



## Delta activity encodes taste information in the human brain

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### ABSTRACT

The categorization of food via sensing nutrients or toxins is crucial to the survival of any organism. On ingestion, rapid responses within the gustatory system are required to identify the oral stimulus to guide immediate behavior (swallowing or expulsion). The way in which the human brain accomplishes this task has so far remained unclear. Using multivariate analysis of 64-channel scalp EEG recordings obtained from 16 volunteers during tasting salty, sweet, sour, or bitter solutions, we found that activity in the delta-frequency range (1–4 Hz; delta power and phase) has information about taste identity in the human brain, with discriminable response patterns at the single-trial level within 130 ms of tasting. Importantly, the latencies of these response patterns predicted the point in time at which participants indicated detection of a taste by pressing a button. Furthermore, taste pattern discrimination was independent of motor-related activation and encoded taste identity rather than other taste features such as intensity and valence. On comparison with our previous findings from a delayed taste-discrimination task (Crouzet et al., 2015), taste-specific neural representations emerged earlier during this speeded taste-detection task, suggesting a goal-dependent flexibility in gustatory response coding. Together, these findings provide the first evidence of a role of delta activity in taste-information coding in humans. Crucially, these neuronal response patterns can be linked to the speed of simple gustatory perceptual decisions – a vital performance index of nutrient sensing.

### 1. Introduction

The internal representation of sensory events is fundamental to the perception of the external world and adaptive behavior. Such a representation is achieved in a spatial distribution of neuronal activation which initiates communication across spatially distributed brain areas (cf. Fries, 2015). Rhythmic neuronal activity or oscillations have been regarded as a key mechanism in the process of neural communication in different species (Buzaki, 2006), for instance by sequencing information into temporal processing windows (cf. Lopes da Silva, 1991), and by linking neural assemblies through phase coherence (Tallon-Baudry, 2003; Fries, 2005, 2015). Oscillatory neural activity has been associated with various brain functions (motor action, Salenius and Hari, 2003; consciousness, Ward, 2003; learning and memory, Kahana, 2006; motivation and reward, Knyazev, 2007; attention, Klimesch, 2012). Recent advances in the field suggest that dysfunctions of the nervous system can often be traced back to disturbed network activity which lead to the concept of “oscillopathies” in neurodegenerative diseases (cf. Nimmrich et al., 2015), for instance revealing pathophysiological beta oscillations

in Parkinson's disease (Little and Brown, 2014), gamma oscillations in Schizophrenia (Mathalon and Sohal, 2015), and both alpha and gamma oscillations in Alzheimer's disease (Nimmrich et al., 2015). Notably, the identification of impaired network functioning necessitates prior characterization of normal activity, beginning with the sensory systems as the initial points of interaction with the external world. Such rhythmic activity is currently well characterized for the visual, auditory, somato-sensory, and olfactory senses in various species (cf. Koepsell et al., 2010), yet insufficiently so for the gustatory system. Only recently have findings provided evidence of the role of slow-wave synchronized activity in taste processing in rodents (Pavao et al., 2014), whereas no studies have characterized the time-frequency dynamics of the human gustatory system.

This lack of knowledge of the frequency by which information is transmitted within the human gustatory system surely does not reflect the importance of the gustatory system. On the contrary, the ability to taste ensures an organism's survival by enabling the identification of nutrients and avoidance of toxins via a discrimination of taste categories (often referred to as *taste qualities*). Accordingly, taste categories have

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been associated with carbohydrates (sweet), electrolytes (salty), acids (sour) or alkaloids (bitter). In rodents, distinct receptors on the tongue respond to chemicals signifying each taste category (Chandrashekar et al., 2006) before the signal is transduced upstream via the gustatory nucleus of the solitary tract in the rostral medulla, and the ventro-posterior medial nucleus of the thalamus to the gustatory cortex in the insula (Carleton et al., 2010). There is evidence of two competing models of taste coding: hardwired, labelled lines with specialized neurons (Chen et al., 2011), and flexible, learning-dependent taste representations (Accolla et al., 2007; Carleton et al., 2010), possibly through broadly tuned neurons (Stapleton et al., 2006). Notwithstanding the unresolved issue of how taste categories are encoded along the peripheral gustatory pathway, at the level of gustatory cortex, however, taste information can be decoded from dynamic activity patterns obtained from neuronal ensembles (Jones et al., 2007) and local field potentials (Pavao et al., 2014) in rodents, and large-scale EEG scalp recordings in humans (Crouzet et al., 2015). The availability of taste information from large-scale recordings enables investigations of the time-frequency dynamics of cortical information transfer in taste perception.

For our investigation, we recorded multi-channel head-surface electroencephalography (EEG) in human participants while they detected salty, sweet, sour, or bitter solutions, in order to investigate the neural mechanism by which the human gustatory system encodes taste information. First, we investigated whether the taste-evoked electrophysiological response would selectively engage a specific frequency band, given that frequency-specific neuronal signatures have been observed in other sensory systems (see Koepsell et al., 2010). Since participants received four different tastants, we were further able to test whether taste-specific content is represented in the frequency-specific activity. Second, we hypothesized that this phenomenon would not be a mere by-product of network activity, but bear functional relevance for perceptual decisions (see Harmony, 2013), by specifically testing whether the timing of the neural gustatory response would predict the timing at which participants detect a taste. Third, because task dependency has been reported with respect to taste-related behavioral responses in humans (Halpern, 1986; Bujas et al., 1989) and cortical activation in rodents (Fontanini and Katz, 2009), we probed the flexibility of human gustatory processing by comparing taste-evoked neural responses between the speeded detection task presented here and a previously reported delayed categorization task (Crouzet et al., 2015).

## 2. Materials and methods

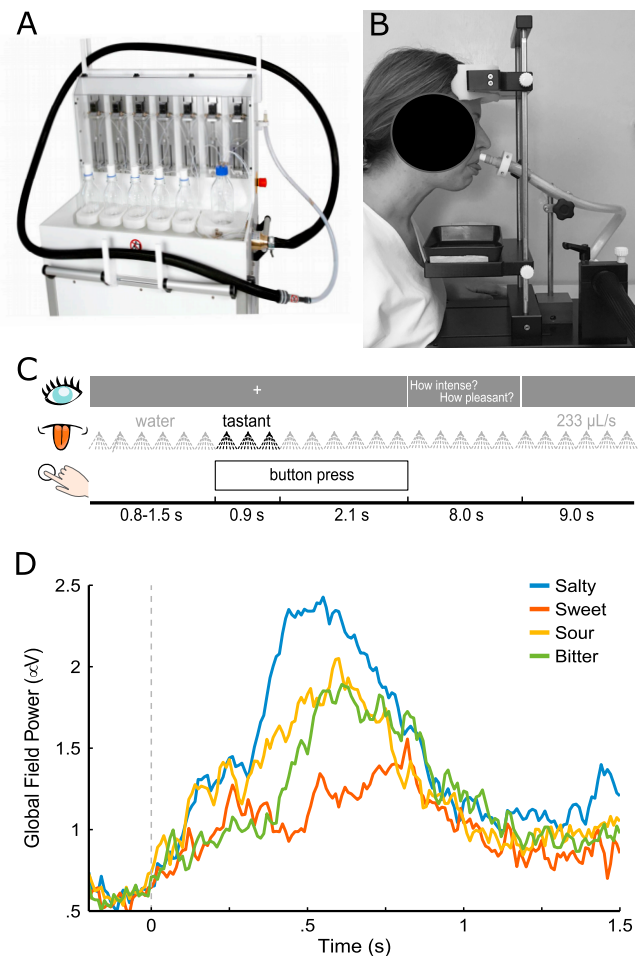
### 2.1. Participants

Sixteen healthy participants (12 women; mean age  $28 \pm 5.1$  SD years; BMI  $22 \pm 3.0$  SD) completed the study. Participants reported having no taste impairments and no history of neurological or psychiatric disease. They signed informed consent prior to the start of the experiment and received monetary compensation for participation. The study protocol conformed to the revised Declaration of Helsinki and was approved by the ethics board of the German Psychological Society.

### 2.2. Stimuli and taste delivery

Tastants were aqueous solutions with a clear taste: 0.65 M sodium chloride (salty; from a local supermarket REWE GmbH, Köln, Germany), 0.039 M citric acid (sour; CAS 77-92-9, Sigma Aldrich, Inc., St. Louis, MO, USA), 0.44 M sucrose (sweet; from a local supermarket REWE GmbH, Köln, Germany), 0.0002 M quinine monohydrate (bitter; CAS, 207671-44-1, Sigma-Aldrich, Inc., St. Louis, MO, USA) and 0.05 M Splenda® (sweet; Tate & Lyle, London, UK) in distilled water. Splenda trials were not included in the present analysis because they were perceptually indistinguishable from sucrose. Concentrations were chosen based on previous studies to be clearly perceivable and to not elicit discomfort or disgust. Taste stimuli were 210  $\mu$ l aliquots delivered at a

flow rate of 233  $\mu$ l/s during 900 ms as aerosol to the anterior part of the slightly extended tongue with the GU002 gustometer (Burghart Messtechnik GmbH, Wedel, Germany; Fig. 1A). The gustometer stores taste and rinse solutions in separate bottles that each supply a syringe pump with a check valve (cf. Iannilli et al., 2015). Solutions and compressed air are transported via separate 5 m long Teflon tubes to a manifold outlet within a spray nozzle that atomizes the liquid. The individual tubes run inside a hose filled with water at 38 °C thereby heating the stimuli, which are, after atomization, delivered at near body temperature to minimize any thermal sensations. The spray nozzle is positioned 1–1.5 cm above the slightly extended tongue so that the spray covers a large area of the anterior tongue's surface. During the experiment, the participant comfortably leans against a forehead rest, which stabilizes the head and holds the spray nozzle in place. In this position, liquids were applied to the slightly extended tongue and not swallowed but collected in a bowl underneath the chin (Fig. 1B). The position was monitored online via camera to ensure that the spray continuously covered the surface of the anterior tongue and to observe movements. The stimulation comprises a regular sequence of spray pulses, during each of which 70  $\mu$ l of liquid are dispensed during 100 ms every 300 ms. The timing and flow rate were



**Fig. 1. Experimental setup.** A: The GU002 gustometer (Burghart Medizintechnik, Wedel, Germany) delivers liquids via separate lines and at constant temperature. B: Vaporized tastants and rinse are applied to the extended, anterior tongue. Tastants are not ingested but collected in a reservoir underneath the participant's chin. C: Schematic depiction of a trial including the display, taste stimulation, and response. Atomized tastants (black) were embedded in a sequence of water (gray). Motor responses were recorded between taste onset and rating prompt. D: Grand-averaged global field power (GFP) for each of four tastes; different tastes are shown in different colors. Stimulus onset is at 0 ms.

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