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Fast Track Report

# Habituation effects of pleasant and unpleasant odors



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#### ABSTRACT

*Objective*: The hedonic value of odors is reflected in chemosensory evoked potentials with more salient unpleasant odors being processed differently from pleasant odors. However, it is not known if this effect is stable over time. It was examined if chemosensory evoked potentials towards pleasant and unpleasant odors change with repeated presentation.

Methods: 42 participants received two pleasant (Peach and PEA) and one unpleasant (H<sub>2</sub>S) intensity matched odors in a block design. Intensity and pleasantness were rated after each presentation. Subjective ratings, as well as N1 and P2 of the first stimulus of each block were compared with the two following stimuli of each block.

Results: Early and late components of the chemosensory evoked potentials had shorter latencies in response to the unpleasant  $H_2S$  compared to PEA and Peach. Pleasantness ratings for  $H_2S$  increased with repeated presentation but were far below neutral even for the third stimulus in a row. In line with this, for  $H_2S$  only, the P2 amplitude diminished with repeated presentation.

Conclusion: We assume that unpleasant stimuli catch more attention first hand. However, repeated presentation leads to reduced emotional salience of unpleasant stimuli only, which is mirrored in a decrease of neuronal activation.

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## 1. Introduction

Attention is modulated by characteristics of the environmental stimuli, whereby those with enhanced intensity and enhanced emotional value evoke enhanced processing (Pourtois et al., 2012). This is also valid for olfaction: intensity and pleasantness of an odor determinate olfactory processing. Unpleasant odors are detected faster than pleasant ones (Bensafi et al., 2002b) and lead to enhanced heart rate acceleration (Alaoui-Ismaili et al., 1997; Bensafi et al., 2002a, 2002b) and odors are detected faster at high than low concentrations (Wang et al., 2002).

Another approach of studying olfactory processing is using chemosensory event related potentials (CSEP). Event related potentials are electrical changes recorded from the brain. This technique visualizes correlates of neuronal activation with very high temporal resolution and allows examination of the sequential processing of information (Picton et al., 1995). Event related potentials consist of early and late components. The early components are suspected to reflect the physical characteristics of the stimulus to a relatively higher degree than later components; late components reflect endogenous processes like subjective emotional evaluation of the stimulus to a relatively higher degree (Kobal et al., 1992). The late P2 compound is modulated by attention: if people attend to an odor, the P2

amplitude is increased (Andersson et al., 2011). It was shown that the unpleasant odor of hydrogen sulfide evokes enhanced P2 amplitudes compared to the pleasant rated vanillin odor (Kobal et al., 1992). Interestingly, this coherence of the P2 amplitude on odor valence could also be found for the very same odor, which was perceived with different pleasantness by the participants. In a study 22 participants rated the olfactory stimulus androstenone using verbal descriptors. Those who used descriptors of human body odor exhibited enhanced amplitudes in the late positive component of event related potentials compared to those participants who used non-body-odor descriptors (Lundstrom et al., 2006). For odor intensity several studies revealed that amplitudes of early and late components of CSEP increase with increased odor concentration (Tateyama et al., 1998) and latencies decrease (Pause et al., 1997; Tateyama et al., 1998). Even at the very first level of olfactory processing, the olfactory epithelium, a difference of neuronal activation due to stimulus intensity and valence has been observed. Increased odor concentration enhances odor processing at the level of the olfactory epithelium and unpleasant odorants evoked larger amplitudes in comparison to their paired pleasant odorants (Lapid et al., 2009).

We aim to see, how neuronal processing of pleasant and unpleasant odors changes with repeated presentation. CSEPs are typically erased using a block design. Hereby 4 to 20 of the same olfactory stimuli are presented in a row, followed by a block of another stimulus in order to prevent habituation by presenting the same odors for

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a long time. This design is repeated several times and at the end potentials are averaged above all stimuli of the same kind. This method is very efficient and proven to be valid for research and clinical purpose (Hummel et al., 2000).

However, it has been shown, that CSEPs are attention dependent (Pause et al., 1997; Croy et al., 2010b) and attention can be directed to the hedonic characteristics of odors (Djordjevic et al., 2012). Furthermore, perception of the hedonic characteristic of stimuli changes with mere exposure (Cain and Johnson, 1978). Therefore potential shifts of attention in the typical block design could influence the CSEPs. We want to know, if there are already habituation effects in the first few olfactory stimuli. A study conducted with visual material revealed, that early components of event related potentials decreased for pleasant and unpleasant pictures with repeated presentation. Late components also showed a small decrease in amplitude with repeated presentation, but even after 90 repetitions pleasant and unpleasant pictures elicited strong late positive potentials, suggesting that the effect of emotional significance is a very robust one (Codispoti et al., 2007). For olfactory stimuli it is not known how neuronal activation develops with repeated presentation. We examine event related potentials in repeated presentation of one unpleasant and two pleasant odors.

#### 2. Materials and methods

#### 2.1. Participants

A total of 42 healthy participants (11 men, 31 women, aged 20 to 38 years mean = 24.5 years, standard deviation = 2.5 years) volunteered for this study. Most of them were graduate students or members of the Technical University of Dresden Medical School. Completion of a detailed medical history form by each participant enabled confirmation of their good physical health. Normal olfactory function was ascertained by the elaborate olfactory Sniffin'Sticks Test (Hummel et al., 2007); scores of all subjects ranged between 31 and 41.75 (mean = 36, standard deviation = 2.5).

The investigations were performed according to the Declaration of Helsinki on Biomedical Research Involving Human Subjects. The protocol was approved by the local Medical Faculty Ethics Review Board (protocol number EK 155052010). After complete explanation of the study to the participants in written form and also during an interview, written informed consent was obtained.

#### 2.2. Chemosensory event related potentials

CSERP were recorded in participants naive to these experiments. They were instructed to keep their eyes open. Monomodal chemosensory nasal stimulation was performed using a stimulator (Olfactometer OM2S, Burghart Instruments, Wedel, Germany) which allows administration of chemical stimuli without causing concomitant mechanical or thermal sensations. This was achieved by embedding chemical stimuli of 200 ms duration in a constantly flowing air stream (8 l/min) applied to the nasal cavity through a canula with an inner diameter of 2 mm inserted approximately 1 cm into the nostril beyond the nasal valve area. Temperature and humidity of the air stream was kept constant (36.5 °C, 80% relative humidity). Rise time of the stimulus concentration was less than 20 ms.

PEA (40% v/v), Peach (40% v/v) and  $H_2S$  (4 ppm) were used for olfactory stimulation. Those odors are considered to be specific stimuli of the olfactory system inducing little or no trigeminal activation. Peach and PEA, which smells like roses, are odors which are known to be perceived as pleasant.  $H_2S$  smells like rotten eggs and is perceived unpleasant (Hummel et al., 2000; Croy et al., 2010a). PEA and  $H_2S$  are odors consisting of only one molecule, while Peach is a mixture. Concentration of the odors remained constant during the experiment, however the participants were not aware of this. As intended, the odors did not differ significantly in intensity (p = 0.07) but in pleasantness

(p < 0.001, compare Table 1). Each participant received 188 olfactory stimuli in total, divided in two sessions. In each session 9 blocks of H<sub>2</sub>S stimuli, 8 blocks of PEA stimuli and 9 blocks of Peach stimuli were included. Each block of the unpleasant H<sub>2</sub>S consisted of 4 consecutive stimuli. In order to minimize effects of expectation, blocks of the pleasant PEA and Peach odors varied between 2 and 5 stimuli. Six of the nine H<sub>2</sub>S blocks of each session were followed by PEA stimuli, three by PEA. In order to prevent memory effects, both sessions were not identical in the sequence of blocks. In total, there were 18 stimuli, where H<sub>2</sub>S was presented first time in a block. There were also 18 stimuli where H<sub>2</sub>S was presented the second time, 18 on the third and 18 on the fourth. For PEA there were 16 stimuli of first presentation and 16 of second presentation, 14 of third, 9 of fourth and 2 of fifth. For Peach there were 18 stimuli of first presentation, 18 of second, 13 of third, 7 of fourth and 3 of fifth. The odors were presented in an attend task and after each stimulus the participants rated stimulus intensity and pleasantness on a scale from 0 to 100. For better visualization, pleasantness ratings were afterwards transformed to -50 to 50 scales. The procedure lasted approximately 1 h per session. Participants were seated in an air-conditioned room that was darkened and acoustically shielded to minimize other concomitant sensory stimuli

EEG was recorded during stimuli presentation from two positions of the international 10/20 system (CZ and PZ) referenced to linked earlobes (A1, A2). Blink artifacts were monitored from an additional recording site (Fp2). Stimulus-linked EEG-segments of 2048 s were digitally recorded at a frequency of 250 Hz (low-pass filter 15 Hz). CSERP were obtained by off-line averaging of at least 8 digitized EEG-segments. Records contaminated by eyeblinks (>50  $\mu V$  in Fp2 lead) or other disturbances (e.g., high-frequency motor artifacts) were discarded during off-line analysis via visual inspection of single trials by a trained observer.

## 2.3. Data analysis

N1 and P2 amplitude and latency of the first three repetitions of PEA, Peach and  $H_2S$  were detected by a trained observer as the highest or lowest value, respectively, in a specified time window (Hummel et al., 2000). Due to unforeseen technical problems, good quality data of each of the nine stimuli (three odors  $\ast$  three presentations) was received only at channel CZ for at least 80% of the participants. Therefore analysis concentrated on this channel.

Data were analyzed using SPSS vs. 19 (SPSS Inc., IL, USA). Ratings of pleasantness and intensity as well as N1 and P2 amplitude and latency were analyzed using analyses of variance (ANOVA) for repeated measurements with the 2 factors odor (3) and repetition (3). Post-hoc tests were interpreted following Bonferroni-adjustment of the p-value.

**Table 1**Intensity and pleasantness ratings.

$\begin{array}{cccccccccccccccccccccccccccccccccccc$					
$\begin{array}{cccccccccccccccccccccccccccccccccccc$		PEA	Peach	$H_2S$	Significance
2nd stimulus 18.4 (13.0) 23.3 (14.0) -30.8 (9.1) in H <sub>2</sub> S p < 0.001 3th stimulus 17.3 (12.8) 22.5 (14.0) 28.0 (10.5)	ricubantinebb	17.4 (12.2)	23.2 (14.0)	-30.5 (8.8)	- 1
3th stimulus 17.3 (12.8) 22.5 (14.0) 28.0 (10.5)	1th stimulus	16.8 (12.1)	23.7 (14.7)	-32.7(9.1)	Significant decrease
	2nd stimulus	18.4 (13.0)	23.3 (14.0)	-30.8(9.1)	in $H_2S p < 0.001$
Intensity overall 40.6 (15.5) 43.0 (17.5) 43.6 (15.6) n.s	3th stimulus	17.3 (12.8)	22.5 (14.0)	28.0 (10.5)	
111c113fty 0 vertil 40.0 (15.5) 45.0 (17.5) 45.0 (15.0) 11.5.	Intensity overall	40.6 (15.5)	43.0 (17.5)	43.6 (15.6)	n.s.
1th stimulus 42.7 (15.6) 49.2 (18.7) 49.2 (17.0) Significant decrease	1th stimulus	42.7 (15.6)	49.2 (18.7)	49.2 (17.0)	Significant decrease
2nd stimulus 42.1 (16.8) 42.9 (17.3) 44.1 (15.5) in Peach and H <sub>2</sub> S	2nd stimulus	42.1 (16.8)	42.9 (17.3)	44.1 (15.5)	in Peach and H <sub>2</sub> S
3th stimulus 40.0 (16.5) 40.9 (17.7) 41.0 (16.3) p < 0.001	3th stimulus	40.0 (16.5)	40.9 (17.7)	41.0 (16.3)	p < 0.001

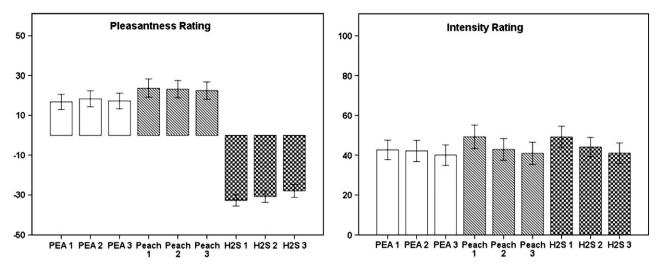


Fig. 1. Intensity and pleasantness ratings. Note: the error bars indicate the 95% confidence interval.

#### 3. Results

## 3.1. Ratings of intensity and pleasantness

The odors did not significantly differ in intensity (p=0.1, compare Table 1 and Fig. 1). A significant decrease of intensity could be observed between the first and third presentation (F41,2 = 39; p < 0.001). Furthermore a significant interaction between odor and presentation was observed (F4,37 = 6.5, p < 0.001). Post hoc analysis revealed, that intensity rating decreased significantly for Peach (t=6.2, p < 0.001) and  $H_2S$  (t=7.1, p < 0.001), but not for PEA (p=0.1).

The odors did differ in rated pleasantness (F2,39 = 329, p < 0.001). Ratings for Peach and PEA were significantly above 0 (p < 0.001), indicating that they were perceived pleasant, whereby Peach was perceived significantly more pleasant than PEA (p < 0.001). Ratings for  $H_2S$  were significantly below 0, indicating that it was perceived as unpleasant (p < 0.001).

Pleasantness ratings for the three odors changed significantly with repeated presentation (F39,6 = 3.7, p = 0.029). Furthermore a significant interaction between odor and presentation was observed (F4,37 = 7.2, p < 0.001). Post-hoc comparison revealed no significant change in perceived pleasantness between the first and the third stimulus presented in a row for the pleasant odors PEA (p = 0.6) or Peach (p = 0.2). For the unpleasant odor H<sub>2</sub>S however, the first stimulus was perceived significantly less pleasant than the fourth (t = 3.8; p < 0.001). However even for the third stimulus of H<sub>2</sub>S the pleasantness ratings were significantly below 0, indicating that it was perceived unpleasant (p < 0.001). The results are visualized in Table 1.

## 3.2. Chemosensory evoked potentials

### 3.2.1. N1 latency

A significant main effect of odor was revealed for the N1 latency (F2,33 = 15.1; p < 0.001, compare Table 2 and Figs. 2 and 3). Post hoc-analysis revealed that the  $H_2S$  odor led to earlier N1 peaks than PEA (p = 0.001) and Peach (p < 0.001). There was no significant difference between PEA and Peach in the N1 latency. No significant effect of repetition (p = 0.7) or of the interaction odor \* repetition (p = 0.3) was found.

## 3.2.2. N1 amplitude

No significant effect of odor (p = 0.2), repetition (p = 0.1) or interaction between odor and repetition (p = 0.2) was seen for the N1 amplitude.

## 3.2.3. P2 latency

A significant main effect of odor was observed for the P2 latency (F2,33 = 9.8, p < 0.001). Post hoc-analysis revealed that  $H_2S$  odor produced earlier P2 peaks than Peach (p = 0.001). No significant effect of repetition (p = 0.8) or of the interaction odor \* repetition (p = 0.4) showed up.

## 3.2.4. P2 amplitude

A significant main effect of odor was found for the P2 amplitude (F2,33 = 12.7; p < 0.001). Post hoc-analysis revealed that  $H_2S$  elicited a higher amplitude than Peach (p < 0.001) and PEA produced a higher amplitude than Peach (p = 0.018). There was no significant

**Table 2** Chemosensory evoked potentials.

			1th stimulus		2nd stimulus		3rd stimulus		Significance
			Mean	SD	Mean	SD	Mean	SD	
N1	Latency	PEA	508.0	84.3	518.8	85.8	518.3	83.5	Main effect of odor p < 0.001
		PEACH	546.1	83.4	527.7	84.7	538.6	88.6	
		$H_2S$	476.2	60.2	472.8	72.5	477.9	76.9	
	Amplitude	PEA	1.8	3.7	1.4	3.0	2.4	3.3	n.s.
		PEACH	2.9	2.7	1.9	2.7	3.3	3.6	
		$H_2S$	2.2	3.1	3.0	2.9	3.0	4.0	
P2	Latency	PEA	619.8	87.1	628.6	95.5	638.5	94.3	Main effect of odor p < 0.001
	-	PEACH	671.2	98.6	654.0	100.6	657.7	100.0	-
		$H_2S$	604.3	69.6	611.5	82.4	611.0	84.0	
	Amplitude	PEA	-8.8	3.9	-8.6	4.4	-7.8	3.6	Main effect of odor p < 0.001
	•	PEACH	-6.1	3.5	-7.2	3.0	-6.9	4.2	Interaction effect odor $*$ repetition p = 0.0
		H <sub>2</sub> S	-9.5	4.0	-9.1	4.7	-8.1	4.2	• •

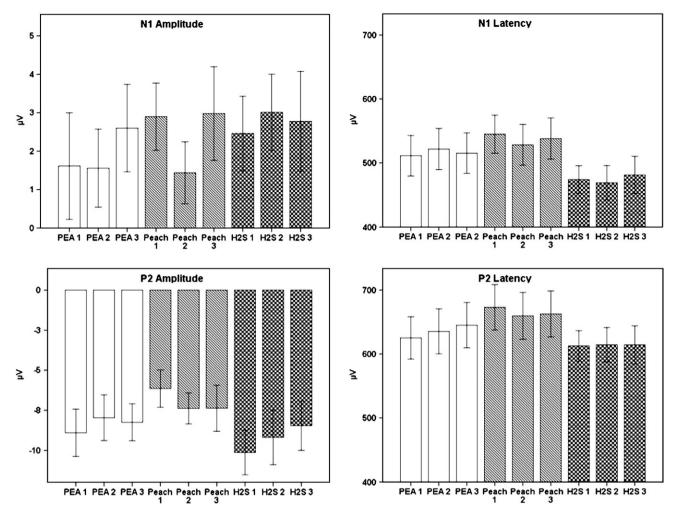


Fig. 2. Averaged values of the N1 and P2 amplitude and latency. Note: the error bars indicate the 95% confidence interval.

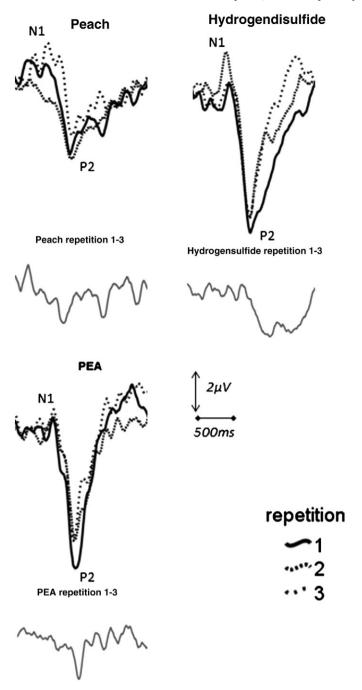
difference in P2 amplitude between PEA and  $H_2S$  (p=0.1). There was no significant effect of repetition (p=0.5). However, a significant odor  $\ast$  repetition interaction was found (F4,33 = 2.6, p=0.04). Post hoc tests revealed, that the P2 amplitude towards  $H_2S$  decreased linearly with repetitions of the stimulus (F1,39 = 4.8, p=0.034). No such effect was observed for Peach or PEA.

## 4. Discussion

Our data revealed that the odors are processed differently in relation to their valence. The unpleasant odor H<sub>2</sub>S produced the earliest response which was due for the N1 as well as for the P2 peak. It is one of the key functions of the olfactory system to warn about potential threats (Stevenson, 2010). Therefore unpleasant odors are likely to draw more attention. This is in line with previous studies, reporting increased autonomic reaction (Alaoui-Ismaili et al., 1997), and reduced reaction time (Bensafi et al., 2002b; Jacob and Wang, 2006) to unpleasant odors. Other studies report an enhanced P2 amplitude for unpleasant odors (Kobal et al., 1992; Lundstrom et al., 2006). We also found the highest P2 amplitude for the unpleasant H<sub>2</sub>S odor, although the comparison between PEA and H<sub>2</sub>S P2 amplitude was not significant after applying Bonferroni-correction. Emotional quality is of high importance in the processing of odors and it has been suggested that humans involuntarily categorize odors according to pleasantness (Bensafi et al., 2002a).

Unpleasant odors might fulfill their warning function by evoking emotions which lead to a behavioral reaction tendency. The olfactory system is especially predisposed to warn about microbial threats by evoking disgust (Stevenson, 2010; Croy et al., 2011). In a fMRI study it has been found, that the unpleasant ammonium sulfide odor in contrast to a pleasant strawberry odor showed higher activation in the left insula (Bensafi et al., 2007), a region involved in disgust processing (Wicker et al., 2003). Interestingly, this was the case not only when actually smelling, but also when only imagining the odors (Bensafi et al., 2007).

The second main outcome of the study is that for the unpleasant H<sub>2</sub>S, repeated presentation attenuated the unpleasantness rating. However, even for the third presentation the H<sub>2</sub>S was rated significantly below neutral. In line with this, a reduction of the endogenously driven P2 amplitude among repeated presentation was found for H<sub>2</sub>S, indicating a reduced neuronal activation. It has been shown that CSEPs are modulated by attention (Pause et al., 1997; Andersson et al., 2011) and that attention towards a stimulus depends on its emotional salience (Pourtois et al., 2012). The diminished unpleasantness ratings of H2S may reflect a reduction of emotional salience with repeated presentation, which is mirrored by a reduced P2 amplitude. We therefore conclude that attention towards the unpleasant odor decreases with repeated presentation. This effect was not seen for the more exogenous driven N1 amplitude. For the pleasant PEA and Peach odors, CSEP do differ significantly over repeated presentations.



**Fig. 3.** Grand average of chemosensory event related potentials in the three repetitions and difference wave forms between the first and third presentation. The curves start at stimulus coset

For researchers and clinicians working with CSEP, our results suggest, that a block design is appropriate for pleasant odors. For unpleasant odors, it should be kept in mind that the P2 amplitude diminishes with repeated presentation.

#### References

- Alaoui-Ismaili, O., Vernet-Maury, E., et al., 1997. Odor hedonics: connection with emotional response estimated by autonomic parameters. Chemical Senses 22 (3), 237–248.
- Andersson, L., Lundberg, C., et al., 2011. Chemosensory attention, habituation and detection in women and men. International Journal of Psychophysiology: Official Journal of the International Organization of Psychophysiology 79 (2), 316–322.
- Bensafi, M., Rouby, C., et al., 2002a. Influence of affective and cognitive judgments on autonomic parameters during inhalation of pleasant and unpleasant odors in humans. Neuroscience Letters 319 (3), 162–166.
- Bensafi, M., Rouby, C., et al., 2002b. Asymmetry of pleasant vs. unpleasant odor processing during affective judgment in humans. Neuroscience Letters 328 (3), 309–313.
- Bensafi, M., Sobel, N., et al., 2007. Hedonic-specific activity in piriform cortex during odor imagery mimics that during odor perception. Journal of Neurophysiology 98 (6), 3254–3262.
- Cain, W.S., Johnson Jr., F., 1978. Lability of odor pleasantness: influence of mere exposure. Perception 7 (4), 459–465.
- Codispoti, M., Ferrari, V., et al., 2007. Repetition and event-related potentials: distinguishing early and late processes in affective picture perception. Journal of Cognitive Neuroscience 19 (4), 577–586.
- Croy, I., Schellong, J., et al., 2010a. Women with a history of childhood maltreatment exhibit more activation in association areas following non-traumatic olfactory stimuli: a fMRI study. PLoS One 5 (2), e9362.
- Croy, I., Schellong, J., et al., 2010b. PTSD, but not childhood maltreatment, modifies responses to unpleasant odors. International Journal of Psychophysiology: Official Journal of the International Organization of Psychophysiology 75 (3), 326–331.
- Croy, I., Olgun, S., et al., 2011. Basic emotions elicited by odors and pictures. Emotion 11 (6), 1331–1335.
- Djordjevic, J., Boyle, J.A., et al., 2012. Pleasant or unpleasant: attentional modulation of odor perception. Chemosensory Perception 5 (1), 11–21.
- Hummel, T., Klimek, L., et al., 2000. Chemosensory evoked potentials for clinical diagnosis of olfactory disorders. HNO 48 (6), 481–485.
- Hummel, T., Kobal, G., et al., 2007. Normative data for the "Sniffin' Sticks" including tests of odor identification, odor discrimination, and olfactory thresholds: an upgrade based on a group of more than 3,000 subjects. European Archives of Oto-Rhino-Laryngology 264 (3), 237–243.
- Jacob, T.J., Wang, L., 2006. A new method for measuring reaction times for odour detection at iso-intensity: comparison between an unpleasant and pleasant odour. Physiology & Behavior 87 (3), 500–505.
- Kobal, G., Hummel, T., et al., 1992. Differences in human chemosensory evokedpotentials to olfactory and somatosensory chemical stimuli presented to left and right nostrils. Chemical Senses 17 (3), 233–244.
- Lapid, H., Seo, H.S., et al., 2009. Odorant concentration dependence in electroolfactograms recorded from the human olfactory epithelium. Journal of Neurophysiology 102 (4), 2121–2130.
- Lundstrom, J.N., Seven, S., et al., 2006. Olfactory event-related potentials reflect individual differences in odor valence perception. Chemical Senses 31 (8), 705–711.
- Pause, B.M., Sojka, B., et al., 1997. Central processing of odor concentration is a temporal phenomenon as revealed by chemosensory event-related potentials (CSERP). Chemical Senses 22 (1), 9–26.
- Picton, T.W., Lins, O.G., et al., 1995. The recording and analysis of event-related potentials. In: Boller, F., Grafman, J. (Eds.), Handbook of Neurophysiology, 10. Elsevier, Amsterdam.
- Pourtois, G., Schettino, A., et al., 2012. Brain mechanisms for emotional influences on perception and attention: what is magic and what is not. Biological Psychology 10, 3–73.
- Stevenson, R.J., 2010. An initial evaluation of the functions of human olfaction. Chemical Senses 35 (1), 3–20.
- Tateyama, T., Hummel, T., et al., 1998. Relation of olfactory event-related potentials to changes in stimulus concentration. Electroencephalography and Clinical Neurophysiology 108 (5), 449–455.
- Wang, L.W., Walker, V.E., et al., 2002. The correlation between physiological and psychological responses to odour stimulation in human subjects. Clinical Neurophysiology 113 (4), 542–551.
- Wicker, B., Keysers, C., et al., 2003. Both of us disgusted in My insula: the common neural basis of seeing and feeling disgust. Neuron 40 (3), 655–664.