

Title: Lexical olfaction recruits olfactory orbitofrontal cortex in metaphorical and literal contexts

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Abstract: The investigation of specific lexical categories has substantially contributed to advancing our knowledge on how meaning is neurally represented. One sensory domain that has received particularly little attention is olfaction. This study aims to investigate the neural representation of lexical olfaction. In an fMRI experiment, participants read olfactory metaphors, their literal paraphrases, and literal olfactory sentences. Regions of interest were defined by a functional localizer run of odor processing. We observed activation in secondary olfactory areas during metaphorical and literal olfactory processing, thus extending previous findings to the novel source domain of olfaction. Previously reported enhanced activation in emotion-related areas due to metaphoricity could not be replicated. Finally, no primary olfactory cortex was found active during lexical olfaction processing. We suggest that this absence is due to olfactory hedonicity being crucial to understand the meaning of the current olfactory expressions. Consequently, the processing of olfactory hedonicity recruits secondary olfactory areas.

Keywords: neural representation, olfaction, metaphor, fMRI, reading, embodiment



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1. Introduction

Recent theories of how lexical and semantic information is represented in the brain often point to embodied accounts (Pulvermüller, 2013). For example, comprehension of action words such as ‘lick’, ‘pick’ and ‘kick’ has been shown to activate portions of the motor and premotor cortices which are typically associated with movements of the tongue, arm and leg, respectively (Hauk, Johnsrude & Pulvermüller, 2004). Hence, bodily movements are partially simulated in response to words that refer to them. Empirical work in support of embodied accounts has mainly focused on concrete concepts, which are associated with one of the five senses (“arm”, “cake”, “bell”). However, little is known about how abstract concepts (e.g., “thought”, “indifference”) are represented. One way to address this question is to embed the same concrete word in different sentential contexts, with the result that the crucial word is used figuratively and therefore acquires a more abstract meaning. Figurative expressions include metaphors, which are thought of mapping abstract conceptual domains onto concrete ones, therefore facilitating comprehension (Lakoff & Johnson, 1980; Gibbs, Lima, & Francozo, 2004). For example, in the expression “She had a rough day”, the abstract concept of “bad” day is mapped onto the concrete concept of “rough” surface. It has been shown that, to understand such sentence, linguistic representations are activated, along with a simulation of the concrete domain of texture (Lacey, Stilla, & Sathian, 2012; for other domains, see Citron & Goldberg, 2014; Desai, Binder, Conant, Mano, & Seidenberg, 2011). This should be particularly true for novel metaphors (e.g., “My husband is an elephant.”) compared to more conventional, “dead” metaphors (e.g., “This is a hard task.”; Keysar, Shen, Glucksberg, & Horton, 2000; Lai & Curran, 2013). In idioms, whose meaning cannot be derived from the meanings of their constituting words (Cacciari, 2014; Gibbs, Nayak, & Cutting, 1989), this effect of sensorimotor activity has been shown to be reduced or even absent (Raposo, Moss, Stamatakis & Tyler, 2009; Schuil, Smits & Zwaan, 2013; see also Cacciari et al., 2011).

Metaphors establish an analogical relationship between two concepts: a source, concrete concept and a target, abstract concept (Yang, Bradley, Huq, Wu & Krawczyk, 2013), which can be activated in parallel. In fact, using conventional textural metaphors such as “She had a rough day”, Lacey et al. (2012) showed activation of the parietal operculum, a somatosensory area that is texture-selective. This finding indicates that metaphors indeed activate areas associated with the source domain, namely perception of texture. Similar results were obtained by Citron and Goldberg (2014), who employed German gustatory metaphors like “Sie bekam ein süßes Kompliment.” (i.e., she received a sweet compliment) and compared these to their literal counterparts (“Sie bekam ein nettes Kompliment” – she received a nice compliment). Their main findings are an activation increase in a left inferior frontal cluster including gustatory cortices for metaphors compared to literal sentences as well as involvement of the left hippocampus and anterior parahippocampal gyrus, including the amygdala. These results provide further evidence for the grounding of metaphors in sensorimotor representations by generalizing to the taste domain. Furthermore, the authors concluded that the metaphorical formulations are more emotionally engaging than their literal renderings at an implicit processing level. In fact, the two types of stimuli had been matched for explicit emotional valence and arousal ratings, but still activated emotion-related brain areas (i.e., amygdala and hippocampus) during reading

comprehension. While reverse inference could be a limitation of this interpretation, the latter finding is supported by a meta-analysis of neuroimaging studies (Bohrn, Altmann, & Jacobs, 2012), by physiological responses to translations of English metaphors (Rojo, Ramos, & Valenzuela, 2014), and has been replicated and generalized to other metaphors not restricted to taste (Citron, Güsten, Michaelis, & Goldberg, 2016). Nevertheless, this novel finding was not originally predicted by the authors. Importantly, the difference between metaphorical and literal expressions was not restricted to their metaphoricity but included the presence versus absence of a taste word. Therefore, the stronger amygdala response could be due to the use of taste words *per se*. Although a control condition showed no amygdala activation in response to taste words in isolation (“sweet” meant literally) compared to their counterparts (“nice”), this null finding could be due to less statistical power. A similar limitation was mentioned by Lacey et al. (2012) in their textural metaphor study.

One sensory system that has been mostly neglected regarding the neural representation of lexical meaning is olfaction. This sense offers very interesting characteristics that can further elucidate the nature of neural representations. Olfaction, as gustation, is a chemical sense. However olfaction, in contrast to gustation, is very difficult to verbalize (Yeshurun & Sobel, 2010; Wilson & Stevenson, 2006). While humans are able to distinguish among an incredible number of odors (McGann, 2017), there seems to be a lack of abstract olfactory categories in most languages, including German and English; however, other languages such as Jahai verbalize specific odor features in the same way in which German verbalizes different colors, shapes or textures (Majid & Burenhult, 2014; see also Wnuk & Majid, 2014). Concerning cognitive processes, verbalization of olfactory impressions seems critical as olfaction strongly relies on verbal translation for efficient working memory maintenance and episodic memory encoding (Rabin & Cain, 1984; Jehl, Royet, & Holley, 1997). This particular link of olfaction to language makes it compelling to investigate.

Odors are processed as configurations, e.g., peanut butter, with no access to their chemical components, and this makes it very difficult to name odors (Howard & Gottfried, 2014). In the case of vision, instead, we have access to both configurations, e.g., a happy face, as well as to their individual features, i.e., nose, mouth, eyes, therefore allowing mapping precision between visual features and lexico-semantic representations. Hence, bottom-up connections between the odor and the language systems are weak, whereas top-down connections, i.e., activation of the olfactory neural network upon presentation of odor-related words, are much more robust (Olofsson & Gottfried, 2015).

Overall, the cortical response to odors remains poorly understood (Price, 1991; Weiss & Sobel, 2012; Wilson & Rennaker, 2010). From the piriform cortex, i.e., the main primary olfactory area, olfactory information is projected to the orbitofrontal cortex (OFC), which receives direct afferent connections from the piriform cortex as well as indirect connections from the dorso-medial nucleus of the thalamus; the latter constitutes the olfactory thalamo-cortical pathway (Wilson & Rennaker, 2010). Since the OFC receives direct afferent inputs also from the amygdala and the entorhinal cortex, thus from most primary olfactory areas, it is considered to be the secondary olfactory area (Gottfried & Zald, 2005). In fact, lesions to the OFC in humans have been reported to induce impairments in discrimination and identification of olfactory stimuli (Jones-Gotman & Zatorre, 1988; Zatorre & Jones-Gotman, 1991). We

will use the terms 'OFC' (as identified in the functional localizer) and 'secondary olfactory cortex' interchangeably.

The present work aims to investigate the neural representation of lexical olfaction in literal and figurative language. The term lexical olfaction refers to the perceptual olfactory vocabulary. To prevent the above-mentioned lack of dissociation between metaphoricity and sensory source domain, the present study implements three experimental conditions: olfactory words were used to build conventional *olfactory metaphors*, their *literal paraphrases*, which did not contain any olfactory expression, and *literal olfactory sentences*. Furthermore, this work aims to examine whether olfactory metaphors are more emotionally engaging than literal olfactory sentences and non-olfactory literal paraphrases. A functional localizer of odor processing was run to examine the neural activation in more detail. The following predictions were generated: (1) the processing of lexical olfaction activates olfactory regions (despite the poor verbalization abilities), (2) reading olfactory metaphors shows a processing difference to reading literal olfactory expressions in olfactory regions, and (3) metaphoricity enhances activation in emotion-related areas.

2. Material and methods

2.1 Participants

Eighteen native German speakers ($M_{age} = 25.83$ years, $SD = 5.04$, age range = 19-39 years, 6 women) recruited by advertisement participated in the present study. Six additional participants were eliminated from the analysis due to technical equipment failure (five participants) and a pronounced functional and anatomical cerebral deviation (one participant). One participant reported to have learned speaking German not until kindergarten. All participants were right-handed by self-report, nonsmokers, had normal or corrected-to-normal vision and hearing, no history of neurological or psychiatric diseases, no dyslexia, no history of legal or illegal drug consumption, and met the criteria for MRI scanning (no claustrophobia, no metallic implants). The study follows the principles set by the Declaration of Helsinki and was approved by the local ethics committee of the Faculty of Psychology (Ruhr-University Bochum, Germany). Participants took part after providing informed consent and either received course credits or were paid 15 € for their participation.

2.2 Stimuli

Thirty-seven sentences were created for each condition. After generating the *olfactory metaphors*, their *literal paraphrases* were created by replacing the metaphorical olfactory word by a literal word, conveying the same overall meaning. Based on the words used for the metaphors and the literal sentences, *literal olfactory sentences* were created. See Table I for examples of the three sentence types. The conditions were carefully matched for various psycholinguistic variables based on a sentence rating task by an independent group of native German speakers ($N = 22$, $M_{age} = 27.32$ years, $SD = 7.93$, 17 women). These participants rated familiarity (i.e., subjective frequency of use and encounter), odor-reference, emotional valence and arousal on 7-point Likert scales. Based on these ratings, two sentences with most extreme values were discarded in each condition. For the descriptive statistics of the remaining 35 sentences per condition, see Table II; all sentences used are reported in

Table A1. This final set of sentences was matched for number of letters and number of words as well as for the logarithmic frequencies of the words (determined using the Wortschatz Leipzig project; <http://wortschatz.uni-leipzig.de>).

As intended, the sentences of the three conditions do not significantly differ in familiarity ($F(2,102) = 0.58, p = .56$), emotional valence ($F(2,102) = 1.21, p = .30$), arousal ($F(2,102) = 0.79, p = .46$), number of letters ($F(2,102) = 0.34, p = .71$), number of words ($F(2,102) = 0.68, p = .51$) and word frequency ($F(2, 676) = .36, p = .70$). Concerning odor-reference, the intended difference is clearly significant ($F(2,102) = 792.77, p < .0001$). Planned comparison of the conditions confirmed that literal olfactory sentences referred more strongly to odor than olfactory metaphors did ($t(68) = 24.21, p < .0001$) and literal paraphrases were least referring to odor ($ts(68) > 9.85, ps < .0001$).

As a visual baseline condition, 35 hash mark string sequences were created by replacing the letters of the first 12 metaphors, the following 12 literal paraphrases, and 11 literal olfactory sentences each with a hash mark; the spaces in between were preserved and the punctuation marks were eliminated. To maintain the participant's attention, eight filler sentences (including the previously discarded sentences) were occasionally presented followed by comprehension questions (see Table A1).

Table I. *Examples of Sentence Types with Approximate Literal Translation in Parenthesis*

Sentence type	
Olfactory metaphor	Er kann ihn absolut nicht riechen. (He cannot smell him at all.)
Literal paraphrase	Er kann ihn absolut nicht ausstehen. (He cannot stand him at all.)
Literal olfactory sentence	Er riecht sehr unangenehm. (He smells very unpleasantly.)
Visual baseline	## ##### ### ##### ##### #####

Note. The visual baseline is matched to the olfactory metaphor.

Table II. *Descriptive Statistics for Olfactory Metaphors, Literal Paraphrases and Literal Olfactory Sentences.*

Variable	Olfactory metaphors	Literal paraphrases	Literal olfactory sentences
	$M(SD)$	$M(SD)$	$M(SD)$
Familiarity	3.46 (1.04)	3.72 (1.03)	3.68 (1.13)
Odor-reference	2.49 (0.70)	1.26 (0.25)	6.10 (0.54)
Emotional Valence	3.30 (1.15)	3.37 (1.25)	3.75 (1.50)
Arousal	3.47 (1.00)	3.48 (1.08)	3.22 (0.83)
Number of letters	32.86 (8.01)	32.14 (7.91)	33.86 (10.00)
Number of words	6.37 (1.33)	6.29 (1.53)	6.74 (2.25)
Word frequency	6.99 (5.34)	6.67 (4.69)	7.05 (5.07)

Note. Familiarity, odor-reference, emotional valence and arousal were rated on 7-point Likert scales, whereby 1 meant not at all familiar/related to odor/emotionally arousing or very negatively valenced, and 7 meant very familiar/related to odor/emotionally arousing or very positively valenced. Word frequencies were determined using Wortschatz Leipzig.

2.3 Procedure

Prior to entering the scanner, participants were first informed about the procedure and the task and completed the informed consent form. After an approximately four-minute-long anatomical scan, participants evaluated olfactorily presented stimuli for the functional localizer run (see 2.5 Localizer). After a short break, participants were instructed to silently read sentences for comprehension and to answer to regularly following comprehension questions by pressing one of two response keys with their right index and middle finger. Written stimuli were visually presented by means of digital goggles using VisuaStim interface (Resonance Technology Company, Inc.) and Presentation® (Neurobehavioral Systems Inc.).

The sentences were centrally presented for four seconds each, in black font on white background. Each sentence was presented in one centered line using three different pseudorandomized orders. The filler sentences were each followed by a comprehension question. These short questions (3-6 words) of no further interest were presented for two seconds, followed by a four-second response window. During the jittered inter-stimulus interval (1500 - 4500 ms, averaging to 3000 ms), a black fixation cross was centrally presented to keep attention and gaze of the participant focused. A total scanning time of approximately 15 minutes was required to complete this part of the experiment, resulting in an overall duration of the experiment of one hour, including preparation, structural scans, odor processing task, and sentence processing task.

2.4 Image acquisition and preprocessing

MRI data were acquired using a 3-Tesla Philips Achieva MRI scanner (Bochum, Germany) with a 32-channel head coil. Mild cushioning minimized head movements. Anatomical T1-weighted scans (MPRAGE sequence) comprised 220 slices with a 8° flip angle and 1 mm³ isotropic voxel size without gaps and were acquired continuously every 8.4 s. The field of view (FOV) was 220 mm with a matrix size of 240x188. T2-weighted echo-planar images (EPI) with blood oxygen level-dependent (BOLD) contrast acquisition used a FOV of 224 x 224 x 90 mm with a 112 x 109 image matrix, a flip angle of 90°, a TR of 2100 ms and a TE of 30 ms. Volumes consisted of 30 slices without gap with 2 x 2 x 3 mm voxel size. During the reading task, 479 functional volumes were recorded (localizer: 850 volumes).

The processing of imaging data was done with SPM8 (Wellcome Trust Centre for Neuroimaging) implemented in Matlab version R2014a (The MathWorks Inc.). The preprocessing included slice time correction to the middle slice of each volume, realign and unwarp, co-registration of the T1-weighted image to the mean T2-weighted image, segmentation of the T1-weighted image and deformation to spatially normalize the images into a standard anatomical space (Montreal Neurologic Institute, MNI), and spatial smoothing using an isotropic 8 mm (full-width half-maximum) Gaussian kernel to account for inter-subject variability.

2.5 Localizer

The olfactory stimulus evaluation localizer consisted of simple odor processing tasks with three different instructions of how participants respond to an odor: (1) detection („Is an odor present? -

Yes/No), (2) valence („Is the odor pleasant/unpleasant? - Yes/No) and (3) identity („Is the odor lemon/garlic/...? - Yes/No). Each trial consisted of one odor, followed by one of three questions. Twelve odors (garlic, sweat, onion, vinegar, rose, lemon, caramel, lavender, banana, apple, nut and jasmine) were selected based on previous work (Bestgen, Schulze, & Kuchinke, 2015). Both the valence and the identity instruction each comprise 24 odor presentations (each of the 12 odors once congruent to the question and once incongruent) and eight neutral ambient air presentations. The detection instruction comprised each 12 odor and four ambient air presentations. Each of these instructions was presented twice, in randomized order and counterbalanced across participants. This leads to a total of 120 odor (48 in the valence instruction, 48 in the identity instruction, 24 in the detection instruction) and 40 ambient air presentations during the localizer run. The procedure was held consistent under all three instructions: A fixation-cross was presented for 2000 ms, followed by the task specific question for 2000 ms and the presentation of an odor for 4000ms. During this interval participants were requested to answer the simple Yes/No question by pressing one of two response buttons. In total, the task lasted 22 minutes. All odor (and ambient air) stimuli were presented using a 24-channel, fMRI compatible and computer-controlled olfactometer with fast onset times and stable concentrations (see Bestgen et al., 2016). Sniffing was not assessed.

Odor onsets were modeled using a GLM that also comprised the 24 subject-specific movement parameters (see section 2.6). The main contrast of odors versus ambient air was computed at the first level, and a simple one-sample *t*-test at the second level. Based on the same computations as outlined in section 2.6, a cluster size threshold of 37 or more voxels was applied to reduce false positives thresholded at $p < .001$ uncorrected that controls the FWE at $p < .05$ for the whole-brain. Significant clusters were used as regions of interest (ROIs).

2.6 Statistical Analyses

Events were modeled using the general linear model (GLM) and convolved with a canonical hemodynamic response function (HRF). 24 subject-specific movement parameters were utilized as regressors of no interest, following the Friston 24 model (Friston, Williams, Howard, Frackowiak, & Turner, 1996; see also Starck, 2014), as well as five regressors of interest for each condition: *olfactory metaphors*, their *literal paraphrases*, *literal olfactory sentences*, filler sentences and questions, and hash mark sequences (visual baseline). For each regressor, the parameter estimates (betas) were computed for all brain voxels, and relevant contrasts of parameter estimates were calculated. The resulting contrast images for all participants were then entered into a series of one-sample *t*-tests at the first level for each condition. On the population level, a whole-brain analysis of all three lexical conditions contrasted to the visual baseline was computed to examine the reading network. Furthermore, a full-factorial model was built that comprised the main three first level contrasts: *olfactory metaphors* versus *visual baseline*, *literal paraphrases* versus *visual baseline*, *literal olfactory sentences* versus *visual baseline*. Effects of interest were computed as pairwise comparisons (*t*-tests) within the full-factorial model.

For the whole-brain analyses, Monte Carlo simulations (10,000 iterations) indicated that a cluster size of 37 or more voxels would reduce false positives to a corrected level of $p < .05$. Accordingly, at the

whole-brain level, all clusters that passed this threshold at $p < 0.001$ uncorrected were family-wise-error (FWE) corrected at $p < .05$ and reported. For the small volume correction (SVC) analyses, a peak level, FWE correction at $p < .05$ was applied. Voxels of interest corresponding to this FWE corrected p-level are reported in MNI coordinate space. ROI analyses results were visualized using rfxplot (Gläscher, 2009).

3. Results

3.1 Olfactory contrast for the functional localizer

The contrast of processing odorants (positive, negative and neutral) versus sniffing ambient air (across all conditions) revealed an olfactory network comprising five, left-lateralized regions (displayed in Fig. 2): the piriform cortex (primary olfactory cortex), the amygdala and hippocampus, the inferior OFC, the medial OFC and the inferior frontal gyrus (IFG). See Table III.

Table III. Five regions identified as being responsive to olfactory processing (across all olfactory conditions) compared to ambient air.

Region	# Voxels	T	x	y	z
Left amygdala, hippocampus, parahippocampal gyrus	251	6.35	-25.5	-18	-9
Left inferior orbitofrontal gyrus (medial and lateral); BA 11/47	350	6.03	-22.5	34.5	-13.5
Left piriform cortex	105	6.00	-31.5	1.5	-12
Left medial orbitofrontal cortex; BA 10/11	69	5.04	-6	57	-7.5
Left inferior frontal gyrus; BA 47	59	5.03	-45	30	-1.5

Note. BA = Brodmann area; # = number of; T = peak T -value; x, y, z = peak voxel MNI coordinates.

3.2 Reading network

At the whole-brain level, the contrast of lexical conditions versus visual baseline (*olfactory metaphors & literal paraphrases & literal olfactory sentences* > hash mark sequences), which examines the reading network, showed large scale activations in the left middle and superior temporal cortex, left occipital cortex, left IFG, and left precentral gyrus. See Figure 1 and Table B.1 for the significant activation peaks.

3.3 Whole-Brain and ROI Analyses

The full-factorial whole-brain analyses comprised the three contrasts of *olfactory metaphors* versus *literal paraphrases*, *literal olfactory sentences* versus *literal paraphrases*, and *olfactory metaphors* versus *literal olfactory sentences*. Five functional ROIs were defined based on the functional localizer and the analyses were conducted using small volume correction (FWE corrected).

The whole-brain analysis of *olfactory metaphors* > *literal paraphrases*, which was expected to replicate the results by Citron and Goldberg (2014), yielded significant clusters of activation in the left medial inferior OFC and in the left angular gyrus, reaching into middle occipital and middle temporal gyrus.

The corresponding ROI analyses showed significant BOLD signal changes in left inferior OFC. The opposite contrast of *literal paraphrases > olfactory metaphors* revealed no significant results.

The contrast *literal olfactory sentences > literal paraphrases*, which was expected to reveal activations based on the processing of lexical olfaction as both conditions are literal, differing only in their source domain, showed left-hemispheric significant BOLD signal changes in inferior OFC and superior frontal gyrus. ROI analyses revealed significant activation in left inferior OFC. The whole-brain analysis of the opposite contrast *literal paraphrases > literal olfactory sentences* resulted in two significant activation clusters in bilateral insulae and right medial frontal gyrus, with the ROI analyses being non-significant. Finally, the analysis of *olfactory metaphors > literal olfactory sentences*, which was expected to reveal activations based on metaphoricity as both conditions contain olfactory words but differ in metaphoricity, yielded no significant activation. Analysis of the opposite contrast of *literal olfactory sentences > olfactory metaphors* resulted in significant BOLD signal changes in right middle and superior temporal gyrus with non-significant ROI analyses. For the percent signal change in the five ROIs, see Figure 2; and for the significant activation peaks revealed in the whole-brain analyses, see Table IV.

Table IV. *Regions Showing Significant Activation in the Whole-Brain Analyses*

Region	# Voxels	T	x	y	z
Olfactory Metaphors > Literal Paraphrases					
Left medial inferior orbitofrontal gyrus; BA 11/47	189	5.56	-27	39	-15
Left angular gyrus, middle occipital gyrus, middle temporal gyrus; BA 39	270	4.19	-42	-69	30
Literal Olfactory Sentences > Literal Paraphrases					
Left inferior orbitofrontal gyrus; BA 11/47	260	4.77	-46.5	34.5	-9
Left superior frontal gyrus; BA 9	39	4.07	-16.5	57	34.5
Literal Paraphrases > Literal Olfactory Sentences					
Left insula	75	4.43	-30	4.5	19.5
Right frontal gyrus, insula	52	4.06	30	30	18
Literal Olfactory Sentences > Olfactory Metaphors					
Right middle and superior temporal gyrus	108	4.61	36	-46.5	6

Note. BA = Brodmann area; # = number of; T = peak *T*-value; x, y, z = peak voxel MNI coordinates.

4. Discussion

The present work investigates the neural representation of lexical olfaction. Furthermore, it examines whether emotion-related areas are involved in the processing of olfactory metaphors relative to literal

sentences. *Olfactory metaphors*, their *literal paraphrases* and *literal olfactory sentences* were silently read for comprehension while we recorded the hemodynamic responses of the participants using functional MRI.

There are three main findings regarding our predictions: (1) the processing of lexical olfaction recruits the left secondary olfactory cortex (or OFC), (2) no processing difference can be found for literal versus metaphorical olfactory expressions in olfactory regions, and (3) no enhanced activation in emotion-related areas can be observed for metaphorical expressions. We suggest that the absence of primary olfactory activation is due to olfactory hedonicity (i.e., degree of pleasantness) being crucial to understand the meaning of the current olfactory expressions, which are associated with the act of smelling rather than with olfactory objects. Therefore, olfactory hedonicity is the relevant feature of the perceptual concept, which is processed in secondary olfactory areas. We argue that the present findings fit well with the action-perception theory of semantic circuits by Pulvermüller (1999, 2013). However, the suggestion by Citron and Goldberg (2014) of metaphors being more emotionally evocative than literal expressions cannot be supported by our findings.

4.1 Lexical olfaction

Processing olfactory metaphors as well as literal olfactory sentences recruits the left inferior OFC (or secondary olfactory cortex), as localized by proper olfaction. Hence, secondary olfactory areas are recruited in the absence of odor - through language only. According to the present results, however, lexical olfaction does not activate primary olfactory areas (the piriform cortex). This is unexpected if we consider previous studies in which primary cortices were found active (e.g., Barrós-Loscertales et al., 2012, using taste words; Citron & Goldberg, 2014, using taste metaphors; González et al., 2006, using smell words; Lacey et al., 2012, using texture metaphors). However, the absence of piriform cortex activation directly points to humans' poor ability in naming odors (Bestgen et al., 2015; see Olofsson et al., 2014), to the weak connection between olfaction and language more generally (Kaeppeler & Mueller, 2013; but see Schulze, Bestgen, Lech, Kuchinke, & Suchan, 2017, for piriform activation to emotional faces), and to the fact that odors are processed as configurations (Olofsson & Gottfried, 2015).

The absence of piriform cortex activation may specifically be due to the stimuli we employed. While González et al. (2006), who found bilateral piriform cortex activation, used words such as "cinnamon" and "garlic", which strongly remind of odors without actually denoting odors, in our study we employed words that are associated with the act of smelling, e.g., "to smell", "sniffer", "stinking", "aromatic", "odor", "fragrance". Hence, processing these words embedded in sentences may well evoke odor-related emotional responses to the text (OFC), but may not at all activate primary olfactory representations (piriform cortex). Interestingly, piriform cortex activation has also been found for odor imagery (Bensafi, Sobel, & Khan, 2007) using two very object-specific odors to be imagined: rotten eggs and strawberry. These stimuli, as well as those used by González et al. (2006), refer to olfactory objects. Imagining concrete olfactory objects seems to be an essentially different process than reading olfactory verbs and adjectives that are not associated with a specific odor but with the act of smelling. Eventually, the absence of piriform cortex activation could indicate that sensorimotor simulation during

language comprehension does not necessarily engage primary cortices. In line with this idea, Tettamanti et al. (2006), for instance, report activation of a fronto-parietal motor circuit in response to motor language, which include the premotor but exclude the primary motor cortex. In relation to such findings, Kemmerer (2015) extensively discusses the role of primary sensorimotor activation with respect to motor verbs; he proposes a multilevel architecture that represents the motor features of verb meanings indeed in the precentral motor cortices, but modulates the retrieval of these motor features as a function of task and context such that the retrieval is not always necessary for word comprehension (see also Kemmerer & Gonzalez-Castillo, 2010, for an elaborate discussion of premotor and primary motor fMRI activation peaks due to motor verbs).

Nevertheless, the processing of lexical olfaction does indeed activate the olfactory OFC, which is the secondary olfactory cortex. This supports the sensorimotor hypothesis and is in line with Pulvermüller's (2013) action-perception theory of semantic circuits. Pulvermüller's theory predicts that reading activates the neural assemblies of the action-perception circuits of the words and of their referents. Therefore, the olfactory system is supposed to be activated besides perisylvian language areas. This perfectly matches what we see in the results: large-scale perisylvian activation reflects the language aspect (see section 4.2), and the OFC activation reflects the olfactory system activation.

The olfactory OFC has consistently been reported in response to low-level odor perception (Gottfried & Zald, 2005; Zald & Pardo, 2000) and corresponding lesions of this region in either hemisphere impair odor identification (Jones-Gotman & Zatorre, 1988). Right OFC has recently been proposed to be actively involved in linking odor percepts to their names (Olofsson et al., 2014) and it has also been suggested that olfactory predictive coding emerges in OFC (Zelano, Mohanty, & Gottfried, 2011). Moreover, the left OFC has been suggested to play a role in the conscious assessment of the emotional quality of odors when judging the degree of odor pleasantness compared to passively smelling odorants (Royet, Plailly, Delon-Martin, Kareken, & Segebarth, 2003). Finally, Royet et al. (2001) found the left OFC to be crucial for olfactory hedonicity judgments, and Zald and Pardo (2000) came to a similar conclusion (see also Kringelbach, O'Doherty, Rolls & Andrews, 2003, for left OFC activation modulation by perceived pleasantness of liquid flavor stimuli). In the case of our stimuli, which mostly use olfactory verbs and adjectives and less often refer to concrete odor-related objects, it is plausible that olfactory hedonicity is crucial to the meaning of the expressions. It is not the association to odor identity which enriches our expressions, but the association to the act of smelling. Importantly, implementing a functional localizer ensured that the activated OFC regions belong to the olfactory network, even though piriform activation is absent. In conclusion, our study provides evidence for the activation of the secondary olfactory cortex in response to metaphorical and literal uses of olfaction terms, therefore adding to the literature on sensorimotor simulation during comprehension of abstract as well as concrete language.

4.2 Reading network

Contrasting lexical conditions with the visual baseline yields a left-hemispheric activation pattern with large-scale middle and superior temporal activation as well as occipital and IFG activation. Frontal and temporal clusters represent perisylvian language activations (Catani, Jones, & Ffytche, 2005; Ferstl,

Neumann, Bogler, & von Cramon, 2008; Jung-Beeman, 2005; Vigneau et al., 2006) and replicate activation of the languages identified by Bolger, Perfetti and Schneider (2005). Activation in the precentral gyrus is most reasonably due to premotor activation in sentence processing (Ferstl et al., 2008; Price, 2000; Stringaris, Medford, Giampietro, Brammer, & David, 2007). Ferstl et al. (2008) suggest the bilateral anterior temporal lobe to be crucial to combine prosodic, syntactic and lexical information to obtain a semantic representation and, similarly, Jung-Beeman (2005) highlights the anterior superior temporal gyrus as crucial for semantic integration. Temporal pole activation is thus compliant with semantic integration processes needed to generate a semantic representation (see Pehrs et al., 2017), while the occipital visual activation points to the reading of words as being visually more demanding than the 'reading' of hash marks, and has been consistently reported for skilled readers (Price, 2012). In sum, this left-lateralized fronto-temporal reading activation matches previous findings and corroborates the importance of these regions in processing written language.

4.3 Metaphoricity

The present study extends previous work on the grounding of abstract concepts through metaphorical mappings to a novel domain, namely olfaction, showing that the comprehension of conventional figurative expressions related to olfaction does indeed recruit the secondary olfactory cortex. In addition, Citron and Goldberg (2014) proposed that metaphorical sentences are more emotionally engaging than their literal counterparts (see also Bohrn et al., 2012, for a review on figurative language processing, and Rojo et al., 2014) and replicated this finding using metaphors not restricted to taste (Citron et al., 2016). However, these findings could not be generalized to the odor domain in the present study. In fact, no significantly increased amygdalar or hippocampal activation could be shown for metaphors compared to literal expressions - neither during the explorative whole-brain analysis nor following the ROI analysis.

While there is a strong link between olfaction and emotion, the capabilities of the language system to activate this link seem weak or to be bound to higher levels of emotional valence (see Bestgen et al., 2015). Eventually, the stronger amygdalar and hippocampal engagement found by Citron and Goldberg (2014) could be due to the source domain of taste which, similarly to odor, is particularly emotionally valenced (Bensafi et al., 2002; Habel et al., 2007; Winter, 2016) but, unlike odor, is more easy to verbalize (Yeshurun & Sobel, 2010). Still, the emotional engagement in Citron and Goldberg (2014) could be due to taste per se rather than metaphoricity. The inclusion of literal taste-related sentences like in the present study would have allowed a better control. More research into which aspects of figurative language contribute to its (if any) stronger suitability to evoke emotion is needed.

4.4 Methodological Limitations and future investigations

As conventional fMRI sequences can suffer from the susceptibility artifact at air-tissue interfaces, image quality in olfactory-specific areas (basal frontal and ventral temporal lobes) can be reduced (Gottfried & Zald, 2005; Ojemann et al., 1997; Zald & Pardo, 2000). It must be taken into account that the current fMRI sequence is not specifically adjusted to meet this technological difficulty. Therefore, the absence of piriform activation for lexical stimuli (which would be arguably less pronounced than for

actual olfactory input), could be partly due to susceptibility artifacts. Future studies should consider these limitations to improve their designs to further extend our knowledge of neural representations.

5. Conclusion

Lexical olfaction recruits olfactory orbitofrontal cortex in metaphorical and literal sentential contexts. This result indicates that modality-specific areas of the human brain contribute to the neural representation of lexical meaning. Considering the weak connection between olfaction and language, it is particularly interesting to witness this sensory contribution in lexical olfaction. The absence of primary olfactory activation is probably due to olfactory hedonicity being central to understanding the meaning of the current olfactory expressions, which are associated with the act of smelling. In line with the action-perception theory of semantic circuits by Pulvermüller (2013), activation in perisylvian language areas has been observed in addition to olfactory system recruitment. However, enhanced recruitment of emotion-related areas due to metaphoricity, as suggested by Citron and Goldberg (2014), could not be extended to the olfactory domain.

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6. References

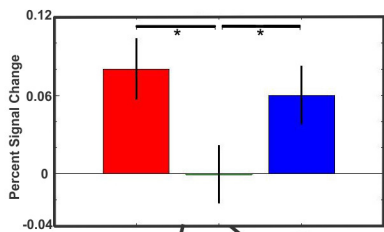
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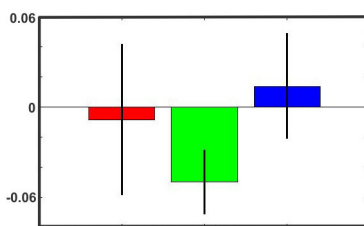
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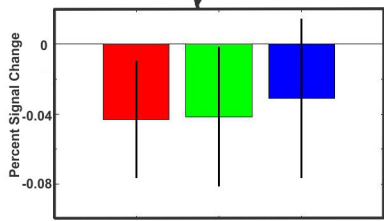
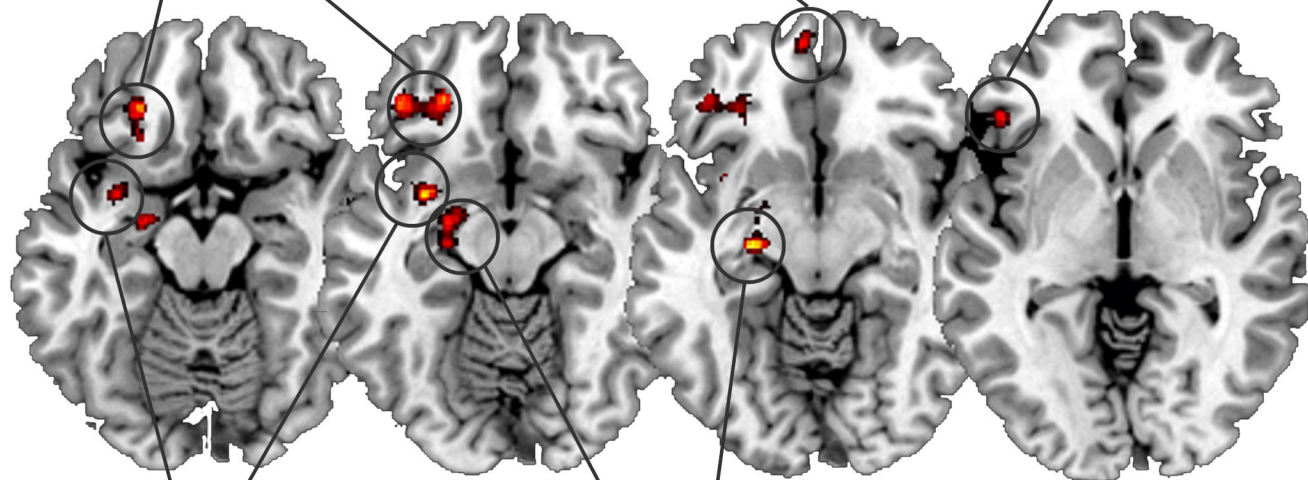
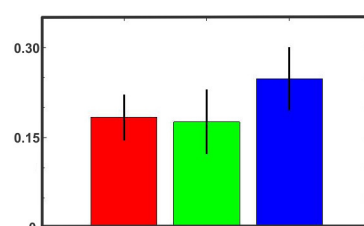
L inferior orbitofrontal gyrus



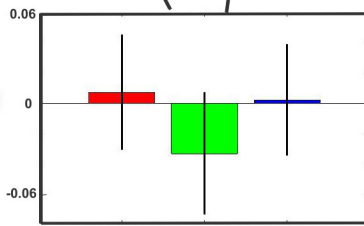
L medial orbitofrontal cortex



L inferior frontal gyrus



L piriform cortex



L Amygdala

- olfactory metaphors
- literal paraphrases
- literal odor sentences

-59

-55

-51

-47

-21

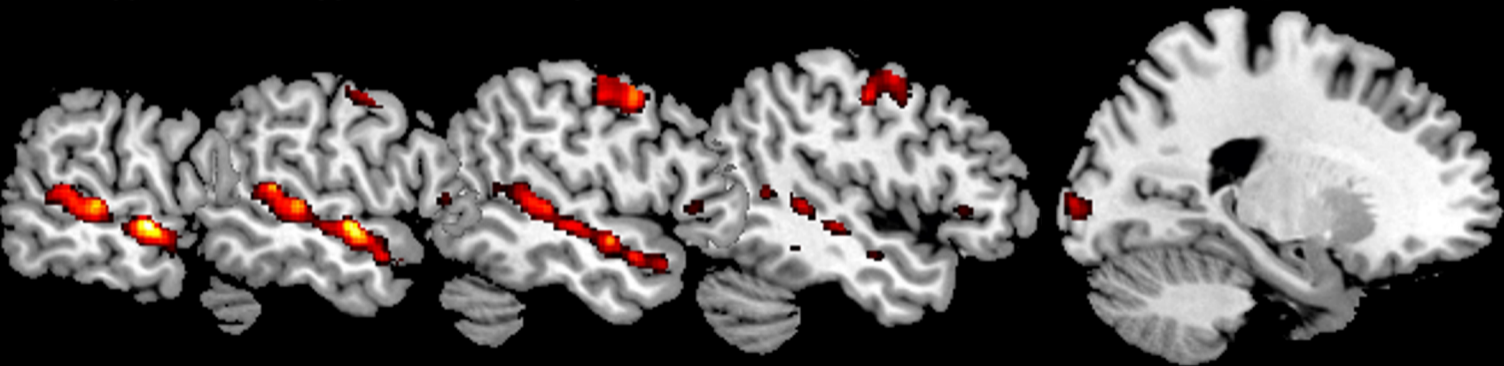


Figure 1. Percent signal change for the processing of olfactory metaphors (red), literal paraphrases (green) and literal olfactory sentences (blue) overlaid on the five functional ROIs as revealed by the functional localizer shown in horizontal slices. A significant difference in signal change can be seen in left inferior orbitofrontal gyrus.

Figure 2. The reading network shown in sagittal slices. Numbers indicate the x coordinates (MNI).

Table A.1. Stimulus Material

No.	Sentence
Olfactory Metaphors	
1.	Er hat einen richtig guten Riecher.
2.	Sie kann ihn absolut nicht riechen.
3.	Er ist ziemlich stinkig wegen der Kündigung.
4.	Es stinkt mir total, dass sie auch kommt.
5.	Es ist ein wirklich anrühiges Lokal.
6.	Sie stänkert schon den ganzen Tag lang rum.
7.	Er macht immer nur Stunk.
8.	Sie kleidet sich äußerst duftig.
9.	Für die Karriere zählt vor allem der richtige Stallgeruch.
10.	Seine geistigen Ausdünstungen sind absolut unbedeutend.
11.	Mir ist sowas von stinklangweilig.
12.	Folge einfach deiner Nase, um das Ziel zu erreichen.
13.	Ich finde das wirklich dufte.
14.	Er hat es wirklich direkt gerochen.
15.	Soweit ich weiß, beschnuppern sie sich noch.
16.	Ich verdufte jetzt gleich.
17.	Sie ist wirklich stinkfaul.
18.	Er wollte erst in das Programm reinschnuppern.
19.	Zu Beginn bieten sie einen Schnupperkurs an.
20.	Sie schnüffelt auf jeden Fall in seinen Sachen rum.
21.	Er ist ein richtig guter Schnüffler.
22.	Er ist eine ausgesprochen gute Spürnase.
23.	Er hat eine absolut ruchlose Tat begangen.
24.	Sie ist heute echt ganz schön muffelig.
25.	Die Vorlesung war mal wieder richtig furztrocken.
26.	Die Party war mal wieder furz langweilig.
27.	Das stinkt eindeutig nach Geld.
28.	Es riecht eindeutig nach Ärger.
29.	Das ist der süße Duft der Freiheit.
30.	Das riecht sehr nach Verrat.
31.	Sie hat ein sehr feines Näschen.
32.	Sie hat es gleich gewittert.
33.	Er ist wirklich stinksauer auf seine Kollegen.
34.	Sie ist stinkwütend wegen der Anschuldigungen.
35.	Er will den ganzen Tag einfach nur rumgammeln.
Literal Paraphrases	
1.	Er hat einen richtig guten Instinkt.
2.	Sie kann ihn absolut nicht ausstehen.
3.	Er ist ziemlich erbost wegen der Kündigung.
4.	Es missfällt mir total, dass sie auch kommt.
5.	Es ist ein wirklich anstößiges Lokal.
6.	Sie motzt schon den ganzen Tag lang rum.
7.	Er macht immer nur Radau.
8.	Sie kleidet sich äußerst grazil.
9.	Für die Karriere zählt vor allem die richtige Abstammung.
10.	Seine geistigen Darbietungen sind absolut unbedeutend.
11.	Mir ist sowas von sterbenslangweilig.
12.	Folge einfach deinem Instinkt, um das Ziel zu erreichen.
13.	Ich finde das wirklich prima.
14.	Er hat es wirklich direkt geahnt.
15.	Soweit ich weiß, lernen sie sich noch kennen.
16.	Ich verschwinde jetzt gleich.

(continued)

Literal Paraphrases (continued)

17. Sie ist wirklich träge.
18. Er wollte erst in das Programm reingucken.
19. Zu Beginn bieten sie einen Orientierungskurs an.
20. Sie stöbert auf jeden Fall in seinen Sachen rum.
21. Er ist ein richtig guter Detektiv.
22. Er ist ein ausgesprochen guter Ermittler.
23. Er hat eine absolut rücksichtslose Tat begangen.
24. Sie ist heute echt ganz schön misstrauisch.
25. Die Vorlesung war mal wieder richtig monoton.
26. Die Party war mal wieder äußerst langweilig.
27. Das bedeutet eindeutig Geld.
28. Es bedeutet eindeutig Ärger.
29. Das ist die süße Verlockung der Freiheit.
30. Das bedeutet Verrat.
31. Sie hat ein sehr feines Gespür.
32. Sie hat es gleich geahnt.
33. Er ist wirklich zornig auf seine Kollegen.
34. Sie ist erzürnt wegen der Anschuldigungen.
35. Er will den ganzen Tag einfach nur faulenzen.

Literal Olfactory Sentences

1. Sie riecht stark nach Parfum.
2. Er riecht sehr unangenehm.
3. Auf der Party hat es sehr nach Zigarettenrauch gerochen.
4. Ich hab den Geruch von Suppe in der Nase.
5. Das duftet richtig lecker.
6. Es stinkt hier ziemlich nach Gülle.
7. Der Hund schnuppert an einem Schild.
8. Das Schwein schnüffelt nach Futter.
9. Es stinkt nach Erbrochenem.
10. In dem Lokal riecht es immer so nach Knoblauch.
11. Der Detektiv hat nach Zwiebeln gerochen.
12. Zu Beginn hat es köstlich gerochen.
13. Seine Sachen riechen immer nach Schweiß.
14. Für diesen Duft würde ich nicht so viel Geld bezahlen.
15. Am Meer riecht es immer so gut.
16. Es duftet ganz herrlich nach Plätzchen.
17. Ihm steigt der Geruch von Kaffee in die Nase.
18. Ihr missfällt der Geruch des Parfums.
19. Seine Schuhe stinken ganz fürchterlich.
20. Der Ermittler nimmt den Geruch von Schwefel wahr.
21. Im Raum des Orientierungskurses riecht es immer nach Fenchel.
22. Es ist schlecht für die Karriere, wenn man immer nach Knoblauch riecht.
23. Ihre Kollegen meiden sie, weil sie streng riecht.
24. Der Geruch von Erdbeeren erinnert mich immer an den Sommer.
25. Es gab riesen Krawall, weil alles nach Essig roch.
26. In der Vorlesung hat es nach Pizza gerochen.
27. Im Ziel riechen die meisten nicht mehr appetitlich.
28. Zu Weihnachten verbreitet sich immer so ein herrlicher Duft.
29. Der Duft von Kuchen liegt in der Luft.
30. Der Gestank ist unerträglich.
31. Das Essen verbreitet einen köstlichen Geruch.
32. Es riecht vorzüglich.
33. Die Butter riecht ranzig.
34. Das Essen riecht verbrannt.
35. Die Blumen duften angenehm.

No. Sentence

Hash mark sequences

1. ## ### #####
2. ### #####
3. ## ### #####
4. ## #####
5. ## ### #####
6. ### #####
7. ## #####
8. ### #####
9. ### #####
10. #####
11. ### #####
12. #####
13. ### #####
14. ## ### #####
15. #####
16. ### #####
17. ### #####
18. ## #####
19. ## #####
20. ### #####
21. ## ### #####
22. ## ### #####
23. ## ### #####
24. ### #####
25. ## ### #####
26. ## ### #####
27. ## ### #####
28. ## ### #####
29. ### #####
30. ### #####
31. ### #####
32. ## #####
33. ### #####
34. ### #####
35. ### #####

Filler sentences with comprehension questions

- 1a. Er hat ein gutes Gespür für den richtigen Duft.
 - 1b. Hat er ein schlechtes Gespür?
 - 2a. Es folgt eine Kündigung, wenn der Laden immer stinkt.
 - 2b. Ist eine Kündigung die Konsequenz?
 - 3a. Es fühlt sich so richtig nach Sommer an.
 - 3b. Fühlt es sich nach Sommer an?
 - 4a. Ich kann das Meer förmlich schon erspüren.
 - 4b. Ist das Meer in der Nähe?
 - 5a. Es duftet so richtig nach Sommer.
 - 5b. Duetet es nach Frühling?
 - 6a. Ich kann das Meer förmlich schon riechen.
 - 6b. Riecht es nach Bergluft?
 - 7a. Sie riecht den Braten.
 - 7b. Ahnt sie etwas?
 - 8a. Das Wetter ist unbeständig.
 - 8b. Ist das Wetter gut?
-

Table B.1. Regions identified as being responsive to reading (across all lexical conditions) compared to seeing hash mark sequences.

Region	# Voxels	T	x	y	z
Left middle temporal gyrus, superior temporal gyrus, temporal pole; BA 21/22/38	2325	7.08	-57	-9	-4.5
Left precentral gyrus; BA 6	723	5.63	-52.5	1.5	45
Left inferior occipital gyrus; BA 19	96	4.86	-37.5	-72	-7.5
Left middle occipital gyrus; BA 18/19	399	4.83	-39	-82.5	-1.5
Left fusiform gyrus	71	4.73	-40.5	-43.5	-15
Left inferior frontal gyrus; BA 45/47	105	4.02	-48	25.5	1.5

Note. BA = Brodmann area; # = number of; T = peak *T*-value; x, y, z = peak voxel MNI coordinates.