Taste laterality studied by means of umami and salt stimuli: An fMRI study

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ABSTRACT

Aim of the present study was to investigate laterality of the gustatory system in the human brain for the taste qualities elicited by MSG (monosodium glutamate) and NaCl (sodium chloride). A total of 23 subjects participated in a block-design functional magnetic resonance imaging (fMRI) study. Liquid stimuli were presented at supra-threshold concentrations and delivered by means of a computer controlled gustometer. Left and right sides of the mouth were stimulated separately in order to correlate statistical parametrical maps to both the site of the stimulus and the specific taste quality. Following the effects of the site of stimulation through primary and secondary gustatory cortices an effort was made to explore the laterality of the gustatory pathways. Our results showed for both tastants a predominance of ipsilateral connections at the thalamus level. Insula left and right regions were both involved for both tastants. In these regions we found a high proportion of ipsilateral connection again for both the tastants. Considering orbitofrontal/prefrontal cortex, left-sided stimulation with NaCl or MSG produced left-sided activation of the orbito-frontal cortex clearly indicating the presence of an ipsilateral path. Finally, the hypothesis of frontal operculum as primary gustatory cortex and lateral prefrontal cortex as secondary was also supported by the results from dynamic causal modeling.

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Introduction

Regarding the cerebral processing of gustatory information it is well established in primates that the primary taste cortex is located inside the anterior insula/frontal operculum (I/FO) (Haase et al., 2009; Rolls and Scott, 2003; Rolls et al., 1996; Yaxley et al., 1990) and the secondary cortical taste area is situated in the caudolateral orbitofrontal cortex (OFC) (Rolls et al., 1990). Similar relations seem to be present in humans but the definition as well as the positions of primary and secondary taste cortices is not yet definitely clarified. Using positron emission tomography (PET) Small et al. (1997a) reported taste induced activations of the FO and bilateral OFC. Frey and Petrides (1999) showed a bilateral activation in the I/FO. Kinomura et al. (1994) among others, observed activations in the insula. By means of functional magnetic resonance imaging (fMRI) de Araujo et al. (2003a) found that stimuli such as sucrose and umami activated areas inside the I/FO and caudolateral OFC. Schoenfeld et al. (2004), found taste-activated brain areas close to the ones mentioned above, with stable activation patterns during repeated stimulation. According to Barry et al. (2001) electric taste stimulation of the tongue activated I/FO, which has also been shown in numerous other studies using natural stimuli (de Araujo et al., 2003b; Faourion et al., 1998; Haase et al., 2009; Small et al., 1997b).
regions of insula and overlying operculum but not in the anterior Insula of fO. Further details about the debate on the definitions of the primary and secondary gustatory cortices are extensively exposed in Small (2010) but also in Veldhuizen et al. (2011).

Because of the open question of the lateralization of gustatory information processing, we wanted to study the laterality of the gustatory pathway in relation to salty (NaCl) and umami (monosodium glutamate: MSG) stimuli using an fMRI approach. While everybody is familiar with salt, the taste of umami (Ikeda, 1909) is the taste of proteins. Umami is present in palatable foods such as meat, fish, tomatoes, mushrooms, and dairy products and it has been shown to stimulate food intake in mammals (Prescott, 2004; Yamaguchi, 1991). In the present study we tried to clarify whether there is laterality in the processing of gustatory information dependent on taste quality. Specifically, we applied salty and umami taste in liquid form to the left and right sides of the tongue/oral cavity, and we recorded the subsequent brain activity by means of fMRI. Based on a region of interest (ROI)-analysis we followed brain activations along the ‘taste map’, as defined in Veldhuizen et al. (2011) in regions such as thalamus, 1/fo, orbital frontal cortex (OFC), prefrontal cortex (PFC) and limbic system. The results should guide us to depict a hypothetical connectivity among brain areas involved with the lateralized taste stimulus that we intended to assess using a formal analytic method, Dynamic casual modeling (DCM) (Friston et al., 2003).

Materials and methods

Participants

Twenty-three healthy, right-handed volunteers participated in this study (13 women; mean age ± standard error = 28.3 ± 1.4 years). The study was approved by the Ethics Committee of the Technical University of Dresden Medical School. Written informed consent was obtained from all subjects prior to the experiment.

Stimuli

Two tastants, NaCl and MSG, were used in diluted form. Stimuli were presented at supra-threshold concentrations of 50 mM for both NaCl and MSG, based on previous studies performed on human umami taste determination (Singh et al., 2010) (de Araujo et al., 2003a; Lugaz et al., 2002; McCabe and Rolls, 2007). Stimulation was restricted to the lateral parts of the tongue and mouth, more than 2 cm distant from the anterior tip of the tongue. Each side was stimulated separately.

Taste delivery system: the gustometer

The liquid stimuli were delivered by means of a computer controlled gustometer (Burghart GU002 – variant GM04; Burghart instruments, Wedel, Germany). The gustometer was placed outside the scanner room; tubings for stimulation were funnelled through a dedicated opening into the scanner room. Stimuli were delivered in a pulse design (total pulse volume 1 ml, total pulse duration 3.3 s) at room temperature (24 °C) through two Teflon™ tubes placed inside the subject’s mouth. Apart from taste, stimulation was void of any cues that would have made subjects aware of the stimulus onset. The small dimension (1.3 mm inner diameter, 1.5 mm outer diameter) made it possible for the tubes to be placed in a comfortable manner inside the mouth. The tubes were positioned on the lateral edges of the tongue in order to separately stimulate the sensory cells in the taste buds located on each side of the tongue.

Olfactory and gustatory screening

The olfactory function of all subjects was investigated using the validated “Sniffin’ Sticks” test (Hummel et al., 2007; Kobal et al., 1996). The subjects included in the study demonstrated a normal sense of smell. Similarly, the gustatory function of the subjects was evaluated by standardized taste test kit, the “taste strips” (Landis et al., 2009; Mueller et al., 2003; Schuster et al., 2009). All subjects included in this study had test scores within the normal range.

Experimental procedure

The fMRI paradigm was built in a 50 s-block design (Fig. 1(b)). According to visually presented information on an MRI-room dedicated screen, subjects were told to maintain the tastants in the mouth as long as a gray field was visible. Then the subjects received the information “swallow” and after 5 s the information “rinse” was given together with 1 ml of water (10.8 s of duration). As evidence that the liquid tastant was maintained to the side of the mouth we did a simulation of the experiment using a food coloring (blue) diluted in water, with a final solution having almost the same fluidity of the original one. The tubings (1.3 mm inner diameter and 1.5 mm outer diameter) were positioned in the tongue in the same way as in the real experiment, the volunteer lied in supine position and we delivered 1 ml of blue-solution for 30 s in his mouth. Right after the instruction ‘swallow’ we took a picture of his mouth; it is visible in Fig. 1(a).

The paradigm was such as AsrBsrBrAsrBsrAsr, where A and B refers to the two different taste qualities, s refers to the instruction “swallow” and r to “rinse”. At the end of each session subjects were instructed to move the set of tubings from one side of the tongue to the other side, without altering their head position in order to avoid any undesired movement artifacts. The order of presentation of A and B conditions and the site of stimulus application (L=left and R=right) were pseudo-randomized across sessions and subjects.

The whole experiment included 4 sessions (two L and two R), including 6 repetitions for condition A and six for condition B, for an acquisition-time total of 20 min per subject.

Psychophysics rating and assessment

After every fMRI session subjects were asked to verbally rate the intensity of the stimuli (on a scale between 0, not perceived, and 10, extremely intense). The rating scores were analyzed by means of the mathematical functions available in Excel (Office 2010; Microsoft, Redmond, WA, USA).

fMRI acquisition

To detect the BOLD (blood oxygenation level dependent) signal, a 1.5 T scanner (SONATA-MR; Siemens, Erlangen, Germany) was used. For each subject the functional images were a total of 168 volumes/session and they were acquired by means of 27 axial-slice mosaic 2D SE/EP sequence (TR=2500 ms/TE=45 ms/FA=90°/matrix=64×64/voxel size = 3×3×3.75 mm³). Moreover, a structural high resolution (0.78×0.78×1 mm³) reference image was added for each volunteer dataset (3D IR/GR sequence: TR=2180 ms/TE=3.93 ms).

fMRI data analysis

The fMRI data analysis was performed by means of SPM5 (Statistical Parametric Mapping; Wellcome Department of Cognitive Neurology, London, UK) implemented in Matlab 7.5 R2007b (Math Works Inc., MA, USA). Spatial pre-processing included: slice timing to reduce the differences in slice acquisition times, realignment and
unwarp to minimize movement effects and susceptibility artifacts, normalization in a stereotactic space and smoothing by means of an $8 \times 8 \times 8$ mm$^3$ FWHM Gaussian kernel (Ashburner and Friston, 2003) in order to improve the signal-to-noise-ratio and reduce residual differences between subjects. Pre-processed functional data were modeled in single-subject first level analyses using the canonical hemodynamic function and its derivative set available in SPM. All scans acquired during mouth rinsing and swallowing were excluded. Statistical parametric maps for group inferences were produced by a second-level random-effects analysis (Penny et al., 2003) using a $2 \times 2$ factorial design (two stimulus conditions, NaCl, and MSG×two sites of stimulus application, L and R). The data from one subject was discarded due to movement artifacts, leaving a final group of 23 subjects.

To assess the laterality of the gustatory pathway, based on the hypothesis described in the Introduction, we applied a ROI analysis of the fMRI imaging data choosing the following regions of interest: thalamus, insula, frontal operculum, orbitofrontal cortex, prefrontal cortex and some areas of the limbic system (including anterior cingulate cortex, amygdala, and hippocampus). The ROIs were depicted using the human atlas available in WFU PickAtlas v2.4 software (Mai et al., 2004; Maldjian and Burdette, 2004; Maldjian et al., 2003). Specifically the thalamus ROI comprehended left and right regions of thalamus with a total of voxels of 728, the insula regions were based on 604 voxels on the left side of the brain and similarly on the right, the frontal operculum comprehended 396 voxels in each side separately, the orbitofrontal cortex in two areas, one was constituted only by Brodmann’s area 47 (615 voxels for each side) and a separate area that was constituted by Brodmann’s areas 10 and 11 (467 voxels); for the prefrontal cortex we used the union of BA 44, 45, and 46 (596 voxels). Finally, for the limbic system we considered amygdala and hippocampus left and right in one ROI of 521 voxels, and separately the anterior cingulate cortex (ACC) defined by the union of BA25 and BA32 (594 voxels).

Spm-fMRI assessment

The statistical parametrical maps were assessed at a voxel height threshold of $p_{FWE}<0.05$, a cluster level of a minimum of 3 voxels, and exclusion masked with p-value in a range of $4E-4<p<2.5E-4$ ($p_{FWE}$ equivalent) dependent on the dimension of the ROI, by an spm-contrast with relative extent depending on the condition (5 voxels minimum to 32 voxels maximum per region on interest). For example, to assess activations inside the I/O as an effect of MSG applied to the left side of the tongue (namely MSG_L), the t-contrast MSG, exclusion masked by the contrast MSG_R was used. Because Guest et al. (2007) demonstrated that thermal stimulation elicited activation in the insular cortex, and Iannilli et al. (2008) found somatosensory processing to involve areas in insular cortex and thalamus, this masking was applied in order to highlight only the areas activated by the tastants, and to hide potential effects by other sensory inputs such as thermal, mechanical, visual or auditory responses. Moreover, this mask allowed to focus on brain activations related to the specific quality of tastants, directly linked with the site of application in the mouth.

All coordinates reported in this manuscript are in MNI space. The Pick-Atlas software toolbox (Mai et al., 2004; Maldjian and Burdette, 2004; Maldjian et al., 2003).
2004; Maldjian et al., 2003) and Atlas of the Human Brain (Mai et al., 2004) were used to identify the brain areas.

**Dynamic causal modeling**

To estimate coupling among brain regions showing activity in relation to lateralized stimulation we implemented a DCM, that is a mathematical method to identify connectivity in functional brain network (Friston et al., 2003). It permits model comparisons among hypotheses, using a Bayesian statistical approach (Bayesian model selection or BMS) (Penny et al., 2004; Stephan et al., 2009).

To develop DCM the following approach was applied: (1). Brain regions resulting from fMRI group analysis were considered as brain areas potentially connected. (2). Using those areas various models were defined, specifying the input, the bilinear and the intrinsic terms. (3). The BOLD fMRI time series was extracted, for each region in the single subject where the activation was statistically significant. (4). Each model was estimated using the single subjects. (5). BMS was defined in order to find the best model, first in single subjects using an FFX approach and then. (6). At a group-level using fixed and random effect methods (Stephan et al., 2009, 2010). Models were fitted using the DCM10 software in SPM-8 (Friston et al., 2003).

The anatomical coordinates of the regions considered in the models were based on the maxima of statistically significant activation clusters resulting from the group analysis (see SPM-fMRI assessment and ROI in functional imaging sections). It included the left VPM thalamic nucleus, left fO and left IFPC (see Fig. 6(a)). For each subject the BOLD fMRI time series was extracted in the volume of interest (VOI) with 10 mm diameter centered in the previously described location, where a subject had no significant activation at the specific coordinate the center of the VOI was adjusted to the next suprathreshold voxel. The threshold for the single subject was set at p<0.001. Among the 23 subjects 12 of them showed suprathreshold activation in those areas. For each subject each model was fitted, and then for each subject the comparison among the models was evaluated. The accuracy of the model is indicated by the free-energy criterion, F (Friston et al., 2007), that approximates what is called the negative log-evidence, so the best model is characterized by the greatest log-evidence. That is why this parameter is used to compare models within and between subjects.

**Results**

**Intensity ratings**

The results of the intensity ratings of the two taste stimuli obtained during functional neuroimaging acquisition showed that subjects did not perceive a significant difference in intensity (I) between the NaCl and the MSG stimuli [(mean ± s.e.)NaCl = 3.6 ± 2.0; (mean ± s.e.)MSG = 4.8 ± 1.9; 2-sample t-test, t11 df = 44 = 1.58, p = 0.12], indicating that stimulus intensity was well matched between the two different tastants. Moreover, the effect between intensity and stimulus presentation site was neither statistically significant for NaCl [(mean ± s.e.),right = 3.1 ± 0.5; (mean ± s.e.),left = 3.8 ± 0.5; t11 df = 44 = 1.25, p, left-right = 0.22) nor for MSG [(mean ± s.e.),right = 4.8 ± 0.5; (mean ± s.e.),left = 4.9 ± 0.4; t11 df = 44 = 2.6, p, left-right = 0.80].

**ROI in functional imaging**

**Thalamus**

To assess the activations related to the site of stimulus application we used the t-contrast ‘tastant-A(B)’, exclusion masked by the t-contrast ‘tastantA(B)_L’ (‘R’). Thus, to look in the thalamus at the effect of NaCl applied on the left side of the tongue (NaCl_L) we used the contrast ‘salt’ exclusion masked by the t-contrast ‘NaCl_R’, and, similarly, for the effects of stimulation of the other side as well as for the effect of the other tantant.

The results are summarized in Table 1 and Fig. 2. The condition MSG_L yielded clusters both in the left and right side of the VPM-thalamus, whereas right-sided stimulation with MSG produced a right-sided VPM-thalamic activation. The condition NaCl_L generated a cluster of activation in the left side of the brain; in contrast, the condition NaCl_R produced no activation in the thalamus at the set statistical level, although at a lower p-value (punc = 0.001, pFWE = 0.06) an activated voxel at the right side was found. Altogether this information seems to indicate a predominantly ipsilateral processing for the stimulus NaCl, as opposed to MSG.

**l/F**

The results of the ROI analysis in the I/F insula and frontal operculum are summarized in Table 1 and Fig. 3. The contrasts used were ‘tastant-A(B)’, exclusion masked by the t-contrast ‘tastant-A(B)_L’ (‘R’), similar to the one illustrated in the previous paragraph. We found that the left-sided application of NaCl produced only one cluster of activation in the left fO. When the same stimulus was applied on right side of the tongue, activations were localized in left insula/fO (3 clusters) and one in the right fO.

MSG stimuli presented on the right side of the tongue produced activations in the right and left side of insula and fO. No suprathreshold clusters were found when MSG was applied on the left side of the tongue. However, searching for a small volume

<table>
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<tr>
<th>Table 1</th>
<th>ROI analysis showing the effect of tastants applied on the left or right side of the tongue.</th>
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<tr>
<td>p(k-cor)</td>
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<tr>
<td>MSG_R</td>
<td>No suprathreshold voxels</td>
</tr>
</tbody>
</table>

Maximum coordinate x,y,z in MNI-space. P value corrected at FWE level. Z: statistical value. k: number of voxels inside the cluster. p(k-cor): p value at the cluster level. ±: Insula; IFPC: frontal Operculum. *Brain area in the left fO shared by both tantants. **Brain area in the right fO shared by both tantants.
correction driven by insula/fO coordinates found in the meta-analysis presented in the work of Veldhuizen et al. (2011), a cluster of 6 voxels was found to be significantly activated in the left fO (Table 1).

OFC and PFC
With a contrast similar to the one described above, we found that the effect of the tastants, when presented on the left side of the tongue, produced an activation in the left OFC for both MSG_L and...
NaCl_L. The application of the liquid stimuli on the right side of the tongue did not produce significant activation in the ROI analyzed (Table 1, Fig. 4).

Limbic lobe

In the limbic lobe the effects of the lateralized stimulation assessed by means of t-contrasts as described above were not statistically significant for either taste quality, NaCl and MSG.

Discussion

Laterality of MSG and NaCl

The primary goal of this study was to elucidate by means of fMRI the laterality of the gustatory system when stimulated by umami and salt. Our results are based on ROI analysis along the ‘taste map’, that, as recently identified by activation likelihood estimation analysis (ALE) (Veldhuizen et al., 2011), includes: thalamus, I/fO, OFC/PFC and some areas in the limbic system. Spm-contrasts were defined in a way that the results would stress the neuronal connection specifically related to the taste quality presented to the left or right side of the tongue.

Results in the thalamic (Fig. 2) region showed bilateral activation following MSG stimulation, with a predominance of ipsilateral processing. Similarly, left and right-sided stimulation of the oral cavity with NaCl produced ipsilateral activation at the thalamic level.

Activations of the I/fO (Fig. 3) were more pronounced for both tastants when they were presented to the right side of the tongue. Overlap among several areas was also observed: both tastants shared an area of activation in the left side of the insular cortex (stressed in
Table 1 by two asterisks) as well as an area in the right frontal operculum (stressed in Table 1 by two open circles).

At the level of the OFC/PFC we found similar activations for both stimuli in the left inferior frontal gyrus (Fig. 4). The two areas are almost overlapping (Table 1). No supra-threshold voxels survived for right-sided stimulation in the OFC/PFC region.

Finally, the absence of activations inside the limbic lobe indicated that – at this level – the information related to the lateralized stimulation is lost.

Altogether our results show a predominance of ipsilateral processing for both tastants. The left stimulus condition has effects on the thalamus, insula and left OFC, while the effects of right-sided stimulation in the OFC/PFC region.

Gustatory pathway models

Information of how activated areas are connected is not directly deducible from fMRI results. Specifically, in the gustatory system it is established, from clinical/anatomical studies, that afferents form the tongue project to the ipsilateral nucleus of the solitary tract (Goto et al., 1983; Jyoichi et al., 1985; Nakajima et al., 1983); from here, studies based mostly on single case report, suggest that second order fibers project to the ventral posterior medial (VPM) thalamus, but the laterality of this projection is controversial. Moreover following the hypothesis presented in neuroimaging studies, the insula and fO seem to be seats of the primary gustatory cortex (Rolls and Scott, 2003) even though it is not precisely defined the location (Small, 2010; Veldhuizen et al., 2011) while the IPFC is the putative secondary gustatory cortex (Rolls, 2000; Rolls and Scott, 2003).

Combining this previews knowledge with our results we can draw a model of the gustatory pathway for the simplest emerging network

![Fig. 4. Activations in the OFC ROI-analysis (P_{FWE-corr} < 0.05, cluster level = 3, t-level in color coded labeled) by the stimulus conditions salt on the left side of the tongue (NaCl_L in orange) and umami on the left side of the tongue (MSG_L in blue). The stimulus conditions NaCl_R and MSG_R did not produce any significant activation at the set statistical level. The relative bargraph showing the contrast estimated and the 90% of confidence interval at the maximum is reported for each activation and it is color coded in each condition, with the relative stimulus condition. For every slice the relative ROI is shown in a small window. The reported coordinates are in MNI space, on the pictures R = right.](image1)

![Fig. 5. Gustatory pathway laterality drawn based on our fMRI-results for NaCl (salt) taste and preview knowledge from neuroimaging, clinical and anatomical studies.](image2)
that is the neural correlate to the left-sided stimulation with NaCl. Fig. 5 illustrates it. Following the classical hypotheses, that fO/Insula constitutes the primary gustatory cortex and lPFC the secondary gustatory cortex, our analyses revealed the path indicated with (a) in Fig. 5. We will refer to it as Model 1 (M1). Beside this first classical model we cannot exclude another possible path, indicated with (b) in Fig. 5. It considers insula and lPFC, both receiving direct input from the thalamus. This idea is supported by neuroimaging studies on humans about the OFC (Elliott et al., 2000), and by findings of pronounced connections between the most anterior section of the lateral subdivision in the OFC/PFC, which is exactly the area that we found to be involved, and both the mediodorsal thalamus and the granular field of the insula (Fuster, 1997; Goldman-Rakic, 1987). We will refer to this model as Model 2 (M2).

Finally for the sake of completeness, we consider a third model in which we hypothesize lPFC receiving input from both insula and thalamus (Model 3, M3).

In order to study the connectivity among those emergent areas involved in lateralization of gustatory perception we implemented a DCM based on the three models described above (Fig. 6(b)). We decided to focus on the specific activations correlated with the NaCl-stimulus that gave us the most linear results on the left side of the brain. In the model the exogenous input (Fig. 6(b) section, red arrows) was thought to influence the thalamus state, while the connections between the involved regions were modeled as intrinsic connection (Fig. 6(b)-section, black arrows).

Comparison of models

Bayesian model selection among the three models was performed for each subject. The results are reported in Fig. 7. M1 was best in nine subjects out of twelve subjects, whereas for three subjects the highest log-evidence was for M2. More relevant are the results about the BMS for the whole group, which were achieved using both the approach ffx and rfx (Fig. 8). The fixed effect results show a maximum log-evidence for M2 equivalent to 2.62 that means a BF over 13, this by convention (Raftery, 1995) indicate positive evidence for M2 at the...
group level. Moreover the BF for M1 was over eight, that means the following model ranking M2>M1>M3 emerged, which was also supported by the model posterior probability with 60% to the advantage of M2, and 36% for M1. The same ranking resulted from the rfx analysis comparisons where it provided 40% expected probability in favor of M2 and the 38% in favor of M1, while the model exceedance probability was estimated as 43% for M1 and 40% for M2. Thus, the current results provide positive evidence that lateralized taste stimulation activates the left VPM thalamic nucleus fibers of which directly project to the left fO, and from here, second order fibers are sent to the left IPFC.

Conclusions

In conclusion the main finding of the present study is that activation by both applied tastants, MSG and NaCl, indicated a predominant ipsilateral link between the nucleus of the solitary tract and the ventral posterior medial nucleus of the thalamus. Moreover, in relation to the stimulation of the left side of the oral cavity the ipsilateral predominance remained evident also at the level of insular cortex and IOFC. Dynamical casual modeling implemented on the left brain network, involving thalamus, fO and IPFC, in the salt condition, indicated as most likely connection the one that goes from thalamus to fO to IPFC. This supports the hypothesis of a primary gustatory cortex located in fO and a secondary g.c. in the IPFC.

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