# **Original Article**

# Smell-Based Memory Training: Evidence of Olfactory Learning and Transfer to the Visual Domain

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## Abstract

Human and non-human animal research converge to suggest that the sense of smell, olfaction, has a high level of plasticity and is intimately associated with visual-spatial orientation and memory encoding networks. We investigated whether olfactory memory (OM) training would lead to transfer to an untrained visual memory (VM) task, as well as untrained olfactory tasks. We devised a memory intervention to compare transfer effects generated by olfactory and non-olfactory (visual) memory training. Adult participants were randomly assigned to daily memory training for about 40 days with either olfactory or visual tasks that had a similar difficulty level. Results showed that while visual training did not produce transfer to the OM task, olfactory training produced transfer to the untrained VM task. Olfactory training also improved participants' performance on odor discrimination and naming tasks, such that they reached the same performance level as a high-performing group of wine professionals. Our results indicate that the olfactory system is highly responsive to training, and we speculate that the sense of smell may facilitate transfer of learning to other sensory domains. Further research is however needed in order to replicate and extend our findings.

Key words: memory, odorants, smell, olfactory disorders, spatial learning

#### Introduction

Olfaction, the sense of smell, is highly associated with learning, and some studies suggest that olfactory sensory abilities even play a role in visual memory (VM) performance. For example, odor discrimination training leads to visuospatial learning enhancement in rats (Zelcer et al. 2006). Conversely, an ablation of the olfactory bulb impairs visuospatial learning in rats (van Rijzingen et al. 1995). The present study focuses on whether olfactory-based memory training in adult human participants would have positive effects both on VM and olfactory perceptual task performance. The olfactory system is characterized by a high level of biological and functional plasticity (Li et al. 2008; Fletcher 2012; Kass et al. 2013). For example,

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healthy adult humans might improve olfactory performance merely by means of repeated olfactory stimulation (Mainland et al. 2002), and to our knowledge, no analogous effects have been reported in the visual system. Olfactory abilities are highly trainable (Hummel et al. 2009; Damm et al. 2014; Morquecho-Campos et al. 2019). Olfactory experts (e.g. perfumers and wine tasters) perform better than nonexperts on olfactory assessments (Royet et al. 2013), and their expertise is correlated with structural reorganizations in memory-associated brain areas (Delon-Martin et al. 2013). A preliminary study, while lacking a matched control group, indicated that odor-based spatial memory training might benefit performance on related visual cognitive tasks (Olofsson et al. 2017). Memory transfer is often studied using visual, and in some cases auditory tasks, and results indicate that while some studies have yielded promising results (Mahncke et al. 2006; Bergman-Nutley and Klingberg 2014), others show no transfer (Owen et al. 2010), or only to tasks that are very similar to the trained task, such that the overall pattern of results remain mixed (Melby-Lervåg et al. 2016; Lindenberger et al. 2017; Teixeira-Santos et al. 2019). Transfer across sensory systems is rarely assessed (see Zelinski 2009, for review). Previous studies investigated whether visual working memory training transfers to improved performance on a similar auditory working memory task, but results are not conclusive (Schneiders et al. 2011; Buschkuehl et al. 2014). As the usefulness of some visual-based cognitive training interventions has been questioned on methodological grounds (Simons et al. 2016), new methods for establishing transfer of learning are warranted. To the best of our knowledge, differences in the cross-sensory transfer have never been systematically addressed using olfaction. Olfaction, with its combination of high levels of plasticity and its close integration with memory encoding regions, might provide a vehicle for transfer effects. This study aimed to test the hypothesis, based on the evidence reviewed above (pronounced olfactory plasticity and transfer effects), that memory training in the olfactory system would lead to significant transfer to a visual task, as well as to nontrained olfactory tasks. We further hypothesized, based on the indirect evidence reviewed above (modest transfer within the visual cognitive domain and lack of evidence of visual transfer to olfactory tasks), that transfer from visual training to olfactory tasks would be less pronounced. To address this hypothesis, we devised two spatial learning board games where olfactory and visual objects were located and matched. Such tasks are known to engage memory encoding networks (Rasch et al. 2007; Kunz et al. 2015), and we used them to establish training-related gain and transfer.

### Materials and methods

#### Participants

This study was approved by the Swedish Ethics Review Authority (2014/621-31/1) and complied with the Declaration of Helsinki for Medical Research involving Human Subjects. Participants (n = 106; age 18–50 years) were recruited to olfactory and VM training conditions by means of advertising, mainly through a designated website for research study advertisements. Exclusion criteria were neurologic or psychiatric disorders, colds, allergies or breathing problems, and olfactory or uncorrected visual impairments. Participants were randomly assigned to either olfactory memory (OM) or VM training groups and were tested by trained research assistants who were blind to the participants' training. Participants were compensated monetarily after completion of the training program. Seventy-two participants completed training, pre- and posttest; 41 with the OM task and 31 with the VM task, The effective sample is higher

than, or similar to, several other studies on this topic, which should provide a sufficient power to detect effects (Hummel et al. 2009; Altundag et al. 2015). Twenty-eight participants did not complete memory training or deviated from the training protocol (17 OM, 11 VM; the OM training was slightly more vulnerable to disruptions from cold and flu). Additionally, six participants were excluded due to technical or experimenter errors during initial testing. The current dataset with 72 participants includes participants who were recruited to a study that was originally conceived as a follow-up, where participants were randomized to identical olfactory and visual training conditions and identical pre- and posttest tasks. The second study, which also included two other training conditions and a novel set of criterion tasks, was scaled down midway through data collection for practical reasons, starting with the visual condition. The data from the follow-up study (11 VM, 20 OM) were instead aggregated with the original study data to achieve more reliable outcomes, which explains the lower number of participants in the visual condition (See Online repository: https://mfr.osf.io/ render?url=https%3A%2F%2Fosf.io%2Fs4dy7%2Fdownload for data). Post hoc exploration indicated that original vs. follow-up datasets showed similar results.

#### Wine professionals

To provide a point of reference for the hypothesized training-related olfactory improvement in the OM group, we additionally recruited 15 wine professionals for testing with the Sniffin' Sticks battery. They were recruited through a professional network email list and were currently active as wine panelists, wine tasting course leaders, wine importers, or wine journalists (data are accessible at Open Science Framework: https://mfr.osf.io/render?url=https%3A%2F%2Fosf. io%2Fs4dy7%2Fdownload). Even though the professionals had a higher mean age than participants in the training groups, we decided that it was more important to have professionals with many years of experience as a bench-mark for olfactory expert performance (Delon-Martin et al. 2013), rather than striving for an age-matched group of young, but less experienced, olfactory experts (e.g. enology students).

#### Training tasks

The OM game included 24 tin cans, containing 12 different kinds of commercially available flavored teas to make up 12 stimulus pairs (stimulus descriptions and sources are accessible at Open Science Framework: https://mfr.osf.io/render?url=https%3A%2F%2Fosf. io%2Fs4dy7%2Fdownload). Two parallel, nonoverlapping sets were created to make the olfactory and visual games more challenging and to involve a larger number of stimuli during the training period, a feature we hoped would help us achieve generalized learning and avoid minimize unknown sources of bias driven by individual stimuli. Prior work in patients with olfactory loss has shown better results from olfactory training when odors are changed during training (Altundag et al. 2015). Odors were placed in white cotton bags to prevent visual identification. The cans were randomly distributed on a board that included 24 squares arranged in a 6 × 4 grid. On each trial, the player sampled two tin cans of choice and compared their content. Upon detecting a match, the matched items were removed from the board. Performance was measured as the number of trials required to empty the board, with fewer trials indicating higher performance. Trial number was also used to compare the difficulty of the two tasks. In order to establish accurate performance logs, each tin can was marked underneath with a barcode that was unique to each can, but mirror inverted for the can holding the matching stimulus (see Supplementary material). Thus, participants could easily verify a match by turning two cans upside down and holding the barcodes opposite each other. However, the mirror-reversed barcodes were not visible while playing, and participants were instructed to only use them to confirm a perceived match, limiting exposure to the barcodes mostly to trials where the cans were immediately removed from the board. Barcodes were thus unlikely to influence memory performance, since they could not be used as a memory cue for the matching task (see Supplementary material).

A VM game was devised as a control task. Two parallel, nonoverlapping sets were constructed. In each set, 12 different language symbols were obtained from Korean and Mandarin Chinese languages, and placed inside the 24 tin cans (see Supplementary material). The two training tasks were similar in all aspects except the engagement of odors vs. visual objects and they were carried out in a similar way. The symbols were unfamiliar to our Swedish participants.

#### Procedure

Completion of the study required training for about 40 days at home (one training session completed each day, average training time was 10 min) and pre- and post-training laboratory assessment. In cases when participants were unable to complete training on a given day, they were instructed to train twice the following day(s) such that their total number of training sessions were kept constant. Posttraining assessments were scheduled after at least 38 days of training and at about 40 days (see Table 1 for details), and participants continued training until the day of return. During the laboratory assessments, participants completed tests with the OM and VM tasks as well tests of olfactory function. During training, participants trained with only one type of game, but alternated between the parallel sets every 5 days.

The games were played individually. Participants were instructed to place all the cans on the game board in a random order and play the game by sampling two cans on each trial, removing the cans if they were matching. Each trial was documented on a scoring sheet as "matching" or "nonmatching." After a minimum of 38 training days, participants returned for the second laboratory assessment. Participants that could not return at 38–40 days from their preassessment were either instructed to continue training for a few more days until they were available for laboratory testing or, if this was not possible, considered as drop-outs.

# Pre-post testing

Pre- and post-training sessions followed the same procedure and consisted of standardized tests of olfactory ability and assessments of the participants' performance in the olfactory and VM games. First, the standardized "Sniffin' Sticks" were used to assess olfactory abilities (see Kobal et al. 1996; Hummel et al. 1997, 2007, for details). Olfactory discrimination was assessed in exact accordance with established protocol. Olfactory threshold was assessed by means of an abbreviated testing protocol (described in Stanciu et al., 2014). Odor sets were replaced within their expiry date. In threshold testing, the experimenter presents the participant with three odorous pens, only one of which contains an odor (n-butanol), and the participant selects the odorous pen in a forced-choice procedure. Across trials, the concentration of the odor stimulus varied as a function of performance, and a threshold value of up to 16 was eventually established. In discrimination testing, three pens are similarly presented, two of which have the same smell and the third has a different smell, and the participant selects the deviating smell in a forced-choice procedure. Discrimination ability is established as a sum score across 16 trials. For naming and identification assessments, participants were presented with familiar odors and were first asked to name it without cues; these answers provided the basis for calculating odor naming accuracy scores (naming is not part of the standard Sniffin' Sticks assessment, but is often added to identification assessments to provide complementary information, see Olofsson et al. 2013). Irrespective of the naming response, odor identification was then assessed by providing four odor name alternatives (one of which was correct) in a forced-choice task. To avoid test-retest effects on the olfactory identification and naming tests, we used an extended version of the Sniffin' Sticks set that contained 32 odors, which were divided into two nonoverlapping sets of 16 (eight odors from the original Sniffin' Sticks set and eight odors from its extension set), for unique use at test and retest, respectively. The use of each of the two alternate sets at pre- and posttest was randomized for each individual to minimize trivial test-retest effects in the identification and naming tasks. Scores on olfactory tasks could range from 0 (min) to 16 (max). Participants were not given any corrective feedback. We hypothesized all four tests would potentially be improved only by olfactory training, resulting in interactions between time and group.

Participants' performance in the training games was assessed. Assessment order (OM first versus VM game first) was randomized

Table 1. Me	an demographic,	Sniffin' sticks, ar	d questionnaire o	data for the olfactor	y and visual trainir	ng groups at j	pre- and posttest
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	Pre-assessment		Post-assessment		
	Olfactory group	Visual group	Olfactory group	Visual group	
Age (±SD)	25.6 (5.0)	27.0 (7.5)	_	_	
n (% female)	41 (66)	31 (71)	_	_	
Education years (±SD)	14.3 (1.7)	14.6 (2.7)	_	_	
Days until posttest (±SD)	—	_	42.7 (5.9)	43.4 (4.1)	
Odor threshold (±SD)	11.2 (3.3)	10.8 (2.8)	11.6 (3.3)	10.8 (2.8)	
Odor discrimination (±SD)	12.3 (2.1)	12.9 (1.8)	13.9 (1.7)	12.3 (1.7)	
Odor identification (±SD)	12.5 2.0)	12.4 (1.7)	12.9 (2.0)	12.8 (2.3)	
Odor naming (±SD)	5.4 (1.9)	6.2 (2.8)	7.1 (2.4)	6.0 (2.4)	
OM task (±SD)	38.1 (10.8)	40.1 (10.5)	28.3 (7.3)	38.5 (9.6)	
VM task (±SD)	33.8 (10.3)	37.9 (8.8)	26.5 (7.2)	24.4 (6.7)	
Self-rated motivation (1-10)	7.5 (1.9)	7.1 (2.3)	5.9 (2.4)	5.9 (2.2)	
Self-rated enjoyment of task (1-10)	7.5 (1.8)	7.0 (1.9)	5.1(2.2)	5.7 (2.5)	
Perceived difficulty of task (1-10)	4.7 (2.9)	4.4 (2.4)	4.8 (2.4)	3.5 (1.9)	

SD = standard deviation; n = sample size.

across participants. The experimenter instructed the participant in how to play the memory games and how to document performance (number of trials) into the accompanying spreadsheet according to the same procedure as training at home. After verifying that the participant had understood the instructions correctly by letting the participant play and document two test trials under supervision, the test leader left the room and returned once the participant was finished with the game. After completion, the test leader controlled that the participant had found and grouped all matching cans correctly and that the spreadsheets were correctly documented.

#### Questionnaires

Before the first and the second testing session, participants filled out an online questionnaire at home that assessed background variables such as level of education, age, gender, and self-rated health, memory, and olfaction. At the post-training session, subjects rated their motivation retrospectively for the first and last weeks of training, how demanding they perceived the game to be, and how much they enjoyed playing the game, on scales ranging from 1 (min) to 10 (max).

#### Data simulation

To provide an assessment of ceiling-level performance in the memory games, we simulated the performance of a group of 10 000 "virtual experts" that explored the stimulus set randomly but with optimal perception and memory of the objects encountered at all previous trials such that performance was optimized. Although variance occurred as a function of random localization of game items on the game board, and the random exploration of novel items, a player with perfect memory would need an average of 18.9 trials (SD = 0.83; code available upon request). Assessment of performance differences due to training was established using *t*-tests and ANOVAs where appropriate.

# Results

# Demographics, olfactory performance, and selfrated variables

Descriptive data are presented in Table 1. T-tests indicated that groups were not different with regards to age (t(1,70) = 0.97), P = 0.34, Hedges's g = 0.23) and education (t(1,70) = 0.47, P = 0.64, Hedges's g = 0.12), and a pearson chi-square test indicated no difference in sex distribution ( $\chi 2 = 0.21$ , P = 0.63, phi = 0.05). The two groups did not differ in terms of baseline performance on any olfactory task (all  $P_s > 0.15$ ). All participants were enrolled in the study for at least 38 days of training. The number of days in the study varied somewhat among participants due to their availability for post-training lab testing (see Table 1) but an independent *t*-test on all participants, except 3 for which these data were lost, indicated groups did not differ in this regard (t(1,67) = 0.54, P = 0.59, Hedges's g = 0.13). We ran ANOVAS to investigate effects of time (pre- vs. post-training) on olfactory control tests and self-reported variables. Odor threshold and identification scores did not differ statistically between groups or as a function of time, nor were there any significant interactions (all Ps > 0.15). Increased performance from preto posttest was observed in odor naming (F(1,68) = 5.36, P = 0.02, $\eta_p^2 = 0.07$ ) and discrimination (*F*(1,68) = 4.25, *P* = 0.04,  $\eta_p^2 = 0.06$ ), but these effects were qualified by interactions between time and group, both for naming (F(1,68) = 7.84, P = 0.01,  $\eta_p^2 = 0.10$ ) and for discrimination ( $F(1,68) = 23.20, P < 0.001, \eta_n^2 = 0.25$ ); these

interactions warranted follow-up ANOVAs targeting each group. These analyses showed training-related effects were present only in the OM group (discrimination F(1,40) = 25.33, P < 0.001,  $\eta_p^2 = 0.34$ ; naming F(1,40) = 21.68, P < 0.001,  $\eta_p^2 = 0.35$ ) but not in the visual group (discrimination F(1,30) = 3.76, P = 0.06,  $\eta_p^2 = 0.11$ ; naming F(1,30) = 0.07, P = 0.79,  $\eta_p^2 = <0.01$ ). Self-rated motivation and enjoyment was initially high in both groups, but declined to moderate levels during the training period, a decline that was significant for motivation (F(1,70) = 29.8, P < 0.001,  $\eta_p^2 = 0.30$ ) and enjoyment (F(1,70) = 37.9, P < 0.001,  $\eta_p^2 = 0.33$ ), but did not differ for the two groups (no main or interaction effects involving group, all Ps > 0.088). Perceived difficulty of the tasks was moderate, similar across the training groups and remained stable during the training period (all Ps > 0.07).

### Memory game performance

Mean performance scores in the training games for each training group at pre- and post-assessment are summarized in Table 1. Participants did not differ significantly in baseline performance in the olfactory (t(70) = 0.76, P = 0.45; Hedges's g = 0.18) or VM game (t(70) = 1.80, P = 0.08; Hedges's g = 0.42). Data from the participants' training logs suggested that the two training conditions were equally difficult across the training period. Mean trials over the training period was 28.8 (SD = 6.2) for the olfactory and 27.5(SD = 7.0) for the visual training game. This difference was not statistically significant (t(70) = 0.83, P = 0.41; Hedges's g = 0.20). As expected, performance increases on assigned game tasks were observed when comparing pre- and post-training scores in both the OM (*t*(40) = 6.02, *P* < 0.001, Cohen's *d* = 0.94), and the VM group (t(30) = 10.80, P < 0.001, Cohen's d = 1.94). However, the magnitude of the pre-post performance increases for the assigned game was not significantly different across training groups (t(70) = -1.69, P = 0.10, Hedges's g = -0.38). On average, neither of the training groups approached the ceiling level of the "virtual experts" (mean trials = 18.9; SD = 0.83; Figures 1 and 2).

The results of a two-factor mixed-design ANOVA showed significant interaction effects between time (pre- vs. post-training) and training modality (odor vs. visual) for both the OM (F(1,40) = 23.80, P < 0.001,  $\eta_p^2 = 0.25$ ) and the VM task (F(1,40) = 7.71, P = 0.007,  $\eta_p^2 = 0.10$ ). These within-subject effects indicate that as expected, the largest performance increases were observed in the game tasks that the participants trained.

To test whether the training regimes differed in associated performance gains, we first investigated between-subject effects of training modality (odor vs. visual) and time (pre- vs. post-training) on the OM and VM task performances, separately. Results for the OM task yielded significant interaction effects of time and training modality (F(1,40) = 9.59, P = 0.003,  $\eta_p^2 = 0.12$ ) but this was not the case for the VM task (F(1,40) = 0.44, P = 0.51,  $\eta_p^2 = 0.01$ ), showing that performance gains were significantly different across groups for the OM game while performance gains were not significantly different across groups for the VM game. The results indicate that olfactory training led to a performance increase in both the olfactory and the visual game, while visual training only led to a performance increase in the visual game (Figures 1 and 2).

Indeed, post hoc comparisons with *t*-tests showed that OM training resulted in improved VM performance (t(40) = 4.42, P < 0.001, Cohen's d = 0.69), but VM training did not result in improved OM performance (t(30) = 0.97, P = 0.34, Cohen's d = 0.17), suggesting that transfer was asymmetrical. Of key importance for



Figure 1. Panel plots of individual game performance measured as trials needed to complete the memory task during the training period for the olfactory training group (A) and visual training group (B). The ceiling level was established by data-simulated "virtual experts" (black solid line).



Figure 2. Average change (blue line) in task performance (trials) estimated as a quadratic function of days of training for the olfactory training group (A) and visual training group (B) with 95% confidence intervals. The ceiling level was established by data-simulated "virtual experts" (black solid line).

our main *a priori* hypothesis, transfer gain for the OM group in the VM task was larger than the corresponding transfer gain for the VM group in the odor memory task, (t(70) = 2.44, P < 0.02, Hedges's g = 0.65; Figure 3A and B). These analyses showed that for the OM training group, the transfer gain on the VM task was, in fact, similar to the training gain in the odor task. Results thus indicate a one-sided transfer of learning from the OM to the VM task.

#### Olfactory baseline performance

Independent samples *t*-tests showed that baseline performance levels were similar for the two training groups in all olfactory tasks (*Ps* > 0.17, Hedges's g < 0.32) and memory games (*Ps* > 0.07; Figure 3). Baseline performances on the olfactory control tasks in the OM group were not significantly correlated with baseline OM game score (*Ps* > 0.25, Hedges's g < 0.42). The results suggest that the two groups were well matched and that initial OM game performance did not depend on varying olfactory acuity.

Follow-up analyses in the OM group revealed no relationship between baseline performances on the olfactory tasks and trainingrelated increase in the OM game (Ps > 0.24), suggesting that OM gains did not depend on baseline olfactory acuity. Transfer from olfactory training to the VM game was also not associated with baseline olfactory test scores (Ps > 0.11).

#### Comparison to wine professionals

When comparing wine professionals to the pre-training OM group, wine professionals performed better on the odor threshold (t(54) = 2.29, P = 0.03, Hedges's g = 0.68) and odor discrimination tasks (t(54) = 2.32, P = 0.02, Hedges's g = 0.69) but not on the odor identification (t(54) = 0.91, P = 0.37, Hedges's g = 0.27) or odor naming tasks (t(54) = 1.86, P = 0.07, Hedges's g = 0.55), although the latter was close to the significance threshold. Following OM training, however, performance was similar to the professionals in all olfactory tasks, including odor naming (t(54) = 0.82, P = 0.42,Hedges's g = 0.24) and odor discrimination (t(54) = 0.41, P = 0.69, Hedges's g = 0.12), odor threshold (t(54) = 1.88, P = 0.07, Hedges's g = 0.56), and odor identification (t(54) = 0.18, P = 0.86, Hedges's g = 0.05). In contrast, and as expected, the VM group post-training still performed more poorly compared with the professionals on odor threshold (t(44) = 2.88, P = 0.006, Hedges's g = 0.89) and odor discrimination (t(44) = 2.54, P = 0.02, Hedges's g = 0.78), but not odor identification (t(44) = 0.04, P = 0.72; Hedges's g = 0.11) or odor naming (t(44) = 0.72, P = 0.47, Hedges's g = 0.22).



Figure 3. (A, B) Boxplots of performance (trials needed) on OM and VM tasks at pretraining (white boxes) and post-training (grey boxes) for the two training groups, and score on the olfactory control tasks, (C) odor discrimination, (D) odor naming, (E) odor identification, and (F) butanol odor threshold. Results are shown for the VM training group and OM training group and for olfactory professionals (Pro; pink boxes). Boxplots are displayed separately for pretraining (white boxes) and post-training (grey boxes), with the exception of professionals who did not participate in training or post-training assessment. The boxes indicate the 25, 50 (median), and 75 percentiles of the distribution (lower, middle, and upper horizontal lines of the box). The upper hinges indicate the maximum value of the variable located within a distance of 1.5 times the interquartile range above the 75-percentile. The lower hinges indicate the corresponding distance to the 25-percentile value. Circles indicate values outside these hinges (outliers). The means and 95% confidence intervals (dots and error bars in blue) are superimposed on the boxplots.

# Discussion

Olfaction is well integrated with the neural systems supporting memory encoding, but the role of smell-based interventions to enhance memory functions is unexplored. Our main result shows that engaging the olfactory system in a memory training task was associated with a transfer effect to a similar VM task, as well as to untrained olfactory tasks. In contrast, participants who trained with the VM task did not show any improvements in the OM task. The transfer effects were observed in olfactory training, but not in visual training, even though task difficulty and learning rates were comparable for the two training tasks. Based on our results, we speculate that memory training that engages the olfactory system might promote cross-sensory transfer to a larger extent than is the case for the visual system (which is the dominant model for cognitive interventions). Our results also emphasize that training-related transfer is often unrelated to the magnitude of gains in the trained task (Bjork 2018).

Further investigations are needed before definitive conclusions can be drawn about the usefulness of olfactory-based cognitive training. It is unclear if it was the multisensory nature of the memory tasks, or unknown differences in cognitive demands, rather than the engagement of olfaction per se, that produced transfer. While this interpretation cannot be ruled out in the present data and should be the focus of further experiments, it should be noted that each training task used one type of sensory stimulus, visual objects, and odors, respectively, that was absent in the other. Thus, we view the sensory complexity as comparable across the two conditions, but to conclusively establish this notion, further experimentation is needed where multisensory complexity of the training tasks is manipulated.

Assuming that olfaction indeed promotes cross-sensory cognitive transfer, the mechanisms are unknown, but previous research in visual cognitive training provides clues that help us speculate about its cause. In visual working memory training, the overlapping neural substrates of the trained and transfer tasks is a key determinant of transfer (Dahlin et al. 2008). Thus, the present observation of "asymmetric transfer," from OM training to VM gain, but not vice versa, might indicate that olfactory input provides a relatively unmediated input to the mediotemporal memory encoding regions (Zelano et al. 2016), whereas the visual system involves extensive prior processing in many intermediate cortical regions (Felleman and Van Essen 1991). From the perspective that these additional processing stages act as information filters, visual processing networks will generate a sparse output (Solomon and Pelli 1994). By this logic, we speculate that the relatively unfiltered olfactory input to the memory encoding regions (see Olofsson and Gottfried 2015) might potentiate transfer effects due to an increased overlap with memory encoding neural networks. We acknowledge that future studies are needed in order to clarify the behavioral and neuronal mechanisms that might explain transfer from olfactory to non-olfactory tasks. Future studies should also investigate whether these effects replicate and generalize to other forms of olfactory-based cognitive training. Of particular interest is the development of digital olfactory technologies that enable online monitoring of olfactory performance and adjusting difficulty levels along with performance gains etc. (see Niedenthal et al. 2019).

In this work, we satisfied several key criteria that are rarely met in cognitive intervention studies (Simons et al. 2016). First, we established a very high level of similarity between the task format of our interventions, as they differed only in the sensory channels that were stimulated, and not the spatial memory format. Second, we were able to monitor performance during training, a rare feature in olfactory-based interventions (Pekala et al. 2016). Our data from the training period ruled out the possibility that trivial retest effects could account for our enhanced learning of the visual task in the OM group; indeed, day-by-day learning rates were on average very small and could not generate strong test-retest effects. Third, we compared results with those obtained from both "virtual experts" with optimal performance (in game tasks), and wine professionals (in olfactory perception tasks), to establish points of reference for training. These features helped support our interpretation that olfactory-based memory training produces substantial transfer effects. Future work is needed to elucidate whether odorbased memory transfer effects might be sustained for several months, as are reported in some visual training studies (Constantinidis and Klingberg 2016; Sandberg and Stigsdotter Neely 2016). Future work should also address how OM training might produce transfer effects onto untrained tasks that share neither the sensory modality nor the task format of the training task (i.e. "far transfer"). Given the present results, odor-based cognitive training might be expected to produce enhanced transfer compared with visual-based training.

We hope that the results of our study will stimulate further research on odor-based cognitive interventions. Such interventions could be useful in older individuals, since olfactory impairments constitute early markers for age-related cognitive impairment and dementia (Olofsson et al. 2009; Stanciu et al. 2014; Devanand et al. 2015). It remains to be seen whether odor learning interventions will permit the transfer to non-olfactory cognition in older individuals, but such studies are warranted given the devastating impact of memory loss and dementia in the aging population (Wimo et al. 2013).

### Supplementary material

Supplementary material can be found at Chemical Senses online and data can be retrieved at Open Science Framework: https://mfr.osf.io/render?url=https%3A%2F%2Fosf.io%2Fs4dy7%2Fdownload.

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# **Conflict of interests**

None declared.

# **Author contributions**

The study concept was developed by J.K.O. All authors contributed to the study design. Data collection and analysis was conducted by authors I.E., J.L, S.J., and E.S., under the supervision of J.K.O and M.L. J.K.O. and I.E. drafted the manuscript, which was revised based on input from all other authors. All authors approved of the final version of the manuscript.

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