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Investigation of Breathing Parameters during Odor Perception and Olfactory Imagery

A.M. Kleemann[1], R. Kopietz[1], J. Albrecht[1], V. Schöpf[1], O. Pollatos[1,2], T. Schreder[1], J. May[1], J. Linn[1], H. Brückmann[1] and M. Wiesmann[1,3]

[1]Department of Neuroradiology, [2]Department of Neurology, Ludwig-Maximilians-University of Munich, Marchioninistr. 15, D-81377 Munich, Germany and [3]Department of Radiology and Neuroradiology, Helios Kliniken Schwerin, Wismarsche Str. 393-397, D-19049 Schwerin, Germany

Correspondence to be sent to: Anna Maria Kleemann, Department of Neuroradiology, Ludwig-Maximilians-University of Munich, Marchionistr. 15, D-81377, Munich, Germany. e-mail: Anna_Maria.Kleemann@med.uni-muenchen.de

Abstract

Compared with visual and auditory imagery, little is known about olfactory imagery. There is evidence that respiration may be altered by both olfactory perception and olfactory imagery. In order to investigate this relationship, breathing parameters (respiratory minute volume, respiratory amplitude, and breathing rate) in human subjects during olfactory perception and olfactory imagery were investigated. Fifty-six subjects having normal olfactory function were tested. Nasal respiration was measured using a respiratory pressure sensor. Using an experimental block design, we alternately presented odors or asked the subjects to imagine a given smell. Four different pleasant odors were used: banana, rose, coffee, and lemon odor. We detected a significant increase in respiratory minute volume between olfactory perception and the baseline condition as well as between olfactory imagery and baseline condition. Additionally we found significant differences in the respiratory amplitude between imagery and baseline condition and between odor and imagery condition. Differences in the breathing rate between olfactory perception, olfactory imagery, and baseline were not statistically significant. We conclude from our results that olfactory perception and olfactory imagery both have effects on the human respiratory profile and that these effects are based on a common underlying mechanism.

Key words: olfaction, olfactory imagery, respiration, sniffing

Introduction

Perception is the process by which information is acquired, selected, and interpreted from the sensory systems. By contrast, imagery occurs when perceptual information is accessed from memory, giving rise to the experience of "seeing with the mind's eye," "hearing with the mind's ear," "smelling with the mind's nose," and so on (Kosslyn et al. 2001; Stevenson and Case 2005).

Olfactory imagery is defined as the ability to experience a sensation of smell when an appropriate stimulus is absent. Compared with visual and auditory imagery, this process is relatively unknown. Some researchers suggest that in the visual, auditory, and motor systems a similar neural mechanism underlies perception and imagery. For instance, eye movements that were detected during visual imagery were similar to those of visual perception (Spivey and Geng 2001; Laeng and Teodorescu 2002; Mast and Kosslyn 2002). An analogue mechanism is suggested for olfaction. Bensafi et al. (2003, 2005) described that olfactory imagery is accompanied by olfactomotor activity, similar to that during odor perception. The primary sensory motor component for olfaction is sniffing, which is often compared with the movement of eyes to accommodate the vision as well as with the movement of ears to accommodate audition in most mammals (Johnson et al. 2003).

The sensation and perception of olfactory stimuli is widely dependent on sniffing, which is an active stage of stimulus transport. The sniff volume is inversely proportional to the concentration of an odorant (Laing 1983; Sobel et al. 2001). Sobel et al. (1998a) suggested that the cerebellum maintains a feedback mechanism that regulates the sniff volume in relation to odor concentration. In summary, previous research has shown that sniffing is not only a simple stimulus delivery method but also necessary for olfactory perception and important for generating neural activity in olfactory brain areas (Sobel et al. 1998a; Mainland and Sobel 2006).

Bensafi et al. (2003, 2005) measured the airflow when subjects were trying to imagine various sights, sounds, or smells and showed that olfactory imagery, but not visual or auditory imagery, was accompanied by spontaneous sniffing. Moreover, the properties of the sniff during olfactory imagery resembled those of sniffing during olfactory perception. Analogous to real odor perception, when imagining a pleasant odor subjects took a larger sniff, and when imagining an unpleasant odor, they took a smaller sniff. Furthermore, blocking the nasal passage reduced the quality of olfactory imagery, and encouraging sniffing increased the quality of olfactory imagery. These results suggest that sniffing plays an important functional role not only in olfactory perception but also in olfactory imagery.

A functional imaging study of Djordjevic et al. (2005) reported that activation patterns during olfactory imagery are similar to those during olfactory perception. In this study, the authors were able to demonstrate that participants did imagine odors. They found increased activation in sensory regions specific for olfaction and in regions involved in mental imagery across different sensory modalities. They also demonstrated a positive relationship between activation of the secondary olfactory cortex and odor imagery performance. These findings demonstrate partially overlapping neural substrates for olfactory imagery and perception in agreement with findings in other modalities including vision, audition, touch, and motion.

Djordjevic et al. (2005) also measured respiration using a polygraph instrumentation system. This system recorded the respiratory movement (expansion and contraction) with 2 stretchable elastic belts attached around the chest and the abdomen of the subjects. However, due to the higher number of artifacts associated with the chest measurement belt, the results reported were based on the data collected with the abdominal belt. Two parameters, the mean amplitude and frequency, were extracted for each subject for all conditions. With their experimental approach, this group did not found any significant differences between the imagery, odorant, and baseline condition.

The goal of the current study was to quantitate the following breathing parameters: respiratory minute volume, respiratory amplitude, and breathing rate, in response to odor stimulation and olfactory imagery. Respiratory minute volume is the volume of air that is inhaled (inhaled minute volume) or exhaled (exhaled minute volume) by a human lung in 1 min. The respiratory amplitude is defined as the depth of inspiration. The respiration rate is the number of breaths taken within 1 min. We analyzed all important breathing parameters supposing that the analysis of a single breathing parameter (e.g., breathing rate) is insufficient to make a statement about the changes in the breathing or sniffing behavior. Secondary we investigated the breathing pattern by analyzing the shape of breathing profiles and searching for local maxima, which could be an indication for potential sniffing behavior. We also performed the fast Fourier transform (FFT) analysis of the breathing patterns in order to compare the frequency spectra between conditions for all individual subjects.

The hypothesis of the present study was that the breathing pattern in human subjects varies during olfactory perception as well as during olfactory imagery. More precisely it was hypothesized that the breathing parameters increase not only when the subjects smell an odor, but also if they imagine it. We supposed that the sniffing behavior, which attends odor perception and olfactory imagery, induces alterations in the breathing shapes and evidences a distinct characteristic, depending on the tested conditions.

Material and methods

Subjects

Fifty-six healthy volunteers (35 females) aged 21–42 years (mean age 28.9 ± 5.2 years) participated in this study. Their olfactory function was verified using the validated olfactory Sniffin' Sticks test (Kobal et al. 1996; Hummel et al. 1997). The protocol was approved by the local Ethics Review Committee, and the study was conducted in accordance with the Declaration of Helsinki/Edinburgh. All subjects gave their written, informed consent. The subjects were informed about the course of the experiment, but they were unaware of the real intention so as not to bias the results of this study.

Odor stimuli

Four odors (banana, rose, coffee, and lemon) were selected from the Sniffin' Sticks test battery (Burghart Instruments, Wedel, Germany), which consists of 16 odors based on pen-like odor-dispensing devices and is an established method to measure nasal chemosensory function (Kobal et al. 1996; Hummel et al. 1997). We employed 4 instead of only one odor in order to avoid adaptation of the olfactory system. Pleasant odors were used because they have been shown to induce a stronger breathing effect than unpleasant odors (Bensafi et al. 2002; Bensafi et al. 2007).

Experimental procedure

The experiment was based on a block design paradigm (Figure 1) with 3 kinds of conditions: odor perception (odor), olfactory imagery (imagery), and baseline. Both odor and imagery blocks were repeated 4 times. In every odorant block (duration 16 s), one of the 4 odors—banana, rose, coffee, and lemon in that order, was presented. In the imagery blocks (duration 16 s), the subjects were required to imagine the smell that was presented in the preceding odor block. The odor and imagery blocks were separated by a baseline condition (duration 32 s).

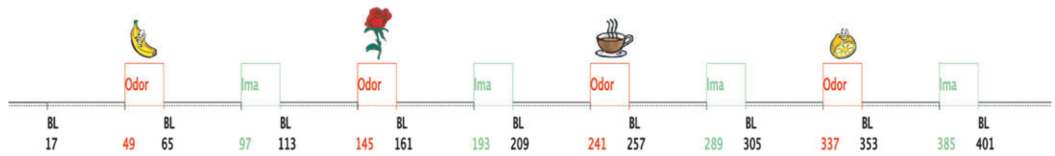

Figure 1 Experimental paradigm (timeline in s). Block design with 3 conditions: odor perception (Odor), olfactory imagery (Ima), and baseline (BL). In every odorant block, 1 of the 4 odors—first banana, then rose, coffee, and at last lemon, was presented. In the imagery blocks the subjects were required to imagine the smell that was presented in the preceding odor block.

The respiratory sensor (OL014, Burghart Instruments) used for this experiment is based on a pressure measuring principle. This sensor measures the pressure difference that arises between the nostril and the environment during breathing. The differential pressure sensor detects the deformation of a thin membrane under pressure using capacitive methods. The signal was recorded at 100 Hz using Lab View 7.0 software (National Instrument, Austin, TX).

During the whole experimental session, the nosepiece of the respiratory sensor was placed in the left nostril of the subjects. Because in other publications of our group, the left nostril was used for monorhinally olfactory stimulation (Weismann et al. 2001; Wiesmann et al. 2004; Wiesmann et al. 2006; Albrecht et al. 2008), we decided to do so to keep the testing conditions constant and reliable across our studies. In order to avoid the slipping out of the nosepiece, the subjects were requested to keep the sensor positioned with their hand. Additionally they were blindfolded and instructed to breathe through the nose. The presentation of odors in the odor condition was not communicated with the subject, whereas the imagery blocks were initiated with the command START and terminated with the command STOP. To detect the offset value of the respiratory sensor, the data recording started 10 s before subjects inserted the nosepiece of the sensor into the nose and ended 10 s after subjects removed the sensor out of the nose. Each experimental session consisted of 2 runs, which were interrupted by a 10-min break. The total experimental duration was half an hour.

Data analysis

Data were processed using Matlab 6.5. We calculated the offset value (mean value of the data recorded before the nosepiece of the sensor was placed in the subjects' nostril and after the sensor was removed from the nostril) and normalized the collected data for each subject about this value. In a second step, the data were smoothed using moving average filter. The window size for the moving average was set at 10.

The respiratory minute volume was determined by computing the integral of the breathing curve during the baseline, odor, and imagery condition. To find the respiratory amplitude, the global maxima of the breathing cycles were detected and subsequently averaged for each subject. The mean interval between 2 ensuing breathing cycles, represented by the global maxima, was calculated as the breathing rate, for all tested conditions.

To enable the comparison of breathing profiles within a condition, local maxima within each breathing cycle were identified. An increase in the number of local maxima is indicative of smell-induced sniffing behavior. The number of local maxima was averaged across all single breathing cycles for each condition. In this case, the global maxima were not considered.

Additionally, an FFT was carried out to analyze the spectra of frequency components for odor, imagery, and baseline condition. The FFT was performed for all breathing cycles within each condition for all subjects.

For the statistical analysis, SPSS for Windows (Statistical Package for the Social Science, Version 17.0, SPSS Inc, Chicago, IL) was used. Data (respiratory minute volume, respiratory amplitude, breathing rate, and the number of local maxima) were submitted to repeated-measures analyses of variance using the general linear model with the "within subject factor" condition (baseline/odor/imagery). We looked for main effects as well as for second-order interactions between these factors. Existing second-order interactions were corrected using Bonferroni correction. The alpha level for all tests was set at 0.05.

Results

Analysis of the recorded data showed that there were significant differences in the respiratory minute volume ($F_{2,222}$ = 23.89, P < 0.001) and respiratory amplitude ($F_{2,222}$ = 8.31, P = 0.001) across all conditions. The respiratory minute volume was significantly increased when the participants smelled an odor (mean: 4.77 ± 3.02 l/min, P < 0.001) or imagined an odor (mean: 4.74 ± 3.10 l/min) compared with the baseline condition (mean: 4.13 ± 2.38 l/min, P < 0.001). In other words, respiratory minute volume increased by 15.5% in the odor condition and by 14.8% in the imagery condition in comparison to baseline (Figure 2). We also found significant differences in the respiratory amplitude between the imagery (mean: 0.30 ± 0.19 l) and baseline condition (mean: 0.28 ± 0.16 l, P = 0.002) as well as between the imagery and odor condition (mean: 0.29 ± 0.18 l, P = 0.03). The amplitude rose by 6.2% in the imagery condition in comparison to baseline (Figure 3) and by 2.9% in comparison to the odor condition. An increase of 3.2% in the respiratory

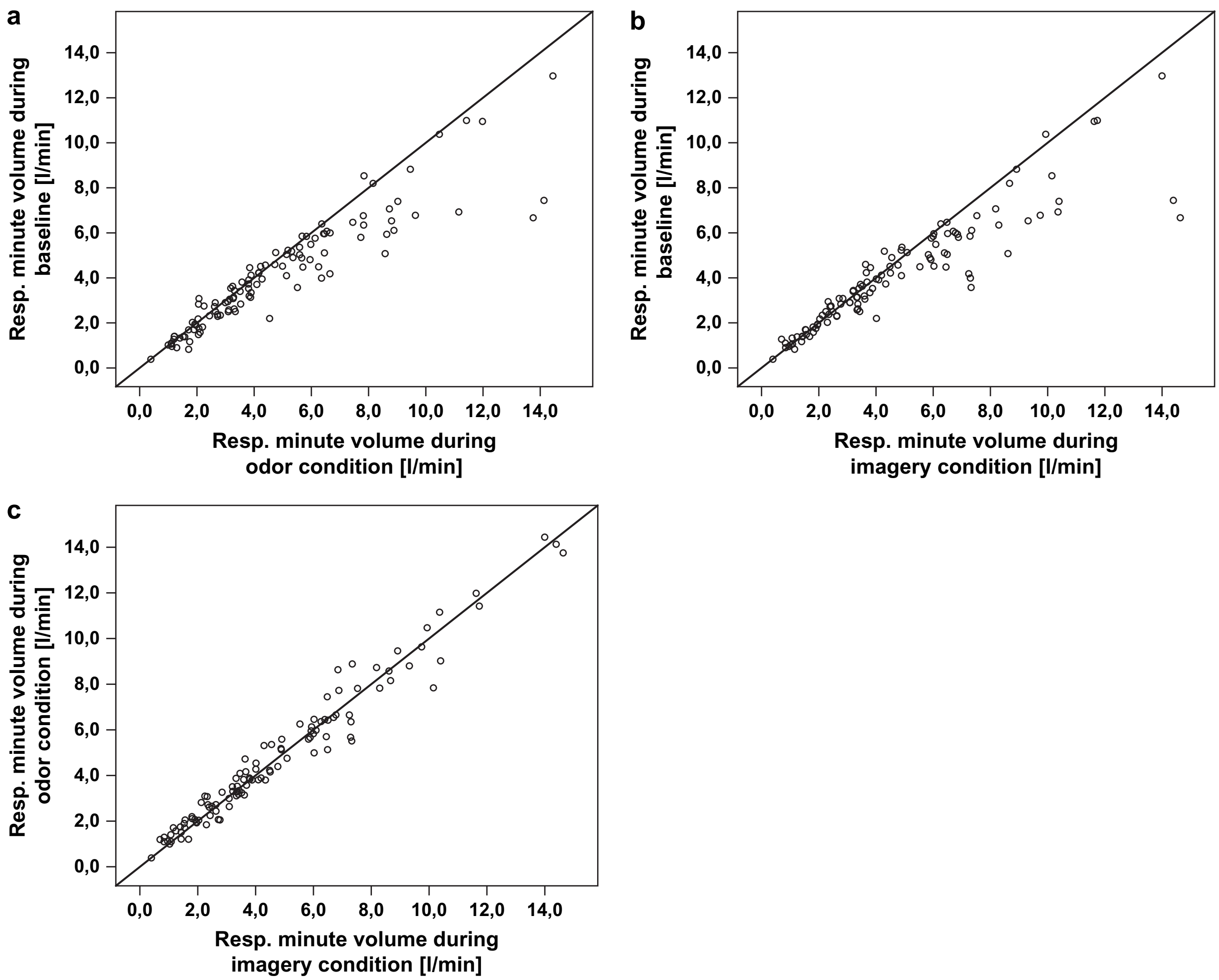

Figure 2 Paired comparison of respiratory minute volume (n = 56) between tested conditions. When there are differences across conditions, the points are mostly above or below the unit slope line. When the conditions are equal, the data points accumulate around the line. **(a)** The difference in respiratory minute volume between olfactory perception and baseline condition was statistically significant ($P < 0.005$). **(b)** The difference in respiratory minute volume between olfactory imagery and baseline condition was also statistically significant ($P < 0.005$). **(c)** The difference in respiratory minute volume between olfactory imagery and olfactory perception was not statistically significant.

amplitude between the odor condition and baseline was observed, although this increase was not statistically significant ($P = 0.13$). Differences in the breathing rate between the conditions were also not statistically significant ($F_{2,222}$ = 1.94, $P = 0.15$, see Figure 4). An overview about the different breathing parameters is presented in Table 1.

Analysis of the breathing profiles showed that the number of local maxima in the breathing cycles within the odor and olfactory imagery condition contained significantly more local maxima than the breathing cycles in the baseline condition ($F_{2,222}$ = 22.41, $P < 0.001$, see Figure 5 and Figure 6). The average number of local maxima in the baseline condition was 4.63, in the imagery condition 5.68, and 6.21 in the odor condition. Correspondingly, the frequency spectra demonstrated a different distribution of frequency components among conditions (see Figure 7, Figure 8, and Figure 9). The highest spectrum peak in all conditions corresponded to the breathing frequency (about 0.25 Hz). Interestingly, the second highest peak was found at a frequency of about 0.7 Hz, and its amplitude varied within the conditions. This peak had its lowest frequency power (amplitude) in the baseline condition (15.32) and its highest power (amplitude) in the imagery condition (25.55). In the odor condition, the peak frequency amplitude was 19.44. This indicates that the frequency of 0.7 Hz occurs more often in the imagery and odor condition in comparison to baseline.

The differences in respiratory minute volume, respiratory amplitude, and number of local maxima between conditions suggest that olfactory perception as well as olfactory imagery are accompanied by sniffing. According to the Fourier transformation analysis, the human sniffing frequency is in the range of 0.7 Hz.

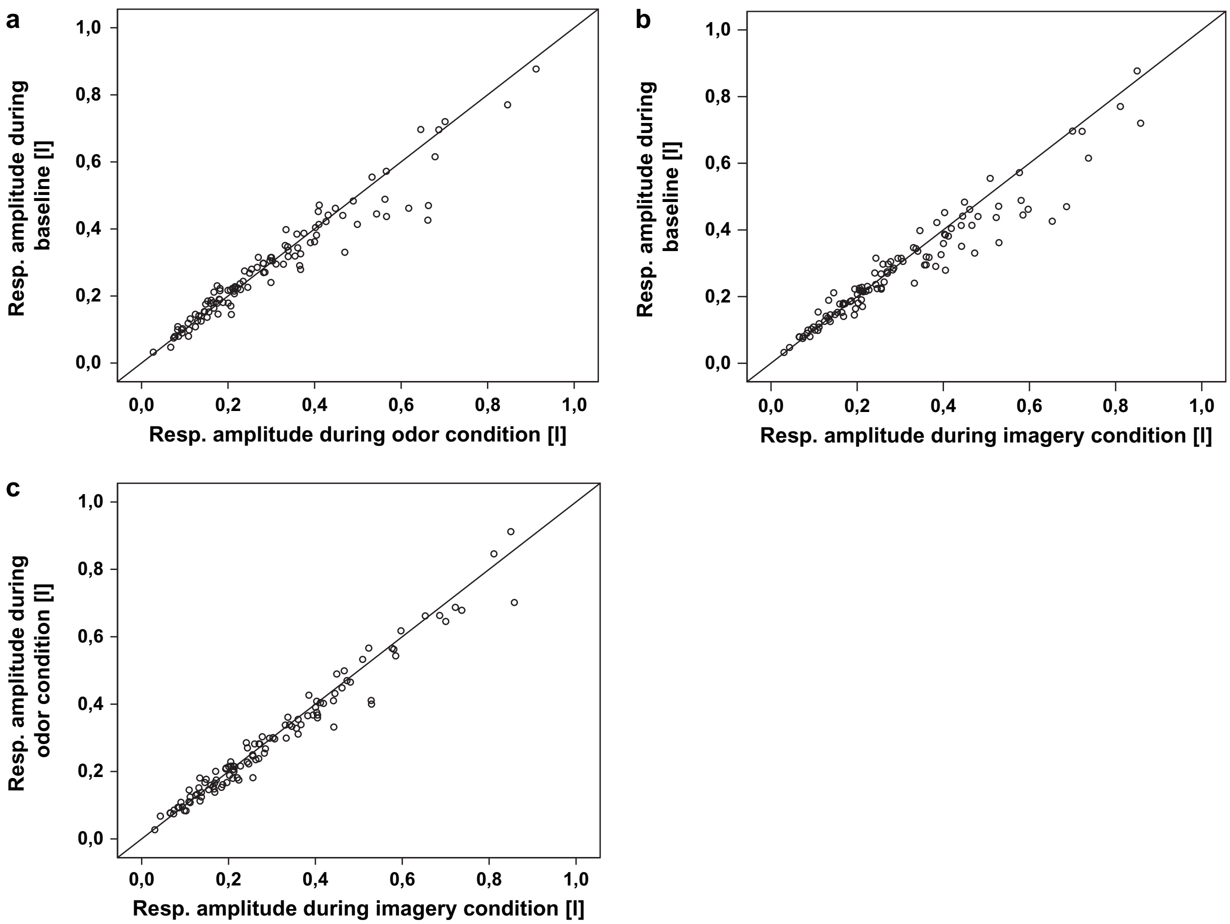

Figure 3 Paired comparison of respiratory amplitude (n = 56) between tested conditions. When there are differences across conditions, the points are mostly above or below the unit slope line. When the conditions are equal, the data points accumulate around the line. **(a)** The difference in respiratory amplitude between olfactory perception and baseline condition was not statistically significant. **(b)** The difference in respiratory minute volume between olfactory imagery and baseline condition was statistically significant ($P < 0.005$). **(c)** The difference in respiratory minute volume between olfactory imagery and olfactory perception was statistically significant ($P < 0.05$).

Discussion

The aim of the present study was to investigate the behavior of the breathing parameters respiratory minute volume, respiratory amplitude, and breathing rate in response to odor stimulation and odor imagery. Measurements were performed on 56 healthy subjects using a respiratory sensor. The results supported our hypothesis, demonstrating that the minute respiratory volume and the respiratory amplitude increase if humans smell or imagine an odor. Intuitively, an increase in the minute respiratory volume can be induced by an increase in the respiratory amplitude or an increase in the breathing rate. In this study however, the breathing rate showed no significant differences between the conditions, and the respiratory amplitude behaved differently from respiratory minute volume. Therefore, we suggest that the differences in the minute respiratory volume are rather caused by changes in the shapes of the breathing profiles. To quantify the changes in the shapes of the breathing profiles in all conditions, the local maxima within one breathing cycle were identified. This parameter was chosen because potential smell-induced sniffing behavior can be expressed as a local increase in the breathing profile. The significant differences in the number of local maxima between experimental conditions suggest that the shape of the breathing profile caused the changes in the minute respiratory volume. Also, the FFT confirms our assumption that both smell and olfactory imagery are accompanied by sniffing. The FFT showed that the second dominant frequency (0.7 Hz) is present in all conditions but has significantly higher amplitude in the odor and imagery conditions compared with baseline.

Our results are consistent with the findings of Bensafi et al. (2003, 2005). They showed that olfactory imagery is accompanied by olfactomotor activity similar to that during odor

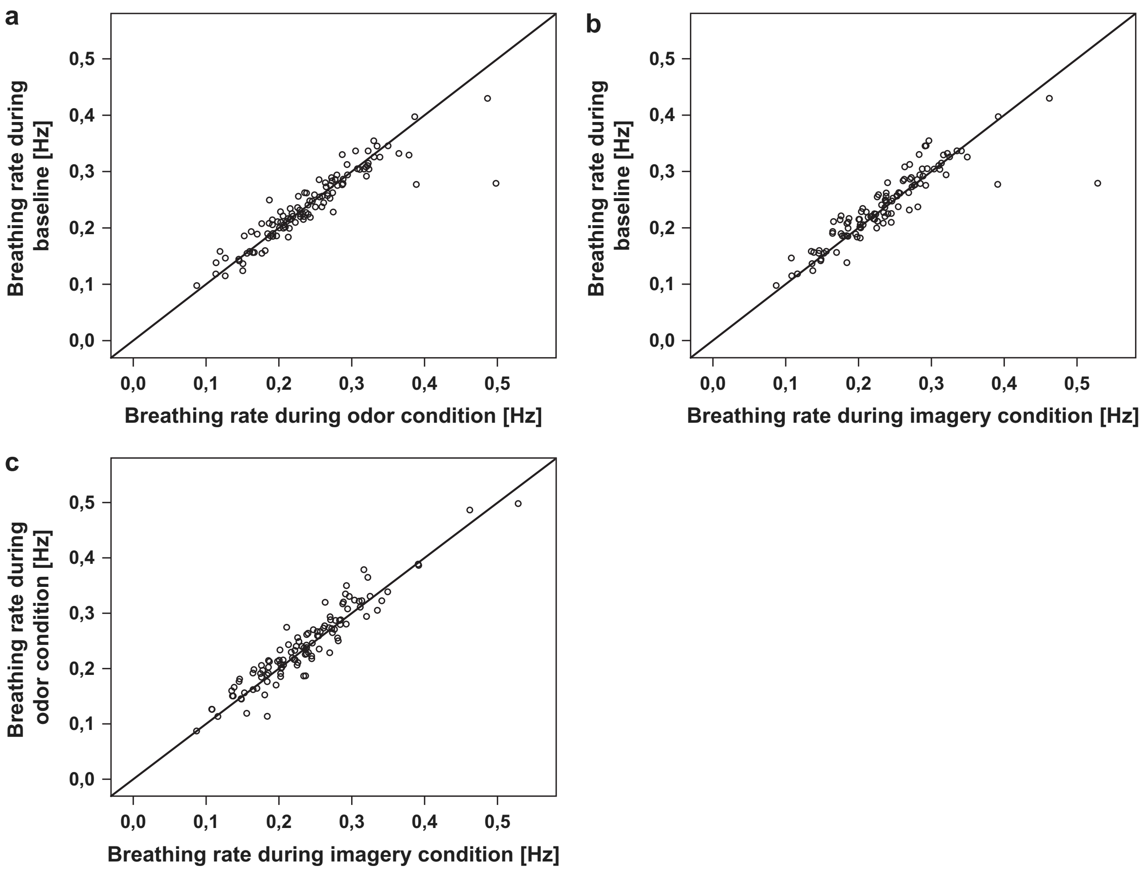

Figure 4 Paired comparison of breathing rate (*n* = 56) between tested conditions. When there are differences across conditions, the points are mostly above or below the unit slope line. When the conditions are equal, the data points accumulate around the line. **(a)** The difference in breathing rate between olfactory perception and baseline condition was not statistically significant. **(b)** The difference in breathing rate between olfactory imagery and baseline condition was not statistically significant. **(c)** The difference in the breathing rate between olfactory imagery and olfactory perception was also not statistically significant.

perception (Bensafi et al. 2003). The results of their experiments clearly pointed out that the sniff was spontaneously generated when participants were trying to imagine a smell but not when trying to imagine sight or sound, and their sniffs were more vigorous during imagery of pleasant versus unpleasant odors. It was also ascertained that the overall vividness of imagery was reduced during the sniff-blocked condition for olfactory but not for visual imagery. Additionally our findings contribute an important extension, namely the fact, that the measurement of the breathing rate is not enough to make a statement about the changes in the breathing or in the sniffing behavior. From the finding that breathing/sniffing rate was equal across conditions cannot be concluded that there are no differences in the breathing (or sniffing) across conditions. The results of this study confirm that it is necessary to analyze the breathing patterns (e.g., amplitude, minute volume, and shape) to evaluate breathing or sniffing behavior.

Table 1 Breathing parameters (respiratory minute volume, respiratory amplitude, breathing rate) and the number of local maxima per respiratory cycle during tested conditions (baseline, odor perception, olfactory imagery). The mean values and standard deviations are presented.

	Baseline	Odor perception	Olfactory imagery
Respiratory minute volume (l/min)	4.13 ± 2.38	4.77 ± 3.02	4.74 ± 3.10
Respiratory amplitude (l)	0.28 ± 0.16	0.29 ± 0.18	0.30 ± 0.19
Breathing rate (Hz)	0.24 ± 0.06	0.24 ± 0.07	0.24 ± 0.07
Number of local maxima per respiratory cycle	4.63 ± 3.91	6.21 ± 5.54	5.68 ± 5.64

Our results confirm that sniffing is involved in both olfactory perception and olfactory imagery. Sniffing is a robust motor activity that is required for the transport of the olfactory stimuli and for olfactory perception. It is also very important for generating neural activity in olfactory brain areas (Sobel et al. 1998a, 1998b). Using functional magnetic imaging (fMRI) Sobel et al. (1998a) found that sniffing induces activation in the human piriform cortex whether an odorant is present or absent. The authors postulated that sniff-induced

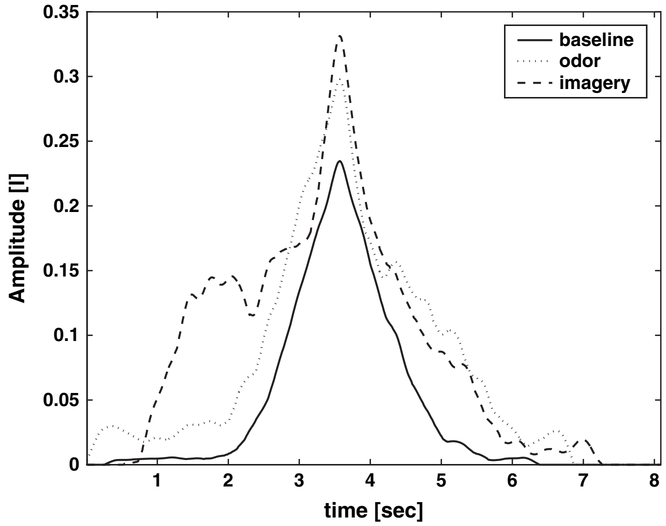

Figure 5 Representative examples of averaged breathing cycles for one subject.

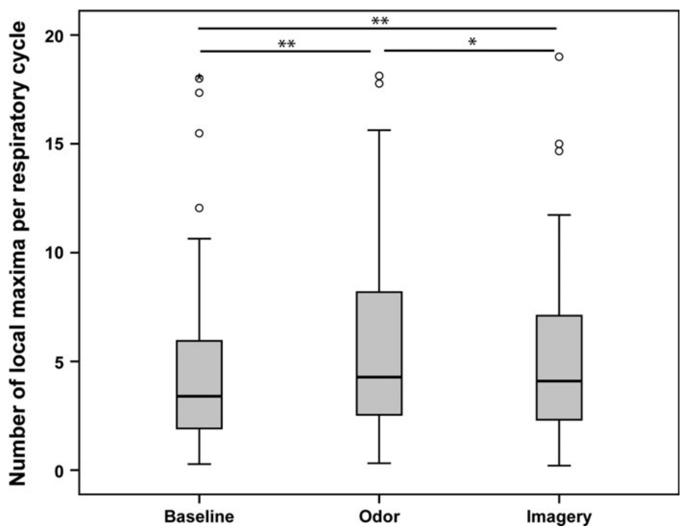

Figure 6 Box plot comparing the number of local maxima per respiratory cycle during olfactory perception, olfactory imagery, and baseline condition. The differences between the conditions were statistically significant (*significant $P < 0.05$; **significant $P < 0.005$).

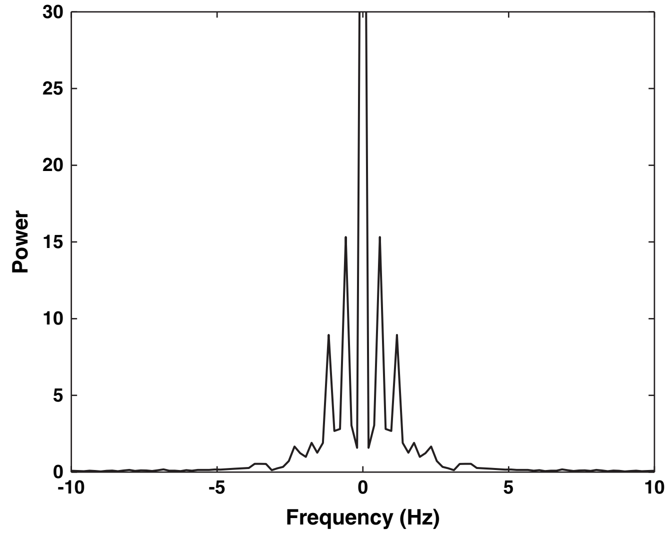

Figure 7 FFT of breathing curves in the baseline condition (n = 56).

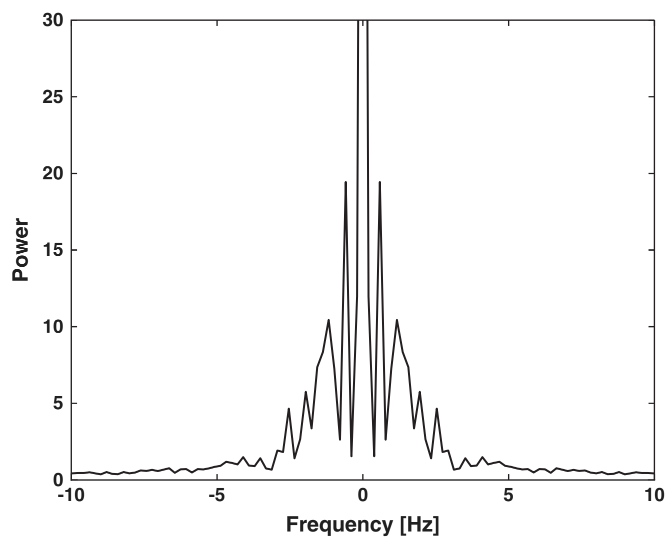

Figure 8 FFT of breathing curves in the odor condition (n = 56).

brain activation is in fact somatosensory stimulation that is caused by airflow through the nostril. Moreover, this group demonstrated that the cerebellum plays a role in human olfaction (Sobel et al. 1998b; Johnson et al. 2003). Given that the sniff volume correlates with the odorant concentration (Laing 1983; Sobel et al. 2001), they suggested that the cerebellum maintains a feedback mechanism that regulates sniff volume in relation to odor concentration.

Our findings confirm the hypothesis that sniffing, the motor component of olfaction, is very important for smelling and functionally involved in odor imagery. During the measurements, we observed that the sniff was spontaneously generated when the participants smelled an odor and when they were trying to imagine a smell. This indicates that both phenomena are based on a similar neural mechanism.

Referring to the mental imagery debate, which contains 2 main theories, the ''perceptual anticipation theory'' (Kosslyn et al. 1995, 2001; Kosslyn and Thompson 2003) and the ''propositional theory'' (Pylyshyn 1973; Pylyshyn 2003), our results support the first theory. The ''perceptual anticipation theory'' posits that the strong anticipation of perceiving an object or scene can actually lead to the creation of a descriptive representation in the early visual cortex resulting in a mental image. In contrast, the propositional theory postulates that mental images are not images at all but rather

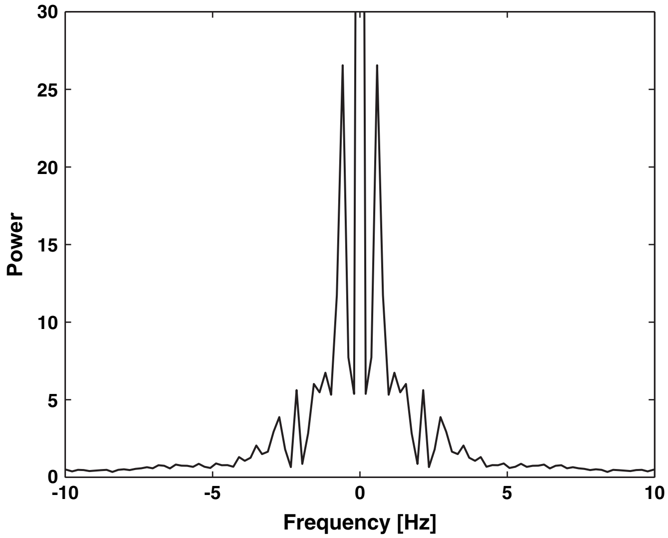

Figure 9 FFT of breathing curves in the olfactory imagery condition (n = 56).

rely on mental descriptions no different in kind from those that underlie language. Our findings, which show that sniffing accompanied not only smelling but also olfactory imagery, are consistent with the perceptual anticipation theory. We were able to show that olfactory imagery exists, and both processes are regulated by similar underling mechanism.

The respiratory sensor we used in the current study was shown to be a suitable device for the measurement of breathing parameters. An additional advantage over other sensors is that our sensor contains no magnetic elements and therefore can be use inside of MRI scanner.

The results of our study demonstrated that it is possible to detect differences in breathing between olfactory imagery, olfactory perception, and baseline. Similar to the study of Djordjevic et al. (2005), we detected no significant differences in the breathing rate. In contrast, we found that the largest differences between conditions were apparent in the minute respiratory volume. Further analysis permitted us to draw the conclusion that main changes in breathing were caused by changes in the breathing profiles. Furthermore, we conclude that the changes in the breathing profile result from sniffing that accompanied both olfactory perception and olfactory imagery.

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