Chem. Senses 30 (suppl 1): i164–i165, 2005 doi:10.1093/chemse/bjh165

Chemotopic Arrangement for Taste Quality Discrimination in the Cortical Taste Area

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Key words: chemotopy, insular cortex, optical intrinsic signal, spatial code, taste

Introduction

Signals from various sensory organs are delivered to the brain where sensory information is generated from the signals. The information is represented on the brain in the form of temporal and spatial codes, which enable us to create inner an representation of the outer world (Florey, 1990). In the neocortex, the information consisting of the spatial codes is principally arranged in the primary sensory area as a receptive field, by way of anatomical column formation. The information consisting of temporal codes, such as frequency and phase dynamics, also plays an important role for synchronization of neural activities or strengthening signal amplitudes. Interaction or integration of the information by way of intra-cortical or cortico-cortical connections enables the temporal and spatial codes to link (Singer and Gray, 1995; Gilbert *et al.*, 1996; Salinas and Sejnowski, 2001).

As for taste information processing, controversy still exists as to whether cortical taste neurons use temporal codes or spatial codes for discriminating taste information in the cortical taste area. However, it may be presumed that cortical taste neurons use spatial codes as well as frequency codes in order to discriminate taste information efficiently. Previous electrophysiological studies predict that there is a chemotopic arrangement for taste quality discrimination in the cortical taste area, but this hypothesis has not been confirmed because of lacking for the evidence with high resolution of spatial dimension. Optical imaging based on intrinsic signals has a high spatial resolution (Frostig *et al.*, 1990) and is useful for studying the functional organization of the brain (Bonhoeffer and Grinvald, 1996). Here, we investigated the spatial aspects of optical intrinsic signal (OIS) responses in the gustatory insular cortex that were elicited by delivering a solution of tastants on the tongue.

Materials and methods

Guinea-pigs were anesthetized with Na-barbiturate. The insular cortex, including rhinal sulcus and middle cerebral artery (MCA), was exposed with dura mater and a thinned skull. Optical intrinsic signals (OISs) were recorded from the insular cortex with a video camera. An area dimension and number of pixels are 8.7×6.5 mm^2 and 320×240, respectively. The focusing depth was adjusted to ~400 μm below the cortical surface. Solutions of tastants were delivered on the tongue in the oral cavity. We used NaCl, sucrose, quinine and HCl for taste stimulation.

Gustatory stimulation was administered by delivering a solution of NaCl, sucrose, quinine and HCl, respectively, on the tongue. The trials were repeated eight to ten times and each trial consisted of a pair of records with and without a stimulation session. During the inter-trial period, the oral cavity was washed with distilled water (DW). OIS data were collected for 7 s with a frame length of 500 ms. There are 14 frames per record. In the stimulating session, the stimulation was applied at frames 3–14, i.e. the stimulation was continued for 6 s. The statistical analysis was applied to the data collected in frames between with and without a stimulation session. We defined the statistically significant pixels ($P < 0.05$) as active signals in response to stimuli. The details of the OIS recording system and the statistical analysis have been described in our recent report (Yoshimura *et al.*, 2004c).

Results

According to the methods above-mentioned, OIS recording and statistical analysis were executed. In the case of sucrose application, a time course comparison of OIS images showed that OIS responses to sucrose appeared at 2.0–3.0 s after the start of tongue stimulation. The responsive area was localized in the rostral part of gustatory insular cortex. In the case of NaCl application, a time course comparison of OIS images showed that OIS responses to NaCl appeared at 2.0–3.0 s after the start of tongue stimulation. The responsive area was localized near the MCA in the gustatory insular cortex. Thus, the sucrose-responsive area is located relatively rostral of the gustatory insular cortex when compared with the NaCl-responsive area.

In order to examine whether OIS responses to sucrose and NaCl solution were responses to the tastants themselves, DW was administered on the tongue. A time course comparison of OIS images clearly showed that no OIS response was generated within the gustatory insular cortex. In order to examine whether OIS responses to the tastants were responses to neural inputs from peripheral organs on the tongue, the tongue was anesthetized by a local injection of lidocaine and sucrose was administered on the tongue. A time course comparison of OIS images clearly showed that no OIS response was generated within the gustatory insular cortex, despite the delivery of the tastants on the tongue. These results indicate that the OIS responses to tastants we observed in this study are responses to gustatory information from the tongue, and not responses to somatosensory information from the oral cavity.

The contribution of tastant concentration to gustatory information processing was investigated by comparing the OIS responses of high concentrations of NaCl with that of lower concentrations of NaCl. When low concentration of NaCl was administered on the tongue, OIS responses began to appear after 2.0–3.0 s. On the other hand, when high concentration of NaCl was administered, OIS response began after 0.5–1.5 s. In addition, in case of high-NaCl applications, the area of statistical spots was wider in rostro-caudal dimension than that of low-NaCl application. As for the temporal dimension, the concentration of tastants may be discriminated by the onset time of responses to taste stimulation.

In the same way, sucrose-, NaCl-, HCl- and quinine-responsive areas were compared. When low-concentration of tastants were administered, the areas of OIS in response to each tastant were spatially separated. Sucrose-, HCl-, NaCl- and quinine-responsive areas were arranged in rostro-caudal direction. When high-concentration of tastants were administered, OIS responses appeared in the rostral part, near the MCA and caudal part to the MCA of the gustatory insular cortex.

The OIS recording methods for investigation of sensory information processing allows a high resolution of spatial dimension. There-

fore, we can identify the relative location between areas in the same window of the brain surface, if each area is responsive to appropriate sensory stimulation and is localized. Based on the data corrected from seven animals, we made chemosensory maps in the insular cortex. To identify relative location of tastant-responsive area clearly, center-of-each-OIS response was plotted on line drawing of insular cortex. It shows that sucrose and HCl-responsive areas locate rostral part of the insular cortex, NaCl-responsive area locates near the MCA, and quinine-responsive area locates caudal part to the MCA of the insular cortex. These results are partially consistent with the cortical taste map investigated by electrophysiological methods (Yamamoto, 1987). Thus, chemotopy for the taste quality of tastants may be organized in the primary cortical taste area. When high-concentration of tastants were administered, sucrose- and HCl-responsive areas appeared near the MCA and caudal part to MCA of the insular cortex respectively in addition to rostral parts, and NaCl-responsive area appeared in the caudal part to MCA in addition to near the MCA, whereas, quinine-responsive area appeared in the rostral part in addition to the caudal part to MCA. Thus, as for high concentration of tastants, chemotopy for the taste quality may be represented in the primary cortical taste area as combinations of high and low threshold tastant-responsive areas.

Discussion

The present results were based on relative location of OIS responses, but not absolute location. Optical imaging based on intrinsic signals enables us to compare relative location over several tastant-responsive areas in the same recording window. For the reason, the OIS recording method is useful for studying spatial aspects of sensory information processing. By using this method, here we demonstrated that chemotopy for the taste quality may be organized in the primary cortical taste area. In addition, as for information processing of tastant concentration, chemotopy for the taste quality may be represented as combinations of high and low threshold tastant-responsive areas. Thus, not only information of taste quality but also information of concentration may be assembled as spatial codes in the primary cortical taste area through the process of taste quality perception.

General taste sensation is recognized as an integration of chemosensory and somatosensory information, which should require both spatial and temporal coding. Gustatory insular cortex neurons receive not only chemosensory afferents, but also somatosensory afferents by way of thalamo-cortical pathways or horizontal cortico-cortical pathways with temporal code information (Katz *et al.*, 2002; Wang and Ogawa, 2002; Yoshimura *et al.*, 2003, 2004a,b). In general, the recognition of the source of sensory information may require neural oscillation and synchronization between functional neuron clusters. It may be presumed that, based on spatial coding in the primary cortical taste area, the brain integrates different sensory information with frequencies and temporal dynamics so as to discriminate complicated taste information. Further study should precisely investigate the contribution of temporal coding to integration of chemical and somatosensory information from the oral cavity.

Acknowledgments

This work was supported by grants from Kanazawa Medical University (Grant for Promoted Research to H.Y., No. S2003-9).

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