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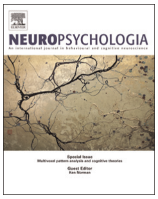

Neural correlates of taste perception in congenital blindness

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ABSTRACT

Sight is undoubtedly important for the perception and the assessment of the palatability of tastants. Although many studies have addressed the consequences of visual impairment on food selection, feeding behavior, eating habits and taste perception, nothing is known about the neural correlates of gustation in blindness. In the current study we examined brain responses during gustation using functional magnetic resonance imaging (fMRI). We scanned nine congenitally blind and 14 age- and sex-matched blindfolded normal control subjects while they made judgments of either the intensity or the (un)pleasantness of four different tastants or artificial saliva that were delivered intra-orally. The fMRI data indicated that during gustation, congenitally blind individuals activate less strongly the primary taste cortex (right posterior insula and overlying Rolandic operculum) and the hypothalamus. In sharp contrast with results of multiple other sensory processing studies in congenitally blind subjects, including touch, audition and smell, the occipital cortex was not recruited during taste processing, suggesting the absence of taste-related compensatory cross-modal responses in the occipital cortex. These results underscore our earlier behavioral demonstration that congenitally blind subjects have of lower gustatory sensitivity compared to normal sighted individuals. We hypothesize that due to an underexposure to a variety of tastants, training-induced cross-modal sensory plasticity to gustatory stimulation does not occur in blind subjects.

1. Introduction

The importance of sight for taste perception is highlighted by the popular French saying “Nous goûtons avec les yeux” (We taste with our eyes). Unlike smell, touch and audition that sense foods both prior (e.g. orthonasal olfaction) and during (e.g. retronasal olfaction) ingestion, vision is the sense that solely (and naturally) perceives food outside the body. On the other hand, taste perception is restricted to the internal experience of food inside the mouth (e.g. sweet, bitter) or digestive tract (e.g. visceral distension). Therefore, the sight of foods builds a mindset of expectations about the internal experience of the foods we eat. In a single eye blink, we gather information about the availability, location, identity, palatability, flavor, texture, intensity, pleasantness, and nutritive and energy contents of the food objects. Through learning, vision powerfully sharpens our expectations about a food and prepares the body to respond accordingly (Feldman and Richardson, 1986; Powley, 2000; Crum et al., 2011). At the brain level, sight modulates the gustatory cortex to respond to tastants according to expectations (Nitschke et al., 2006; Veldhuizen et al., 2011). Stimulus-specific representations can also be activated before the experience of the stimulus. For example, seeing taste-related (compared to non-taste-related) words or pictures of foods (compared to non-foods) produces activity in the hedonic-hunger network, that includes visual and reward areas together with primary (insula and overlying operculum) and secondary (orbitofrontal) taste cortices (Barros-Loscertales et al., 2011; review in Van der Laan et al., 2011).

It is not surprising that vision also affects the perception of tastants and flavors (Delwiche, 2012). For example, adding color to a drink or a food can increase or lower a person's ability to discriminate or identify tastants and flavors, even if he/she is instructed that color only contains non-relevant information (Zampini et al., 2007; Levitan et al., 2008; Spence et al., 2010; reviews in Verhagen and Engelen, 2006; Zampini and Spence, 2012). Cross-modal influences of vision on taste perception go even beyond the characteristics of the consumed food and extend to the visual aspects of the cutlery (Harrar and Spence, 2013), dishes (Harrar et al., 2011), ambiance lighting (Wheatley, 1973) and social cues (e.g. facial expressions and body shapes of the dining partners; Bartholomeuf et al., 2010), suggesting that eating and drinking are

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complex and multisensory rewarding experiences in which context plays an important role.

Visual cues also play an important role in food consumption, especially when one is hungry. The physiological state of hunger or satiety, coded by the gustatory system, directs visual attention towards relevant visual stimuli in an alliesthesia-dependent fashion. For example, hungry sighted participants perform worse than sated controls in attentional tasks that require ignoring food items (Piech et al., 2010). Furthermore, when visual input is blocked, e.g. by wearing a blindfold, participants eat nearly 20% less (Linné et al., 2002).

What are the effects of the (congenital) absence of vision on the development of the taste system? People who are blind from birth experience numerous obstacles related to selection and access of food products, as well as in the preparation of meals (Bilyk et al., 2009). For example, during grocery shopping, many blind individuals rely on a memorised list of food items. This is in sharp contrast with sighted persons whose food-choice is to a large extent based upon the appealing visual aspects of foods such as their color, shape, label or packaging. Blind subjects also eat slower compared to (blindfolded or not) sighted subjects (Linné et al., 2002). We recently provided evidence that congenitally blind individuals have lower taste detection and identification thresholds (Gagnon et al., 2013), a result that contrasts sharply with their increased sensitivity to touch, sound and odour (review in Kupers and Ptito, 2014). We further showed that blind subjects have a better intuitive eating attitude compared to sighted, meaning that they rely more strongly on their physiological feeling of hunger, rather than on external and situational cues, when deciding what and how much to eat (Gagnon et al., 2013; 2014a). We here test whether the reduced taste sensitivity in congenitally blind subjects is reflected at the neuronal level by attenuated blood oxygenation-level dependent (BOLD) responses in the primary and/or secondary taste cortices. Based on studies showing that blind individuals are less exposed to various tastants (Bilyk et al., 2009) and that occipital activation by non-visual sensory stimulation in blind subjects is training-induced (Kupers and Ptito, 2014), we hypothesized that they will activate less strongly their taste cortex and will not recruit their occipital cortex in a gustatory task.

2. Methods

2.1. Participants

Twelve congenitally blind (7 females) and 14 blindfolded sighted control (5 females) subjects participated in this study. All participants were right-handed, as assessed with the Edinburgh Handedness Inventory (Oldfield, 1971). Blind participants were recruited through either the Nazareth & Louis Braille Institute, the MAB-Mackay center and/or the Canadian National Institute for the Blind. Demographic data of the blind subjects are given in Table 1. Prior to the fMRI study, all participants were first screened for olfactory impairments using the Sniffin' Sticks screening 12-test battery (Hummel et al., 2001), and they were also familiarized with the gustometer. This led to the rejection of one blind anosmic male and one blind female who was unable to perform the training task. All other participants scored higher than 8 on the smell identification test. An additional blind female participant was removed from the fMRI data analysis because of head movements during scanning. The resulting blind (5/9 females; [mean ± SEM] age: 45 ± 5 y; body mass index (BMI): 27.5 ± 1.4 kg/m^2) and sighted (6/14 females; age: 39 ± 4 y; BMI: 29.0 ± 1.9 kg/m^2) groups were matched for age, gender and BMI. The local Ethics Research Committees of the Centre de Recherche Interdisciplinaire en Réadaptation [CRIR 838-0413] and of the Regroupement de Neuroimagerie du Québec [CMER RNQ 10-11-027] approved the experimental protocol and all participants gave their written informed consent prior testing.

2.2. Familiarization session

Pleasantness and intensity of the tastants were rated by indicating a number from 0 to 10 (pleasantness) or from -5 to 5 (unpleasantness), using the fingers of both hands. Prior to scanning, all participants were trained to use the pleasantness and intensity scales and familiarized with the rating procedure using the hands. Participants were also acquainted with the gustometer, consisting of a mouthpiece attached to syringes (60 mL) through separate tubing (1.7 m length; 3 mm diameter); all participants were allowed to explore the gustometer haptically or visually.

2.3. MRI data acquisition

Subjects were scanned using a 3-T Siemens Magnetom Trio MR scanner (Siemens, Erlangen, Germany) equipped with a 32-channel head coil (Invivo, FL, USA). All scanning sessions took place between 9 a.m. and 6 p.m. In order to limit possible side effects related to the ingestion of quinine, participants were instructed to eat a meal or a snack before the scanning session. Prior to the functional imaging runs, we acquired a T_1-weighted volume covering the whole head, using a magnetization prepared rapid gradient echo (MP-RAGE) sequence with the following parameters: repetition time (TR)/echo time (TE)/inversion time (TI)/flip angle (FA) of 2.3 s/2.98 ms/900 ms/9°, 256×256 matrix, spatial resolution of $1 \times 1 \times 1$ mm^3 voxels). Next, we collected single shot gradient echo-planar images (EPI) covering the whole brain in an oblique orientation to the commissural plane (TR/TE of 2.95 s/30 ms, 90° flip angle, 64×64 matrix, FoV of 192×192 mm, 45 slices with no gap, $3 \times 3 \times 3$ mm^3 voxels). In each of the two functional runs, 340 dynamic images were acquired. Finally, we acquired a field map (FLASH, TR/TE short/TE long/FA 497 ms/4.92 ms/7.38 ms/60°, 64×64 matrix with a resolution of $3 \times 3 \times 3$ mm^3 voxels, 45 slices) to correct for static magnetic field inhomogeneities. We tried to restrict head motion by placing comfortable padding around participants' heads.

2.4. Stimuli and stimulation equipment

Four different tastants ("weak sweet": sucrose 0.05 M; "strong sweet": sucrose 0.15 M; "weak bitter": quinine hydrochloride 0.04 mM; "strong bitter": quinine hydrochloride 0.08 mM) and artificial saliva (potassium chloride 1.25 mM + sodium bicarbonate 0.125 mM) dissolved in distilled water were freshly prepared before the start of the fMRI sessions. During scanning, tastants and artificial saliva were manually delivered at a rate of 3 mL/3 s, using the gustometer. Prior to stimulus onset, an audio cue (Nordic Neuro Lab) warned the experimenter of the upcoming stimulus. This was followed by an auditory countdown to ensure a relatively constant flow of 3 mL/3 s. A 3 mL volume of water was administered after each tastant for mouth rinsing. Participants were asked to swallow all liquids during the scanning sessions.

2.5. Experimental fMRI procedure

Blindfolded participants underwent two fMRI runs, each with 30 stimulus presentations, resulting in a total of 60 stimulus presentations. In both runs, the four tastants were administered five times, whereas the artificial saliva was administered 10 times; tastants and artificial saliva were presented in a pseudo-randomized fashion. The 3-s lasting taste stimuli were separated by an inter-stimulus interval varying between 27 and 38 s (Fig. 1). An

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