-scale mapping based on linkage disequilibrium methods are likely to be useful in narrowing the interval containing the PTC locus.

2.9. Possible identification of a family of bitter taste receptors and the PTC gene

Two groups of investigators have identified genes that may be bitter taste receptors (Alder *et al.* 2000, Matsunami *et al.* 2000). The bitter genes identified are G-protein coupled receptors, which is the expected structure of taste receptors, and at least one of these genes has been shown to be functional (Chandrashekar *et al.* 2000). Of the putative bitter receptors sequenced to date, five are located in areas of linkage to PTC (5p15, T2R1; 7q31, T2R3, T2R4, T2R5) and therefore are candidates for the PTC receptor.

The most definitive demonstration that a candidate gene is responsible for the PTC phenotype is the discovery of an allele that co-segregates with the taste phenotype. Sequencing efforts are underway to identify allelic variability within these genes, and to examine the relationship between genotype and phenotype.

3.0. Identification of the PTC loci will further our understanding of sensory biology and the genetics of complex traits

One of the investigators to first describe the heritability of the PTC polymorphism demonstrated differences in chemosensory experience by small experiments, interjected between dinner courses at a meeting of American Association for the Advancement of Science in 1934 (Blakeslee 1935). These experiments highlighted the individual differences in our sensory world. After almost 70 years, the origins of that variability, apparently due in large part to genetic factors, remains a conundrum. Through the characterization of PTC genetics, we will be in a better position to understand the origins of these individual sensory experiences. This achievement would assist in elucidating the mechanism of taste transduction. In addition, the mapping of the PTC genes will provide a powerful tool to examine the genetic basis for food preferences and the relationship between taste status and health outcomes. It also provides a testing ground for current gene-mapping methodology, which have not yet been successful for complex traits.

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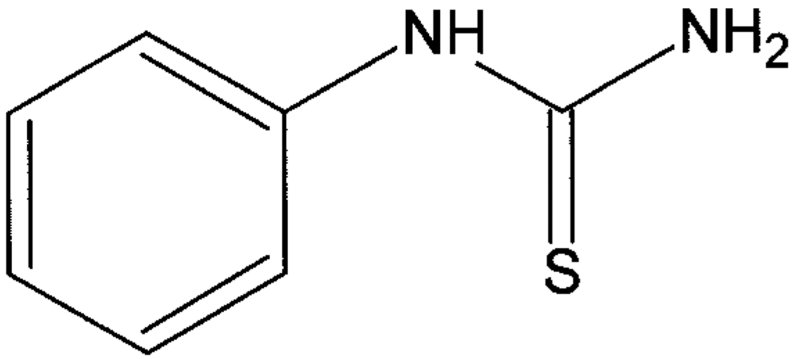
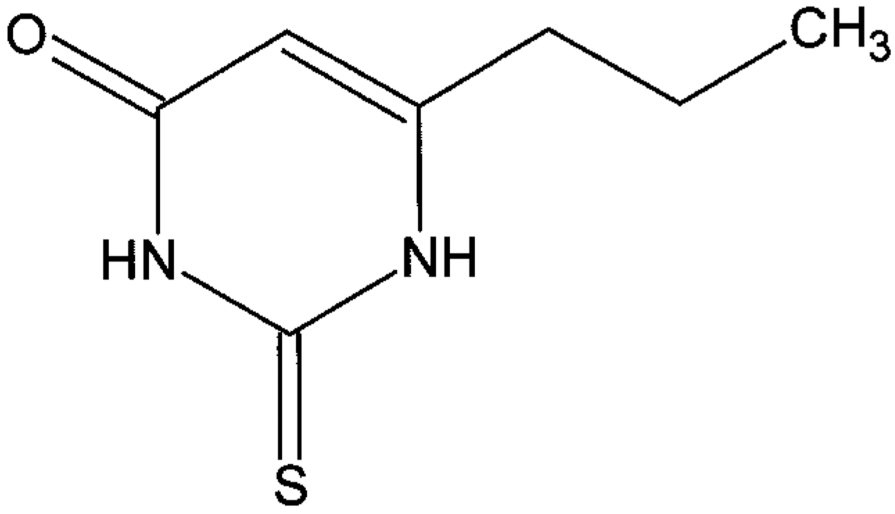


Phenythiocarbamide
PTC



Propylthiouracil
PROP

Figure 1.
Chemical structure of PTC and propylthiouracil.

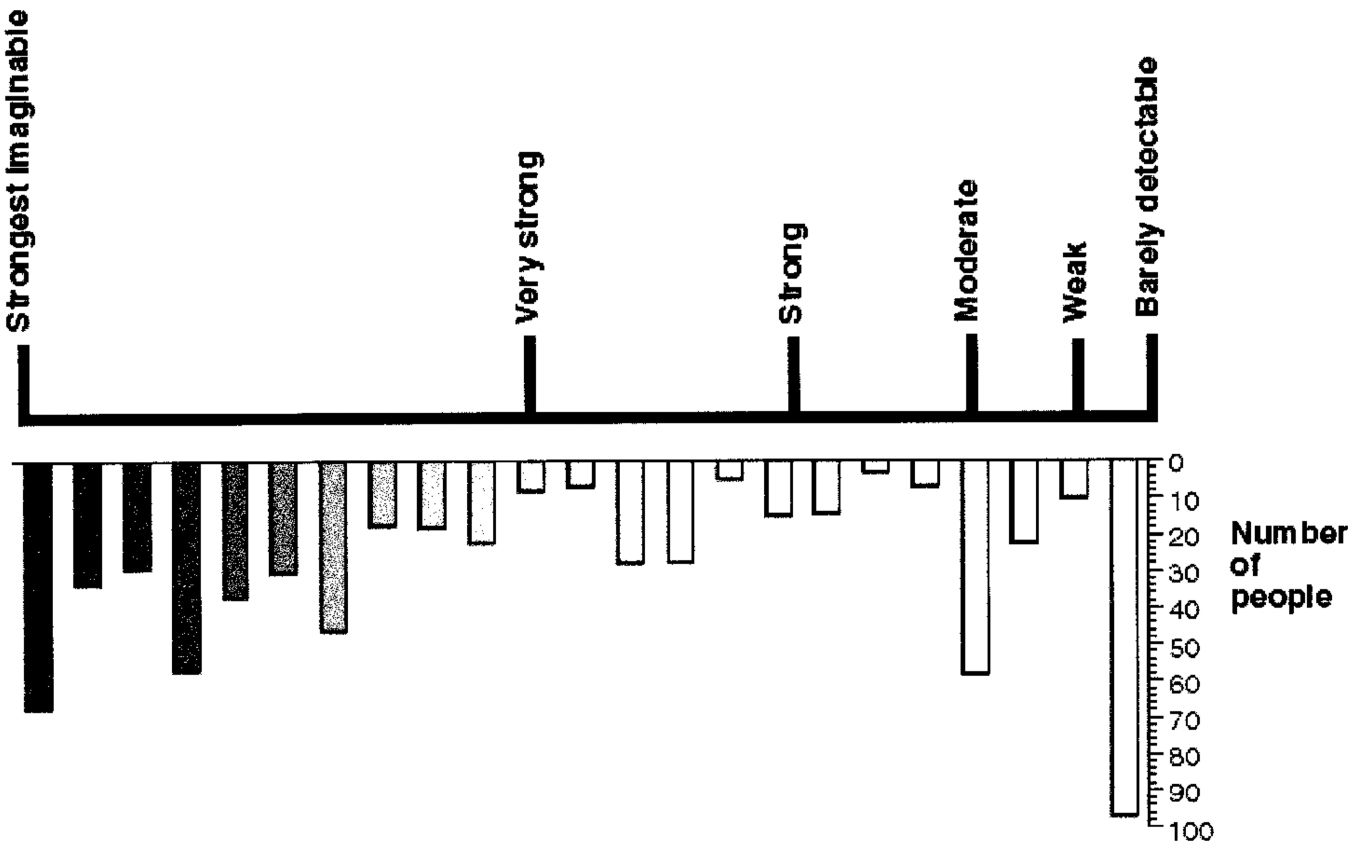


Figure 2.
Distribution of the ratings for a suprathreshold concentration of propylthiouracil, adjusted for sex and age effects.

Table 1

Worldwide population variation in nontaster frequency.

Country or continent	Group	*n*	% Nontaster	Reference
Africa	Africans	74	2.7	Barnicot 1950
Africa	Amhara	123	12.2	Bat-Miriam *et al.* 1962
Africa	Arabs from Syria	400	36.5	Parr 1934
Africa	Armenians from Syria	294	32.0	Parr 1934
Africa	Assiut	480	24.0	Boyd 1950
Africa	Bari	70	7.1	Rife 1953
Africa	Billen, Ethiopian	104	3.9	Bat-Miriam *et al.* 1962
Africa	Boarij Syria	119	32.0	Boyd 1950
Africa	Bush	85	7.1	Jenkins 1965
Africa	Cyrenaicans	65	20.0	Jenkins 1965
Africa	Dinka	132	34.8	Rife 1953
Africa	Egyptians	208	24.1	Parr 1934
Africa	Egyptians	569	22.0	Boyd 1950
Africa	Egyptians	1078	8.2	Hashem and Khalifa 1968
Africa	Egyptians, Bagdad Christians	60	27.0	Boyd 1950
Africa	Egyptians, Bagdad Jewish	168	17.0	Boyd 1950
Africa	Egyptians, Bagdad Moslems	322	29.0	Boyd 1950
Africa	Fezzanites	52	17.3	Jenkins 1965
Africa	Galla	110	15.5	Bat-Miriam *et al.* 1962
Africa	Giriama Bantu	208	3.8	Allison 1951
Africa	Guraghe	108	13.9	Bat-Miriam *et al.* 1962
Africa	Hadza in North Tanzania	118	23.7	Barnicot and Woodburn 1975
Africa	Ibadan, Western Nigeria	191	13.7	Kalmus 1967
Africa	Kenyan	375	4.8	Sunderland and Rosa 1975
Africa	Kgalagadi	38	5.2	Jenkins 1965
Africa	Libyans	167	19.8	Sunderland and Rosa 1975
Africa	Melinde Arabs	63	25.4	Allison 1951
Africa	Meshghara Syria; Christians	96	30.0	Boyd 1950
Africa	Meshghara Syria; Moslems	171	18.0	Boyd 1950
Africa	Mixed Sudanese	51	17.6	Rife 1953
Africa	N Falasha	24	8.3	Bat-Miriam *et al.* 1962
Africa	Nigeria	970	12.6	Odeigah 1994
Africa	Nigeria	2013	12.5	Scott-Emuakpor *et al.* 1975
Africa	Northern Sudanese	100	4.0	Rife 1953
Africa	Nuer	110	18.2	Rife 1953
Africa	S Falasja	109	8.3	Bat-Miriam *et al.* 1962
Africa	Shilluk	105	20.0	Rife 1953
Africa	Tigré	119	5.0	Bat-Miriam *et al.* 1962
Africa	Tripolitanians	50	21.5	Jenkins 1965

Country or continent	Group	*n*	% Nontaster	Reference
Africa	Urban Bantu	86	2.3	Jenkins 1965
Australia	Aboriginal	50	NG	Lugg 1968
Australia	Aborigines	NG	50.0	Simmons *et al.* 1957
Australia	Aborigines	152	49.3	Simmons *et al.* 1954a
Central America	Miskito in Nicaragua	96	20.8	Stefano and Molieri 1976
Central America	Rama in Nicaragua	79	1.3	Stefano and Molieri 1976
Central America	Mexican	1689	10.4	Kalmus *et al.* 1964
Central America	Sumo in Nicaragua	85	8.2	Stefano and Molieri 1976
China	Chinese Immigrants	66	10.6	Barnicot 1950
China	Chinese Immigrants	167	6.0	Parr 1934
China	Han Lan Zhou City	538	11.0	Zhang *et al.* 1988
China	Dong Xiang Gansu Province	831	18.4	Zhang *et al.* 1988
China	Kazak Gansu Province, Akscu	161	19.3	Zhang *et al.* 1988
China	YuGru Gansu Province, Sunan County	486	23.0	Zhang *et al.* 1988
China	Hui Gansu Province, Linxia County	1323	17.6	Zhang *et al.* 1988
China	Tu Qinghai Province, Huzhy County	801	18.4	Zhang *et al.* 1988
China	SaLa Qinghai Province, Xuhua Country	1077	8.5	Zhang *et al.* 1988
China	Tibetan Gansu Province	914	13.6	Zhang *et al.* 1988
China	Mongolian Gansu, Suhua County	332	16.0	Zhang *et al.* 1988
China	Bao'an Gansu, Jishishan Country	545	5.1	Zhang *et al.* 1988
China	Han Chinese in Shanghai	106	10.0	Guo *et al.* 1998
Europe	Cumbria	854	19.7	Mitchell *et al.* 1977
Europe	Danes	314	31.8	Mohr 1951
Europe	England, Derbyshire	653	36.8	Cartwright and Sunderland 1967
Europe	England, Lancaster	835	27.5	Cartwright and Sunderland 1967
Europe	England, Northeast	777	28.9	Sunderland 1966
Europe	English	581	28.0	Akcasu *et al.* 1974
Europe	Finns	202	29.2	Allison and Nevanlinna 1952
Europe	Finns	761	22.1	Eriksson *et al.* 1970
Europe	Irish from Dublin	618	27.0	Boyd 1950
Europe	Isle of Man	699	27.8	Mitchell *et al.* 1977
Europe	Lapps	140	6.9	Allison and Nevanlinna 1952
Europe	Nellim Fisher Lapps	76	10.5	Eriksson *et al.* 1970
Europe	Nellim Skolt Lapps	138	29.7	Eriksson *et al.* 1970
Europe	Norwegian Lapps	255	17.6	Monn 1969
Europe	Salamis Island	183	32.2	Panayotou *et al.* 1983
Europe	Sardinians	541	27.1	Maxia *et al.* 1975
Europe	Sevettijärvi Skolt Lapps	251	28.3	Eriksson *et al.* 1970
Europe	Spaniards	306	24.8	Pons 1955
Europe	Spaniards, San Sebastian, Spain	172	27.0	Boyd 1950
Europe	Swedish	1051	12.8	Romanus 1965

Country or continent	Group	*n*	% Nontaster	Reference
Europe	Swedish, Southern	200	32.0	Akesson 1959a
Europe	Åland, Main Island	522	26.2	Eriksson and Forsius 1964
Europe	Sottunga	38	18.4	Eriksson and Forsius 1964
Europe	Kökar	121	34.7	Eriksson and Forsius 1964
Europe	Welsh	252	NG	Beach 1953
Europe	Welsh	398	28.0	Boyd 1950
Europe	Welsh, Carmarthenshire	271	35.2	Partridge 1962
Europe	Welsh, Pembrokeshire	1005	27.6	Pullin and Sunderland 1963
Europe	Yugoslavian	459	30.9	Grünwald and Herman 1963
Greenland	Eskimos from Umanaq	129	53.5	Alsbirk and Alsbirk 1972
India	Ahom	123	21.1	Sengupta and Dutta 1991
India	Angami Nagas	150	6.3	Seth and Seth 1973
India	Anglo-Indians	160	28.1	Bhattacharya 1964
India	Audich Brahman	200	35.0	Parikh *et al.* 1969a
India	Audichya Brahmans	200	37.0	Vyas *et al.* 1962
India	Bado Gadaba	409	53.6	Das *et al.* 1963
India	Bagatha	483	37.9	Babu *et al.* 1996
India	Baghdadi Jews	200	20.5	Sirsat 1956
India	Bareng Paroja	439	49.9	Das *et al.* 1963
India	Bene-Israel Jews	200	20.0	Sirsat 1956
India	Bengali Brahims of Lucknow	300	27.7	Deb and Shukla 1981
India	Bhangi Harijans	200	43.0	Vyas *et al.* 1962
India	Bhil	188	45.2	Vyas *et al.* 1962
India	Bod Mali	70	20.0	Babu *et al.* 1996
India	Bodh of Lahaul	110	11.8	Chowdhury 1988
India	Bohras	130	45.4	Hakim *et al.* 1973
India	Brahim of Orissa	56	33.9	Tripathy 1969
India	Brahims	165	20.0	Chandraiah and Bahadur 1975
India	Brahims of Narendra Nagar	170	29.4	Rani and Seth 1981
India	Brahmin	132	26.5	Srivastava and Tyagi 1967
India	Brahmin, Maharashtrian	58	27.5	Singh and Bagga 1994
India	Brahmins	242	23.6	Tiwari and Bhasin 1967
India	Brahmins of Bhimtal	217	17.5	Singh 1975
India	Chandraseniya Kayasth Prabhu	200	46.5	Sanghvi and Khanolkar 1949–50
India	Chenchu	132	37.9	Simmons *et al.* 1953a
India	Chenchu	227	55.1	Sirajuddin 1977
India	Chettibalija	155	40.0	Devi *et al.* 1995
India	Chitpavan	200	34.5	Sanghvi and Khanolkar 1949–50
India	Cutchi Lohana	200	39.0	Vyas *et al.* 1962
India	Danguria	126	15.1	Srivastava 1961

Country or continent	Group	*n*	% Nontaster	Reference
India	Delhi and Madras	301	28.0	Akcasu *et al.* 1974
India	Delhi students	102	29.0	Bhatia *et al.* 1979
India	Desasth	200	42.5	Sirsat 1956
India	Desasth Rigvedi Brahman	100	36.0	Sanghvi and Khanolkar 1949–50
India	Dhanka	211	56.3	Vyas *et al.* 1962
India	Dhobis	165	4.8	Ranganayaki and Injeti 1979
India	Dhobis	205	12.7	Balakrishna *et al.* 1992
India	Dhodia	83	42.2	Vyas *et al.* 1962
India	Dogra Brahmins	111	39.7	Sharma and Bhalla 1981
India	Dogra Rajputs	79	38.0	Sharma and Bhalla 1981
India	Dubla	207	45.4	Vyas *et al.* 1962
India	Gadaba	193	15.0	Babu *et al.* 1996
India	Gamit	200	53.5	Vyas *et al.* 1962
India	Gorkhas	202	14.4	Parmar 1968
India	Harijans	77	31.2	Chandraiah and Bahadur 1975
India	Hill Kolams	224	50.9	Ramesh *et al.* 1981
India	Hill Rajputs, Cis-Himalayan	159	24.5	Bhalla *et al.* 1980
India	Hindu Gujjars	200	56.5	Balgir 1992
India	Hindus	334	59.0	Dhesi *et al.* 1972
India	Immigrant Burmese	208	19.7	Agrawal 1966
India	Iranis	200	25.0	Sirsat 1956
India	Jalaris	215	15.8	Rao and Jaikishan 1995
India	Jalary	103	47.6	Reddy 1983, Reddy 1988
India	Jatapu	158	25.3	Babu *et al.* 1996
India	Jats	564	38.0	Chattopadhyay 1971
India	Jat-Sikhs	536	59.3	Dhesi *et al.* 1972
India	Juang of Orissa	75	38.7	Das *et al.* 1978
India	Kapol Vania	200	51.5	Vyas *et al.* 1962
India	Karana of Orissa	41	36.6	Tripathy 1969
India	Karnataka	353	45.6	Srivastava 1980
India	Kashmiri	800	11.8	Parveen *et al.* 1990
India	Kayastha	114	29.0	Srivastava and Tyagi 1967
India	Kayasthas of Lucknow	300	30.0	Deb and Shukla 1981
India	Keet	223	36.8	Das 1971
India	Keet of Assam	223	36.8	Das and Buragohain 1969
India	Khandayat of Orissa	49	18.4	Tripathy 1969
India	Khasis	317	21.8	Miki *et al.* 1960
India	Khattri	75	29.3	Srivastava and Tyagi 1967
India	Khojas	222	41.4	Hakim *et al.* 1973
India	Kodava of Kodagu	233	32.8	Saheb *et al.* 1979
India	Koli	128	38.3	Vyas *et al.* 1962

Country or continent	Group	*n*	% Nontaster	Reference
India	Kolis, Cis-Himalayan	142	27.5	Bhalla *et al.* 1980
India	Konda	234	53.4	Das and Mukherjee 1964
India	Konda Dora	350	35.1	Babu *et al.* 1996
India	Konda Kammaras	413	36.1	Babu *et al.* 1984
India	Kondhs or Orissa	51	64.7	Tripathy 1966
India	Kota of Nilgiri Hills	534	40.8	Ghosh 1973
India	Koya Dora	359	12.8	Babu *et al.* 1996
India	Koya Dora	569	51.0	Goud and Rao 1979a
India	Koya Dora	505	28.5	Parmar 1968
India	Kumaonis	194	12.4	Seth 1962
India	Kurmi Mahato	111	49.5	Basu *et al.* 1966
India	Lad Vania	200	33.5	Parikh *et al.* 1969a
India	Ladakhis	53	5.7	Bhalla 1972
India	Lahaulis	274	12.7	Sharma 1967
India	Lampadi	142	45.1	Goud and Rao 1979a
India	Lepchas	154	7.2	Miki *et al.* 1960
India	Leva Patidars	200	32.5	Vyas *et al.* 1962
India	Lower Caste	130	9.2	Srivastava and Tyagi 1967
India	Mahars	200	43.0	Parikh *et al.* 1969b
India	Manne Dora	380	34.5	Ramana and Naidu 1992
India	Manne Kolams	343	55.7	Ramesh *et al.* 1981
India	Manzai Mali	317	27.4	Babu *et al.* 1996
India	Maratha	200	42.5	Sanghvi and Khanolkar 1949–50
India	Maratha, Maharashtrian	989	31.4	Singh and Bagga 1994
India	Mathur Kayasths	422	57.8	Mathur *et al.* 1983
India	Mikir of Assam	114	11.4	Dass 1976
India	Misgars	153	45.1	Hakim *et al.* 1973
India	Moplahs	186	48.4	Hakim *et al.* 1973
India	Muslim	39	20.5	Srivastava and Tyagi 1967
India	Muslim	106	38.7	Bhattacharjee 1956
India	Muslim Gujjars	200	42.5	Balgir 1992
India	Muslims	105	20.0	Chandraiah and Bahadur 1975
India	Muslims	250	42.4	Hakim *et al.* 1973
India	Muslims of Lucknow	300	28.0	Srivastava 1976
India	Naika	78	46.2	Vyas *et al.* 1962
India	Naikpod	154	64.3	Goud and Rao 1979a
India	Nicobarese	83	18.6	Agrawal 1968
India	Nokte Naga	271	13.7	Kumar 1955
India	Non-Jat Sikhs	285	56.3	Dhesi *et al.* 1972
India	Northern Pahira	206	41.6	Basu *et al.* 1966
India	Ollaro	227	52.6	Das and Mukherjee 1964

Country or continent	Group	*n*	% Nontaster	Reference
India	Other castes of Orissa	49	28.6	Tripathy 1969
India	Pachhimaha	87	14.9	Srivastava 1964
India	Pallar	110	43.6	Buchi 1955
India	Paniyan	204	12.7	Das and Ghosh 1954
India	Panjabis	322	32.0	Sharma 1962
India	Paraja of Orissa	85	41.3	Das *et al.* 1978
India	Pardhans	140	62.9	Goud and Rao 1979a
India	Pardhans	202	51.5	Ramesh *et al.* 1981
India	Pareng	232	52.9	Das and Mukherjee 1964
India	Parsis	200	21.5	Sirsat 1956
India	Pathan	150	26.0	Srivastava 1974
India	Raj Gonds	163	54.6	Goud and Rao 1979a
India	Raj Gonds	239	47.3	Ramesh *et al.* 1981
India	Rajbanshi	580	40.7	Das *et al.* 1967
India	Rajputs	45	8.9	Srivastava and Tyagi 1967
India	Rajputs	229	25.3	Tiwari and Bhasin 1967
India	Rajputs of Palampur	87	29.9	Bagga and Seth 1992
India	Rana	155	18.1	Srivastava 1964
India	Rana of Orissa	29	31.0	Das *et al.* 1978
India	Rarhi Brahmin	143	35.1	Bhattacharjee 1956
India	Rastogis of Lucknow	300	17.0	Rastogi and Tyagi 1975
India	Reddys	183	21.3	Chandraiah and Bahadur 1975
India	Relli	175	1.7	Ranganayaki and Injeti 1979
India	Riang	401	16.2	Kumar and Sastry 1961
India	Samantha	250	9.2	Babu *et al.* 1996
India	Savara	200	26.5	Babu *et al.* 1996
India	Sayyad	150	26.7	Srivastava 1974
India	Scheduled, Maharashtrian	1073	35.4	Singh and Bagga 1994
India	Shompens of Nicobar	54	33.3	Agrawal 1969
India	Sikkimese Lepchas	107	13.1	Bhattacharjee *et al.* 1978
India	Sindhi	480	29.2	Khullar 1965
India	Southern Pahira	671	65.7	Basu *et al.* 1966
India	Spitians	110	12.0	Sharma 1967
India	Suddha	200	26.5	Sanghvi and Khanolkar 1949–50
India	Sukla	100	33.0	Sanghvi and Khanolkar 1949–50
India	Swangla of Lahaul	100	14.0	Chowdhury 1988
India	Talavia Dubla	212	42.9	Vyas *et al.* 1962
India	Tibetan refugees	230	17.4	Patel 1971
India	Tibetans	216	10.7	Sharma 1967
India	Tibetans	400	14.7	Tiwari 1966

Country or continent	Group	*n*	% Nontaster	Reference
India	Tibetans	106	12.2	Bhalla 1972
India	Uttar Pradesh	344	34.9	Srivastava 1959
India	Vadabalija of Penticotta	266	36.5	Reddy 1983, Reddy 1988
India	Vadabalija of Vadapeta	213	39.9	Reddy 1983, Reddy 1988
India	Vadabaljas	200	12.5	Ranganayaki and Injeti 1979
India	Vadnagara	108	25.0	Sirsat 1956
India	Vaisha	67	34.3	Srivastava and Tyagi 1967
India	Vaishya	351	35.3	Das 1971
India	Vaishya of Assam	351	35.3	Das and Buragohain 1969
India	Visa Oswal Jain	200	30.0	Parikh *et al.* 1969a
India	Vyshyas	131	17.6	Chandraiah and Bahadur 1975
India	Wad Balgel	114	66.7	Agrawal 1964
India	Weavers	112	24.1	Chandraiah and Bahadur 1975
Jamacia	Jamaicans	682	9.4	Terry 1950
Japan	Ainu	328	6.4	Simmons *et al.* 1953b
Japan	Ainu-Japanese	275	5.1	Simmons *et al.* 1953b
Japan	Formosans	3172	6.8	Rikimaru 1936a
Japan	Formosans	5933	7.1	Rikimaru 1936b
Japan	Japanese	295	7.1	Saldanha 1958
Japan	Japanese	314	33.1	Yanagida 1988
Japan	Japanese	656	8.0	Tsuji 1957
Japan	Japanese	915	9.4	Sato *et al.* 1997
Japan	Japanese	916	23.0	Suzuki 1949
Japan	Japanese	921	9.1	Fukuoka 1936
Japan	Japanese	1600	12.0	Matsunaga *et al.* 1954
Japan	Japanese	5871	13.1	Rikimaru 1936a
Japan	Japanese	8824	14.3	Rikimaru 1936b
Japan	Natives	1756	1.8	Rikimaru 1936b
Korea	Koreans	771	15.1	Kang *et al.* 1967
Middle East	Armenians from Beyrouth and Ghazir	311	25.0	Boyd 1950
Middle East	Aschkenasim	245	31.5	Parr 1934
Middle East	Balkan immigrants in Israel	101	21.8	Sheba 1962
Middle East	Berber in Israel	464	33.6	Guttman *et al.* 1967
Middle East	Cochin immigrants in Israel	41	31.7	Sheba 1962
Middle East	Cochin in Israel	402	42.0	Guttman *et al.* 1967
Middle East	Djerva immigrants in Israel	383	42.0	Guttman *et al.* 1967
Middle East	European Ashkenazim immigrants	440	20.7	Sheba 1962
Middle East	Gerba immigrants in Israel	41	41.5	Sheba 1962
Middle East	Habbanite	506	19.8	Bonne *et al.* 1972
Middle East	Iraqi and Persian immigrants in Israel	336	16.1	Sheba 1962
Middle East	Kurdistan immigrants in Israel	129	14.0	Sheba 1962

Country or continent	Group	*n*	% Nontaster	Reference
Middle East	Kurdistan immigrants in Israel	455	26.8	Guttman *et al.* 1967
Middle East	Libya immigrants in Israel	501	22.4	Guttman *et al.* 1967
Middle East	North-African immigrants in Israel	340	15.0	Sheba 1962
Middle East	Samaritans in Israel	125	6.4	Bonne 1966
Middle East	Semenites	59	32.3	Parr 1934
Middle East	Sephardim	175	28.0	Parr 1934
Middle East	Yemen immigrants in Israel	261	18.0	Sheba 1962
Middle East	Yemen immigrants in Israel	498	26.3	Guttman *et al.* 1967
New Guinea	Pygmies in Netherland New Guinea	178	36.0	Graydon *et al.* 1958
New Guinea	West Nakanai, New Britain	352	34.4	Simmons *et al.* 1956
North America	Alaskan Eskimos	68	26.0	Allison and Blumberg 1959
North America	American Indians admixed	110	12.8	Parr 1934
North America	American Indians, Kansas	183	6.1	Parr 1934
North America	American students, Gentile	232	20.3	Rife and Schonfeld 1944
North America	American students, Jewish	82	14.7	Rife and Schonfeld 1944
North America	Americans of African ancestry	107	7.5	Setterfield *et al.* 1936
North America	Americans of African ancestry	533	23.5	Parr 1934
North America	Americans of European ancestry	210	28.0	Taylor 1961
North America	Americans of European ancestry	291	35.4	Matson 1938
North America	Americans of European ancestry	477	17.8	Setterfield *et al.* 1936
North America	Blackfeet Indians	129	8.5	Matson 1938
North America	Caucasian Americans, USA	439	30.9	Parr 1934
North America	Caucasian Americans, USA	3643	29.8	Parr 1934
North America	Flathead Indians	442	17.4	Matson 1938
North America	Mennonite	1157	25.0	Koertvelyessy *et al.* 1982
North America	Micmac Indians	496	29.1	Chiasson 1963
North America	Papago Indians Arizona	70	1.4	MacRoberts 1964
North America	Ramah, New Mexico, USA	269	2.0	Boyd 1950
Polynesia	Cook Island	215	16.3	Simmons *et al.* 1955
Polynesia	Eastern and Central Islands	126	7.9	Simmons and Graydon 1957
Philippine	Negritos	73	13.7	Pascasio *et al.* 1974
Philippine	Philippine, non-Negrito	200	2.0	Pascasio *et al.* 1974
Puerto Rico	Puerto Ricans	1693	10.3	Thieme 1952
Russia	Kharkov	486	37.0	Boyd 1950
Russia	Kirghiz children	734	29.1	Ibraimov and Mirrakhimov 1979
Russia	Kirghiz students	640	19.6	Ibraimov and Mirrakhimov 1979
Russia	Russian students	245	31.9	Ibraimov and Mirrakhimov 1979
Russia	Siberians	137	5.8	Rychkov and Borodina 1969
Russia	Tiflis	455	23.0	Boyd 1950
Russia	Zagorsk	237	41.0	Boyd 1950

Country or continent	Group	*n*	% Nontaster	Reference
South America	Amoreeiras	70	8.6	Kalmus 1957
South America	Ashkenazic Jews in Brazil	244	27.9	Saldanha and Becak 1959
South America	Brazilian patients and staff	162	35.1	Kalmus, 1957
South America	Brazilian students	148	33.8	Kalmus 1957
South America	Brazilians of African ancestry	90	12.1	Kalmus 1957
South America	Brazilians of African ancestry	123	10.6	Saldanha 1962
South America	Buzios, Victoria	73	13.7	Kalmus 1957
South America	Caboclos	74	24.3	Kalmus 1957
South America	Caboclos, admixed	18	11.1	Kalmus 1957
South America	Carajas, Brazil	86	0.0*	Kalmus 1957
South America	Carajas, Brazil	86	0.0*	Junqueira *et al.* 1957
South America	Chileans	316	17.4	Saldanha and Nacrur 1963
South America	Curitiba	92	26.0	Freire-Maia and Quelce-Salgado 1960
South America	Highland Quechua, Peru	319	3.1	Frisancho *et al.* 1977
South America	Ilhabella	77	20.8	Kalmus 1957
South America	Ilhabella, admixed	43	16.3	Kalmus 1957
South America	Japanese immigrants	89	9.0	Kalmus 1957
South America	Japanese immigrants in Brazil	300	12.7	Beiguelman 1962
South America	Jivaro Indians, Ecuador	327	2.1	Sunderland and Ryman 1968
South America	Kaingangs	77	2.6*	Kalmus 1957
South America	Kaingangs	77	2.6*	Fernandes *et al.* 1957
South America	Lowland Mestizo, Peru	805	7.3	Frisancho *et al.* 1977
South America	Lowland Quechua, Peru	672	7.1	Frisancho *et al.* 1977
South America	Manaus Amazonia	90	15.6	Kalmus 1957
South America	Piracicaba, admixed	41	9.8	Kalmus 1957
South America	Presidente Prudente	73	8.0	Freire-Maia and Quelce-Salgado 1960
South America	Rio de Jan, admixed	203	11.9	Kalmus 1957
South America	Russian immigrants in Brazil	60	43.3	Freire-Maia *et al.* 1960
South America	Salvador, Ba	34	38.0	Freire-Maia and Quelce-Salgado 1960
South America	Southern Peruvian Quechua	522	2.9	Garruto *et al.* 1975
South America	Tucano Indians, Brazil	128	6.3	Montenegro 1964
South-East Asia	Burmese medical students	300	12.0	Than-Sint and Mya-Tu 1974
South-East Asia	Chinese immigrants in Singapore	50	2.0	Lugg 1955
South-East Asia	European immigrants in Singapore	50	19.6	Lugg 1955
South-East Asia	Malay	237	16.0	Thambipillai 1955–56
South-East Asia	Malay immigrants	50	15.6	Lugg 1955
South-East Asia	Malay, Negrito	50	18.0	Lugg 1956–57
South-East Asia	Malay, Senoi	50	4.0	Lugg 1956–57
South-East Asia	Tamil Indians in Singapore	50	26.8	Lugg 1955

Country or continent	Group	*n*	% Nontaster	Reference
South-East Asia	Thailand	56	5.4	Simmons *et al.* 1954b
South-East Asia	Thailand	460	9.7	Boobphanirojana *et al.* 1970
South-West Asia	Iraqi	110	21.8	Shah and Sattar 1981
South-West Asia	Kurdish in Iran	346	27.5	Lightman *et al.* 1970
South-West Asia	Turkey	315	5.0	Akcasu *et al.* 1974
South-West Asia	Turkey	366	11.2	Bokesoy and Togan 1987
South-West Asia	Turkey	684	4.1	Akcasu and Ozalp 1977
South-West Asia	Turkey	2000	20.0	Say *et al.* 1966

Studies varied in the methods to classify nontasters.

*May represent the same dataset published twice.

#Refers to the subcontinent of India.

NG = not given.