

Odorant-specific Patterns of Sniffing during Imagery Distinguish 'Bad' and 'Good' Olfactory Imagers

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Abstract

There are large individual differences in the self-reported ability to form vivid olfactory mental imagery. Based on such self-reports, subjects have been classified as 'bad' or 'good' imagers. The present study examined whether a differential strategy in re-enacting the olfactomotor response during imagery may explain the dissociation between 'bad' and 'good' olfactory imagers. As previously reported, odor imagery was accompanied by sniffing. Although 'bad' and 'good' olfactory imagers did not differ in their overall sniffing volume, they used different strategies when re-enacting the motor component of olfaction during imagery. Particularly, as in real perception, 'good' but not 'bad' imagers generated bigger sniffs when imagining a pleasant smell compared with an unpleasant smell ($P < 0.02$). Furthermore, preventing sniffing significantly hampered mental imagery of pleasant odors in 'good' but not 'bad' imagers ($P < 0.03$). Taken together, these results suggest (i) the validity of the dissociation between 'bad' and 'good' olfactory imagers as revealed by self-report; (ii) that sniffing may be a causal factor in the creation of olfactory imagery; and (iii) that sniff measurements may serve as a reliable non-verbal tool in exploring individual differences in odor imagery.

Key words: hedonics, individual differences, mental imagery, olfaction, sniffing

Introduction

Mental imagery is defined as the creation of a neural representation in the absence of an external stimulus or event (Freeman, 1981). A large body of research suggests that in the visual (Farah, 1988, 1989a; Farah *et al.*, 1988; Kosslyn *et al.*, 1995, 1999, 2001), auditory (Zatorre and Halpern, 1993; Halpern and Zatorre, 1999) and motor (Jeannerod, 1995; Jeannerod and Frak, 1999) systems, similar neural mechanisms underlie perception and imagery. For example, in vision, eye movements during imagery re-enact those during perception (Spivey and Geng, 2001; Laeng and Teodorescu, 2002; Mast and Kosslyn, 2002). A similar mechanism was suggested for olfaction within a study considering the differences between 'memories' and 'imaginings' (Perky, 1910). Perky described observations of subjects instructed to either recreate memories, or (in contrast) imagery of odors. He noted that 'of 56 memories, 96% involved movement of the nostrils, and 86% very definite movements, a sniffing in and out of the nostrils and a jerking of the head'. In contrast, Perky noted that 'of 57 imaginings, 46 or 80% gave no per-

ceptible movement (of the nostrils)'. Whereas the debate regarding the dissociation between imagery and memory recall is beyond the scope of this study, we previously found, using standard methods for generation of mental imagery, that olfactory imagery was accompanied by olfactomotor activity similar to that during perception (Bensafi *et al.*, 2003). Specifically, we found that when asked to imagine smells, human subjects spontaneously sniffed. Furthermore, subjects took a larger sniff during imagery of a pleasant smell compared with imagery of an unpleasant smell, as if they perceived real smells. Moreover, sniffing did not merely accompany the mental representation of smell, but rather functionally contributed to its vividness and emotional tone.

Vividness ratings are often used to obtain an indication of the degree to which imagery experience resembles perceptual experience (Sheehan, 1983; Richardson and Patterson, 1986). Based on vividness estimations, Gilbert and collaborators found large individual differences in the ability to form vivid olfactory images. In view of this populational variance, they

proposed the categories of 'low' and 'high' olfactory imagers (Gilbert *et al.*, 1997, 1998). In the present study we set out to ask whether the strategy of re-enacting the olfactomotor response during imagery, namely sniffing, underlies the dissociation between 'bad' and 'good' olfactory imagers. We first asked whether 'bad' and 'good' imagers differed in their overall amount of imagery-related sniffing (Experiment 1). We then conducted a novel analysis of data previously published in brief form (Bensafi *et al.*, 2003) and asked whether 'bad' and 'good' imagers differed in the extent to which their imagery related sniffs were tailored to the odors they were imagining (in real perception, sniffs of diluted and/or pleasant odors are more vigorous than sniffs of intense and/or unpleasant odors) (Experiment 2). Finally, we asked whether preventing sniffing would have a differential impact on self-reported imagery quality in 'bad' and 'good' imagers (Experiment 3).

Experiment 1

The aims of Experiment 1 were twofold. We first set out to replicate previous findings whereby human subjects sniffed when they were asked to imagine smells. Also, in past experiments (Bensafi *et al.*, 2003), participants were asked to imagine different stimuli across modalities (e.g. imagine the smell of chocolate, the sight of a mountain or the sound of a siren). This raised the possibility that the specific identity of the stimulus evoked particular task demands. Thus, here we asked whether olfactory-specific imagery-dependent sniffing would persist when using the same imagined stimuli across modalities. Second, we set out to determine whether the strategy of re-enacting the olfactomotor response during odor imagery serves to predict the dissociation between 'bad' and 'good' olfactory imagers.

Methods

Subjects

Ten subjects (nine females and one male, mean age 19.37 ± 1.19 years) of the University of California at Berkeley were tested. All subjects provided written informed consent to procedures approved by the Berkeley Committee for the Protection of Human Subjects. Exclusion criteria included history of head or nasal passage trauma, history of neurological disease, history of repeated or current sinus infection, chronic use of medication, including oral contraceptives, and alcohol, drug or tobacco abuse.

Procedures

After completing a demographics questionnaire and providing written informed consent, participants were taken into the testing room (11 × 8 ft) and seated comfortably in a dental chair in front of a computer monitor. The testing room was coated in stainless steel to prevent ambient odors, was maintained at constant temperature and humidity, and was served

by high-throughput HEPA and carbon air filters. During the experiment, subjects were alone in the closed experimental room, and were monitored via a one-way mirror from the adjacent control room.

Subjects were fitted with a small nasal mask (Respironics, Murrysville, PA) coupled to a high sensitivity pneumatograph (model #4719, Hans Rudolph, Inc. Kansas City, MO) that measured nasal airflow. Subjects were deceived and told that the mask was fitted at this time for a second experiment that would be explained and take place later. The experimenters were careful not to use the word 'sniff' in any form when giving experimental instructions. Any reference to olfaction was through the word 'smell'. Subjects were completely unaware of our capability to measure nasal flow, and hence that nasal respiration was being monitored in any way. Furthermore, subjects were unaware of any experimental interest in airflow, and were told that the experiment focused on the imaginability of different stimuli. The pneumatograph signal was transduced by a spirometer (ADInstruments, NSW, Australia), amplified (PowerLab 16SP, ADInstruments) and recorded at 1 KHz using Chart 4.1.1 software (ADInstruments). Nasal inhalation volume across imagery conditions was compared by first measuring the volume of the first nasal inhalation following trial onset for each trial, and then computing the mean first nasal inhalation volume for each modality (auditory, olfactory and visual).

The same three objects (apple, bubblegum and gasoline) served as stimuli in all three modalities (auditory, olfactory and visual). Instructions to imagine were (i) for auditory imagery: 'imagine the sound of blowing a bubble/of crunching an apple/of filling gasoline in a tank'; (ii) for olfactory imagery: 'imagine the smell of bubblegum/of an apple/of gasoline', and (iii) for visual imagery, 'imagine the sight of bubblegum/of an apple/of a gasoline pump'. Each stimulus was presented five times, giving a total of 45 trials per study.

Each trial began with a 15 s center-monitor fixation period. Following fixation an instruction to imagine a particular stimulus was displayed for 15 s [typical duration of odor imagery trials ranged from few seconds to a minute (Lyman and McDaniel, 1990; Algom and Cain, 1991; Carrasco and Ridout, 1993; Djordjevic *et al.*, 2004c)]. Following the 15 s allowed for imagery creation, the following three questions were presented in succession on-screen: (i) 'How clear and vivid was the image?'; (ii) 'How pleasant was the image?' (iii) 'How arousing was the image?'. Subjects keyed in their response on a scale from 1 (not at all) to 9 (very). The order of trial types, and questions following trials, were counter-balanced. All presentation of stimuli, recording of subject responses and recording of airflow data were linked to the clock of one central computer.

Results

For the purpose of the present study, we averaged subject's vividness ratings within modality for each subject. Thus, for

each subject we computed an 'olfactory vividness index' which consisted of the average of vividness estimates from all olfactory imagery trials. The *K*-means method was used to determine the number of subjects within each sub-group. The analysis of vividness ratings separated the subjects into six 'good' and four 'bad' imagers [$F(1,8) = 14.321$; $P < 0.0055$].

An analysis of variance (ANOVA) comparing sniffing during imagery of smells, sights, sounds and during baseline of ongoing nasal inhalation revealed a significant main effect of sniffing [$F(3,27) = 5.672$, $P < 0.0038$]. That main effect reflected that sniffing was greater during imagery of smells compared with imagery of visual [$t(9) = 2.838$, $P < 0.01$], auditory [$t(9) = 2.118$, $P < 0.032$] and baseline of ongoing nasal inhalation [$t(9) = 2.985$, $P < 0.008$] (Figure 1a). This both replicated our previous findings (Bensafi *et al.*, 2003) and extended them in that imagery-dependent sniffing was evident even when the same stimuli were used across sensory modalities.

However, there was no significant differences between 'bad' and 'good' olfactory imagers in sniff volume during olfactory [$F(1,8) = 0.042$, NS] (Figure 1b), auditory [$F(1,8) = 0.341$, NS] and visual [$F(1,28) = 0.431$, NS] imagery or during a baseline of ongoing nasal respiration [$F(1,28) = 0.041$, NS]. Multiple regression analyses revealed no significant relationships between 'olfactory vividness index' and sniffing during imagination of smells [$F(4,9) = 1.560$, NS] (Figure 1c). Thus, the present findings showed that 'bad' and 'good' olfactory imagers did not differ in their overall sniff volume during odor imagery.

Experiment 2

In Experiment 1 we replicated our previous finding whereby subjects spontaneously sniffed when imagining an odor. Furthermore, this effect was persistent even when using the same imaginary stimulus across sensory modalities, thus reducing the possibility that the result reflected task demands. How-

ever, 'bad' and 'good' olfactory imagers did not differ in their overall extent of sniffing. To address the possibility that this null result reflected a lack of power related to sample size, we set out to reanalyze previously published data that was collected in a similar manner (Bensafi *et al.*, 2003) but not previously analyzed separately for 'bad' and 'good' olfactory imagers.

Methods

Subjects

Thirty students (24 females, mean age 20.8 ± 3.32 years) were selected using the same criteria as in Experiment 1.

Procedures

Procedures were identical to Experiment 1 with the exception that each session consisted of 45 imagery trials, 15 different stimuli in each of three modalities: auditory (doorbell, rain-fall, siren, typing on a keyboard, vacuum cleaner, explosion, dog barking, person crying, gunshots, person yelling, bird singing, piano, children laughing, fans in a stadium, ocean waves), olfactory (pepper, peanut butter, bathroom cleaner, licorice, rotten egg, rotten meat, urine, garbage, skunk, cookies baking, banana, peppermint, chocolate, rose, leather) and visual (stereo system, map of campus, windmill, bruise, scar, execution, house burning, mushroom cloud, baby smiling, sunset, flowers, tropical beach, fireplace, spoon, street). Examples of the three trial types are (i) 'imagine the sound of a door bell'; (ii) 'imagine the smell of peanut butter'; and (iii) 'imagine the sight of a windmill'.

Results

The statistical analysis (*K*-means, two clusters) of overall vividness ratings separated the 30 subjects into 11 'good' and 19 'bad' imagers [$F(1,28) = 50.065$; $P < 0.0001$]. All subjects sniffed when imagining smells [$F(3,87) = 22.290$, $P < 0.0001$], but there was no significant differences between 'bad' and 'good'



Figure 1 Experiment 1. **(a)** Sniffing during imagery of smells, sights, sounds and during baseline of ongoing nasal inhalation. Sniffing was significantly (*) greater during imagery of odors compared with imagery of sights, sounds and during the baseline condition. **(b)** Sniffing during olfactory in 'bad' and 'good' imagers. Sniffing during olfactory imagery was not significantly different between 'bad' and 'good' olfactory imagers [$F(1,8) = 0.044$, NS]. **(c)** The 'olfactory vividness index' as a function of sniff volume. No significant relationship was observed between olfactory imager status and sniff volume [$F(4,9) = 1.443$, NS]. Each element corresponds to a subject (10 participants in total in Experiment 1). * $P < 0.05$.

olfactory imagers in sniffing during olfactory [$F(1,28) = 1.361$, NS] (Figure 2a), auditory [$F(1,28) = 1.794$, NS] and visual [$F(1,28) = 1.188$, NS] imagery or during a baseline of ongoing nasal stimulation [$F(1,28) = 2.967$, NS]. A complementary multiple regression analyses between the 'olfactory vividness index' and sniff volume during visual, auditory and olfactory imagery also revealed no significant association between 'olfactory vividness index' and sniffing during imagination of smells [$F(4,29) = 0.957$, NS] (Figure 2b). Thus, as in Experiment 1, 'bad' and 'good' olfactory imagers did not differ in their extent of sniffing during olfactory imagery.

The above analysis suggested that 'good' and 'bad' olfactory imagers did not differ in their overall sniff volume. However, use of the olfactomotor system in imagery may be reflected in the odorant- (or image-) specific pattern of sniffing, rather than overall volume. Specifically, in perception the olfactomotor system reduces sniff volume when encountering intense (Johnson *et al.*, 2003; Laing, 1983) or unpleasant (Bensafi *et al.*, 2003; Frank *et al.*, 2003) odorants. Thus, the difference between 'good' and 'bad' olfactory imagers may be in the odorant-specificity of olfactomotor activation rather than overall olfactomotor enactment as reflected in overall volume. To address this, we analyzed the data by pooling for each subject a correlation score be-

tween the pleasantness ratings of the olfactory images and the sniff volume associated with each trial (15 trials in total for each participant). In order to ensure parametric assumptions, raw Pearson correlations scores were converted using Fisher transformation. We then analyzed these converted scores using an ANOVA with imager status ('good' and 'bad') as a between-factor variable. The analysis revealed that participants with low scores of vividness exhibited a lower score of correlation between sniff volume and odor imagery pleasantness compared with those who scored high in their vividness ratings [$F(1,28) = 6.256$; $P < 0.0186$] (Figure 2c). Therefore, although they did not differ in their overall sniff volume during imagery, 'bad' and 'good' olfactory imagers used different strategies when re-enacting the motor component of olfaction during imagery. This conclusion was supported by two additional analyses. The first analysis consisted of a regression analysis and revealed a positive relationship between sniff volume and pleasantness ratings in 'good' [$F(1,164) = 4.459$, $P = 0.0362$] but not in 'bad' [$F(1,284) = 1.611$, $P = 0.2055$] olfactory imagers (Figure 2d,e). The second analysis compared sniff volumes for the most unpleasant imagined odors (i.e. urine and garbage) and for the most pleasant imagined odors (i.e. banana and chocolate), and showed a significant difference in sniff

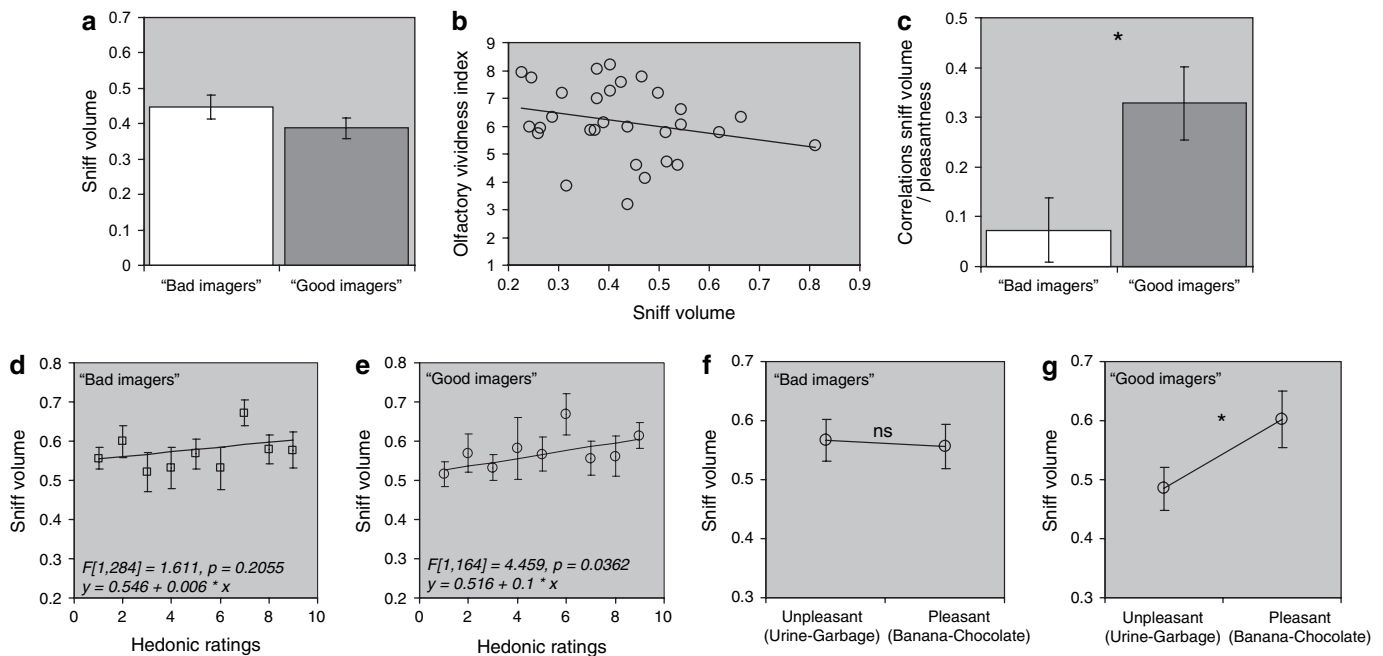


Figure 2 Experiment 2. (a) Sniffing during olfactory imagery in 'good' and 'bad' imagers. Sniffing during olfactory imagery was not significantly different between 'bad' and 'good' olfactory imagers [$F(1,28) = 1.361$, NS]. (b) The 'olfactory vividness index' as a function of sniff volume. No significant relationship was observed between olfactory imager status and sniff volume [$F(4,29) = 0.957$, NS]. Each element corresponds to a subject (30 participants in total in Experiment 2). (c) 'Good' olfactory imagers showed greater scores of correlations between sniff volume and pleasantness than did 'bad' olfactory imagers. (d, e) Sniff volume as a function of hedonic ratings in 'bad' (d) and 'good' (e) imagers. Regression analyses revealed a positive significant relationship between sniff volume and pleasantness in 'good' [$F(1,164) = 4.459$, $P = 0.0362$] but not 'bad' [$F(1,284) = 1.611$, $P = 0.2055$] olfactory imagers. (f, g) Sniff volume during imagery of the most unpleasant smells (urine and garbage) and the most pleasant smells (banana and chocolate) in 'bad' (f) and 'good' (g) olfactory imagers. Sniff volume during imagery of pleasant odors was greater than sniff volume during imagery of unpleasant odors in 'good' but not in 'bad' olfactory imagers. * $P < 0.05$, ns = non-significant.

volume between the two categories of imagined smells in 'good' [$t(42) = 1.942, P < 0.05$], but not in 'bad' [$t(74) = 0.19, NS$] olfactory imagers (Figure 2f,g).

Experiment 3

Experiment 2 revealed that both 'bad' and 'good' imagers sniffed during olfactory imagery, but that they differed in the odorant-specificity of this sniffing. Thus, two scenarios may underlie the greater ability of the 'good' imagers. One is that the odorant-specific re-enactment of the olfactomotor system enabled 'good' imagers to create vivid imagery. In other words, the odor-specificity of the sniff may have been a causal factor in imagery creation. By contrast, a second scenario is that odor-specific sniffing was the result of better imagery, and that this imagery was created by sniff-independent mechanisms.

To dissociate these two possibilities, we set out to prevent sniffing during olfactory imagery. If the first possibility is correct, and sniffing is a causal factor in imagery creation, then preventing sniffing should hamper imagery of pleasant odors to a greater extent than imagery of unpleasant odors, and more so in 'good' than in 'bad' imagers. In contrast, if the second possibility is correct, and 'good' imagers benefit from additional mechanisms unavailable to 'bad' imagers, then preventing sniffing should have an equal effect on imagery in both 'good' and 'bad' imagers, and for both pleasant and unpleasant odors.

Methods

Subjects

Forty subjects (31 females, mean age 20.2 ± 2.96 years) were selected using the same criteria as in Experiment 1.

Procedure

Experiment 3 was identical to Experiments 1 and 2 except that we omitted the auditory trials and we tested each subject under two conditions: blocked-sniff and free-sniff. In the blocked-sniff condition, sniffing was prevented by blocking the nose with a nasal clip. The order of conditions (blocked-sniff and free-sniff) was counterbalanced across subjects. In subjects where blocked-sniff occurred before free-sniff, the nasal clip was placed at the beginning of the experiment. Halfway through the experiment, the experimenter entered the room, removed the clip and told the subject that they (the experimenters) had made a mistake, and that the clip should not have been used in this experiment. The opposite procedure was executed when free-sniff occurred before blocked-sniff.

Pleasant and unpleasant stimuli were selected from Experiment 2. Here, we identified the most unpleasant (urine and garbage) and the most pleasant (banana and chocolate) imagined odors, and the most unpleasant (house burning and execution) and the most pleasant (baby smiling and sun-

set) imagined sights (for the mean ratings of these stimuli, see Bensafi *et al.*, 2003). These stimuli were interspersed within lists of various imagery trials during the experiment. Specifically, in order to prevent stimulus familiarity effects, two different lists of stimuli were used. 'List A' consisted of 12 olfactory imagination trials (pepper, peppermint, garbage, leather, coconut, peanut butter, bathroom cleaner, banana, wet dog, rotten eggs, incense, rotten meat) and 12 visual imagination trials (execution, street, clock, cemetery, bird, clown smiling, sunset, mad dog, tropical beach, vacuum cleaner, tornado, spoon), and 'List B' consisted of 12 olfactory imagination trials (rose, cigarette, popcorn, sweat, fresh paint, cookies baking, strong cheese, licorice, urine, baby powder, chocolate, skunk) and 12 visual imagination trials (stereo system, house burning, mushroom cloud, computer, map of campus, dairy cow, windmill, bruise, fireplace, scar, baby smiling, flowers). Half of the subjects were asked to imagine the stimuli from 'List A' under the blocked-sniff condition and the stimuli from 'List B' under the free-sniff condition. The other half of the participants were instructed to imagine the stimuli from 'List B' under the blocked-sniff condition, and the stimuli from 'List A' under the free-sniff condition. The order of trial types was randomized.

Results

As in Experiments 1 and 2, in order to distinguish 'bad' olfactory imagers from 'good' olfactory imagers, we built an 'olfactory vividness index' by averaging the olfactory vividness ratings during the natural free-sniff condition for each participant. Here also, the *K*-means method was used to determine the number of subjects within each sub-group. Given the larger number of subjects (40 here), and in order to distinguish very 'bad' olfactory imagers from very 'good' olfactory imagers, we used a *K*-means analysis with three clusters. The analysis showed that the three clusters contained respectively seven 'bad', 22 'medium' and 11 'good' olfactory imagers [$F(2,37) = 60.693, P < 0.0001$]. Furthermore, there was no difference in olfactory vividness between 'bad' imagers from Experiment 2 and 'bad' imagers from Experiment 3 [$t(24) = 1.621, NS$] and 'good' imagers from Experiment 2 and 'good' imagers from Experiment 3 [$t(24) = 0.381, NS$].

To discover whether blocking sniffing influences the quality of pleasant and unpleasant olfactory mental imagery differently in 'bad', 'medium' and 'good' olfactory imagers, we conducted three-way mixed ANOVAs including sniffing (blocked and free) and modality (olfaction and vision) as within-factors variables and imager status ('bad', 'medium' and 'good' olfactory imagers) as a between-factor variable for both the pleasant and the unpleasant trials. Given that vividness ratings were used to separate 'bad' from 'good' imagers, the effect of sniffing on that measure was not analyzed. Data were analyzed for hedonic and arousal ratings.

The analysis revealed a significant imager status \times sniffing \times modality interaction for the pleasant trials regarding hedonic

ratings [$F(2,37) = 4.711, P < 0.0209$]. This reflected a significant increase of pleasantness for the pleasant olfactory imagined trials following sniffing specifically in the group of 'good' olfactory imagers [$t(10) = 2.141, P < 0.03$] (Figure 3a), but not in 'medium' (Figure 3b) or 'bad' olfactory imagers (Figure 3c) ($P > 0.05$ in all cases). Similar comparisons during visual imagery did not reveal any significant effect of sniffing on pleasantness of visual imagery in 'bad', 'medium' or 'good' olfactory imagers ($P > 0.05$ in all cases).

No significant effects of sniffing were observed during imagery of unpleasant trials ($P > 0.05$ in all cases) (Figure 3d–f). The statistical analyses did not reveal any interactions or effect of sniffing for arousal ratings. In other words, increasing sniffing increased the pleasantness of pleasant smells in 'good' olfactory imagers, but had no effect on the pleasantness of an unpleasant smell in that same group of imagers. Taken as a whole, these results suggest that sniffing is not a mere product of olfactory imagery, but is indeed a causal factor in odor imagery creation

Discussion

The present study had two goals. The first was to test replication of our finding previously reported in brief format whereby odor imagery was accompanied by spontaneous sniffing (Bensafi *et al.*, 2003). Odor-imagery-related sniffing was clearly evident in the subjects tested in this study. This combines with our previous report (Bensafi *et al.*, 2003) to suggest that olfactory imagery-related sniffing is a robust effect.

A second goal was to explore the novel question of whether the strategy of re-enacting the olfactomotor response during imagery underlies the dissociation between 'bad' and 'good' olfactory imagers. Experiment 1 showed that 'bad' and 'good' olfactory imagers did not differ in their overall sniff volume. However, a difference between these two populations was seen in Experiment 2 in the odor-hedonic specificity of olfactomotor activation rather than overall sniffing activity. Specifically, 'bad' and 'good' olfactory imagers used different strategies when re-enacting the motor component of olfaction during imagery. As in real perception, the 'good' imagers sniffed more when imagining pleasant odors than they did when imagining unpleasant odors. In contrast, the 'bad' imagers did not modify their sniffs in accordance with imagined odor valence.

To ask whether sniffing was causal in the generation of imagery, we blocked sniffing. In a previous study we contrasted blocked sniffing with encouraged sniffing and found that encouraged sniffing improved imagery across subjects [$F(1,19) = 6.192, P < 0.023$]. Encouraged sniffing, however, may lead to increased effects of task demands. Therefore, we omitted the encouraged sniffing condition here, and compared baseline imagery to imagery with a nasal blocker. Consistent with the notion that re-enactment of sniffing strategies underlies the dissociation between 'good' and 'bad' imagers, blocking sniffing hampered imagery only in the 'good' imagers, where it hampered imagery of pleasant odors. The specificity of this manipulation further negates concerns regarding potential confounds of task demands. Specifically, one may claim that,

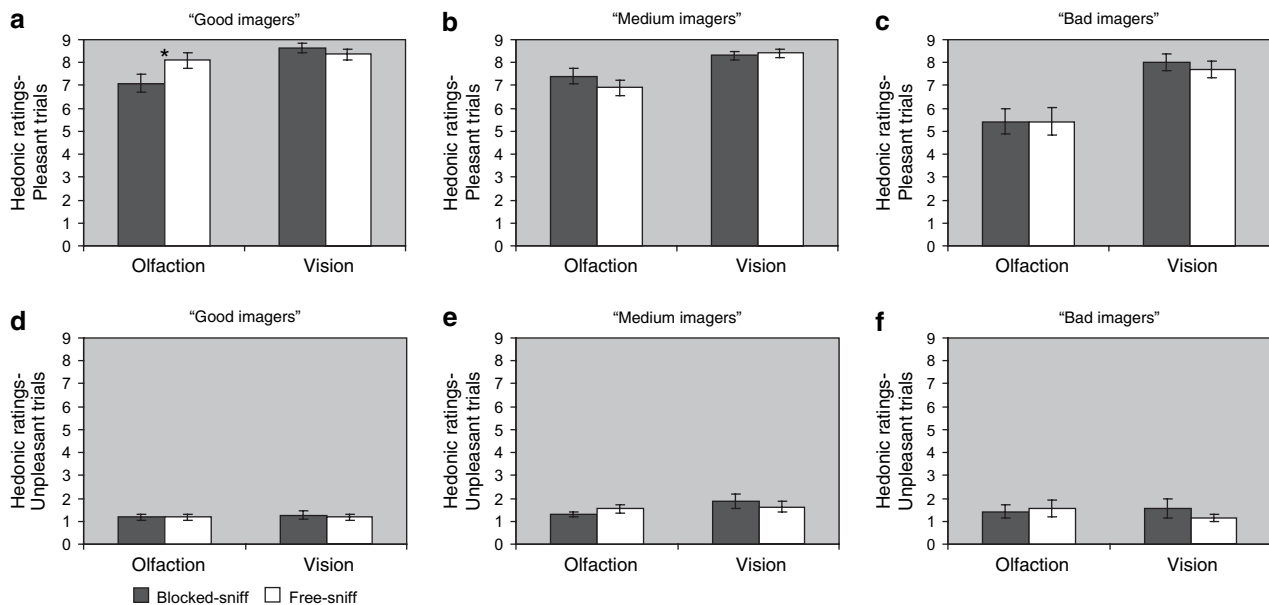


Figure 3 Experiment 3. (a–c) Effect of sniffing on the pleasantness of pleasant olfactory and visual imagery in 'good' (a), 'medium' (b) and 'bad' (c) olfactory imagers. The pleasantness of pleasant imagined odors is significantly ($*P < 0.05$) greater during the free-sniff condition (white bar) than during the blocked-sniff condition (black bar) in 'good' olfactory imagers, but not in 'medium' and 'bad' olfactory imagers. (d–f) Effect of sniffing on the pleasantness of unpleasant olfactory and visual imagery in 'good' (d), 'medium' (e) and 'bad' (f) olfactory imagers. No significant effects of sniffing were observed for the unpleasant trials ($P > 0.05$ in all cases).

due to task demands, subjects lowered their vividness ratings of olfactory imagery either knowingly or unknowingly under the condition of blocked nasal respiration. It would be difficult to explain, however, how tens of naive subjects would have known to do so for the pleasant but not the unpleasant imagined stimuli, a behavior consistent with the esoteric expectations of only a very small number of people who study sniffing.

Overall, these results are of special interest when considering the debate over the validity of using vividness scales in mental imagery studies (Chara, 1989; Marks, 1989b; McKelvie, 1990). For example, regarding classification of 'bad' and 'good' imagers, Ahsen (1986) suggested that by using vividness scales, a subject could, by 'pure accident', be categorized as a 'good' imager or a 'bad' imager depending entirely on 'which foot' he/she started at the beginning of the test. In other words, rather than accepting these differences as representing differences in mental imagery, one may consider that 'good' and 'bad' imagers are two populations who use the rating scale differently. In line with this, some researchers questioned the use of vividness scales on the grounds that subjects may bias their scores and performances by an excess of confidence, or again, because such methods are susceptible to demand-characteristics (see McKelvie, 1990, 1994). This view is, however, challenged by a large body of research showing positive correlations between individual differences in reported mental imagery on the one hand, as assessed in the Vividness of Visual Imagery Questionnaire or VVIQ (Marks, 1973), and perception and/or cognitive performances on the other hand (for a list of studies, see Marks, 1989a). Furthermore, EEG recordings have suggested increased cerebral activity during imagery in 'good' as compared with 'bad' imagers (Marks and Isaac, 1995), suggesting that these labels do reflect a genuine difference in neural activity during imagery. Our results showed that beyond their differences in vividness, 'good' and 'bad' olfactory imagers used different sensorymotor mechanisms when trying to imagine smells: imagers who were qualified as 'good' used an olfactomotor strategy that resembled that during perception in that they sniffed more when trying to imagine pleasant smells. This result shows that demand-characteristics and overconfidence bias are unlikely to be determinants of group differences in our study. In other words, the present findings suggest that the odor-hedonic sniffing pattern may be viewed as an objective and reliable tool to explore individual differences in olfactory mental imagery.

One may finally ask how the current results reflect on the ongoing debate regarding the existence of olfactory mental imagery, a subject of considerable controversy (Engen, 1987; Lyman and McDaniel, 1990; Schab, 1990; Algom and Cain, 1991; Algom *et al.*, 1993; Carrasco and Ridout, 1993; Crowder and Schab, 1995; Cain and Algom, 1997; Elmes, 1998; Herz, 2000; Djordjevic *et al.*, 2004a,b,c, 2005). In support of olfactory mental imagery, one may point to (i) that olfactory imagery improved odor detection (Djordjevic *et al.*, 2004c) and recognition memory (Lyman and McDaniel, 1990); (ii) the

observed similarity in perceptual grouping of perceived and imagined smells (Carrasco and Ridout, 1993); (iii) the similarity in relative contributions of real and imagined odors to the perception of an odor mixture (Algom and Cain, 1991; Algom *et al.*, 1993; Cain and Algom, 1997); and (iv) that perception and imagination of smells involved common neural substrates (Djordjevic *et al.*, 2005; Henkin and Levy, 2002; Levy *et al.*, 1999). Whereas the existence of odor imagery may be evidenced by these reports, the process by which an olfactory image is created remains unknown. In the visual modality, common neural mechanisms underline perception and imagery (Farah *et al.*, 1988; Farah, 1989a,b; Kosslyn *et al.*, 1995, 1999, 2001; D'Esposito *et al.*, 1997). More specifically, eye movements during imagery mimic those during perception (Spivey and Geng, 2001; Laeng and Teodorescu, 2002; Mast and Kosslyn, 2002; Kosslyn, 2003). Similarly, common motor mechanisms underline perception and imagery in the olfactory modality (Bensafi *et al.*, 2003; Kosslyn, 2003). In accordance with the implication of olfactomotor activity in odor mental imagery, it has been reported that sniffing can trigger 'phantom perceptions' in patients who suffer from olfactory hallucinations (Leopold, 2002). Our findings are in line with this, and suggest that sniffing is functionally involved in odor imagery. In conclusion, combined with numerous findings in animals (Adrian, 1942; Freeman, 1960, 1981, 1983; Macrides, 1975; Bressler and Freeman, 1980; Ketchum and Haberly, 1991) and humans (Teghtsoonian *et al.*, 1978; Sobel *et al.*, 1998a,b, 2000, 2001), the present experiment suggests that sniffing, the motor component of olfaction, should be studied together with smelling, the sensory component of olfaction, in paradigms exploring mental imagery of smells. Here, complementary to bottom-up processes which respond to changes in odor content (Laing, 1983; Bensafi *et al.*, 2003; Johnson *et al.*, 2003), top-down processes used during olfactory imagery may also drive sniffing. In turn, sniffing does not merely accompany, but rather functionally contributes to olfactory mental imagery. Thus, future studies on odor imagery may consider sniffing as a reliable non-verbal measure of olfactory mental imagery.

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