



Remembering the past with slow breathing associated with activity in the parahippocampus and amygdala

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HIGHLIGHTS

- ▶ The perfumes induced memory retrieval and specific emotional responses.
- ▶ The perfumes increased tidal volume and decreased respiratory frequency.
- ▶ The perfumes activated the right parahippocampus and the right amygdala.
- ▶ The synchronization between the activation of the limbic areas and the breathing cycle.

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ABSTRACT

Breathing plays an important role in perception of odors and the experience of emotions. We used the dipole tracing method to analyze brain areas related to odor-induced autobiographical memory and emotions estimated from averaged electroencephalograms triggered by inspiration onset during odor presentation. Odor stimuli were perfumes subjects named that elicited a specific, pleasant and personal memory as well as two pleasant odors for controls. The perfumes induced specific emotional responses during memory retrieval, arousal level of the memory, feelings of pleasantness and a sense of familiarity with the odor. Respiration measurement indicated that tidal volume increased and respiratory frequency decreased during presentation of perfume stimuli, showing a deep and slow breathing pattern. Throughout the olfactory stimulation, electroencephalograms and respiration were simultaneously recorded. In the averaged potentials, low frequency oscillation was phase-locked to inspiration. Dipole analysis showed that perfumes activated more widespread areas of the right parahippocampal cortex and converged in the right amygdala compared to control odors. Slow breathing synchronized with odor-induced autobiographical memory and emotions may be subconsciously stored in the parahippocampal cortex and amygdala.

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The primary role of breathing is regulation of homeostasis to maintain life. However, breathing plays an important role in perception of odors [22] and the experience of emotions [13]. When odor molecules are in the air, inspiration delivers them to the olfactory nerve in the nasal mucosa and to the olfactory bulb. From the olfactory bulb, signals ascend to the primary olfactory cortex, which includes all brain regions receiving direct input from the olfactory bulb, namely, the anterior olfactory cortex, ventral tectal, anterior hippocampal continuation and indusium griseum, olfactory tubercle, piriform cortex (Pir), anterior cortical nucleus of the amygdala, periamygdaloid cortex and rostral entorhinal cortex (ENT) [5,27]. Through projection to the amygdala (AMG) and

hippocampus (HC), information finally converges in the orbitofrontal cortex (OFC) [14,20].

As odor molecules evaporate, these areas are activated by every breathing cycle, and simultaneously emotions are expressed with these breathing cycles. With two breaths more than one and three breaths more than two, inspiration causes more emotion and is increasingly associated with memory retrieval [13].

This unique anatomical process of olfaction with information input directly to the limbic system is immediately associated with breathing changes. How the respiratory pattern changes is dependent on emotional states induced by the odor. Unpleasant odors, for example, increase respiratory rate (fR) and decrease tidal volume (V_T), whereas pleasant odors are related to deep and slow breathing [14]. Thus, the limbic system is inspired by odor and expresses emotional state in breathing alterations.

Among the links between emotions and odor, an association between odor and autobiographical memory has been well

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established [7,21]. Memories induced by odors enable individuals to mentally travel back into their personal past. It has been reported that odor-evoked autobiographical memories are experienced more emotionally than memories evoked by visual or auditory stimuli [26]. Sensations of familiarity, reality and nostalgia accompany autobiographical memories induced by odor.

In a previous study, we tested whether odors associated with autobiographical memories can trigger pleasant emotional experiences and whether respiration changes during stimulation with these odors [15]. That study showed that autobiographical memory retrieval was associated with increasing V_T and decreasing fR during presentation of these odors more than during presentation of control odors [15]. Our interest in the present study was the brain regions related to odor-induced autobiographical memory and emotions observed with slow and deep breathing. To determine the brain areas related to odor-induced autobiographical memory, the dipole tracing method was used. Dipole analysis enabled us to find the generators of potentials measured from surface electrodes. Averaging potentials that increase signal to noise ratio improves accuracy of the estimated locations. Because odor perception is dependent on inspiration we used the onset of inspiration during presentation of odor stimuli for averaging electroencephalograms (EEGs). In averaging this activity, we found alpha rhythm oscillations referred to as “inspiration related potentials” [14]. Using the dipole tracing method, we found source generators of inspiration-related potentials during presentation of odor stimuli in the Pir, ENT, AMG, HC and OFC in the millisecond range after inspiration onset [14]. In this study, we focused on the brain areas estimated from averaged potentials triggered by onset of inspiration during odor stimuli that induced autobiographical memory.

A total of 23 subjects (8 males, 15 females) were chosen from 264 subjects (aged 20–59 years) on the basis of a pre-test interview [15]. Three months prior to the procedure, we asked subjects to identify the name of a perfume that elicited a specific, pleasant and personal memory. We confirmed that the perfumes identified did not cause unpleasant feelings related to memories evoked by smelling them. All subjects provided written informed consent, and the study was approved by the Ethics Committee of the Showa University School of Medicine.

Nineteen electrodes were attached to the subjects according to the International 10–20 system, with the reference electrode on the right earlobe. An EEG and electro-oculogram were recorded and stored in a digital EEG analyzer (DAE-2100, Nihon Kohden, Tokyo, Japan). The EEG was sampled at 1000 Hz through a 0.016–30-Hz bandpass filter. Impedances were kept below 10 k Ω . Signals of the onset of odor stimulation and respiratory flow (described later) were obtained simultaneously by the EEG and oculogram recordings and stored in the EEG analyzer. The subject put on a nose mask with a transducer connected to a respiratory monitor (CPX, Arco System) to measure V_T , fR and end-tidal CO_2 concentration (ETCO₂). Respiratory flow data obtained with the respiratory monitor were also stored in the EEG analyzer. Inspiration flows downward from 0 level, and expiration flows upward. The onset of inspiration (0 level) was used as a trigger for averaging potentials. Eye blinks measured with oculogram and artifactual activity exceeding $\pm 50 \mu V$ was excluded for averaging. A perfume stimulus (Perfume) reported from the pre-test interview by each subject was prepared for olfactory presentation. Two control odors were presented: β -phenyl ethyl alcohol (PEA) and chamomile, as used in a previous study [15]. Both were categorized as a “pleasant odor” but did not induce autobiographical memories, as confirmed before [15]. The three kinds of odorant-dipped litmus strips were prepared 30 min before the experiment and left exposed to the air until the smell of alcohol disappeared. For perfume stimuli, 50 μL were attached to the tip of the litmus strip. Ten microliters of PEA diluted 5% with ethanol and Roman chamomile oil diluted 30% with

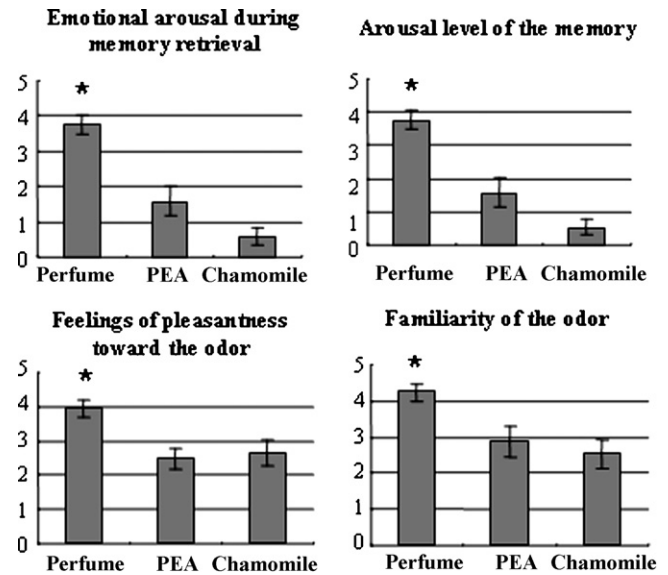


Fig. 1. Perfume-induced emotional arousal during memory retrieval, arousal level of the memory, and feelings of pleasantness and familiarity of the odor had higher scores during perfume presentation than during presentation of control odors. * $P < 0.05$.

ethanol were applied to the other litmus strips. Each odor was presented for 30 s with a 30-s air interval in front of the inspiratory side of a one-way valve connected to the transducer. During the 30-s air interval, we confirmed that V_T , fR and ETCO₂ returned to baseline level on the PC screen-connected CPX. The three odors (perfume, PEA and chamomile) were presented in randomized order, and each odor was tested ten times. We confirmed that ETCO₂ maintained at a resting level throughout the experiment.

We used 10 subjective scales for each odor after the experiment. Emotional change during memory retrieval, emotional arousal during memory retrieval, strength of feeling back in time during memory retrieval, comfortableness of the memory context, vividness of the memory context, pleasantness of the memory, arousal level of the memory, feelings of pleasantness toward the odor, subjective intensity of the odor and familiarity of the odor were measured [15]. Scales consist of 5 levels (level 1 = not at all strong or very unpleasant; level 5 = extremely strong or very pleasant) about perceived odor-induced emotion and memory.

Three subjects reported that the perfume did not evoke an autobiographic memory and another three subjects recognized the odor of perfume associated with a past experience after the experiment, therefore, data for 17 subjects who reported that they actually felt taken back in time to the memory of the past were used in the analysis for all odors. Among these subjective scales, perfume-induced emotional arousal during memory retrieval, arousal level of the memory, and feelings of pleasantness and familiarity of the odor had higher scores during perfume presentation than during presentation of control odors, as shown in Fig. 1 (one-way repeated measures ANOVA with the Bonferroni test, $P < 0.05$). Respiration measurement showed that V_T increased and fR decreased during perfume stimulation (Fig. 2), showing a deep and slow breathing pattern. Throughout the olfactory stimulation, EEG and respiration were simultaneously recorded. Inspiration onset during each stimulation was used as a trigger for averaging EEG activity. Potentials were averaged within and across subjects (grand averaged potentials).

In the averaged potentials, low frequency oscillation was phase-locked to inspiration activities during odor stimulation. Fig. 3 shows an example of perfume stimuli. These wave forms are termed “inspiration phase-locked alpha band oscillation ($I-\alpha$)”. We also

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