Current Biology

Taste Quality Decoding Parallels Taste Sensations

Highlights

- Large-scale electrophysiological response patterns code for taste quality in humans

- Taste quality is represented early in the central gustatory system

- Neural response patterns correlate with subjective perceptual experience

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In Brief

Taste allows discriminating nutritious and harmful food constituents. Crouzet et al. show that the earliest taste-evoked neural responses in the human cortex code for taste quality (e.g., salty or sweet). These neural response patterns were correlated with perceptual decisions, indicating that they form the basis of subjective taste experience.

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Taste Quality Decoding Parallels Taste Sensations

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http://dx.doi.org/10.1016/j.cub.2015.01.057

SUMMARY

In most species, the sense of taste is key in the distinction of potentially nutritious and harmful food constituents and thereby in the acceptance (or rejection) of food. Taste quality is encoded by specialized receptors on the tongue, which detect chemicals corresponding to each of the basic tastes (sweet, salty, sour, bitter, and savory [1]), before taste quality information is transmitted via segregated neuronal fibers [2], distributed coding across neuronal fibers [3], or dynamic firing patterns [4] to the gustatory cortex in the insula. In rodents, both hardwired coding by labeled lines [2] and flexible, learning-dependent representations [5] and broadly tuned neurons [6] seem to coexist. It is currently unknown how, when, and where taste quality representations are established in the cortex and whether these representations are used for perceptual decisions. Here, we show that neuronal response patterns allow to decode which of four tastants (salty, sweet, sour, and bitter) participants tasted in a given trial by using time-resolved multivariate pattern analyses of large-scale electrophysiological brain responses. The onset of this prediction coincided with the earliest taste-evoked responses originating from the insula and opercular cortices, indicating that quality is among the first attributes of a taste represented in the central gustatory system. These response patterns correlated with perceptual decisions of taste quality: tastes that participants discriminated less accurately also evoked less discriminated brain response patterns. The results therefore provide the first evidence for a link between taste-related decision-making and the predictive value of these brain response patterns.

RESULTS

All organisms require efficient mechanisms for taste classification to enable adaptive ingestion-related behavior. Accordingly, most animals are able to detect taste qualities bearing nutritional and/or behavioral relevance [1]. Humans can proficiently categorize prototypical substances of basic tastes [7]. The present study characterizes the dynamic neuronal activity in distributed cortical networks during tasting and its role for taste quality discrimination (i.e., perceptual decision-making) using time-resolved multivariate pattern analysis (MVPA) and electrical neuroimaging of head-surface electrophysiological recordings in humans.

Sixteen human participants tasted salty, sweet, sour, and bitter solutions (see Supplemental Experimental Procedures and Figure 1A) and performed a delayed four-alternative forced-choice (4AFC) taste discrimination task on each trial. The tastes evoked a significant electrophysiological response relative to the pre-stimulus period (global field power, GFP; see [8]) starting at 150 ms after taste onset (Figure 1B) corresponding to the first gustatory potential (P1; [9, 10]). Accordingly, the GFP showed the earliest signal increase for bitter (at 150 ms) and salt (152 ms) followed by sour (190 ms) and sweet (270 ms). Differences in the topographical distribution of the electric field independent of the electric field strength (global map dissimilarity, GMD; topographic ANOVA with 5,000 permutations, $p < 0.05$ for 50 consecutive time points [100 ms], but $p < 0.05$ for 15 consecutive time points [30 ms] for visualization of pairwise comparisons; see [8]) indicated that the underlying neuronal generators varied between taste qualities at around the same time (at 148 ms; Figure 1C).

After observing these topographical differences between tastes in the average across trials, time-resolved MVPA was used to evaluate whether the single-trial, instantaneous topographical pattern of electrophysiological activity carries information about taste quality. While human electrophysiological data are conventionally analyzed by averaging across numerous trials and subjects, MVPA leverages information in the topographical pattern on single trials in single subjects [11–13], thereby allowing to directly relate on a single-trial basis brain responses with subsequent behavior. Therefore, MVPA in humans offers the opportunity to relate this information to the subjective perception reported by the participants [14]. For each time point, classifiers were trained to perform multi-class, one-versus-one, or one-versus-all taste discrimination by using the single-trial electrophysiological activity of individual participants. A random sample corresponding to 90% of the
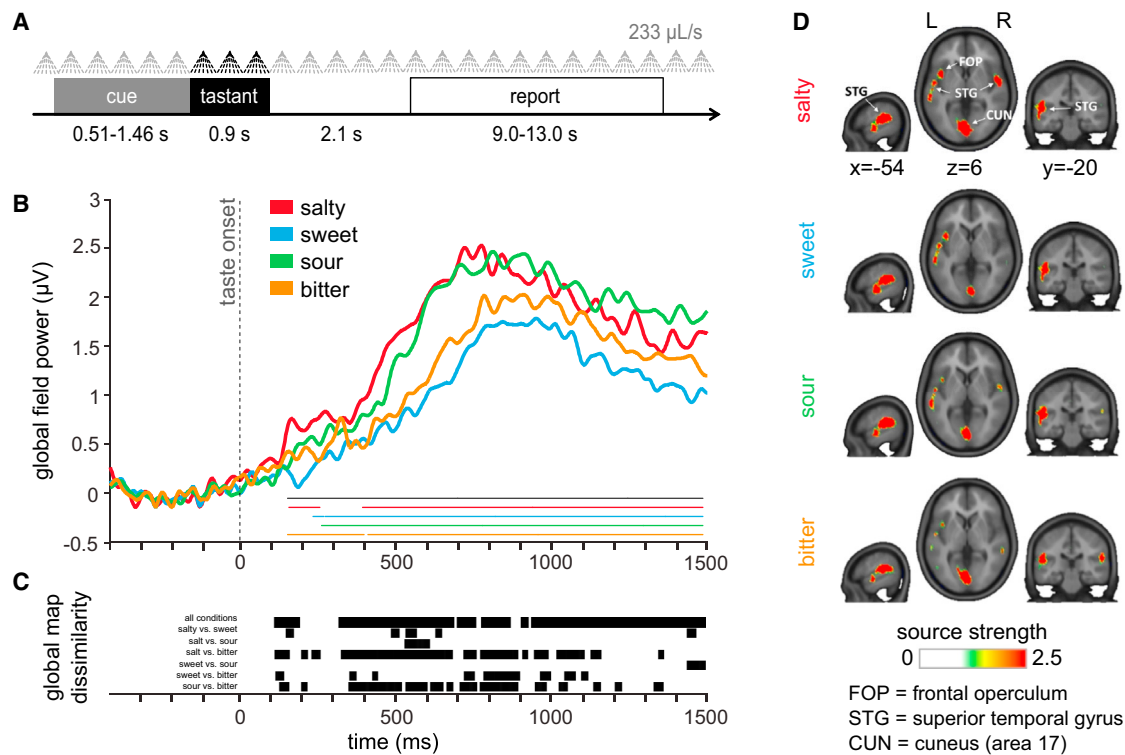
Figure 1. Event-Related Responses to Different Tastes Exhibited Differences in Electric Field Strength and Distribution

(A) Schematic of an experimental trial. Atomized tastants (indicated in black) were embedded in a regular stream of water sprays (gray).

(B) Global field power (GFP) for each taste category (averaged across participants). The time period during which the GFP differed from pre-stimulus levels is marked with a gray line for all tastes and with colored lines for individual tastes. Only p <0.05 lasting for at least 100 ms are shown.

(C) Periods of significant topographical differences (global map dissimilarity) between taste categories are indicated in black. The top row depicts the main effect of taste categories (only p <0.05 lasting for > 100 ms are shown); subsequent rows represent all pairwise comparisons: salty versus sweet, salty versus sour, salty versus bitter, sweet versus sour, sweet versus bitter, and sour versus bitter (p <0.05 for > 30 ms).

(D) Estimates of neural sources underlying the initial GFP-normalized taste-evoked responses (P1) include the frontal operculum and insula (predominantly of the left hemisphere), the bilateral superior temporal gyrus, and the cuneus for all tastes.

trials was utilized for training, leaving the remaining 10% for testing (120 cross-validations; Figure 2A).

In the multi-class analysis, the classifier was trained using data from all four tastes to provide an answer to the following question: "Which taste is this?" (any of sweet, salty, sour, or bitter; 25% chance performance). This is equivalent to the 4AFC tasks performed by the subjects. Taste quality could be decoded significantly above chance level at as early as 175 ms after stimulus onset at the group level (Figure 2B) and for most individual participants (Figure S2), indicating that taste quality is among the first attributes of a taste processed by the brain (see [6]). Notably, individual electrodes failed to provide sufficient information for discriminating between taste qualities above chance level (Figure S2). This result indicates that taste quality was encoded in multivariate spatial activity patterns that univariate measures are not sufficiently sensitive to detect as it has been shown previously in the visual domain (e.g., [12]). Interestingly and in contrast to similar analyses in the visual domain [12, 13], decoding accuracy outlasted taste presentation and remained above chance level during the entire analysis period (1,500 ms). This finding suggests that taste category information remains available during and beyond stimulus presentation, probably until the tastant is removed from the tongue.

Participants correctly categorized the tastes in 86% of all trials (salty: 72.9%; sweet: 96,0%; sour: 83.0%; bitter: 93.0%). The majority of the categorization errors occurred due to the confusion of salty with sour tastants (84% of all errors in salt trials) and sour with salty tastants (75% of all errors in sour trials). These confusions allowed us to evaluate whether this perceptual similarity stemmed from neuronal similarity between salty- and sour-evoked response patterns; we therefore investigated whether the classifiers were susceptible to the same confusion.

To this end, classifiers were trained to discriminate between all pairs of tastes (one-versus-one classification; Figure 2D). For one-versus-one classification, a classifier was trained using only data from two tastes to provide an answer to the question: "Is this taste X or taste Y?" (50% chance performance). Note that such classification of taste X versus taste Y is identical to classifying taste Y versus taste X. This analysis is most useful for studying which tastes share similar underlying neuronal representations and therefore are frequently confused by the classifier. The classifier's pattern of confusion showed a remarkable resemblance to the participants' pattern of confusion, i.e., taste quality could be decoded best for salty versus sweet and poorest for salty versus sour (Figure 2D).
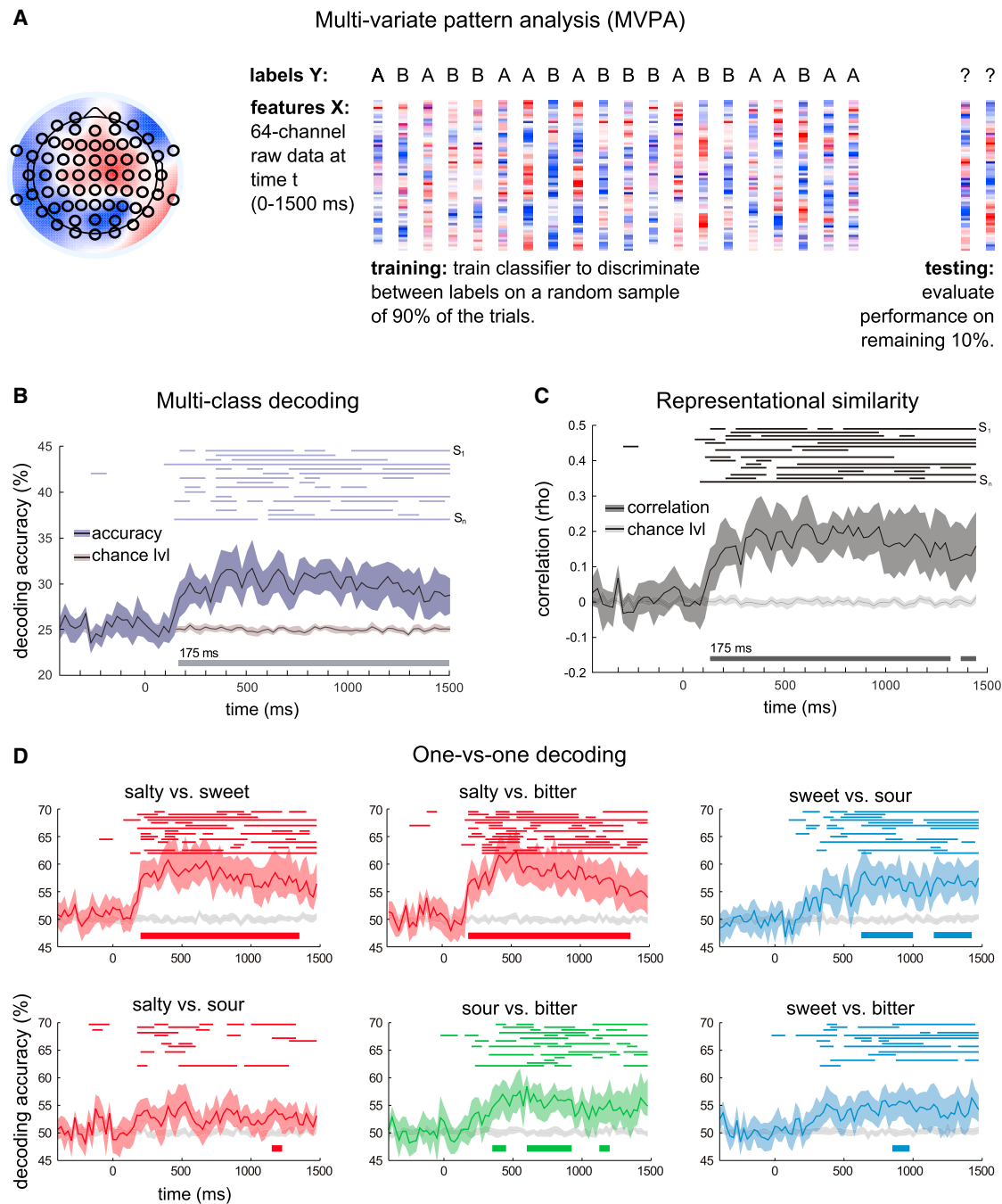
Figure 2. MVPA Yielded Significant Decoding Starting at 175 ms and a Close Relation to the Pattern of Errors of the Participants

(A) For a given participant and time point, a random sample of 90% of the trials was used to train a classifier to discriminate between brain responses (EEG scalp topography) associated with two (one-versus-one classification) or four (multi-class discrimination) tastants. Classification performance was then evaluated by using the remaining 10% of the trials. The entire procedure was repeated for 120 cross-validations.

(B) Multi-class decoding: classifiers were trained to provide at each time point an answer to the following question: "Which taste is this?" The black curve indicates decoding accuracy averaged across participants (shaded area: bootstrapped 95% confidence interval; light gray curve: average chance level). The thin (top) and thick (bottom) horizontal lines correspond to the period of significant decoding for individual participants and at the group level, respectively.

(C) Representational similarity analysis: behavioral confusion matrices were correlated with neural confusion matrices at each time point to estimate the similarity between taste representations in perceptual space and in neuronal space. Conventions are as in (B).

(D) One-versus-one decoding: classifiers were trained to provide at each time point an answer to the following question: "Is this taste X or taste Y?" Conventions are as in (B).

To further quantify this resemblance, we explored the representational similarity between subjective and neural taste representations. Since the multi-class decoding analysis corresponded to the participants' behavioral task (i.e., answering "Which taste is this?"), we obtained a dynamic neural confusion matrix that represented for each time point the proportion of trials in which the classifier categorized taste X as taste Y. These matrices are a representation of the neuronal space in which taste categories are coded since they show which taste-evoked neural patterns are similar and thus are frequently confused by the classifier. We also obtained each subject's behavioral confusion matrix, which is a representation of subjects' perceptual space, since it shows which taste categories are subjectively similar and therefore are most frequently confused by the subjects. Neural and behavioral confusion matrices were significantly correlated starting at 175 ms after stimulus presentation (Figure 2C). Thus, the time at which the classifiers' error patterns correlated with that of the participants also coincided with the earliest time at which the neuronal signal carried information about taste quality as indicated by the multi-class analysis. This result confirms that the information used by the classifiers for decoding formed the basis for the perceptual decision-making of each participant.

The relatively low decoding performance for salty versus sour tastants and the good decodability of salty versus bitter could imply that the former tastes are represented by similar neuronal response patterns while the latter tastes are represented by different patterns. However, tastes that the classifier could discriminate accurately could as well be represented by similar patterns, albeit at different latencies. For example, was the excellent decoding performance for salt versus bitter (Figure 2D) possible because bitter evoked the same neuronal response pattern as salt, but with a 200-ms delay? If so, a classifier trained to answer "Is this salt?" at time t should also be able to answer "Is this bitter?," but at time t + 200 ms. We tested for this possibility using one-versus-all decoding and a neural template analysis [12] across tastes and time. For one-versus-all decoding, a classifier was first trained at a given time point using data from all tastes to answer the following question: "Is this taste A?" (rather than taste B, C, or D) (Figure 3A). In the neural template analysis, a classifier trained for a given taste at a given time point (referred to as "train time" in Figure 3C) was then used to answer the same question for all other time points (referred to as "test time" in Figure 3C) and that taste. This corresponds to panels 1, 6, 11, and 16 in Figure 3C where the classifier is trained and tested on the same taste. Moreover, a classifier trained to detect taste A at a given time point was also used to detect all other tastes and all time points. If, for example, the salt-evoked neural pattern at 200 ms was identical to the bitter-evoked pattern at 400 ms, a template obtained by training the classifier on the salty taste at 200 ms should allow decoding of the bitter taste at 400 ms. In such a case, significant off-diagonal decoding accuracy should be found specifically along the tilted diagonal in the diagrams in Figure 3C (see illustration in Figure 3B). Clearly, no effects along the tilted diagonal were found for any combination of tastes tested, indicating that one-versus-one taste decoding was not in fact grounded on similar, albeit latency-shifted, neural patterns but rather was grounded on entirely distinctive neural patterns.

Furthermore, the neural template analysis confirmed the similarity of salty and sour taste representations. Specifically, when trained on salty taste, the classifier could accurately decode both salty (Figure 3C, 1) and sour tastes (Figure 3C, 9). On the other hand, classifiers trained on sour were only barely able to decode salty taste (Figure 3C, 3) and failed to perform better than chance at decoding sour (Figure 3C, 11). This asymmetry in across-taste decoding performance between classifiers trained on salty and sour can be explained by the lower signal-to-noise ratio in the sour condition (see Figure S1), which would specifically impair the template obtained during training [12]. The absence of off-diagonal decoding also has important implications for the dynamics of neuronal taste quality coding. Specifically, the panels representing training and testing on the same taste (especially 1, 6, and 16 in Figure 3C) showed effects only along the main diagonal, indicating that a classifier trained at time t can be only used for decoding at time t, but not at other time points. Such generalization to other time points would be reflected by significant off-diagonal decoding along the vertical or horizontal dimension (see Figure 3B). Thus, the neural patterns carrying the information that allows for the persistent decoding of taste quality are changing from one moment to the next.

To rule out the possibility that taste features other than quality influenced decoding performance, we next correlated participants' ratings of pleasantness and intensity with decoding performance for each pairwise comparison (e.g., salty versus sour). Overall, participants rated the tastes as moderately intense (mean: 55.0; range: 46.6–63.0; on a 100-point visual analog scale) and moderately pleasant (mean: 44.5; range: 34.6–62.9). No correlation was found between decoding performance and difference ratings of pleasantness (rho = 0.08, p = 0.45) or intensity (rho = 0.11, p = 0.26; Figure S3), indicating that decoding performance was not influenced by differences in perceived intensity and pleasantness between tastes.

To identify the neural network underlying the earliest taste-evoked response that carried taste quality information, we estimated the cortical generators of the P1 component [10] of the taste-evoked response for each taste [15]. Areas previously associated with gustatory processing in general and taste *quality* processing in particular [16–18], including the anterior and mid insula and the overlying frontal operculum (see [19]), the parietal operculum [20, 21], the superior temporal gyrus, and the cuneus (e.g., [22]), were activated by all tastes (Figure 1D). These observations suggest that the earliest sweep of activation through the gustatory network not only codes that *any* taste was detected but already allows for taste *quality* discrimination. Yet, future studies will have to assess whether individual structures within this network are indeed differentially activated by different tastes.

DISCUSSION

A full account of gustatory processing in humans must factor in the chemical, the neural, and the perceptual domains: phenomenological taste experiences are the result of a cascade starting with the binding of a chemical to a receptor, the elicitation of a signal that is further transduced, and the resulting neural stimulus representations. All three domains can be represented as a space—an abstract representation in which distances
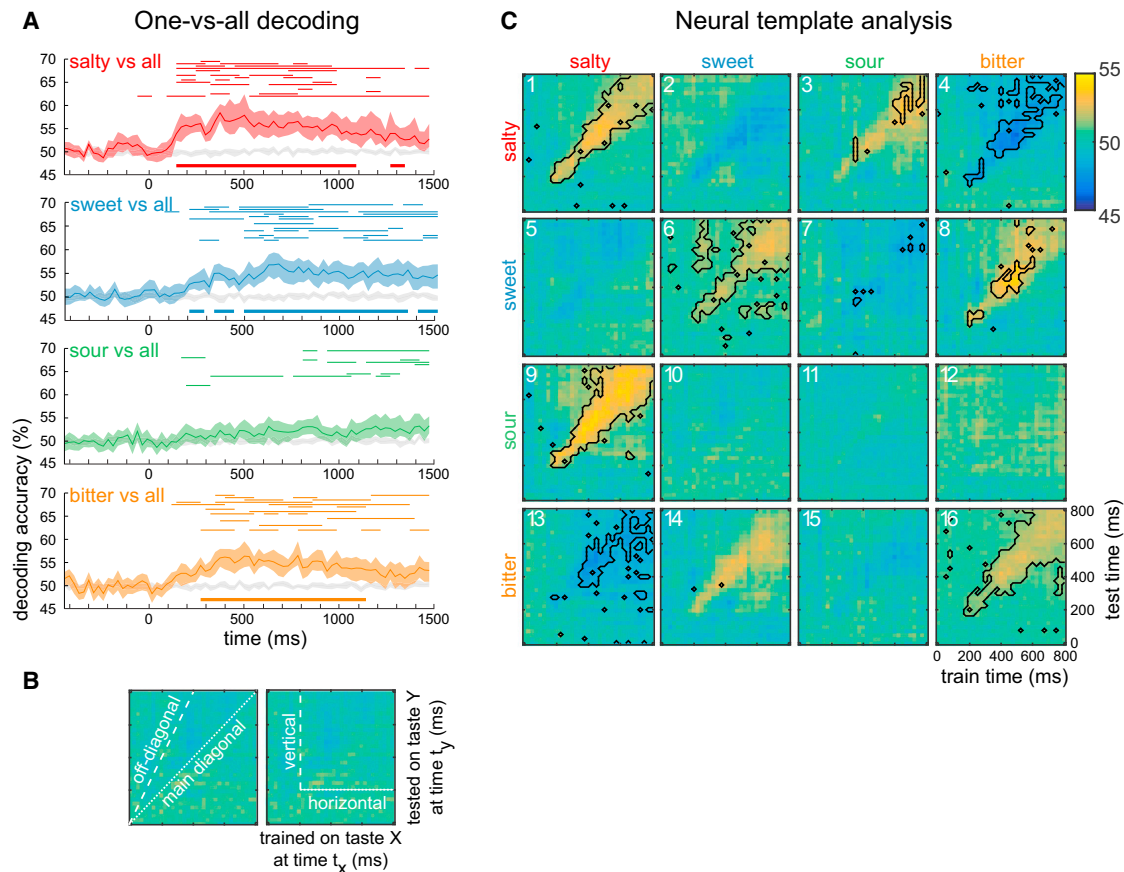
Figure 3. One-versus-All Decoding and Neural Template Analyses Reveal that Different Tastes Are Represented by Distinctive Neural Patterns

(A) For one-versus-all decoding, classifiers were trained to provide at each time point an answer to the following question: "Is this taste X?" Colored curves indicate decoding accuracy averaged across participants (shaded area: bootstrapped 95% confidence interval; light gray curve: average chance level). The thin (top) and thick (bottom) horizontal lines correspond to the period of significant decoding for individual participants and at the group level, respectively.

(B) Illustration of the hypothetical patterns in the neural template analysis. Classifiers were first trained to discriminate taste X versus all other tastes at a given time point (training time t_x). This classifier was then tested by using it to discriminate taste Y at all time points (testing time t_y). Left: significant decoding along the main diagonal indicates that tastes X and Y are represented by similar neural patterns at the same latency. By contrast, significant decoding along the tilted, off-diagonal dimension indicates that tastes X and Y are represented by similar neural patterns but at different latencies. The off-diagonal illustrated here would correspond to a constant latency shift of 200 ms for taste Y relative to taste X. Right: significant decoding along the horizontal and vertical dimensions indicates that both tastes are represented by the same neural pattern and that this pattern generalizes across time.

(C) Neural template analysis testing for the generalization of decoding across time and tastes [12] based on one-versus-all classification. Panels depict the performance of different classifiers trained on one taste at different time points and tested on the same or a different taste at all time points. Time points of significant decoding are highlighted with contour lines. Note that the main diagonals in panels 1, 6, 11, and 16 are equivalent to the results shown for one-versus-all decoding in (A).

correspond to similarity relations [23]. For example, in the neural space, each dimension corresponds to the activity of one neural unit or, as in our case, electrode. If two tastants evoke neural patterns that are close in neural space, their response patterns are similar. Likewise, two tastes that are close in perceptual space are expected to taste similar. While considerable effort has been made to elucidate how the chemical space is encoded within the neural space, e.g., by identifying receptors for different tastants on the tongue [1] and also by characterizing response patterns of peripheral or cortical gustatory neurons [2, 4, 24, 25], the mapping of the neural space onto perceptual space—the role of neural response patterns in subjective gustatory perception and gustatory-related behavior—has received

little attention. Thus, the present study investigated this mapping in humans. Specifically, we used MVPAs of electroencephalographic recordings and psychophysical data to study how and when taste identity is represented in cortical neuronal responses and how the neuronal responses relate to perceptual decisions. We found that taste quality discrimination relied on transient large-scale neural response patterns.

Based on these neural response patterns, classifiers could accurately predict which of four tastes was presented in a given trial. Our findings are in line with previous electrophysiological studies in rodents indicating that neuronal response patterns along the gustatory processing pathway, including the nucleus of the solitary tract [26], parabrachial nucleus [27], and gustatory

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cortex [28], allow accurate classification of taste quality. For each taste, the time at which taste quality information was available coincided with the latency of the first taste-evoked response, suggesting that taste quality represents one of the most elementary taste features. In all sensory systems, the initial event-related response is associated with the representation of sensory stimulus features such as the size of a visual stimulus [29] and the loudness of sound [30] as well as the intensity of tastes [31, 32] and odors [33]. Importantly, we excluded that other phenomenological experiences like intensity and pleasantness, which are processed in the insula [34, 35], contributed to taste quality discrimination and influenced decoding performance. Notably, taste quality information could be decoded throughout and beyond the stimulation interval, but the exact patterns that carried this information were changing from moment to moment, implying that cortical taste representations are highly dynamic.

We demonstrate that the information encoded in the multivariate neural response patterns is also the basis for gustatory perceptual decision-making: the more similar the multivariate response patterns of any two tastes were (and thus, the less a classifier could discriminate between them), the more these tastes were confused by the participants. To our knowledge, our study is the first to show that the subjective discriminability of tastants is related to their neural dissimilarity and thus reveals a neural-perceptual mapping.

Source estimations provided a visualization of likely predominant sources for this early response, which originated mainly in the insular cortex and the overlaying opercula, areas that have been previously associated with taste processing in functional neuroimaging [19] and electrophysiological [10] studies. The insular cortex, in particular, has been linked to taste quality processing in rodents [36], primates [37], and humans [19]. Our results extend previous findings by revealing the earliest time (150 ms) at which the insula is likely involved in taste quality processing. Importantly, GMDs indicated that different subpopulations within the insular-opercular network are activated by each taste to a different extent. Note that this finding is equally compatible with different proposals for the gustotopic organization of the insula, which argue for either extensive [4], partial [36], or minimal [2] spatial overlap between populations of neurons tuned to different tastants. Advancements in and the combination of multivariate and imaging techniques will have to resolve whether these differences result from activation of specialized but segregated areas within a cortical region, e.g., the insula-opercular cortex, or from differences in distributed neuronal activation patterns within a region.

Together, our results provide the first evidence that taste quality is encoded at the earliest level of the taste processing cascade and, at the same time, corroborate the notion that taste-evoked brain responses in the human brain occur much earlier [10, 32, 38] than traditionally proposed [39, 40]. Notably, the early taste-evoked responses reported here are in strong alignment with electrophysiological studies in awake rodents [6, 25, 41]. Thus, our findings offer fundamental insights into the mental chronometry of taste quality processing and its relation to taste-related decisions, which provide the perceptual foundation for food intake and weight management. We anticipate that our results will ignite further investigations using time-resolved whole-brain responses to understand taste intensity and valence coding, which also contribute to gustatory gratification.

EXPERIMENTAL PROCEDURES

Data were recorded from healthy humans (n = 16) during the tasting of salty (sodium chloride), sweet (sucrose), sour (citric acid), and bitter (quinine) solutions. Taste stimuli were given as 210-μl atomized aliquots delivered during a 900-ms period. To minimize oro-tactile responses, we embedded taste pulses in a constant stream of water pulsed at 3.3 Hz by using a computer-controlled GU002 gustometer (Burghart Messtechnik). In each trial, participants performed a delayed 4AFC taste discrimination task and rated the intensity and pleasantness of each taste (see Figure 1A and Supplemental Information for a detailed description of the protocol).

Electroencephalogram (EEG) was recorded from 64 channels (actiCAP amplifier, Brain Products) at a sampling rate of 500 Hz. Data were cleaned of artifacts using independent component analysis and rereferenced to average reference (see Supplemental Information for a detailed description of EEG recording and preprocessing).

Time-resolved MVPA was applied to the single-trial data to test whether brain response patterns differ between tastes. Linear classifiers based on L2 regularized logistic regression [42] were used to find the optimal projections of the sensor space for discriminating between two (discrimination between two tastes) or more (multi-class discrimination between all four tastes, corresponding to the participants' behavioral task, or one-versus-all discrimination) conditions at each time point. This allowed us to assess how and when taste category information was available in the EEG data. For each time point, the performance of the classifier was determined by using a Monte-Carlo cross-validation (CV) procedure (n = 120) in which the entire dataset was randomly split into a training set (90% of the trials) and a test set (the remaining 10% of the trials) at each CV (Figure 2A; see Supplemental Information for a detailed description of the MVPA).

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures and three figures and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2015.01.057.

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