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CO_2 Modulates the Central Neural Processing of Sucrose Perception

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Introduction

The five universally accepted tastes, sweet, salty, sour, bitter, and umami (a savory sensation elicited by monosodium glutamate) have specific receptors in oral, pharyngeal and laryngeal regions [1].

The most credited candidates to the function of human primary taste cortex are the frontal operculum and the anterior insula; while the opercular cortex and the orbitofrontal cortex are thought to code for secondary gustatory functions, while the amygdale and the dorsolateral prefrontal cortex are involved as hierarchically superior processing units [2]. Conversely, more is known on the peripheral pathway of taste, including the molecular dynamics of many receptors [3].

In addition to the basic tastes, the gustatory system appears responsive to CO_2 but the presence of specific CO_2 peripheral receptors and central neural pathway is still debated [4]. In the absence of a dedicated neural processing and cortical representation, CO_2 might still induce a powerful modulation of different gustatory inputs, implying that sweetness, bitterness, sourness, saltiness, and umami, or their combination in specific beverages, may be perceived as profoundly different in the presence of carbonation.

Everyday experience provides ample evidence in favor of this hypothesis. Among the different interferences carbonation may produce, the modulation of sweet perception appears of particular practical interest, given the widespread use of CO_2 in sweet beverages [5]. In particular, the contribution of carbonation to taste may not even be properly gustatory in nature, given that the CO_2 stimulation operates on mechanical and chemical trigeminal receptors that provide tactile, proprioceptive, chemosensory and nociceptive information from face, mouth, and nose [6].

A new, powerful tool to extend our knowledge of hPTC has been recently provided by fMRI, which has already proven essential in conveying extremely valuable information on the functional anatomy of other neural sensory pathways. In this study, we investigated the effect of carbonation on the brain processing of sweet stimuli. The cortical representation of taste-related neural responses has been studied by a Philips 3 T scanner in an echo planar blood oxygenation-level–dependent (BOLD) experiment, while gustatory stimuli were delivered by computer-controlled automatic injectors.

Methods

The study involved nine volunteers (mean age 23 years, 5 men and 4 women), not reporting any olfactory, gustatory, neurological or psychiatric disorder, and free from the use of any medication. Informed consent was given by all the participants and the study was approved by the local ethics committee. The brain functional examination was performed through the acquisition of time-series of Magnetic Resonance (MR) images using a 3 Tesla MR scanner (Philips, Eindhoven, The Netherlands) during the delivery of gustatory stimuli.

Two computer controlled automatic injectors delivered the stimuli directly triggered by the MR radiofrequency pulses, while the subjects laid still in the scanner.

A total of two different gustatory stimuli were used, each a variation of a commercial beverage differing only for the presence of carbonation agent: 1) carbonated, sweetened with sucrose, 2) non-carbonated, sweetened with sucrose. All the tastants were kept at controlled low temperature (4°C). Each MRI-compatible injector (Spectris Solaris, MedradTM) delivered two solutions both in the quantity of 10 ml each (speed of injection: 5ml/sec). To avoid cross-contamination of stimuli, each stimulus was delivered by the principal line of a specific injector, while the secondary line delivered water. The alternation of stimuli and water prevented physical and perceptual overlapping between the different tastes. The subjects held the solution or the water in their mouth for 10 seconds and then swallowed it, following acoustic cues given 1 second prior to the injection and swallowing phases.

Stimulation and washing periods were composed of three phases (Injection=2 sec, Tasting=10 sec, Swallowing= 3 sec), and were separated by a resting period of 15 seconds.

MRI acquisition and pre-processing

The functional time-series, consisting in the repetition of whole brain volumes, were acquired with a Philips Achieva scanner at 3T (IRCCS SDN Naples, Italy) by means of T2*-weighted gradient echo planar imaging sequences (TE 35 ms; matrix 96 × 96; FOV 210 ×210 mm; in-plane voxel size, 2.1875 × 2.1875 mm; flip angle 90°; slice thickness 4 mm).

Functional volumes consisted of twenty-two bi-commissural slices, acquired with a volume repetition time (TR) of 2000 ms with an inter-slice time of 90 ms. A total of 610 volumes were acquired for each subject, and the first two volumes were discarded to ensure steady-state

longitudinal magnetization. Subsequently, a high-resolution structural volume was acquired via a T1-weighted 3D TFE SENSE sequence (sagittal; matrix 256 × 256; FOV 256 × 256 mm; 181 slices; slice thickness 1 mm; no gap; in-plane voxel size 1 mm × 1 mm; flip angle 8°; repetition time TR 7.658 ms; TE 3.483 ms) to provide the anatomical reference for the functional scan.

Functional data were pre-processed using BrainVoyager™ QX, version 1.9 (Brain Innovation, Maastricht, The Netherlands), correcting the slice timing dispersion and the motion in the time series, and removing linear and non-linear "drifts" in the time courses (temporal high pass filter of two cycles). Finally, functional data were aligned with T1-volumes and warped into the standard anatomical space of Talairach and Tournoux. The resulting time-series were filtered in space with a spatial smoothing Gaussian kernel of 5 mm FWHM.

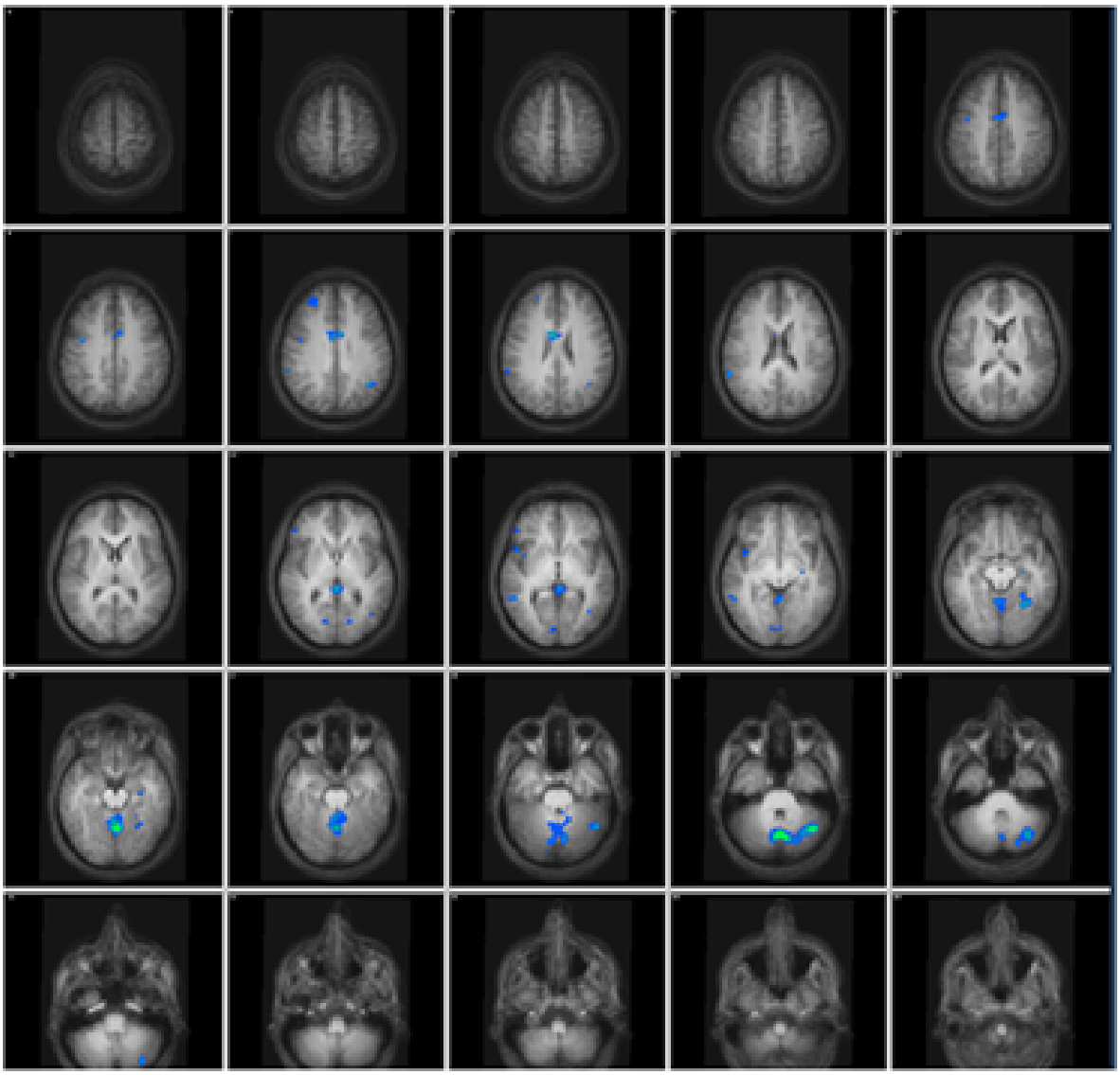

Figure 1: The presence of (carbonation versus non-carbonated beverages) in the sucrose sweetened solutions produces relative decrease (blue) in taste-related brain activity, evident in the right hemisphere in the insular cortex, latera orbitofrontal cortex, ventrolateral prefrontal cortes, bilaterally in the cingulate cortes, the tempero-parietel and tempero-occipital junction, and the cerebellar vermis and in the left side in the inferior occipito-temporal cortex and the hemispheric cerebellar cortex.

Data analysis

The statistical processing of fMRI data was carried out through BrainVoyager™, by analyzing the random effects of a General Linear Model (n=9, P[cluster corrected]<0.05), after correction of serial correlation [AR-1], Z-transformation of predictors, and correction for multiple comparisons through randomization.

Carbonated versus non-carbonated sucrose sweetened solutions were analyzed. The functional contrast was projected on the average anatomy of the Talairach-transformed T1-weighted 3D TFE SENSE of all the subjects, after reaching a threshol of $P<0.05$.

Results

The presence of carbonation (carbonated versus non-carbonated beverages) in a sucrose sweetened solutions produced (Figure 1) a relative decrease in taste-related brain activity, evident in the right hemisphere in the insular cortex, lateral orbitofrontal cortex, ventrolateral prefrontal cortex, bilaterally in the cingulate cortex, the temporo-parietal and temporo-occipital junction, and the cerebellar vermis and in the left side in the inferior occipito-temporal cortex and the hemispheric cerebellar cortex.

Discussion

In the present study, we investigated the central neural pathway in response to gustatory stimulation by sucrose and the modulation of sweet perception operated by carbonation, monitoring the changes in blood oxygenation with BOLD fMRI.

According to some authors, carbonation plays such a large role in the sensory profiles of beverages containing sugar as to inhibit their perception.

In our experiment, the presence of carbonation decreased the neural processing of sweetness, in keeping with the behavioral decrease in sensitivity. This neural effect was present in a widespread cortical and subcortical pattern (Figure 1).

The negative modulation of behavioral taste sensitivity and of the neural processing of sweetness operated by carbonation, deserves a discussion in the light of the increasing brain activity that carbonation is able to produce.

Studies about taste interactions showed a consistent pattern of mixture suppression in which sucrose sweetness tended to be both the least suppressed quality and the strongest suppressor of other tastes. The regulation of food intake is, among others, driven by a combination of sensory information, somatosensory signals of gastric fullness and chemical signals indicative of nutrient depletion.

The presence of carbonation is able to induce evident effects on the brain, by interacting strongly with the central processing of sweetness. These data support the view that carbonation is able to markedly interact with sweetness perception, reducing the global sensitivity to sucrose.

In conclusion these findings provide insightful information on the interaction between carbonation and sweet taste processing, and may help design new beverages where pleasantness and diet requirements would reach the best possible compromise.

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