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The functional neuroanatomy of odor evoked autobiographical memories cued by odors and words

Artin Arshamian [a,b,*,1], Emilia Iannilli [a,1], Johannes C. Gerber [c], Johan Willander [b,d], Jonas Persson [b], Han-Seok Seo [a], Thomas Hummel [a], Maria Larsson [b]

[a] Smell and Taste Clinic, University of Dresden Medical School, Dresden, Germany
[b] Department of Psychology, Stockholm University, Sweden
[c] Department of Neuroradiology, University of Dresden Medical School, Dresden, Germany
[d] Center on Autobiographical Memory research, Aarhus University, Denmark

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ABSTRACT

Behavioral evidence indicates that odor evoked autobiographical memories (OEAMs) are older, more emotional, less thought of, and induce stronger time traveling characteristics than autobiographical memories (AMs) evoked by other modalities. The main aim of this study was to explore the neural correlates of AMs evoked by odors as a function of retrieval cue. Participants were screened for specific OEAMs and later presented with the odor cue and its verbal referent in an fMRI paradigm. Because the same OEAM was retrieved across both cue formats (odor and word), potential cue dependent brain activations were investigated. The overall results showed that odor and word cued OEAMs activated regions typically associated with recollection of autobiographical information. Although no odors were presented, a verbal cuing of the OEAMs activated areas associated with olfactory perception (e.g., piriform cortex). However, relative to word cuing, an odor cuing of OEAMs resulted in more activity in MTL regions such as the parahippocampus, and areas involved in visual vividness (e.g., occipital gyrus and precuneus). Furthermore, odor cues activated areas related to emotional processing, such as limbic and tempopolar regions, significantly more. In contrast, word cues relative to odor cues recruited a more widespread and bilateral prefrontal activity. Hippocampus activity did not vary as function of the remoteness of the memory, but recollection of OEAMs from the 1st vs the 2nd decade of life showed specific activation in the right OFC, whereas the 2nd reflected a higher activation in the left inferior frontal gyrus.

1. Introduction

Autobiographical memory (AM) concerns personally experienced events (Conway & Pleydell-Pearce, 2000). The recollection of autobiographical events is a complex and effortful process that draws on a variety of cognitive processes. The functional complexity is reflected in the extensive patterns of brain activation typically observed in neuroimaging studies of AM. Functional magnetic resonance imaging (fMRI) studies have demonstrated that prefrontal, medial and lateral temporal, as well as retrosplenial/cingulate cortices are associated with autobiographical recollection (for reviews, see; Cabeza & St Jacques, 2007 and Svoboda, McKinnon, & Levine, 2006). However, the laterality of these activations has varied widely across studies, presumably due to experimental variations in for example control tasks and design protocols (Greenberg et al., 2005).

Most of the behavioral and neuroimaging research on AM has focused on events triggered by verbal or visual stimuli (e.g., words or pictures). In a seminal study, Rubin, Groth, and Goldsmith (1984) reported that AMs cued by odors were less thought and spoken of than memories cued by pictures and words. Current behavioral findings indicate that the age of memories recollected varies as a function of the sensory modality. Specifically, memories evoked by odors have been localized to the first decade of life rather than to young adulthood which is the typical finding for memories evoked by verbal and visual information (Chu & Downes, 2000; Larsson & Willander, 2009). In a similar vein, evidence pertaining to the chronological distribution of odor memory representations shows that the retention of first odor-to-object associations was higher than for auditory-to-object associations, suggesting that retroactive interference for olfactory information is negligible (Yeshurun, Lapid, Dudai, & Sobel, 2009).

Further, the experiential qualities of odor-evoked memories differ from AMs evoked by verbal or visual information. Odor evoked autobiographical memories (OEAMs) are experienced as more emotional, and associated with stronger feelings of being brought back in time to the occurrence of the event compared to

* Correspondence to: Frescati Hagväg 14, Room 340, Department of Psychology, Stockholm University, SE-106 91 Stockholm, Sweden. Tel.: +46 8 161491; fax: +46 8 159342.
E-mail address: artin.arshamian@psychology.su.se (A. Arshamian).
[1] These authors contributed equally to this work.

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memories evoked by verbal or visual cues (Chu & Downes, 2000; Herz & Schooler, 2002; Rubin et al., 1984; Willander & Larsson, 2006, 2007). However, although behavioral evidence is available, few studies have explored whether the observed behavioral differences also are reflected in the neural activity subserving the recollection of olfactory evoked autobiographical information.

The neural underpinnings of autobiographical memories that involved odors was first investigated by Herz, Eliassen, Beland, and Souza (2004), in which a pre-scan interview protocol was adopted. Five participants were asked whether they could recall a positive memory representing both the sight and scent of a perfume. The participants were then presented with the odors and the corresponding pictures of the perfumes in an fMRI paradigm. The results indicated that odor-cued memories were related to stronger activations in the amygdala and hippocampal regions than picture-cued recollections. This observation is significant in that it addresses the "direct-synapsing hypothesis" that illustrates the direct synapsing from the olfactory bulb to the amygdala that may subserve the stronger emotional connotation in olfactory processing (Herz & Cupchik, 1995, Herz, 1998; Herz and Schooler, 2002; Herz et al., 2004; Willander & Larsson, 2006, 2007). Because most of the fMRI studies investigating AM have used different cues to evoke different memories, knowledge regarding cue-specific effects of a specific memory representation on brain activity is limited.

For more than a decade, brain-imaging studies have explored the notion that recollection entails a reactivation of areas that were activated during encoding (Heil, Rosler, & Hennighausen, 1994; Nyberg, Habib, McIntosh, & Tulving, 2000; Persson & Nyberg, 2000; Roland & Gulyás, 1995; Vaidya, Zhao, Desmond, & Gabrieli, 2002; Wheeler, Petersen, & Buckner, 2000; for reviews, see Buckner & Wheeler, 2001; Danker & Anderson, 2010). Support for an encoding-retrieval overlap in episodic memory has been obtained for a variety of stimuli including visual, auditory, olfactory, motoric, emotional, and verbal information (Gottfried, Smith, Rugg, & Dolan, 2004; Nyberg et al., 2000, 2001; Vaidya et al., 2002; Wheeler & Buckner, 2003, 2004; Wheeler et al., 2000, 2006). Thus, available evidence indicates that recollection of episodic information produces a reactivation of the sensory regions that were initially activated during encoding of the specific episode.

The overall aim of the present fMRI study was to explore the neural underpinnings of AMs evoked by odors as function of cue modality. This was accomplished by exposing pre-selected individuals to a set of odors known to spontaneously elicit specific OEAMs. In the scanner, each specific OEAM was cued by an odor and by its verbal referent. Given that participants retrieved the same AM across both cue formats, we could specifically examine potential brain activation differences as a function of the retrieval cue. Because olfactory cued memories elicit richer experiential qualities than other sensory cues, we hypothesized that, in addition to the core autobiographical memory network (Svoboda et al., 2006), brain regions involved in emotional processing and vividness (e.g., amygdala, insula, precuneus, and visual cortex) would be engaged during odor cued OEAM. Moreover, given that the same specific OEAM should be recollected in the word cue condition, we predicted that verbally cued olfactory memories also should induce activity in the core AM regions along with areas associated with emotional processing, but the latter possibly to a lesser extent. Furthermore, as all of the OEAM were presumed to have had an olfactory stimulus present during encoding we predicted that verbally cued olfactory memories would reactivate brain regions associated with olfactory perception (e.g., piriform cortex, Gottfried, 2010) and imagery (e.g., insula and orbitofrontal cortex (OFC), Bensafi, Sobel, & Khan, 2007; Djordjevic, Zatorre, Petrides, Boyle, & Jones-Gotman, 2005).

Finally, we explored potential effects of memory remoteness on brain activity. Based on previous work by Moscowitch and others suggesting a permanent role of the hippocampus in autobiographical memory retrieval (Multiple Trace Theory—MTT; e.g., Moscovitch et al., 2005) it is of interest to determine whether the hippocampal involvement also could be generalized to retrieval of olfactory evoked information. Further, given that prefrontal cortex (PFC) is a key region for retrieval of autobiographical information we explored whether the well documented clustering of childhood representations (1st decade) is reflected in PFC activity.

2. Material and method

2.1. Participants

The participants were recruited through posted advertisements at the University of Dresden Medical School (Germany) after the study had been approved by the local Ethics Committee (protocol number EK 290112008). Participants provided informed consent. Given that the prevalence rate of olfactory evoked autobiographical memories is low (about 16% has been suggested by previous studies: Willander & Larsson, 2006, 2007) it was necessary to pre-select individuals for the fMRI study. In the preselection phase, individuals were presented with a test set of 20 odors that has been used in previous work targeting olfactory AM (Willander & Larsson, 2006, 2007). A prerequisite for study inclusion was that each participant was able to spontaneously generate a minimum of two autobiographical odor memories and that the memories could be located with relatively exact space and time references. A total of 67 individuals were screened for OEAM and of which 24 individuals were selected based on the inclusion criterions. From the pool of 24 participants, 18 were able to participate in the fMRI study. However, due to technical problems three participants were excluded from the fMRI analysis, yielding a final sample of 15 right-handed participants (8 women; *mean age* =24.7 years, *age range* 20–28 years). All participants were in good health and had normal olfactory functions ascertained by means of the "Sniffin' Sticks" test kit (Hummel, Sekinger, Wolf, Pauli, & Kobal, 1997; Kobal et al. 2000).

2.2. Stimuli

Olfactory stimuli: The test set of odors used in the preselection phase has been extensively used in the previous work targeting AM in Swedish samples (Willander & Larsson, 2006, 2007). Given that five of the 20 odors from the original test set were highly associated with Swedish culture, these were replaced with odors more familiar to the German population. The following odors were used: cloves, beer, red wine, chlorine, anise, tobacco, Glühwein (mulled wine), bitter almond, cinnamon, whiskey, tar, garlic, soap, cardamom, lily of the valley, liniment (Vick's vaporub), herb liqueur (Jägermeister), lavender, rubber, and leather. All odors were natural except for the latter three that were synthetic. The test odors were presented in opaque glass bottles and covered with cotton pads to prevent visual inspection.

Two odors typically perceived with positive valence were selected as control odors for the olfactory baseline measurements in the MR scanner (see below): phenyl ethyl alcohol (PEA) and linalool. The smell of PEA is often described as flowery or rose-like whereas linalool is lime-like. Experimental and control odors were rated with regard to perceived intensity (1=not at all, 7=very intense) and pleasantness (1=not at all, 7=very pleasant). Statistical *t*-tests indicated no significant differences in perceived intensity between the control (*mean*=4.33, SD=1.62) and experimental odors (*mean*=4.7, SD=1.46), $t(14)=-1.04$, $p>0.05$, or between control (*mean*=4.77, SD=1.0) and experimental odors (*mean*=4.93, SD=1.2), $t(14)=-0.47$, $p>0.05$ in perceived pleasantness.

For the fMRI-session a custom-made olfactometer was used, and odors were presented intranasally through a Teflon^{TM} tubing (inner diameter 4 mm). To avoid mechanical stimulation, odors were embedded in a constant flow of odorless humidified air.

Verbal stimuli: For verbal stimuli the respective verbal references for the presented odors were chosen. Because González et al. (2006) reported that exposure to verbal semantic odor information alone activates piriform cortex, amygdala and insula the respective names for the control odors (i.e., rose, citrus) were used as control for the verbal stimuli. In the scanner, the odor name was presented as a lower case white word on a black background. The projection was made on a semitransparent MRI-room compatible blackboard.

In both conditions, the participants were exposed to the same frame rate, 20 s black screen (On-block), empty in the odor condition and with a word in the verbal stimulus, and a 20 s gray screen (Off-block).

2.3. Preselection session

In the pre-selection phase participants were exposed to 20 olfactory cues (see above) and asked to relate any autobiographical memory for the given cue. Thirty sec/odor was allowed for retrieval. In instances when a memory was evoked, the

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