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COMMENTARY

Which format for odor images?

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Abstract

Olfactory mental images are defined as short-term memory representations of olfactory events that give rise to the experience of "smelling with the mind's nose." The present paper reviewed converging evidences that support the view that as visual mental images, odor mental images preserve some aspects of olfactory percepts. The role of olfactomotor mechanisms in recalling olfactory mental images from long-term memory to short-term memory is also discussed.

Key words: olfactory cortex, olfactory mental imagery, perception, semantics, sniffing

Many people can experience vivid visual memories by imagining them. Cognitive psychologists defined such visual mental images as short-term memory representations of visual events that give rise to the experience of ''seeing with the mind's eye.'' One central question raised in the literature of mental imagery processes focuses on the format (type of code) of the representations that underlie the experience of imagery. The issue is whether only propositional representations are used in imagery (Pylyshyn 2003) or whether sensorial-type (depictive) representations also play a role (Kosslyn et al. 2001). Arguments toward the latter theory come from studies in the visual modality showing that primary visual cortex is activated during visual mental imagery (Kosslyn and Thompson 2003). Understanding this question is crucial because it will have significant implications for the mechanisms underlying sensory perception in general. As primary sensorial cortices are the first areas of the brain to receive inputs from the sensorial receptors, if mental imagery affects the activity in these areas, it could thus modulate perception. Another important question in the mental imagery domain is whether such relationship between mental imagery and perception is a general principle in brain function: could it be generalized to other modalities such as the sense of smell? Over the last 2 decades, several studies using behavioral, psychophysical, and brain imaging methods have questioned the existence of odor images. In this paper, we review findings, including an original report by Kleemann et al. (2008), converging to support the view that as visual mental images, odor mental images preserve some aspects of olfactory percepts.

The first argument in favor of this view is that olfactory mental imagery and olfactory perception are not independent mechanisms. The overlap between mental imagery and perception is well documented in the visual (Farah 1989; Kosslyn et al. 1995), auditory (Halpern and Zatorre 1999), and motor (Jeannerod and Frak 1999) systems, and its characteristics in the olfactory domain have been questioned (Elmes 1998; Gilbert et al. 1998; Herz 2000; Stevenson and Case 2005). Similarity in the relative contributions of real and imagined odors to the perception of an odor mixture (Algom and Cain 1991) and similarity in perceptual grouping of perceived and imagined smells (Carrasco and Ridout 1993) have been shown. Additional support comes from the observed improvement of recognition memory (Lyman and McDaniel 1990) and odor detection (Djordjevic et al. 2004) when tested concurrently with odor imagery.

The second argument stipulates that as visual mental imagery, olfactory mental imagery shares many neural processes with real olfactory perception. Neuropsychological (Farah 1988) and neuroimaging (Kosslyn et al. 2001) methods have demonstrated similarities between visual perception and visual imagery, to the extent that common neural substrates are implied in both processes. Similarly, in olfaction, Djordjevic and collaborators (Djordjevic et al. 2005) used positron emission tomography to show that mental imagery of odors is associated with increased activation in a number of regions involved in odor processing, namely, orbitofrontal cortex, anterior insula, and piriform cortex. More recently, Bensafi et al. (2007) used functional magnetic resonance imaging to measure activity in subjects who alternated between smelling and imagining pleasant and unpleasant odors. Activity induced by imagining odors mimicked that induced by perceiving real odorants not only in the particular brain regions activated but also in its hedonic-specific pattern. For both real and imagined odors, unpleasant stimuli induced greater activity than pleasant stimuli in the left frontal portion of piriform cortex and left insula. These findings combine with findings from Djordjevic's study to suggest that the format of odor images is not exclusively propositional-like and may include some sensorial-like features. Nevertheless, these evidences do not weigh definitively against the propositional theory and a fortiori against a role of semantics in generating odor images. As the famous perfumer Edmond Roudnitska noted: "if you have been in love with a woman who used Arpège and if, several years later, someone mentions in your presence the name Arpège, won't your mind call forth the particular form of this perfume just as quickly as if you had the bottle right under your nose?" (Roudnistka 1983). On a neural point of view, such claim has been recently evidenced by a functional imaging study by Gonzalez et al. (2006) who showed that linguistic odor labels may modulate patterns of activity in human primary olfactory cortex (Gonzalez et al. 2006).

In sum, the above-reviewed findings lend support to the view that generating imagery of sensory events involves activation of primary olfactory structures common to real perception. This has been well documented in vision, and its current iteration in olfaction suggests that this is a general principle in brain function.

Now, the question that ensues is: by what mechanisms are odor images generated in the human brain? In the visual system, eye movements during visual imagery reenact those occurring during visual perception (Spivey and Geng 2001; Laeng and Teodorescu 2002). Comparison with the visual system is, however, tricky because major differences exist between the 2 modalities: first information from olfactory receptors reaches central structures without any direct thalamic relay and second olfactory areas are phylogenetically older than visual areas, the former being an allocortex and the latter an isocortex. Despite these differences, the olfactory modality shares a major mechanism with the visual system: both integrate a sensory component (the smell itself for olfaction and the visual input for vision) and a motor component (the sniff for olfaction and eye movement for the visual system). Indeed, olfactory perception is not simply induced passively by the stimulus but also comprises a motor action. Research in both animals and humans suggests that sniffing, the motor component of olfaction is a prominent characteristic of olfactory perception (Adrian 1942; Freeman 1981; Sobel et al. 1998). A question raised in the recent literature was whether the olfactomotor system is involved in the generation of olfactory mental images. Such mechanism was suggested for olfaction within a 1-century-old study (Perky 1910). Using standard methods for generation of mental imagery, Bensafi and collaborators (Bensafi et al. 2003, 2005) found that as odor perception, olfactory imagery was accompanied by increased sniff volume activity. A recent report by Kleemann and colleagues (Kleemann et al. 2008) obtained converging findings. In their study, they compared sniffing during 3 conditions: a control condition whereby participants were not asked to do any task, a perception task in which subjects were asked to smell odors, and a mental imagery task in which participants were asked to imagine odors. They showed that both odor perception and odor imagery lead to a significant increase in respiratory activity compared with the control condition. An important contribution of Kleemann's report was that olfactomotor activity during odor perception and during odor imagery was similar not only in terms of respiratory volume but also in its temporal characteristics as revealed by the frequency spectra analysis between conditions. Whereas the highest spectrum peak in the 3 conditions corresponded to 0.25 Hz breathing frequency, odor imagery and odor perception were characterized by a large peak at the frequency of 0.7 Hz as compared with the control condition. This novel finding strengthens the notion that olfactomotor activity during odor imagery mimics that during perception not only in a particular sniff parameter (respiratory volume) but also in the overall sniff pattern.

A question that may be raised from the above findings is by what mechanisms does sniff affect olfactory imagery? As described above, eye movements during visual imaging mimic those that would occur during actual perception of the equivalent visual scene, and blocking these movements reduces image quality, suggesting that a sensorimotor trace of a visual representation could be stored in memory and later reactivated to help recall the representation. We suggest that such a mechanism also exists in olfaction. To decipher such processing, Kosslyn (Kosslyn 2003) proposed that mental images are generated from information stored in long-term memory. A straightforward and inexpensive solution for the brain could be to have direct access to the long-term store. The problem, however, is that information in long-term memory is implicit and inaccessible, in contrast to short-term stored information, which is explicit and accessible. The research presented above supports the theory that the role of sniffing during olfactory imagery is to activate an internal representation stored in long-term memory, which will in turn be used to generate the so-called mental image that includes a sensorial-type representation. The information is thus made explicit and accessible thanks to the sniff.

To conclude, the studies reviewed above converge on the general idea that, as visual images, odor images include also sensorial-type representations and involve the reactivation of a sensorimotor trace to be recalled. As a perspective, it would be important to understand how linguistic-like and sensory-like representations interact in the human brain to generate olfactory images. That experts and perfumers, who have extensive knowledge about linguistic and semantic attributes of smells, report high abilities in odor imagery ability (Gilbert et al. 1998; Holley 2002) suggests that experience and training may facilitate such interaction between linguistic-like and sensory-like representations.

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