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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.

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 (Gibbs, Lima, & Francozo, 2004; Lakoff & Johnson, 1980). 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

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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 (Wilson & Stevenson, 2006; Yeshurun & Sobel, 2010). 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 (Jehl, Royet, & Holley, 1997; Rabin & Cain, 1984). 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 1 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