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Olfaction and its dynamic influence on word and face processing: Cross-modal integration

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Abstract

The article specifies several important aspects related to the sense of smell in vertebrates. The idea that odors exert effects in the human brain though being not consciously perceived is introduced. Functional aspects related to cross-modal sensory interaction between olfaction and vision are highlighted. In particular, studies making use of electrophysiological methods providing high temporal resolution reveal an early processing stage around 300 ms and a later stage around 700 ms after stimulus onset. The early stage has been associated with subconscious olfactory information processing, whereas the later stage most likely reflects conscious odor perception. Specific interactions are described between olfaction and language and between olfaction and face processing in correlation with both stages of olfactory information processing. A consciously perceived odor can negatively affect language and face processing if these stimuli are presented and associated simultaneously, whereas simultaneous subconscious odor processing has the potential to improve memory formation in other stimulus modalities. Strikingly, the subconscious effect seems not to depend on odor valence.

Besides a better understanding of the sense of olfaction itself, these findings on cross-modal integration support the idea that neural representations exist for semantic contents (object meaning) independent from particular sensory modalities. These representations can be referred to as meta representations because the information they contain is derived from a great variety of sensory information integrated into a semantic representation of an object. It is suggested that such meta representations represent the basic units for cognition and that they provide inputs during dreaming.

Keywords: Olfaction; Words; Faces; Cognition; Brain imaging; Cross-modal integration

Contents

Abbreviations: PET, positron emission tomography; fMRI, functional magnet resonance imaging; CSERP, chemosensory event-related potential; EEG, electroencephalography; MEG, magnetoencephalography; OERP, olfactory event-related potential; BOLD, blood oxygenation level dependent; PEA, phenylethyl alcohol; H_2S, hydrogen sulfide; CO_2, carbon dioxide.

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1. Introduction

Human olfaction as a field of research attracts people as it has never done before. Besides a growing number of scientists who dedicate their time to augment the understanding of this particular sense, also journalists, economists and even marketing people are fascinated. Most likely, the idea that olfactory stimulation is more closely and more directly related to emotion and memory than any other sensory modality turned it from a lower sense to an exciting phenomenon. The absence of evidence is not an evidence for absence! This sentence fits very well the notion that odors exert effects though being not consciously perceived. As stated by Le Guérer (2002), ‘‘Odors, more sheltered from intellectual analysis than the other sense impressions, are the tools for intuitive and emotional knowledge of the world, as is reflected in everyday language and in many colloquial expressions’’ (‘‘to have a nose for something’’; ‘‘something smells to heaven’’). It seems strange but somehow such colloquial expressions can get you remarkably close to the point. It might well be that one major consequence of olfaction in humans is the creation of an overall judgement related to the environment which is in clear contrast to vision which produces a detailed image of it. Nevertheless, serious scientific investigations through empirical studies are the essential approach and, nowadays, an increasing number of people spend both time and money for research to increase scientific knowledge about the human sense of smell.

1.1. Vertebrate aspects

To date, olfaction has been well investigated in mammalian species with respect to its peripheral sensory characteristics and neuroanatomic projections. Starting in 1991, Buck and Axel (1991) contributed to a better understanding of odor perception on the basis of receptors on the olfactory epithelium; this work was eventually honoured by the Nobel Prize Committee in 2004. They found a multigene family (about 1000 genes; roughly 2/3 constitute so-called pseudo-genes) coding for certain proteins to be expressed solely in the olfactory epithelium. In addition, odorant receptor gene expression was found to be organised in distinct zones (Ressler et al., 1993) (Fig. 1).

In a paper on the development of the vertebrate main olfactory system, Lin and Hgai (1999) reviewed empirical evidence about the stereotyped projections of olfactory receptors to their first dendritic (second neuron) targets in the olfactory bulb, where they form a precise spatial map (see also Ressler et al., 1994; Buck, 1996). It is worthwhile to stay at this stage of olfactory information processing for a moment. From a morphological perspective, a simple display of olfactory bulbs (first olfactory relay station) belonging to different species of familiar mammals demonstrates their relative enormous size compared to the rest of the brain (Fig. 2). We certainly know that size alone does not necessarily relate to functional competence; however, the relatively large volumes of olfactory bulbs in those mammalian species might somehow reflect the relative importance of olfaction at least for brain functions in mammals other than the human species, as can be seen in Fig. 2. In an article about the evolution of vertebrate olfactory systems, Heather Eisthen mentioned that much research into the location and the extent of olfactory bulb projections in vertebrates has been stimulated by Edinger’s suggestion that the telencephalon was originally an olfactory structure that was invaded by other sensory systems over the course of vertebrate evolution (Eisthen, 1997; Edinger, 1904). The idea that the telencephalon did originally develop as a neural structure to process olfactory information is intriguing and potentially helpful at the same time in terms of trying to understand the human brain. The human brain bears a long history and some structures might have been designed under other selective pressures than suggested today. See Fig. 3 showing an opossum brain (axial slice) with a large olfactory bulb and direct projections to the telencephalon.

In fact, even lower vertebrates such as fish have surprisingly large peripheral olfactory systems suggesting an important role of olfaction in the underwater world, too (Hamdani and Døving, 2007) (Fig. 4).

In the mammalian brain, from the olfactory bulbs further up along the afferent path towards the brain the next relay station is the so-called primary olfactory cortex, consisting of the anterior olfactory nucleus, the olfactory tubercle, the anterior and posterior piriform cortex, the periamygdaloid region, the anterior and posterior cortical nuclei of the amygdala, as well as the nucleus of the lateral olfactory tract, the medial nucleus of the amygdala and the rostral entorhinal cortex (e.g., Savic, 2001; Gottfried and Zald, 2005). Finally, projections continue to the secondary olfactory cortex, which comprises the orbitofrontal cortex, parts of the insula, other parts of the amygdala, hypothalamic structures, the mediodorsal thalamus and the hippocampus (e.g., Savic, 2001; Gottfried and Zald, 2005). Olfaction is the only sense that connects to the orbitofrontal cortex with only 2 synapses in between bypassing the thalamus which relays information from other senses before they reach neocortical areas.

1.2. Human aspects

Looking again at Fig. 2 which shows size adapted brains of different mammals, one easily notices the relatively small olfactory bulbs in the human brain. The instantly arising question is ‘‘Does this demonstrate that olfaction is not very influential in humans’’? Despite its rather small peripheral