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Expiration: The moment we experience retronasal olfaction in flavor

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ABSTRACT

Respiration is essential for smell perception. Previously we found that 8–12-Hz cortical rhythms were phase-locked to inspiration onset during the presentation of odor stimuli; this is referred to as inspiration phase-locked alpha band oscillation (I-α). Generators of I-α estimated with a dipole fitting model were found in the piriform, the entorhinal cortex (ENT), the amygdala (AMG), the hippocampus (HI) and the orbitofrontal cortex (OFC). Such olfactory perception is said to occur via the orthonasal olfaction route. Another route is the retronasal olfaction route. In this study, we investigated the link between respiration phase and retronasal olfactory perception. Electroencephalograph (EEG) and respiratory flows (separately measured with mouth and nose) were simultaneously recorded during stimulation of subjects' tongues with liquids of chocolate, sucrose and water. The percentage of subjects correctly identifying the chocolate taste was higher when subjects were asked to breathe through the nose than when they were breathing through the mouth. In the averaged EEGs triggered by the onset of expiration measured from the flow through the nose, a 8–12-Hz oscillation was observed. Generators of this potential were found in the left ENT, HI, AMG and OFC in the order of milliseconds after expiration onset. Perception of retronasal olfaction is dependent on expiration, and combining retronasal olfactory information with gustatory information and somatosensation enable us to identify flavors when drinking and feeding.

Respiration is essential for smell perception. When we inspire, odor information reaches the olfactory receptors located in the nasal mucosa and their signal is transmitted to the olfactory bulbs. From the olfactory bulbs, information ascends directly to the olfactory limbic areas: the prepiriform, piriform (PIR), entorhinal cortex (ENT), amygdala (AMG) and hippocampus (HI). This peculiar sensory process accompanying inspiratory activity is not observed with other sensory modalities; unlike other sensory processes, olfactory information ascends to these limbic areas without passing through the thalamus. Therefore, every breath activates these limbic areas and immediately changes emotions.

To investigate the relationship between olfactory perception or olfactory-evoked emotions and inspiratory activity, we previously performed simultaneous recordings of electroencephalograph (EEG) and respiration flow during odor stimulation to see if there was any link between cortical rhythm and inspiration activities [7]. We assumed that if perception of odor depended on inspiration, we could find an inspiration-related potential during presentation of olfactory stimulation in the averaged potentials triggered at inspiration onset. We found that 8–12-Hz cortical rhythms were phase-locked to inspiration during the presentation of odor stimuli; this is referred to as inspiration phase-locked alpha band oscillation (I-α). To identify the generator of this rhythmic cortical potential, we used a dipole tracing method incorporating a scalp–skull–brain head model (SSB/DT) [5–7], which enabled us to detect generators of event-related potentials in the order of milliseconds. Generators of I-α were found in the PIR, the ENT, the AMG, the HI and the orbitofrontal cortex (OFC), and these processes transmitting olfactory information were detected from the onset of inspiration. At 300 ms after inspiration onset, dipoles were localized in the OFC, which plays a role in the identification and recognition of odors through emotion and memory. The synchronization of these areas of activation with respiratory cycles was confirmed in humans [7] as well as in animal studies [4,10].

In such olfactory perception, olfactory signals originating outside the body are sensed by inspiring or sniffing through the external nares of the nose. This is the orthonasal olfaction route. Another route is the retronasal olfaction route, in which odor molecules released from the food or drink are drawn up into the nose from the nasopharynx and reach the olfactory epithelium located in the nostrils [15]. This olfactory route plays a role in perceiving flavors combined with taste and texture of food. It is interesting to note that if we pinch the nose, it is difficult to identify the kind of food. However, if we open the nose, we are able to recognize the kind of food. On the tongue, there are five categories of qualities of taste, sweet, salty, sour, bitter, and umami. By incorporating retronasal olfaction with gustatory information and somatosensation, we are able to experience flavor.

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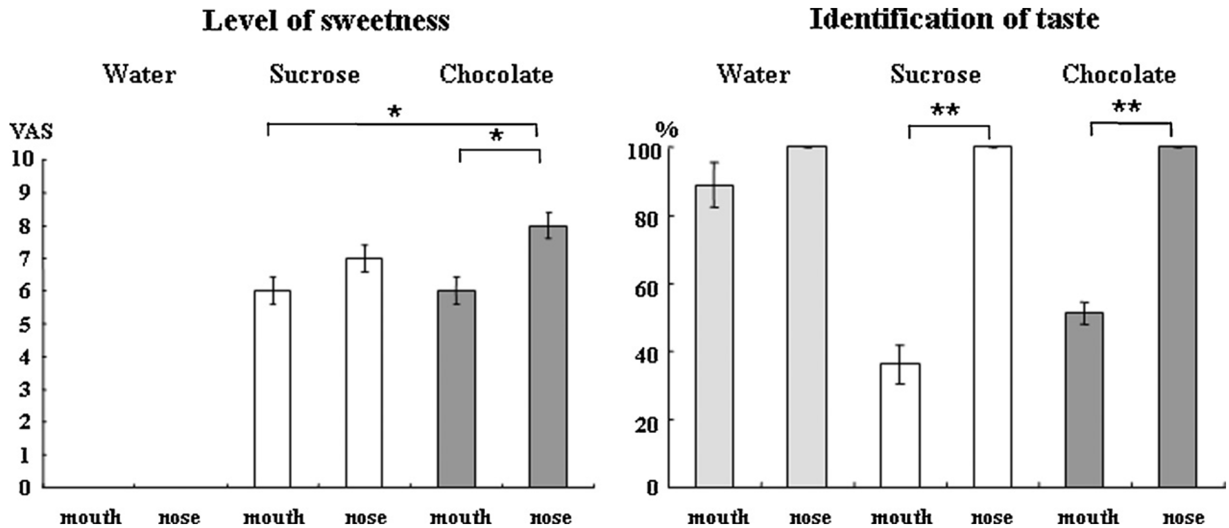

Fig. 1. Percentages of subjects correctly identifying chocolate.

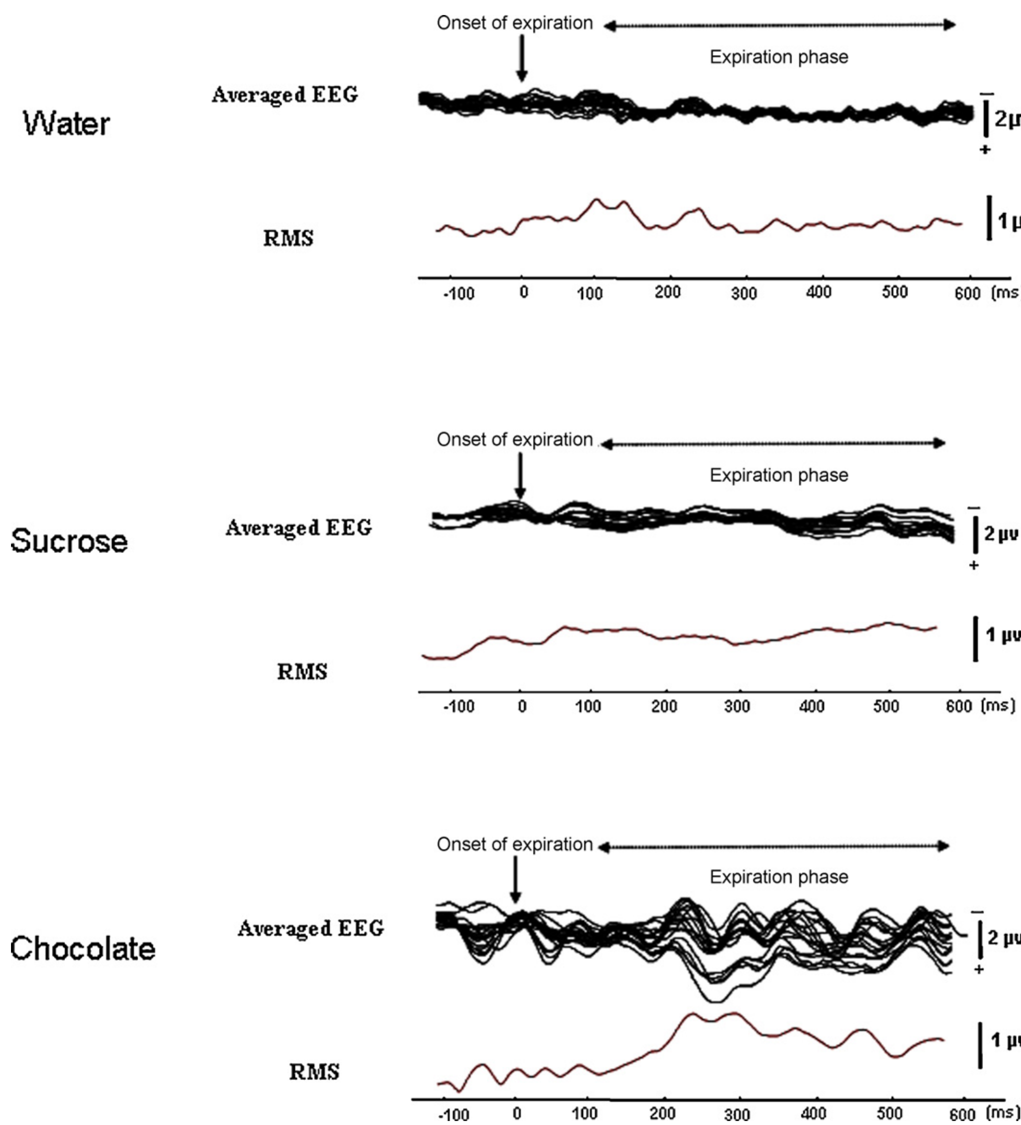

Fig. 2. Grand-averaged potentials triggered by the onsets of expiration measured during breathing through the nose during each exposure to stimulus. Root mean square values (RMSs) were indicated below each averaged potentials.