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Working Memory Across Nostrils

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Whether olfactory working memory involves verbal representations or neural images of odor per se remains unclear. This study investigated whether verbal representation influences performance in an olfactory delayed-match-to-sample task and used monorhinal presentation to generate hypotheses as to the underlying anatomy of this mechanism. The main findings were that (a) nameable odorants were easier to remember than hard-to-name odorants and (b) the nameability effect was more pronounced when the evaluation was done across nostrils. Considering these results within a proposed model implies dual representation in olfactory working memory: All odors, nameable and hard to name, are represented both perceptually and verbally.

Keywords: olfaction, working memory, short-term memory, verbal, monorhinal

Whether olfactory working memory (OWM) involves verbal representations or neural images of odor per se remains unclear. Evidence supporting verbal-dependent memory performance was obtained by comparing memory for common (thus presumably nameable) versus uncommon (hard-to-name) odors. Common odors were recognized better than uncommon odors, both across altering retention intervals (de Wijk, Schab, & Cain, 1995) and across nostrils when using monorhinal presentation (Savic & Berglund, 2000). Furthermore, immediate and delayed odor recognition performance was enhanced by learning to associate veridical or generated names to odors (Jehl, Royet, & Holley, 1997) and was related to accuracy in odor naming (Murphy, Cain, Gilmore, & Skinner, 1991). Developmental studies also demonstrated the importance of semantic processing for odor memory (Larsson & Backman, 1997; Lehrner, Gluck, & Laska, 1999). Taken together, these results suggest that odor memory is dependent in large part on verbal representations.

In turn, there is also evidence for perceptual rather than verbal OWM. Using an experimental paradigm in which errors in memory could be attributed as deriving from the substitution of similar verbal codes or of similar olfactory codes revealed that a substantial proportion of the errors were olfactory (White, Hornung, Kurtz, Treisman, & Sheehe, 1998). In addition, previous odor familiarity did not improve performance in an odor recognition task (Engen & Ross, 1973). Also, although expert wine judges show superior olfactory recognition, the ability to recognize odors and the ability to name odors were not positively correlated (Parr, Heatherbell, & White, 2002). Studying serial position effects for nameable and hard-to-name odors revealed that the overall rate of recognition was remarkably similar for the two sets of odors; in both cases, serial position effects did not resemble those obtained with verbal stimuli (Miles & Hodder, 2005). Taken together, these results suggest that odor memory is dependent in large part on sensory representations.

In addition to the unknown relative contributions of verbal versus sensory mechanisms in OWM, the neural substrates of OWM are also unclear. Because verbal information is processed predominately by the left hemisphere and olfactory processing is largely ipsilateral (Price, 1987, 1990), monorhinal presentation of an odor could help identify the brain systems that underlie OWM. Odors are named more correctly when presented to the left nostril (Herz, McCall, & Cahill, 1999; Homewood & Stevenson, 2001), yet right nostril dominance was obtained in familiarity ratings (Broman, Olsson, & Nordin, 2001) and odor discrimination (Zatorre & Jones-Gotman, 1990). However, this right nostril advantage was observed only during discrimination of unfamiliar odors (Savic & Berglund, 2000).

In this experiment, we set out to test OWM across nostrils, using an olfactory delayed-match-to-sample (DMTS) task with nameable and hard-to-name odors. This type of task is widely used to tap into working memory in a variety of protocols (Curtis, Rao, & D'Esposito, 2004; Grady et al., 1998; Jokisch & Jensen, 2007) because it gauges an elementary phenomenological attribute of working memory, namely the holding of information in temporary storage during the planning and execution of a task (Dudai, 2002).

Considering the aforementioned predominantly ipsilateral nature of olfactory projections (Price, 1987, 1990), we hypothesized that nonverbal OWM images would result in no effect of nameability and better overall performance within the same nostril and in contrast that verbal OWM images would result in a main effect of nameability and a possible left nostril advantage.

Materials and Method

Participants

Twenty-one healthy normosmic participants (12 women and 9 men), ranging in age from 21 to 40 (M = 28.19 ± 3.85 years), participated in the study after providing informed consent. A

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six-item questionnaire revealed that 17 of the participants were strongly right handed, and the remaining 4 participants were moderately right handed.

Odorants

Thirty odorants composed of both pure molecules and blends were used in the study (Table 1). The pure molecules were manufactured by Sigma-Aldrich (Rehovot, Israel), and the blends by Sensale (Ramat-Gan, Israel).

Procedure

Experiments were conducted in an odorant-nonadherent stainless-steel–coated room subserved by high-throughput HEPA and carbon filtration. Each participant participated in two sessions, 24 hr apart.

In the first session, nameability ratings were obtained per participant. Participants were requested to assign a single object descriptor to each odorant and to rate on a visual analogue scale ranging from *not at all* to *very* how well the object described the odorant. For each participant, the 10 most nameable and 10 most hard-to-name odorants were selected for further experimentation. Next, participants performed the DMTS task where 48 pairs of odorants were presented. The 2 odorants in each trial consisted of the same odorant or different odorants and were presented in succession with 12 s between the items in a pair and 25 s between trials. The 12-s interstimulus interval was chosen following previous results obtained by others (Bromley & Doty, 1995; de Wijk et al., 1995; Engen, Kuisma, & Eimas, 1973), suggesting that odor memory does not decrease with time (up to 40 s) and that 12 s allows optimal performance for odor recognition. For presentation, a jar containing the odorant was placed under the blindfolded participant's nostril, alternating the side and balancing the order of odorants presented to the right versus left side. Also, the order of nostrils tested was randomly assigned across trials. In the same-nostril and across-nostril trials, one nostril was tested on each trial by asking the participant to hold the other nostril closed by pressing his or her finger on the outer side of the nostril and inhaling only through the open nostril for 1.5 s (indicated by an auditory tone). In the both-nostrils condition, participants were requested only to sniff, without blocking their nostrils. All interactions with participants, such as instructions on which nostril to block, when to sniff, and so forth, were computer generated by digitized voice with no direct interaction with an experimenter. Participants were not instructed to name or not to name the odors during the DMTS task because we did not want to manipulate their strategy by suggestion.

To record respiration, participants were fitted with a pair of small tubes nestled at the opening of each nostril (Johnson, Russell, Khan, & Sobel, 2006). Pressure across the tubes was pro-

Table 1
Odorant Nameability and Usage

Odorant	Nameability rating ($M \pm SE$)	No. participants (out of 21) defining this odor as nameable	No. participants (out of 21) defining this odor as hard to name	No. participants (out of 21) defining this odor as not in the most nameable or hard-to-name odorants
α,α-dimethylphenethyl butyrate	341.22 ± 69.98	0	19	2
Banana essence	754.72 ± 70.41	17	1	3
Blue cheese essence	548.77 ± 76.62	4	1	16
Bornyl acetate	535.05 ± 85.43	2	12	7
Cheetos snack essence	820.66 ± 80.32	17	0	4
Cola essence	702.88 ± 85.17	12	0	9
Ethyl decanoate	359.22 ± 64.44	2	13	6
Eucalyptus essence	827.05 ± 76.87	11	0	10
Fresh baguette essence	681.33 ± 62.14	17	1	4
Fresh cut grass essence	460.72 ± 48.61	7	3	11
Grapes essence	762.27 ± 79.70	18	1	2
Heptyl alcohol	417.22 ± 75.11	0	17	4
Hexyl hexanoate	375.66 ± 75.88	0	16	5
Hydroxycitronellal	629.55 ± 87.55	3	8	10
Isoamyl phenylacetate	660.72 ± 89.48	8	5	8
Iso-phorone	554.94 ± 83.99	1	14	6
Lemon essence	761.55 ± 83.18	15	1	5
Licorice essence	948.44 ± 47.38	19	0	2
Maple syrup essence	531.55 ± 86.12	5	5	11
Methyl anthranilate	719 ± 79.72	1	12	8
Methyl hexanoate	259.77 ± 44.09	0	15	6
Methyl octanoate	345.5 ± 65.12	0	15	6
Mint essence	1,057.94 ± 20.06	13	0	8
Nonanoic acid	431.55 ± 80.66	1	15	6
Nonyl acetate	322.22 ± 56.17	1	18	2
Peanut butter essence	673.72 ± 67.81	13	0	8
Pentanol	648.72 ± 91.86	1	3	17
Rose essence	597.22 ± 71.34	7	4	10
Watermelon essence	828.27 ± 65.44	15	0	6
β-ionone (mainly trans)	408.22 ± 82.17	0	10	11

cessed with a spirometer (ADInstruments, Grand Junction, CO), amplified (PowerLab 4SP, ADInstruments), and digitally recorded at 100 Hz using Chart Version 5.3 software (ADInstruments). This measurement was used to validate that participants were following task instructions (i.e., properly blocking their nostril and sniffing at the tone) and to define which nostril took in more air as a function of the nasal cycle (Bojsen-Moller & Fahrenkrug, 1971).

In the second session, conducted on the day after the first session, participants again performed the DMTS task where 48 pairs of odorants were presented. After completing the DMTS task, participants scored the odorants for nameability, familiarity, pleasantness, and intensity, using a 250-mm visual analogue scale.

Altogether, the DMTS task included 96 pairs of odorants. In one third of the trials, sample and match were presented in the same nostril (same-nostril condition); in one third of the trials, sample was presented in one nostril and match in the other (across-nostril condition); and in one third of the trials, sample and match were delivered to both nostrils (both-nostrils condition). Odorant order was randomized, and test side was counterbalanced. This design resulted in 12 types of trials: 3 (nostril side: same nostril, across nostrils, or both nostrils) × 2 (nameability: nameable or hard-to-name odorant) × 2 (odorant: same or different pair). There were eight repetitions of each type of trial.

Statistics

The overall response time and number of errors in the discrimination task was compared between the nameable and hard-to-name odorants and nostril side in a repeated measures analysis of variance (ANOVA) model with nostril as the within-subject factor and nameability class as the between-subjects factor. The ANOVA analysis was followed by Tukey's Honestly Significant Difference (HSD) post hoc test to test for the influence of nostril side on the observed nameability effect. A p value of less than .05 was considered significant.

The obtained ratings of the respective odorant qualities were analyzed using Pearson correlation analysis on the difference between the two sets of odorants (nameable and hard to name). To discover whether differences in quality, which are not related to nameability, were present between the two sets of odorants, we correlated odorant nameability with the respective rating score of familiarity, pleasantness, and intensity.

Analyses were restricted to trials in which sample and match were the same. This was done to eliminate potential variance resulting from differences in difficulty across the different trials. In other words, some different trials were easy and others were hard, and we wanted to avoid variance resulting from this difference.

Results

Odorant Assignment

We obtained nameability ratings per participant for each of the 30 odorants. For each participant, the 10 most nameable and 10 most hard-to-name odorants were selected for further experimentation (a total of 20 odorants). The nameable and hard-to-name odorant groups included different odorants for each participant. No single odorant was unanimously deemed nameable or hard-to-name by all 21 participants (see Table 1). This is important because it strengthens the claim that the effects reflected nameability and not some other aspect of the odorants.

We calculated the difference between the nameable and hard-to-name odorants in mean nameability, familiarity, pleasantness, and intensity ratings for each participant. Pearson correlation analysis revealed a significant correlation between the difference in nameability ratings and difference in familiarity ratings (r = .6, $p < .005$). In other words, more familiar odorants were easier to name. No correlation was found between the difference in nameability ratings and the difference in pleasantness ratings (r = .319, p = .17) or the difference in intensity ratings (r = .22, p = .345).

Psychophysical Results

We examined differences in response accuracy with a 2 (nameability: nameable or hard-to-name odorants) × 3 (nostril side: same nostril, across nostrils, and both nostrils) repeated-measures ANOVA. This revealed significant response accuracy differences between nameable and hard-to-name odorants, $F(1, 20) = 8.75$, $p < .0077$, reflecting more mistakes when the odorants were hard to name. Planned comparisons revealed that this effect was mainly because of significant differences between nameable and hard-to-name odorants delivered across nostrils, $F(1, 20) = 7.24$, $p < .015$, and not to the same nostril, $F(1, 20) = 2.34$, $p = .14$, or to both nostrils, $F(1, 20) = 3.42$, $p = .078$ (Figure 1). We observed no nostril-side effect, $F(2, 40) = 0.48$, $p = .617$, or Nameability × Nostril Side interaction, $F(2, 40) = 0.33$, $p = .72$. The lack of

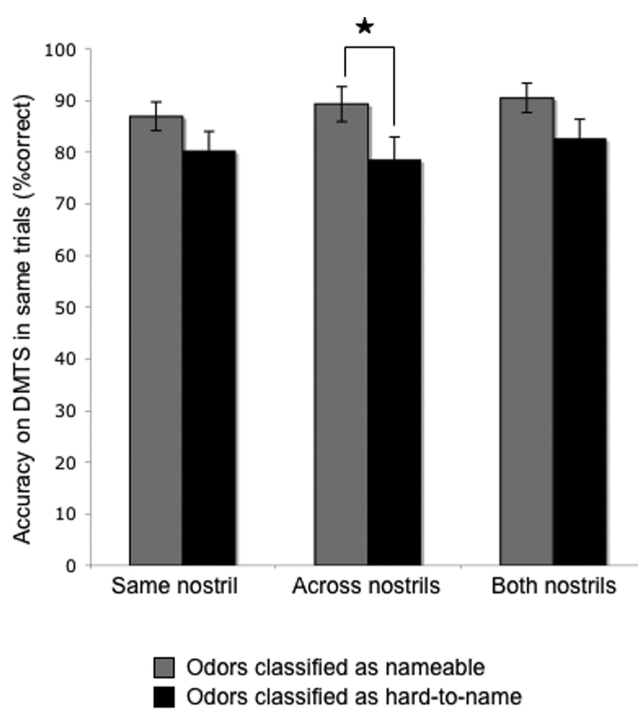

Figure 1. Mean response accuracy (±SEM) for nameable odorants (gray bars) and hard-to-name odorants (black bars) when sample and match were presented to the same nostril, across nostrils, or both nostrils. Response accuracy was significantly higher for nameable odorants than for hard-to-name odorants when presented across nostrils. DMTS = delayed match to sample. $^{*}p < .015$ (planned comparison).

nostril-side effect reveals that there was similar overall performance when odorants were presented within the same nostril or across nostrils. In a more detailed analysis, we divided the same-nostril condition into trials in which sample and match were presented to the left nostril (LL) and trials in which sample and match were presented to the right nostril (RR); the across-nostrils condition was divided into trials in which sample was delivered to the right nostril and match to left nostril (RL) and trials in which sample was delivered to the left nostril and match to right nostril (LR). In a 2 (nameability) ×5 (nostril side) ANOVA, we again obtained an effect of better performance for nameable odorants, $F(1, 20) = 6.733$, $p < .017$. Tukey's HSD post hoc test showed that there was a significant difference between nameable and hard-to-name odorants in the RL condition ($p < .04$, planned comparison $p < .0094$).

A similar 2 (nameability) × 3 (nostril side) ANOVA that was used to analyze differences in response time (RT) for all trials revealed a significant effect of nameability, $F(2, 40) = 5.16$, $p < .035$, reflecting longer RT for hard-to-name odorants. Moreover, a Nameability × Nostril Side interaction was evident, $F(2, 40) = 4.97$, $p < .011$. Tukey's HSD post hoc test revealed that the nameability effect (longer RT for unnameable odorants) was unveiled only when participants were tested across nostrils ($p < .0005$). More so, longer RT was measured when the odorant was delivered across nostrils, then in both nostrils, only with the hard-to-name odorants ($p < .025$) and not with the nameable odorants ($p = .99$). The 2 (nameability) ×5 (nostril side) ANOVA again revealed a nameability main effect, $F(1, 20) = 5.51$, $p < .03$, and Nameability × Nostril Side interaction, $F(4, 80) = 3.16$, $p < .018$ (Figure 2a). Tukey's HSD post hoc test revealed that the nameability effect occurred only in the RL ($p < .039$) and the LR ($p < .0033$) conditions, and not in the RR ($p = 1$) and LL ($p = .99$) conditions. Consistent with our notion of an across-nostril effect, whereas performance was equal when nameable or hard-to-name odorants were presented within the same nostril (points/participants distributed evenly around the *y*-axis; Figure 2b), performance was better for nameable versus hard-to-name odorants when presented across nostrils (17 of 21 points/participants above the *x*-axis; Figure 2b).

In other words, the RT data converged with the accuracy data to suggest overall better performance for nameable odorants compared with hard-to-name odorants. In addition, the RT data revealed that this nameability effect derived from trials in which sample and match were delivered across nostrils.

Sniffing Behavior

To test whether our findings were related to differences in the volume of air that entered each nostril, we reanalyzed the data using high flow and low flow instead of right and left nostril designations. We examined differences in response accuracy with a 2 (nameability: nameable or hard-to-name odorants) × 4 (nostril volume: high flow–high flow, low flow–low flow, high flow–low flow, or low flow–high flow) repeated-measures ANOVA.

No difference in number of errors was observed between the high flow–high flow and the low flow–low flow conditions (planned comparison: $p = .803$ for nameable odorants and $p = .84$ for unnameable odorants), suggesting that better performance in

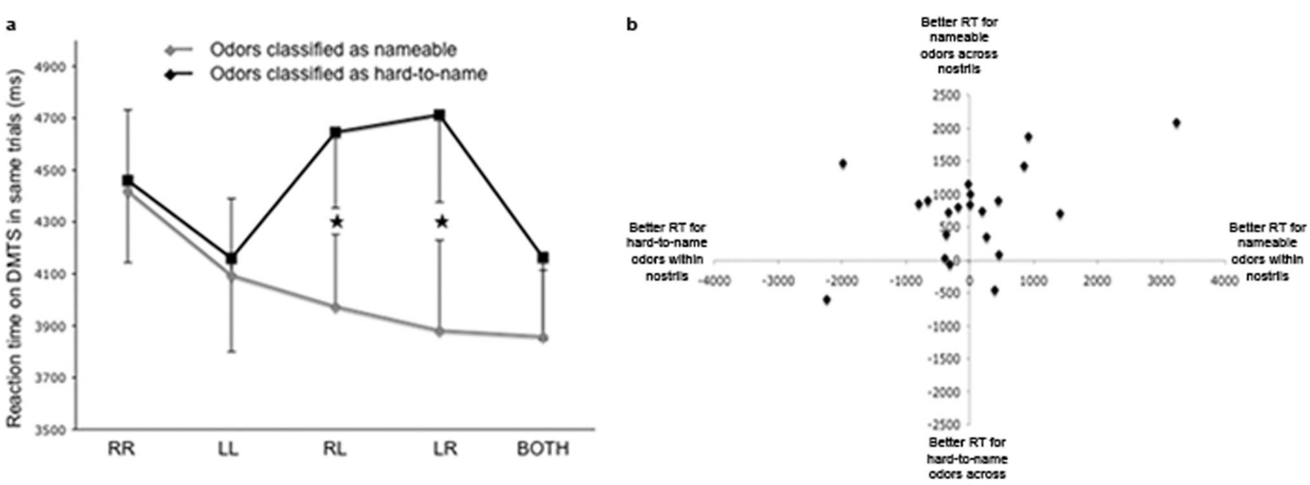

Figure 2. A: Mean reaction time (±SEM) for nameable odorants (gray line) and hard-to-name odorants (black line) when sample and match were presented to the right nostril (RR), to the left nostril (LL), or to both nostrils (BOTH); sample was presented to the right nostril and match to the left nostril (RL); and sample was presented to the left nostril and match to the right nostril (LR). Reaction time was significantly faster for nameable odorants than for hard-to-name odorants in the RL and LR conditions. B: Reaction time (RT) for nameable odorants and hard-to-name odorants when odorants were presented within the same nostril (*x*-axis) and when they were presented across nostrils (*y*-axis). Each dot represents 1 participant; $y > 0$ reflects better performance (smaller RT) for nameable versus hard-to-name odorants when presented across nostrils, and $x > 0$ reflects better performance (smaller RT) for nameable versus hard-to-name odorants when odorants were presented within the same nostril. DMTS = delayed match to sample. $^*p < .039$ for RL; $^*p < .0035$ for LR (Tukey's Honestly Significant Difference post hoc test).

this study was not because of a larger volume of air flowing into one nostril or the other.

Discussion

This study investigated whether verbal representation influences performance in OWM that was taxed in a DMTS task, and it used monorhinal presentation to probe the underlying anatomy of this mechanism.

Our main findings were that (a) nameable odorants were easier to discriminate than hard-to-name odorants and (b) the nameability effect was more pronounced when the evaluation was done across nostrils. The first finding suggests the contribution of verbal representation to OWM, a notion that is congruent with other studies that have shown better memory performance for familiar odors in short-term (de Wijk et al., 1995; Savic & Berglund, 2000) and long-term (Larsson, 1997; Lyman & McDaniel, 1990; Rabin & Cain, 1984) memory. However, the second finding is novel and suggests complex bimodal representation.

The question posed in this study can be considered within a model with three levels of processing (Figure 3). The model assumption is ipsilateral-only connectivity in the low-level olfactory system, based on the anatomical (Price, 1987, 1990) and functional (Gordon & Sperry, 1969) evidence. However, one should keep in mind that functional evidence for cortical contralateral projections exists in rats (Wilson, 2001) and humans (Porter, Anand, Johnson, Khan, & Sobel, 2005; Savic & Gulyas, 2000). With the ipsilateral connectivity in mind, we can further discuss the following questions:

1. *Does OWM involve only low-level perceptual representation?* If the comparison of match to sample took place in only the olfactory bulbs we would expect overall better performance when odors are presented within the same nostril than across nostrils because there is minimal direct exchange of information between the two bulbs (Shipley & Adamek, 1984). Therefore, that such an effect was not evident implies that the process takes place upstream of the olfactory bulb.

2. *Does OWM involve only high-level perceptual representation?* If the comparison of match to sample took place only in the piriform cortex, we would expect similar performance for nameable and hard-to-name odors when odors were presented to the same nostril or across nostrils. This is because nameable and hard-to-name odorants could be represented (a) in the same way, and then we would expect similar performance for both types of odorants in all orders of odorant presentation, or (b) in a different way; for example, a nameable odorant is more familiar and its perceptual representation is more accessible; therefore, the performance for nameable odorants would be better then for hard-to-name odorants. In that case, we would expect better performance for nameable odorants when presented in the same nostril or across nostrils. Our finding of different patterns of performance when odors were presented to the same nostril or across nostrils implies an involvement of language areas in the DMTS task.

3. *Do hard-to-name odors generate verbal representation?* If hard-to-name odors generate only an olfactory sensory image (and no verbal representation), better performance is expected when hard-to-name odors were presented in the same nostril than when presented across nostrils. This is because of the ipsilateral nature of the olfactory system. However, our finding of similar performance in both cases implies that hard-to-name odors were not represented as a sensory image alone.

4. *Does OWM involve only verbal representation?* If the odors were represented only verbally, we would expect an overall left-nostril advantage because of the left hemisphere dominance in language. Lack of such an effect in our results implies that the representation was not verbal alone.

Thus, the conclusions we draw using the model imply dual representation in OWM: All odors, nameable and hard to name, are represented both perceptually and verbally. One may argue that odors are encoded in memory as the olfactory percept and are additionally labeled with a name. The name can act as a handle or retrieval cue. It is important to notice that naming would help in OWM tasks that use as foils odors that are not highly similar to the targets, in which names would differentiate between the targets and foils. Hence, although we do not address here the question of whether OWM represents a dedicated modality-specific working memory buffer or shares cognitive space with other modalities in working memory, our findings do indicate at least an interaction with the phonological loop (Baddeley, 2007) on one hand and with a potential pure sensory representation on the other. Finally, it is noteworthy that predominant models of working memory assume in addition that the working memory system performs mental operation(s) over the information in temporary storage (Baddeley, 2007). Our study, however, did not probe potential mental operations over the DMTS task. Future analysis of this point could hence cast additional light on the nature of the postulated OWM system.

Could this conclusion explain the difference between evaluation of nameable and hard-to-name odorants when presented across nostrils? The quality of the verbal representation may be different for nameable and hard-to-name odors. Nameable odors could be described with a concrete item like *peach*, whereas hard-to-name odors could be described with a more general, category-reflecting word like *fruity*. When match and sample are presented to the same nostril or to both nostrils, the generated description is similar even in the case of a hard-to-name odor where the odor is described with more general terms.

However, when the odor is presented across nostrils there might be a slight difference in the right- and left-nostril–generated description, especially when the odor is hard to name. This could explain the

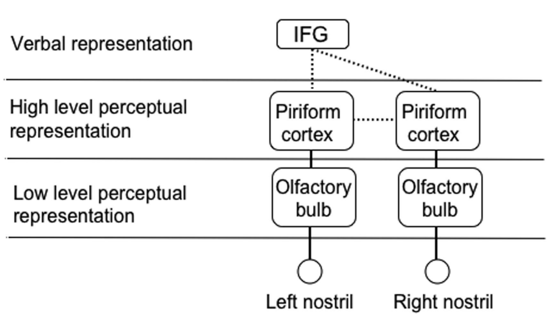

Figure 3. A model with three levels of processing: olfactory bulb (low-level perceptual representation), piriform cortex (high-level perceptual representation), and inferior frontal gyrus (IFG, verbal representation). The unbroken lines represent known connectivity, and the broken lines represent plausible connectivity.

finding of better performance for nameable odors than for hard-to-name odors only when odors are presented across nostrils.

The assumption of variation in odor description when presented across nostrils is based on evidence for alteration of nostril characteristics and hemispheric lateralization in olfaction tasks. One study found that the difference in airflow between the nostrils causes each nostril to be optimally sensitized to different odorants, so that each nostril conveys a slightly different olfactory image to the brain (Sobel, Khan, Saltman, Sullivan, & Gabrieli, 1999). Additionally, odors were rated as more pleasant when sniffed through the right nostril and were more accurately named when sniffed through the left nostril (Herz et al., 1999). Also, significantly higher familiarity ratings were found in right-nostril stimulation (Broman et al., 2001). However, the higher familiarity ratings in the right nostril were more strongly associated with low than high familiarity. Thus, the difference between the nostrils was more pronounced when the odors were less familiar. This finding is in agreement with the assumption that the variation in right- or left-nostril–generated description is more significant when the odor is hard to name (less familiar).

Our model could be used to explain the lack of right-nostril advantage: The finding of lack of right-nostril superiority in odor discrimination is in accordance with some studies (Broman et al., 2001; Bromley & Doty, 1995; Savic & Berglund, 2000) but not with others (Savic & Berglund, 2000; Zatorre & Jones-Gotman, 1990). Zatorre and Jones-Gotman (1990) concluded that there is a perceptual asymmetry in olfactory discrimination. We would like to generate a hypothesis that could resolve apparent inconsistencies across studies. In our data analysis, we considered only errors that derived from trials in which sample and match were the same. We did not use trials in which sample and match were different because we did not measure subjective similarity ratings between two different odors in a pair and thus could not determine whether the difficulty of the task was equivalent for the nameable and hard-to-name odors. Zattore and Jones-Gottman and Savic and Berglund (2000) analyzed errors deriving from same-item pairs and different-item pairs. Zattore and Jones-Gottman found that the right-nostril advantage was primarily present for the similar items, as compared with the dissimilar items. We might explain these results with our model: When odors are similar, two different odors can be described using the same general description, such as *fruity*, and thus result in an error. It might be that because participants are more verbal when using the left nostril, they add similar descriptions to similar odors and make a mistake in thinking it is the same odor, while when using the right nostril they slightly incorrectly describe the first odor and then slightly incorrectly describe the second odor, and the difference between the descriptions is enough to make them think that the two similar odors are different, thus generating a correct response.

Our results of similar performance for unilateral and bilateral nostril presentation may appear contradictory to the results obtained in a multiple-target odor memory test, in which significantly better performance was measured when both sides of the nose were tested than when either side was tested alone (Bromley & Doty, 1995). However, the latter effect was obtained when the retention interval was 30 or 60 s, although not when it was 10 s (an interval that is closer to the 12-s interval used in our experiment). Thus, it is possible that a bilateral advantage materializes when the task becomes harder, that is, as the memory interval becomes longer. Evidence that strengthens this claim is that in our data, significantly faster response time was obtained for sampling with both nostrils than across nostrils only in the harder task, discrimination of hard-to-name odors.

Finally, the above is a discussion of a speculative model that serves to explain both our and other findings on OWM. However, a true measure of the neural substrates of this task, whether verbal, pure sensory, or a combination of both, awaits more direct measurement of brain function during task performance. With this in mind, the key findings of this study remain that OWM involves verbal representation and that the representation quality varies as a function of odor nameability.

References

Baddeley, A. D. (2007). *Working memory, thought, and action.* Oxford, England: Oxford University Press.

Bojsen-Moller, F., & Fahrenkrug, J. (1971). Nasal swell-bodies and cyclic changes in the air passage of the rat and rabbit nose. *Journal of Anatomy, 110*(Pt. 1), 25–37.

Broman, D. A., Olsson, M. J., & Nordin, S. (2001). Lateralization of olfactory cognitive functions: Effects of rhinal side of stimulation. *Chemical Senses, 26,* 1187–1192.

Bromley, S. M., & Doty, R. L. (1995). Odor recognition memory is better under bilateral than unilateral test conditions. *Cortex, 31,* 25–40.

Curtis, C. E., Rao, V. Y., & D'Esposito, M. (2004). Maintenance of spatial and motor codes during oculomotor delayed response tasks. *Journal of Neuroscience, 24,* 3944–3952.

de Wijk, R. A., Schab, F. R., & Cain, W. S. (1995). *Odor recognition memory.* Mahwah, NJ: Erlbaum.

Dudai, Y. (2002). *Memory from A to Z : Keywords, concepts, and beyond.* Oxford, England: Oxford University Press.

Engen, T., Kuisma, J. E., & Eimas, P. D. (1973). Short-term memory of odors. *Journal of Experimental Psychology, 99,* 222–225.

Engen, T., & Ross, B. M. (1973). Long-term memory of odors with and without verbal descriptions. *Journal of Experimental Psychology, 100,* 221–227.

Gordon, H. W., & Sperry, R. W. (1969). Lateralization of olfactory perception in surgically separated hemispheres of man. *Neuropsychologia, 7,* 111–120.

Grady, C. L., McIntosh, A. R., Bookstein, F., Horwitz, B., Rapoport, S. I., & Haxby, J. V. (1998). Age-related changes in regional cerebral blood flow during working memory for faces. *NeuroImage, 8,* 409–425.

Herz, R. S., McCall, C., & Cahill, L. (1999). Hemispheric lateralization in the processing of odor pleasantness versus odor names. *Chemical Senses, 24,* 691–695.

Homewood, J., & Stevenson, R. J. (2001). Differences in naming accuracy of odors presented to the left and right nostrils. *Biological Psychology, 58,* 65–73.

Jehl, C., Royet, J. P., & Holley, A. (1997). Role of verbal encoding in short- and long-term odor recognition. *Perception & Psychophysics, 59,* 100–110.

Johnson, B. N., Russell, C., Khan, R. M., & Sobel, N. (2006). A comparison of methods for sniff measurement concurrent with olfactory tasks in humans. *Chemical Senses, 31,* 795–806.

Jokisch, D., & Jensen, O. (2007). Modulation of gamma and alpha activity during a working memory task engaging the dorsal or ventral stream. *Journal of Neuroscience, 27,* 3244–3251.

Larsson, M. (1997). Semantic factors in episodic recognition of common odors in early and late adulthood: A review. *Chemical Senses, 22,* 623–633.

Larsson, M., & Backman, L. (1997). Age-related differences in episodic odour recognition: The role of access to specific odour names. *Memory, 5,* 361–378.

Lehrner, J. P., Gluck, J., & Laska, M. (1999). Odor identification, consistency of label use, olfactory threshold and their relationships to odor memory over the human lifespan. *Chemical Senses, 24,* 337–346.

Lyman, B. J., & McDaniel, M. A. (1990). Memory for odors and odor names: Modalities of elaboration and imagery. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 16,* 656–664.

Miles, C., & Hodder, K. (2005). Serial position effects in recognition memory for odors: A reexamination. *Memory & Cognition, 33,* 1303–1314.

Murphy, C., Cain, W. S., Gilmore, M. M., & Skinner, R. B. (1991). Sensory and semantic factors in recognition memory for odors and graphic stimuli: Elderly versus young persons. *American Journal of Psychology, 104,* 161–192.

Parr, W. V., Heatherbell, D., & White, K. G. (2002). Demystifying wine expertise: Olfactory threshold, perceptual skill and semantic memory in expert and novice wine judges. *Chemical Senses, 27,* 747–755.

Porter, J., Anand, T., Johnson, B., Khan, R. M., & Sobel, N. (2005). Brain mechanisms for extracting spatial information from smell. *Neuron, 47,* 581–592.

Price, J. L. (1987). The central olfactory and accessory olfactory systems. In T. E. Finger & W. L. Silver (Eds.), *Neurobiology of taste and smell* (pp. 179–204). New York: Wiley.

Price, J. L. (1990). Olfactory system. In G. Paxinos (Ed), *The human nervous system* (pp. 979–1001). San Diego, CA: Academic Press.

Rabin, M. D., & Cain, W. S. (1984). Odor recognition: Familiarity, identifiability, and encoding consistency. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 10,* 316–325.

Savic, I., & Berglund, H. (2000). Right-nostril dominance in discrimination of unfamiliar, but not familiar, odours. *Chemical Senses, 25,* 517–523.

Savic, I., & Gulyas, B. (2000). PET shows that odors are processed both ipsilaterally and contralaterally to the stimulated nostril. *NeuroReport, 11,* 2861–2866.

Shipley, M. T., & Adamek, G. D. (1984). The connections of the mouse olfactory bulb: A study using orthograde and retrograde transport of wheat germ agglutinin conjugated to horseradish peroxidase. *Brain Research Bulletin, 12*(6), 669–688.

Sobel, N., Khan, R. M., Saltman, A., Sullivan, E. V., & Gabrieli, J. D. (1999, November 4). The world smells different to each nostril. *Nature, 402,* 35.

White, T. L., Hornung, D. E., Kurtz, D. B., Treisman, M., & Sheehe, P. (1998). Phonological and perceptual components of short-term memory for odors. *American Journal of Psychology, 111,* 411–434.

Wilson, D. A. (2001). Receptive fields in the rat piriform cortex. *Chemical Senses, 26,* 577–584.

Zatorre, R. J., & Jones-Gotman, M. (1990). Right-nostril advantage for discrimination of odors. *Perception & Psychophysics, 47,* 526–531.

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