

---

# Emotional Processing of Odors: Evidence for a Nonlinear Relation between Pleasantness and Familiarity Evaluations

---

Sylvain Delplanque<sup>1</sup>, Didier Grandjean<sup>1,3</sup>, Christelle Chrea<sup>1</sup>, Laurence Aymard<sup>2</sup>, Isabelle Cayeux<sup>2</sup>, Bénédicte Le Calvé<sup>2</sup>, Maria Inés Velazco<sup>2</sup>, Klaus R. Scherer<sup>1,3</sup> and David Sander<sup>1,3</sup>

<sup>1</sup>Swiss Center for Affective Sciences, University of Geneva, rue des Batoirs 7, 1205 Geneva, Switzerland <sup>2</sup>Firmenich, SA, Route des Jeunes 1, 1227 Geneva, Switzerland and <sup>3</sup>Department of Psychology, University of Geneva, 40 Bld du Pont d'Arve, 1205 Geneva, Switzerland

Correspondence to be sent to: Sylvain Delplanque, Swiss Center for Affective Sciences, University of Geneva, rue des Batoirs 7, 1205 Geneva, Switzerland. e-mail: sylvain.delplanque@pse.unige.ch

---

## Abstract

Pleasantness, familiarity, and intensity are 3 interdependent dimensions commonly used to describe the perceived qualities of an odor. In particular, many empirical studies have demonstrated a positive correlation between familiarity and pleasantness. However, on the basis of both theoretical and methodological perspectives, we questioned the validity of such a relation for malodors. We report 2 studies based on subjective judgments of a large sample of odorants (Experiment 1) associated with autonomic recordings (Experiment 2). Multivariate exploratory analysis performed on the data splits the whole odorant set into 2 subsets composed, respectively, of unpleasant and pleasant odorants. Subsequent correlation analyses have shown that the relation between pleasantness and familiarity is specific for the pleasant odors in the 2 experiments. Moreover, autonomic activity was more important in response to malodors than to pleasant odors and was significantly correlated with unpleasantness ratings in the subset of unpleasant odors. These 2 studies argue in favor of a functional dissociation in the relations between both subjective and autonomic responses to odors as a function of pleasantness and indicate that researchers in the olfactory domain should consider the relations between pleasantness and familiarity as more complex than linear.

**Key words:** electrodermal activity, emotion, familiarity, hedonicity, human olfaction, pleasantness, subjective scales

## Introduction

Subjective odor perception is a complex process that is often investigated with the aid of several dimensions. For instance, pleasantness (or hedonicity), familiarity, and intensity are 3 standard dimensions that are mostly used to describe the subjective qualities of an odor. Many studies have demonstrated a considerable variability in the ratings along those dimensions within and between participants for a given odorant (for further details, see Distel et al. 1999), and it has also been demonstrated that these dimensions are not independent. In particular, a positive correlation between the familiarity and the pleasantness of odors seems to constitute a reliable and unchallenged result in olfactory research (e.g., Engen and Ross 1973; Lawless and Cain 1975; Ayabe-Kanamura et al. 1998; Distel et al. 1999; Royet et al. 1999; Bensafi et al. 2002c; Sulmont et al. 2002). For simplicity, the more familiar an odor, the more pleasant it is judged. This relation between familiarity and pleasantness

was mainly explained with the mere exposure effect (Cain and Johnson 1978; Sulmont et al. 2002), a theory of hedonic value in memory claiming that the repeated exposure to a stimulus is sufficient for the enhancement of one's attitude toward it (e.g., to induce an increase of subjective preference; Zajonc 1968; Harmon-Jones and Allen 2001). However, one can question the validity of this relation on the basis of several empirical data and both theoretical and methodological points of view.

From an empirical point of view, it has been demonstrated that the odors that were equally well identified across age cohorts were rated as significantly more unpleasant than those for which the identification was sensitive to aging, although the odors did not differ with regard to their rated familiarity (Konstantinidis et al. 2006). Consequently, pleasantness judgments could be affected, whereas familiarity judgments remained stable across ages, showing that the

positive correlation between pleasantness and familiarity seems not to be systematic. This latter point has already been highlighted by several authors, especially when malodors are concerned (Ayabe-Kanamura et al. 1998; Distel et al. 1999; Royet et al. 1999; Sulmont et al. 2002). Using faces and words, Monin (2003) demonstrated that the positive valence of a stimulus increased its perceived familiarity, even in the absence of prior exposure. This “good-is-familiar” phenomenon was illustrated in a series of experiments during which participants were asked to judge the faces and words according to their familiarity and their attractiveness. The author pointed out a positive linear correlation between the 2 dimensions for pleasant material, but he also emphasized the weakness of this correlation when unpleasant stimuli were concerned. Thus, the fact that familiarity and pleasantness possess different relations as a function of pleasantness is not specific to the olfactory domain.

From a theoretical point of view, the olfactory system provides information about the identity and the quality of objects which is crucial for evaluation of food and alerts the organism to potentially harmful substances (Köster 2002). From an adaptive perspective, one can wonder why it could be pertinent for the olfactory processes to be equally sensitive to familiar influences when facing a pleasant and an unpleasant odor. In theory, judging a malodor as less unpleasant following a few exposures could be unfavorable to individual survival. In fact, the prevalence of unpleasant information over pleasant information for individual survival has already been demonstrated with many behavioral, physiological, and cognitive measures in other modalities (e.g., Cacioppo and Gardner 1999; Baumeister et al. 2001). From this perspective, the positive correlation between pleasantness and familiarity is completely understandable as far as the pleasant domain is concerned. In contrast, one would expect this correlation to be weaker, if not nonexistent, for the unpleasant domain. Moreover, the functional dichotomy in the relation between the 2 dimensions could be conceivable because olfactory information may be processed differentially as a function of whether the odor is pleasant or unpleasant, and researchers should perhaps not consider the pleasantness dimension as a continuum but rather as hedonic categories (for a review, see Rouby and Bensafi 2002).

However, to our knowledge, none of the scientific publications showing the positive correlation between familiarity and pleasantness questioned and demonstrated the existence of functional subsets of unpleasant and pleasant odors. One key reason for that could be, from a methodological perspective, that studying the correlation between pleasantness and familiarity does not allow one to highlight hypothetical differences as a function of hedonic categories because a correlation is blind to the existence of subsets in the data. In the latter case, a high correlation may result that is entirely due to the arrangement of the 2 subsets, but which does not represent the “true” relation between the 2 variables.

With regard to all of the preceding points, we propose that the positive correlation between pleasantness and familiarity is more specific to the pleasant domain, whereas this relation is weaker, if not nonexistent, for malodors. Thus, in a first experiment, we scrutinized the relations between pleasantness and familiarity ratings of a large sample of odorants (48). To this aim, we performed an alternative method of analyzing the data using exploratory multivariate techniques (e.g., cluster analysis). The cluster analysis is an exploratory data analysis tool that aims to segment different groups on the basis of a series of variables, without any a priori assumption about the existence and number of groups, in a way that the degree of association between 2 elements is maximal if they belong to the same group and minimal otherwise. In a second step, we examined the relation between pleasantness and familiarity within each potentially extracted group of odors.

## Experiment 1

### Material and methods

#### *Participants*

Sixty-six participants ( $28.2 \pm 7.52$  years, 14 males) took part in this experiment. They all self-reported a normal sense of smell.

#### *Stimuli*

We decided to use complex stimuli, mainly taken from everyday life, thought to elicit a wider spectra of cognitive and emotional responses as compared with monomolecular stimuli (Distel et al. 1999) and to be judged more easily (Royet et al. 1999). Thus, 51 odorants provided by Firmenich, SA (Switzerland) were selected on the basis of previous evaluations and analyses made in the company’s sensory analysis department (Table 1).

These odorants represent a wide spectrum of pleasant and unpleasant odorants, including several families, from fruity odors (e.g., lime, fig, and tutti frutti) to floral notes (e.g., lavender and geraniol) to animal odors (e.g., body odor, leather, and civet).

Odorants were presented in felt-tip pens that had a length of approximately 14 cm; the inner diameter of the cylindrical pens was 1.3 cm. The pen’s tampon was filled with 2 ml of pure odorants or odorants dissolved in propylene glycol, and the final concentrations were adjusted so that the pens were subjectively judged by a small sample of Firmenich employees as 1) well perceived without being too strong and 2) without any notable difference in perceived intensity among all of the odorants. The use of this highly practical system provided by Burghart (Germany) prevents contamination by the environment. An additional pen without any odorant was added in the selection as a control.

**Table 1** Names of the 51 odors and the cluster type they belong to in the 2 experiments

Odor name	Cluster type Experiment 1	Cluster type Experiment 2
Agarwood smoke	p	Not used
Aladinate	p	u
Amyl acetate (banana)	p	p
Classical detergent fragrance	p	p
Basil	p	p
Beer	p	p
Landes wood	p	p
Bornyl acetate (pine, camphoraceous, herbal, and balsamic)	p	p
Cake	p	p
Carbinol (1-octen-3-ol, mushroom)	p	p
Cassis bud	p	p
Classical shampoo fragrance	p	p
Fig	p	p
Geraniol	p	p
Green tea	p	p
Honey	p	Outlier
Classical soap fragrance	p	p
Lavender	p	p
Lilac	p	p
Lime	p	p
Linalol (floral)	p	p
Magnolia grandifolia	p	p
Methyl salicylate (wintergreen)	p	p
Neroli	p	p
Peach	p	p
Classical body lotion fragrance	p	p
Pineapple	p	p
Resinoid Incense	p	Not used
Tiare	p	p
Tutti frutti	p	Outlier
Body odor	u	u
Butter popcorn (rancid butter)	u	p
Caproic acid (sharp, sour, and rancid odor)	u	Outlier
Dynascone	u	u
Famboisone	u	u
Ghee	u	u
Isobutylquinoleine	u	u

**Table 1** Continued

Odor name	Cluster type Experiment 1	Cluster type Experiment 2
Isovaleric acid (rancid cheese, sweaty, and putrid)	u	Outlier
Leather	u	Outlier
Melonal (melon like)	u	u
Octamile	u	u
Octanol (oily)	u	u
Paracresol (phenolic odor)	u	u
Sclarymol (sulfury and onion)	u	u
Skunk	u	u
Sulfox (rotten egg)	u	u
Vetyver	u	Not used
Yoghurt	u	u
Diacetyl (butter, fermenting perspiration)	Outlier	u
Durian	Outlier	u
Isobutyric acid (rancid cheese, sweaty, and putrid)	Outlier	u

p, pleasant cluster; u, unpleasant cluster.

### Scales and measures

The participants were asked to judge the pleasantness, from “very unpleasant” (left of the scale = 0 cm) to “neutral” (middle of the scale = 5 cm) to “very pleasant” (right of the scale = 10 cm), and the familiarity from “not familiar at all” (left) to “very familiar” (right). Because the intensity of the odor can modulate its perceived pleasantness (de Graaf et al. 1996; Ayabe-Kanamura et al. 1998; Distel et al. 1999; Royet et al. 1999) and thus could be the mediator of any relation between familiarity and pleasantness, participants were also asked to judge the subjective intensity of the odorant from “not perceived” (left) to “medium” (middle) to “very strong” (right). They were also informed that they could use all of the intermediate positions. The judgments were performed on paper sheets. The data were acquired using the FIZZ sensory software (Biosystèmes, Couternon, France), which automatically scanned and measured the distance of the vertical draft from the origin of the scale for all questionnaires.

### Experimental procedure

Participants performed 2 sessions of judgments, separated at least by 1 day but by less than 2 weeks. During each session, participants smelled 26 pens in random order. The interval between 2 odorants varied from 30 to 45 s to avoid sensory adaptation. Before testing, participants were instructed on how to smell the odorants in order to minimize the intra- and interparticipant breathing pattern variability

using a procedure as described in previous studies (Hudry et al. 2003; Jung et al. 2006). The instructions were as follows: when the participants heard the signal from the experimenter, they had to 1) take the selected pen from the display shelf, 2) breathe out deeply through the mouth; 3) open the cap of the pen and breathe in once and evenly with the odorant pen opened near the nose (about 1 cm below both nostrils); 4) close the pen and replace it in the display shelf; and 5) rate the 3 scales and wait for the signal to proceed to the next trial. The participants were explicitly asked not to smell the odorant again. They sat in a wide room (volume  $\approx 55 \text{ m}^3$ ) with all of the windows opened (surface opened  $\approx 3.4 \text{ m}^2$ ). This setup associated with the use of the pens provides good conditions to prevent odorant diffusion and contamination.

## Results

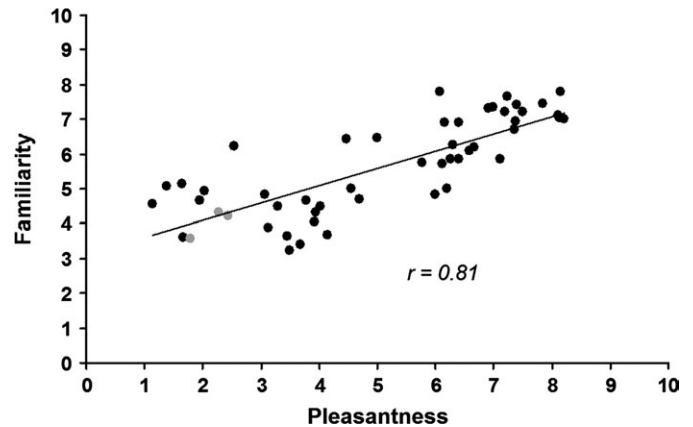
Individual scores were averaged per odorant. The fact that the pen without odorant (blank) was perceived as not intense at all (mean ratings =  $0.15 \pm 0.19$ ) showed that the task was performed correctly by the participants. The data concerning the pen without odorant were excluded from the following analyses. Moreover, because outliers (i.e., extreme values) have a profound influence on the value of the correlation coefficient, we excluded odorants that were outside the range of  $\pm 2$  standard deviations (SDs) around their ratings mean for each scale. This procedure led to the exclusion of 3 odorants, 1 (isobutyric acid) being rated as not intense enough and 2 others (diacetyl and durian) being rated as too intense. The following analyses were thus performed on 48 odorants with Statistica Software (Statistica 7.0, Statsoft, Tulsa, OK).

### Correlations between intensity, pleasantness, and familiarity ratings

*Intensity versus other scales.* The analyses did not reveal any significant correlation between the perceived intensity of the odor and its perceived familiarity ( $r = 0.03$ , nonsignificant [NS]) nor between intensity and pleasantness ratings ( $r = -0.28$ , NS). However, because the intensity could mediate any relation between familiarity and pleasantness, we investigated the correlations between the 2 dimensions and their partial correlations while controlling for intensity.

*Familiarity and pleasantness.* We found the expected significant positive correlation between familiarity and pleasantness ( $r = 0.77$ ,  $P < 0.001$ ). This significant relationship was found for 57 of the 66 participants ( $\approx 86\%$ ) and was even stronger (see Figure 1) when it was controlled for intensity ( $r = 0.81$ ,  $P < 0.001$ , significant for 59 of the 66 participants, i.e.,  $\approx 89\%$ ;  $r = 0.82$ ,  $P < 0.001$ , when the outliers are included and controlled for intensity). Thus, this result indicates that the proportion of common variation in pleasantness and familiarity is about 66% when controlling for intensity.

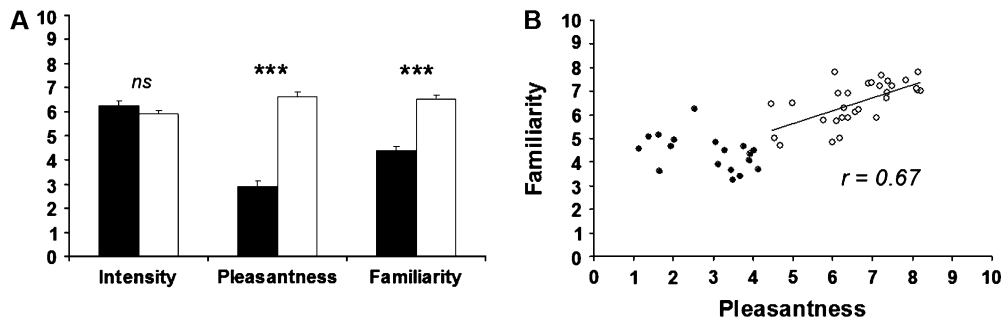
*Cluster analysis.* In order to examine the homogeneity in the sample from which a correlation was calculated, we submit-



**Figure 1** Mean rating scores of familiarity as a function of pleasantness for the 48 odorants (black dots). The correlation coefficient for the significant positive partial correlation (controlled for intensity), the linear regression line, and the position of the 3 odorants excluded for intensity reasons (gray dots) are also indicated.

ted the data of pleasantness, familiarity, and intensity to a cluster analysis using Statistica 7.0 software (Statsoft). We applied Ward's method on City-block (Manhattan) distances (City-block [Manhattan] distance is simply the average difference across dimensions. In most cases, this distance measure yields results similar to the simple Euclidean distance. However, in this measure, the effect of single large differences [outliers] is dampened because they are not squared. Ward's method uses an analysis of variance (ANOVA) approach to evaluate the distances between clusters. In short, this method attempts to minimize the sum of squares of any 2 [hypothetical] clusters that can be formed at each step. In general, this method is regarded as very efficient; however, it tends to create clusters of small size [see "Electronic Statistics Textbook" for further details; StatSoft, Inc. 2007].) To select the number of clusters yielded by cluster analysis, we examined the dendrogram for changes in level and selected the number of clusters corresponding to the largest difference between 2 consecutive levels. The largest change occurred at the level of 2 clusters (distanced from each other  $>65\%$  of the total linkage distance) whose characteristics are represented in Figure 2A.

An examination of the odorants included in each cluster (see Table 1) showed that the first cluster corresponded to the unpleasant and less familiar odorants ( $n = 18$ , mean pleasantness  $2.9 \pm 0.98$ , familiarity  $4.37 \pm 0.72$ , and intensity  $6.26 \pm 0.79$ ), whereas the second cluster included principally the pleasant and familiar odorants ( $n = 30$ , mean pleasantness  $6.64 \pm 1.03$ , familiarity  $6.52 \pm 0.89$ , and intensity  $5.93 \pm 0.64$ ). ANOVAs revealed that the 2 clusters differed in pleasantness and familiarity but not in intensity ( $F_s(1,46) = 145.8, 72.27, \text{ and } 2.43$ ;  $P_s < 0.001, 0.001, \text{ and } \text{NS}$ ;  $\eta_s^2 = 0.76, 0.61, \text{ and } 0.05$ , respectively). Thus, this analysis highlighted the fact that pleasantness and familiarity are not similar between the 2 groups extracted by cluster analysis.



**Figure 2** (A) Mean ratings (+standard error of the mean) of intensity, pleasantness, and familiarity as a function of the clusters. Black, unpleasant cluster; white, pleasant cluster. (B) Mean ratings scores of familiarity as a function of pleasantness for the 48 odorants grouped by cluster. Black, unpleasant cluster; white, pleasant cluster. The correlation coefficient for the significant positive correlation for the pleasant cluster and the regression line are also indicated. \*\*\* $P < 0.001$ ; NS, nonsignificant.

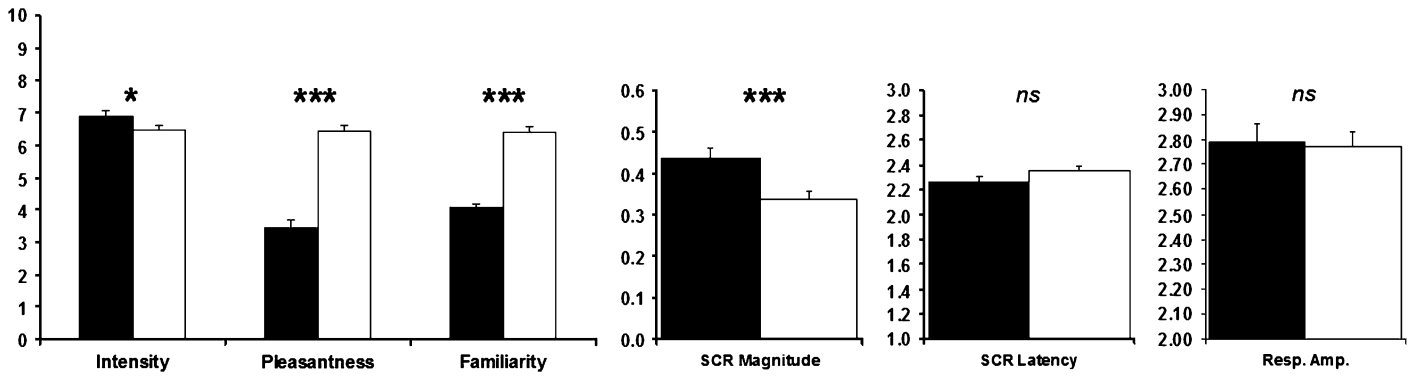
In a final step, we examined the relations between pleasantness and familiarity within each cluster of odorants. We found no significant correlation for Cluster 1 (unpleasant and less familiar odorants) before and after controlling for intensity ( $r = -0.43$ , NS and  $r = -0.33$ , NS, respectively). On the contrary, there was a significant positive correlation for Cluster 2 (pleasant and familiar odorants) before and after controlling for intensity ( $r = 0.64$ ,  $P < 0.05$  and  $r = 0.67$ ,  $P < 0.05$ , respectively). This result is illustrated in Figure 2B. Further individual analyses revealed that this correlation was significant for 51 of the 66 participants ( $\approx 77\%$ ; 44 of the 66 participants after controlling for intensity,  $\approx 66\%$ ).

## Discussion

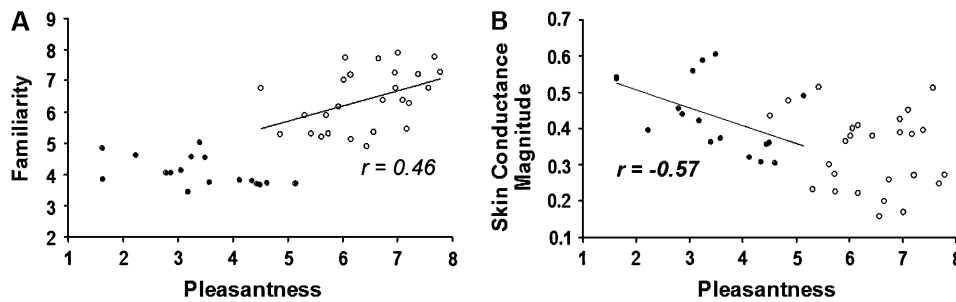
At first glance, we replicated the classical positive correlation between pleasantness and familiarity as previously described (e.g., Engen and Ross 1973; Lawless and Cain 1975; Ayabe-Kanamura et al. 1998; Distel et al. 1999; Royet et al. 1999; Bensafi et al. 2002c; Sulmont et al. 2002). However, with a large sample of odorants and participants, our results suggest that the positive correlation between pleasantness and familiarity is specific to the pleasant domain and does not exist for malodors.

One could question whether this result could be due to a bias in the selection of odorants. Indeed, one could object that the unpleasant odors we used were all weakly familiar, a property that is not specific to unpleasant odors because objectively often encountered malodors should exist (e.g., Rouby and Bensafi 2002). However, the fact that a positive correlation between subjective ratings of familiarity and pleasantness was depicted consistently in many studies suggests that the subjective evaluation of familiarity for malodors can be dissociated from the objective probability of encountering them. Indeed, of course, if malodors were (objectively and subjectively) as familiar as pleasant odors, no positive correlation between ratings of familiarity and pleasantness would be observed. Although our specific aim was to test subjective evaluations of familiarity and pleasantness, further research aimed at comparing subjective and objective

familiarity of odors would help clarifying this issue. One could also object that the absence of neutral odors in our design artificially leads to the constitution of a pleasant and unpleasant subset of odorants. This reasoning is also applicable to the familiarity dimension. However, a closer examination of the pleasantness, familiarity, and intensity ratings revealed that they did not differ from normal distributions (Kolmogorov–Smirnov test,  $d_s = 0.16$ , 0.11, and 0.09; NS, respectively). This observation means that the odorants were homogeneously distributed along the pleasantness and the familiarity axes and that the constitution of 2 groups of odors was more linked to differential relations between the dimensions than to an artificial segregation of odors based on one dimension alone. Another explanation of our results could be that the unpleasant odors we selected have a similar degree of familiarity, whereas pleasant odors are more distributed along this dimension. However, unpleasant and pleasant odors are distributed in a very similar way along the familiarity and pleasantness axes (SDs of familiarity ratings = 0.72 and 0.82; SDs of pleasantness ratings = 0.98 and 1.03, respectively). Consequently, if the relation between familiarity and pleasantness is as true for the unpleasant odors as it is for the pleasant odors, it should be observed in our data. However, results have shown that increasing the pleasantness in the malodor domain does not increase the familiarity. Considering these points, it seems improbable to us that our results can be accounted for by a bias in the odorant selection. Lastly, we cannot rule out the hypothesis that the lack of significant correlation for the unpleasant cluster could be due to a lower number of odorants ( $n = 18$ ) as compared with the pleasant cluster ( $n = 30$ ). To tackle this issue, we built 100 random selections of 18 pleasant odors and performed correlation analyses between familiarity and hedonicity mean ratings for each selection. Ninety-six of them were significant ( $0.47 < r_s < 0.85$ ; all  $P_s < 0.045$ ), showing that 18 odorants should be sufficient to highlight a correlation for the unpleasant odorants, with a probability of obtaining it by chance inferior to 5%, if the relation between familiarity and hedonicity would have



**Figure 3** Mean ratings (+standard error of the mean) of intensity, pleasantness, and familiarity; SCR magnitude (in microsiemens); SCR latency (in s); and amplitude of the respiration (Resp. Amp. in volts) as a function of the clusters. Black, unpleasant cluster; white, pleasant cluster. \* $P < 0.05$ ; \*\*\* $P < 0.001$ ; and NS, nonsignificant.



**Figure 4** (A) Mean ratings scores of familiarity as a function of pleasantness for the 43 odorants grouped by cluster. The correlation coefficient for the significant positive correlation for the pleasant cluster is also indicated. (B) Mean ratings scores of SCR magnitude (in microsiemens) as a function of pleasantness for the 43 odorants grouped by cluster. The correlation coefficient for the significant negative correlation for the unpleasant cluster is also indicated. Black, unpleasant cluster; white, pleasant cluster.

been as strong as for the pleasant odors. Moreover, we can argue that a sample of 18 odors (and even less) was sufficient to show a significant classical familiarity–hedonicity correlation in other studies (Ayabe-Kanamura et al. 1998; Distel et al. 1999; Bensafi et al. 2002c).

The relation between familiarity and pleasantness in the pleasant domain could be related to the mere exposure influence (Zajonc 1968; Harmon-Jones and Allen 2001), an effect of hedonic value on memory consisting of an enhancement of one’s attitude toward a stimulus following its repeated exposure. The past exposures to an odorant could enhance its perceptual fluency, making it more prototypical and familiar, leading to an increase in its attractiveness (Monin 2003). Sulmont et al. (2002) brought forward elements in favor of this idea in the sense that in their study, the more familiar and pleasant the odors, the more simple they were rated, whereas the number of perceived notes remained relatively independent of familiarity, suggesting that simplicity is not related to physical complexity. Another explanation is that the increase in fluency itself may produce feelings of pleasantness and thus increase positive affective responses (see Reber et al. 1998; Seamon et al. 1998; Winkielman et al. 2003). In both cases and as suggested by Monin (2003), experiencing this exposure effect enough times could lead to the development in

the perceiver of an implicit association between liking a stimulus and prior exposure to it. This latter mechanism would explain the “liking-is-familiar” effect in conditions of a single presentation of odorants. Concerning malodors, the influence of another mechanism based on the repression theory was proposed by Doop et al. (2006). The repression theory postulates that unpleasant memories degrade faster than pleasant memories (Holmes 1970; Walker et al. 2003). This effect, which may explain the prevalence of pleasant semantic associations with olfactory stimuli (Doop et al. 2006), could also explain why familiarity may have less influence on pleasantness judgments in the unpleasant domain.

From a functional perspective, the most familiar odors are more attractive because their positive consequences or their absence of negative consequences are well known from past exposures (Zajonc 2001), whereas the consequences associated with less familiar odors (i.e., more novel) are less known and the odors could present a greater potential threat. It seems very adaptive for malodor processing to avoid as much as possible the influence of the exposure to the odorant (i.e., increasing familiarity) to maintain negative attitudes toward potential dangerous stimulation.

To summarize, the data of this first experiment suggest the existence of a nonlinear relation between pleasantness and

familiarity evaluations as expressed in subjective ratings. A speculative functional explanation for such an effect is that malodors have a greater immediate biological significance to individual survival than pleasant odors, implying that they should not be similarly influenced by their familiarity. One should also expect the 2 hedonic functional categories, besides influencing our subjective judgment of the odor, to induce different autonomic responses. Indeed, for instance, there is notable literature on the importance of skin conductance responses (SCRs) to biologically significant threatening stimuli (for a review, see Öhman and Mineka 2001). Whereas some authors reported empirical data that showed differential SCRs to unpleasant and pleasant odors (Alaoui-Ismaili, Robin, et al. 1997; Alaoui-Ismaili, Vernet-Maury, et al. 1997; Brand et al. 2000), other authors did not report this effect (Bensafi et al. 2002a, 2002b; Møller and Dijksterhuis 2003). This absence of coherent findings could be due to the influence of other subjective dimensions because, for instance, the intensity of the odorant and/or its emotional arousal is positively correlated with the SCRs (Bensafi et al. 2002b, 2002c), a point that is not taken into account in most of the studies.

In order to examine the link between subjective ratings and biological significance, we decided to conduct a second experiment, during which we investigated the relations between intensity, pleasantness, and familiarity ratings of odorants and the autonomic responses (SCRs) they induced. As in the first experiment, we used cluster analysis to isolate potential subsets of odors without any a priori assumption. The main objective of this second experiment was to test whether subjective and autonomic levels could entertain specific functional relations as a function of the subset. Given the hypothesis that malodors have a greater immediate biological significance or a greater pertinence to the individual than do pleasant odors, we expected the relation between the smelled odors and the electrodermal responses they evoke to be particular for malodors even when controlling for the influence of intensity and familiarity.

## Experiment 2

The results of this experiment constitute part of a broader study investigating electrophysiological correlates of novelty processing of odorants (Delplanque S, Grandjean D, Chrea C, Aymard L, Cayeux I, Velazco MI, Sander D, and Scherer KR). During this experiment, we recorded many other physiological indices, but according to our purposes, we reported only the results concerning SCRs.

### Material and methods

#### Participants

Eighteen psychology students ( $26.9 \pm 6.1$  years, 9 male) took part in this experiment. They all self-reported a normal sense of smell. None of them were participants in Experiment 1.

#### Experimental procedure

The participants were asked to smell 48 different odorants (see Table 1) that were delivered in a different random order for each participant. To prevent subjects from undergoing sensory adaptation, the interval between 2 odorants was more than 30 s (Jehl et al. 1994). Each stimulus was delivered with the odor pen opened near the nose (about 1 cm below both nostrils) for 2 s by an experimenter sitting near the participant. Before testing, participants were instructed on how to smell the odorants in order to minimize the intra- and interparticipant breathing pattern variability. This procedure has been described in other studies (Hudry et al. 2003; Jung et al. 2006). The instructions were the same as for Experiment 1 except that the participants were asked to rest and relax for 15 s without any movement before rating the 3 scales and to wait for the signal to proceed to the next trial.

#### Scales and measures

After each odorant presentation, intensity, pleasantness, and familiarity judgments were performed on paper sheets; participants rated the odorants on the 3 continuous scales by tracing a vertical draft with a black marker pen across the 10-cm horizontal line. The participants were asked to judge the subjective intensity, pleasantness, and familiarity using the same rules and material as in Experiment 1.

#### Apparatus and physiological recordings

Physiological signals were assessed with the TEL 100 Remote Monitoring System of Biopac Systems (Santa Barbara, CA), with separate settings for electrodermal and respiratory activities. Signals were transferred from the experimental room to the MP100 Acquisition Unit (16-bit A/D conversion) in an adjacent room and stored on computer hard disc (sampling rate 500 Hz). Skin conductance was recorded (low-pass filtered: 1 Hz) by the constant-voltage method (0.5 V). Beckman Ag–AgCl electrodes (8-mm diameter of active area) were filled with Biopac electrolyte gel and attached to the palmar side of the middle phalanges of the second and third fingers of the participant's nondominant hand. Specific SCRs to odors were measured in microsiemens and analyzed off-line. They were scored in magnitude as changes in conductance starting in the 1- to 4-s interval after the beginning of the inspiration phase and were square root transformed to normalize the data (Dawson et al. 2000). The latency of the SCRs was measured from the onset of the inspiration phase to the beginning of the response. Moreover, because the SCRs could be evoked by the respiration itself (Schneider et al. 2003), we also assessed respiratory activity ( $\mu\text{V}$ ) by placing a respiration belt on the participant that measured abdominal expansion and contraction.

#### Results

As in the first experiment, we excluded odorants that were outside the range of  $\pm 2$  SDs around their ratings mean

for each scale and physiological measures. This procedure led to the exclusion of 5 of the 48 odorants, 1 (isovaleric acid) being rated as too unpleasant, 2 (leather and honey) being rated as not intense enough, 1 (tutti frutti) being rated as too familiar, and 1 (caproic acid) evoking SCRs that were too extreme. The following analyses were thus performed on 43 odorants.

#### *Correlations between intensity, pleasantness, familiarity ratings, and electrodermal activity*

*Correlations of the subjective ratings between the 2 experiments.* We checked whether the ratings obtained during the 2 experiments on the same scales with the same 40 common odorants were coherent. The correlation analyses between each subjective scale revealed significant positive correlations (intensity:  $r = 0.61$ ,  $P < 0.001$ ; pleasantness:  $r = 0.93$ ,  $P < 0.001$ ; and familiarity:  $r = 0.82$ ,  $P < 0.001$ ). Thus, these results showed that the 2 groups of participants rated the odorants in a similar way.

*Correlations between ratings and physiological responses.* Again, we found a positive correlation between familiarity and pleasantness ( $r = 0.75$ ,  $P < 0.001$ ), these 2 dimensions being negatively correlated with the skin conductance magnitude ( $r = -0.38$ ,  $P < 0.01$  and  $r = -0.51$ ,  $P < 0.001$ , respectively). Intensity was negatively correlated with pleasantness of the odorant ( $r = -0.33$ ,  $P < 0.05$ ). When controlling for the intensity with partial correlations, there was still a relation between pleasantness and familiarity ( $r = 0.76$ ,  $P < 0.001$  and  $r = 0.78$ ,  $P < 0.001$  when the outliers were included) as well as between the 2 latter dimensions and the skin conductance magnitude ( $r = -0.51$ ,  $P < 0.001$  and  $r = -0.38$ ,  $P < 0.05$ , respectively). Whether the intensity was controlled or not, there was no significant correlation between any variable and the respiratory amplitude and latency of the SCRs.

*Cluster analyses.* A cluster analysis (identical to that in Experiment 1) was performed on the ratings of familiarity, pleasantness, intensity, magnitude and latency of the SCRs, and amplitude of the respiration in response to the 43 odorants. Based on the same rules as in Experiment 1, this analysis yielded 2 clusters (distanced from each other  $>70\%$  of the total distance) whose properties are represented in Figure 3.

An examination of the odorants included in each cluster (see Table 1) showed that the first cluster corresponded to the unpleasant and less familiar odorants ( $n = 17$ , mean pleasantness  $3.42 \pm 0.99$ , familiarity  $4.07 \pm 0.45$ , intensity  $6.89 \pm 0.68$ , and skin conductance magnitude  $0.44 \pm 0.1$ ), whereas the second cluster included principally the pleasant and familiar odorants ( $n = 26$ , mean pleasantness  $6.42 \pm 0.86$ , familiarity  $6.39 \pm 0.93$ , intensity  $6.48 \pm 0.59$ , and skin conductance magnitude  $0.34 \pm 0.1$ ). ANOVAs revealed that, except for the amplitude of the respiration ( $F(1,41) < 1$ ) and the latency of the SCRs ( $F(1,41) = 2.69$ , NS, and  $\eta^2 = 0.62$ ), the 2 clusters differed in pleasantness, familiarity, intensity,

and SCR ( $F_s(1,41) = 105.2, 87.16, 4.36$ , and  $9.61$ ;  $P_s < 0.001, 0.001, 0.05$ , and  $0.001$ ;  $\eta_s^2 = 0.71, 0.68, 0.08$ , and respectively). A covariance analysis on electrodermal responses indicated that the difference between the 2 clusters remained significant ( $F(3,39) = 4.61$ ,  $P < 0.01$ , and  $\eta_s^2 = 0.262$ ) when controlling for intensity. Thus, the difference in skin conductance was mainly due to the difference in pleasantness and/or familiarity of the odorants and was not an intensity bias.

Finally, we examined the correlations between the scales within each cluster of odorants. There was no significant correlation of any variable with the intensity, the amplitude of the respiration, or the latency of the SCRs. Because both the intensity and the amplitude of the respiration could still be mediators of any relationship between familiarity, pleasantness, and SCR latency or magnitude, we investigated the partial correlations of the variables while controlling for intensity and respiration.

Once more, we found a significant positive correlation between pleasantness and familiarity for Cluster 2 (see Figure 4A: pleasant and familiar odorants,  $r = 0.46$ ,  $P < 0.05$  after controlling for intensity and respiration and  $r = 0.44$ ,  $P < 0.02$  before controlling) that we did not observe for Cluster 1 (unpleasant and less familiar odorants,  $r = -0.47$ , NS and  $r = -0.5$ ,  $P < 0.05$  before controlling). Moreover, for this latter cluster, we found a negative correlation between pleasantness and SCRs (see Figure 4B:  $r = -0.57$ ,  $P < 0.05$  and  $r = -0.5$ ,  $P < 0.05$  before controlling), which was not observed for the pleasant and familiar odorants ( $r = -0.18$ , NS and  $r = -0.15$ , NS before controlling).

## Discussion

The objective of this second experiment was to argue in favor of a functional dissociation in the relations between both subjective and autonomic responses to odors as a function of odor pleasantness. To this end, we performed an exploratory multivariate analysis on the ratings of familiarity, hedonicity, intensity, and skin conductance magnitude and latency. This analysis, performed without any a priori assumption on the existence of subsets in the odorant set, led to the constitution of 2 groups of odors. In a first pleasant and familiar group of odorants, we demonstrated the existence of a positive correlation between familiarity and pleasantness, whereas no systematic relation was found between any subjective ratings and the SCRs. In a second unpleasant and less familiar group of odorants, we did not find the classical positive correlation between familiarity and pleasantness, whereas SCRs were on average of greater magnitude than for the pleasant group. Moreover, within this group of malodors, the more unpleasant the odor, the greater the SCRs. All of these effects were maintained when we controlled for the influence of the intensity of the odor and respiration amplitude.

The subjective results are similar to Experiment 1, and the fact that unpleasant odors elicited greater autonomic activity

than did pleasant odors constitutes a sign of greater autonomic implication in response to malodors. Moreover, the particular relation between subjective ratings of unpleasantness and the autonomic activity only for malodors constitutes a functional specificity of unpleasant odor processing. Because SCRs are particularly important in response to biologically significant threatening stimuli (for a review, see Öhman and Mineka 2001), unpleasant odors possess a greater immediate biological significance than do pleasant odors. Taking both the subjective and the autonomic results together, we can conclude that unpleasant and pleasant odors are processed in different ways in order to maintain adaptive attitudes toward them.

## General discussion

The results of our 2 experiments can be understood in the mobilization–minimization hypothesis framework (Taylor 1991). This theory claims that negative events evoke stronger and more rapid physiological, cognitive, emotional, and social responses than do positive events. However, this greater mobilization for unpleasant events is followed by other physiological, cognitive, and behavioral responses that minimize and even erase the impact of that event. From this perspective, the greater autonomic reactivity that we observed for unpleasant odors as compared with pleasant odors corresponds to stronger mobilization for a negative event, whereas the lack of influence of familiarity for malodors is the result of the greater minimization of that type of event. As suggested earlier, the mechanisms selected for adaptive purposes lead to 1) a functional dichotomy in the relation between pleasantness and familiarity on a subjective level and 2) a greater implication of the autonomic system in response to malodor on a physiological level.

This dichotomy is conceivable because olfactory information may be processed differentially as a function of whether the odor is pleasant or unpleasant, as predicted by models which suggest that different evaluative channels are used for the processing of positive versus negative stimuli (e.g., Cacioppo et al. 1999; Sander, Koenig, et al. 2005). In this framework, researchers should not consider the pleasantness dimension as a continuum but rather as hedonic categories (for a review, see Rouby and Bensafi 2002). Indeed, Rouby and Bensafi highlighted that the linguistic domain is more marked for unpleasant odorants than it is for pleasant odorants within and between many different cultures. These authors noticed several specific autonomic (e.g., SCRs) and cerebral activities in response to malodors. They proposed that a “quick and dirty” route of processing is engaged during malodor perception, whereas a slower and cognitively more complex route is engaged during neutral or pleasant odor perception. One can suspect that this latter road is more sensitive to higher order associations with specific semantic retrieval about the odor (even implicit) and thus is more influenced by its familiarity (LaBarba and Kingsberg 1990;

Royet et al. 1999; Larsson 2002). Interestingly, a closer examination of the SD of the pleasantness ratings revealed a significant inverse U shape (quadratic regression; Experiment 1:  $r = 0.76$ ,  $F(2,47) = 32.06$ , and  $P < 0.001$ ) accounting for a greater intersubject variability in the pleasantness ratings for subjectively neutral odors than for unpleasant and pleasant odors. In other words, the existence of hedonic categories on the individual level could explain why the odors are rated as neutral when the mean across all subjects is considered. Thus, as argued by Rouby and Bensafi (2002), our findings could suggest the existence of hedonically based functional categories rather than a continuum on the odor pleasantness dimension.

An alternative interpretation of the nonlinear relation that we observed would be that the relation between subjective hedonicity and subjective familiarity would not depend on hedonic category but would obey to other rules than the classical positive linear correlation. In order to bring arguments in favor of this hypothesis, we performed quadratic regressions on the ratings obtained for the 2 experiments. The quadratic regressions were significant for the hedonicity–familiarity dimensions (Experiment 1:  $r = 0.82$ ,  $F(2,47) = 46.12$ , and  $P < 0.001$ ; Experiment 2:  $r = 0.79$ ,  $F(2,47) = 32.71$ , and  $P < 0.001$ ) as well as for the SCR magnitude–hedonicity variables in the second experiment ( $r = 0.54$ ,  $F(2,47) = 8.1$ , and  $P < 0.001$ ). These results, again, highlight the weakness of the hedonicity–familiarity relationship for malodors, the correlation being reinforced as the pleasantness increases. Moreover, they confirm the particular relation between malodors and electrodermal activity, the correlation being reduced as pleasantness increases. However, from a methodological perspective, one can object that this kind of regression is as blind as the linear correlation to the existent of subgroups in the data. In sum, whether the relation between hedonicity and familiarity depends on hedonic categories or obey to nonlinear rules is still an open question. Further research is needed to directly assess whether there is a dissociation between the processing of pleasant versus unpleasant odors.

Finally, and from a broader perspective, the negative bias described above may be integrated in a larger theoretical framework suggesting that negative events are also typically more relevant for the individual and therefore have more impact on behavioral and physiological levels (Sander, Grandjean, and Scherer 2005). Indeed, positive events, if they are equally relevant than negative events, for example, when related to strong needs (e.g., intense hunger), could also induce strong peripheral responses. Further research is needed to test such predictions based on the relevance concept rather than the negative–positive dimension. In this framework, we would like also to emphasize the importance of the experimental contexts as well as intra- and interindividual differences for this issue (see Sander, Grandjean and Scherer (2005)). Indeed, the results we obtained on both subjective and autonomic levels should be deeply influenced by

the internal state of the participant in association with specific odorants. For instance, Rolls ET and Rolls JH (1997) demonstrated a specific decrease in the ratings of pleasantness of a food-related odor after participants ate that food to satiety. One can speculate that the relation between pleasantness and familiarity is also modified when hungry participants are asked to judge pleasant odors containing several highly relevant food-related odors. In this latter case, one can also predict the relation between electrodermal activity and subjective ratings to be modified because the food-related odor is particularly goal conducive and possesses a great immediate biological significance for a starving individual. Thus, further studies are needed in order to specify the influence of biologically pertinent variables and to test the stability of the relations that we highlighted in our 2 experiments.

In summary, these 2 studies questioned the validity of the existence of a simple linear and positive relation between familiarity and pleasantness of odors. On the basis of both subjective ratings and autonomic recordings, we brought forward new arguments in favor of a functional distinction between unpleasant and pleasant odor perception. We claim that these functional differences account for the biological relevance of malodors for individual survival. The results that we presented could be of particular importance for brain imaging studies dealing with the functional and anatomical bases of odor perception. Indeed, many interesting results are based on correlations between cerebral activities and subjective ratings. Thus, a misunderstanding about the relations between the subjective dimensions of odor perception would be detrimental where the attribution of functional properties to cerebral structures or networks is concerned. In general, we hope that our results will invite researchers in the field to consider the relations between pleasantness and familiarity separately for unpleasant and pleasant odors.

## Funding

FIRMENICH SA and the National Center of Competence in Research (NCCR) Affective sciences financed by the Swiss National Science Foundation (n° 51NF40-104897) and hosted by the University of Geneva.

## Acknowledgements

We thank H el ene Goichon and G eraldine Coppin for the experimental and participants schedules management and for the help in data collection. We also thank Christian Margot and all the people from the Perception and Bioresponses Department of the Research and Development Division of Firmenich, SA for their precious advices and their theoretical and technical competences.

## References

- Alaoui-Ismailli O, Robin O, Rada H, Dittmar A, Vernet-Maury E. 1997. Basic emotions evoked by odorants: comparison between autonomic responses and self-evaluation. *Physiol Behav.* 62:713–720.
- Alaoui-Ismailli O, Vernet-Maury E, Dittmar A, Delhomme G, Chanel J. 1997. Odor hedonics: connection with emotional response estimated by autonomic parameters. *Chem Senses.* 22:237–248.
- Ayabe-Kanamura S, Saito S, Distel H, Martinez-Gomez M, Hudson R. 1998. Differences and similarities in the perception of everyday odors: a Japanese-German cross-cultural study. *Ann N Y Acad Sci.* 855:694–700.
- Baumeister RF, Bratslavsky E, Finkenauer C, Vohs KD. 2001. Bad is stronger than good. *Rev Gen Psychol.* 5:323–370.
- Bensafi M, Rouby C, Farget V, Bertrand B, Vigouroux M, Holley A. 2002a. Influence of affective and cognitive judgments on autonomic parameters during inhalation of pleasant and unpleasant odors in humans. *Neurosci Lett.* 319:162–166.
- Bensafi M, Rouby C, Farget V, Bertrand B, Vigouroux M, Holley A. 2002b. Psychophysiological correlates of affects in human olfaction. *Neurophysiol Clin.* 32:326–332.
- Bensafi M, Rouby C, Farget V, Bertrand B, Vigouroux M, Holley A. 2002c. Autonomic nervous system responses to odours: the role of pleasantness and arousal. *Chem Senses.* 27:703–709.
- Brand G, Millot JL, Biju C. 2000. Comparison between monorhinal and binorhinal olfactory stimulations in bilateral electrodermal recordings. *C R Acad Sci III.* 323:959–965.
- Cacioppo JT, Gardner WL. 1999. Emotion. *Annu Rev Psychol.* 50:191–214.
- Cacioppo JT, Gardner WL, Berntson GG. 1999. The affect system has parallel and integrative processing components: form follows function. *J Pers Soc Psychol.* 76:839–855.
- Cain WS, Johnson F Jr. 1978. Liability of odor pleasantness: influence of mere exposure. *Perception.* 7: 459–465.
- Dawson ME, Schell AM, Filion DL. 2000. The electrodermal system. In: Cacioppo JT, Tassinari LG, Berntson GG, editors. *Handbook of psychophysiology.* 2nd ed. Cambridge: Cambridge University Press. p. 200–223.
- de Graaf C, van Staveren W, Burema J. 1996. Psychophysical and psychohedonic functions of four common food flavours in elderly subjects. *Chem Senses.* 21:293–302.
- Distel H, Ayabe-Kanamura S, Martinez-Gomez M, Schicker I, Kobayakawa T, Saito S, Hudson R. 1999. Perception of everyday odors—correlation between intensity, familiarity and strength of hedonic judgement. *Chem Senses.* 24:191–199.
- Doop M, Mohr C, Folley B, Brewer W, Park S. 2006. Olfaction and memory. In: Brewer W, Castle D, Pantelis C, editors. *Olfaction and the brain.* Cambridge: Cambridge University Press. p. 65–82.
- Engen T, Ross BM. 1973. Long-term memory of odors with and without verbal descriptions. *J Exp Psychol.* 2:221–227.
- Harmon-Jones E, Allen JJB. 2001. The role of affect in the mere exposure effect: evidence from psychophysiological and individual differences approach. *Pers Soc Psychol Bull.* 27:889–898.
- Holmes DD. 1970. Differential changes in affective intensity and forgetting of unpleasant personal experiences. *J Pers Soc Psychol.* 15: 234–239.
- Hudry J, Perrin F, Ryvlin P, Manguiere F, Royet JP. 2003. Olfactory short-term memory and related amygdala recordings in patients with temporal lobe epilepsy. *Brain.* 126:1851–1863.
- Jehl C, Royet JP, Holley A. 1994. Very short term recognition memory for odours. *Percept Psychophys.* 56:658–668.
- Jung J, Hudry J, Ryvlin P, Royet JP, Bertrand O, Lachaux JP. 2006. Functional significance of olfactory-induced oscillations in the human amygdala. *Cereb Cortex.* 16:1–8.
- Konstantinidis I, Hummel T, Larsson M. 2006. Identification of unpleasant odors is independent of age. *Arch Clin Neuropsychol.* 21:615–621.

- Köster EP. 2002. The specific characteristics of the sense of smell. In: Rouby C, Schaal B, Dubois D, Gervais R, Holley A, editors. *Olfaction, taste, and cognition*. Cambridge: Cambridge University Press. p. 27–43.
- LaBarba C, Kingsberg SA. 1990. Cerebral lateralization of familiar and unfamiliar music perception in nonmusicians: a dual task approach. *Cortex*. 26:567–574.
- Larsson M. 2002. Odor memory: a memory system approach. In: Rouby C, Schaal B, Dubois D, Gervais R, Holley A, editors. *Olfaction, taste, and cognition*. Cambridge: Cambridge University Press. p. 231–245.
- Lawless HT, Cain WS. 1975. Recognition memory for odors. *Chem Senses*. 1:331–337.
- Møller P, Dijksterhuis G. 2003. Differential human electrodermal responses to odours. *Neurosci Lett*. 346:129–132.
- Monin B. 2003. The warm glow heuristic: when liking leads to familiarity. *J Pers Soc Psychol*. 85:1035–1048.
- Öhman A, Mineka S. 2001. Fears, phobias, and preparedness: toward an evolved module of fear and fear learning. *Psychol Rev*. 108:483–522.
- Reber R, Winkielman P, Schwarz N. 1998. Effects of perceptual fluency on affective judgments. *Psychol Sci*. 9:45–48.
- Rolls ET, Rolls JH. 1997. Olfactory sensory-specific satiety in humans. *Physiol Behav*. 61:461–473.
- Rouby C, Bensafi M. 2002. Is there a hedonic dimension to odors? In: Rouby C, Schaal B, Dubois D, Gervais R, Holley A, editors. *Olfaction, taste, and cognition*. Cambridge: Cambridge University Press. p. 140–159.
- Royet JP, Koenig O, Gregoire MC, Cinotti L, Lavenne F, Le Bars D, Costes N, Vigouroux M, Farget V, Sicard G, et al. 1999. Functional anatomy of perceptual and semantic processing of odors. *J Cogn Neurosci*. 11:94–109.
- Sander D, Grandjean D, Scherer KR. 2005. A systems approach to appraisal mechanisms in emotion. *Neural Netw*. 18:317–352.
- Sander D, Koenig O, Georgieff N, Terra JL, Franck N. 2005. Processus émotionnel dans la schizophrénie: étude de la composante d'évaluation. *L'Encéphale*. 31:672–682.
- Schneider R, Schmidt S, Binder M, Schaefer F, Walach H. 2003. Respiration-related artifacts in EDA recordings: introducing a standardized method to overcome multiple interpretations. *Psychol Rep*. 93:907–920.
- Seamon JG, McKenna PA, Binder N. 1998. The mere exposure effect is differentially sensitive to different judgment tasks. *Conscious Cogn*. 7:85–102.
- StatSoft, Inc. 2007. *Electronic statistics textbook*. Tulsa (OK): StatSoft. Available from: <http://www.statsoft.com/textbook/stathome.html>. Accessed 5 Mar 2008.
- Sulmont C, Issanchou S, Köster EP. 2002. Selection of odorants for memory tests on the basis of familiarity, perceived complexity, pleasantness, similarity and identification. *Chem Senses*. 27:307–317.
- Taylor SE. 1991. Asymmetrical effects of positive and negative events: the mobilization-minimization hypothesis. *Psychol Bull*. 110:67–85.
- Walker RW, Skowronski JJ, Thompson CP. 2003. Life is pleasant—and memory helps to keep it that way! *Rev Gen Psychol*. 7:203–210.
- Winkielman P, Schwarz N, Fazendeiro T, Reber R. 2003. The hedonic marking of processing fluency: implications for evaluative judgment. In: Musch J, Klauer C, editors. *The psychology of evaluation: affective processes in cognition and emotion*. Mahwah (NJ): Lawrence Erlbaum. p. 189–217.
- Zajonc RB. 1968. Attitudinal effects of mere exposure. *J Pers Soc Psychol Monogr*. 9:1–27.
- Zajonc RB. 2001. Mere exposure: a gateway to the subliminal. *Curr Dir Psychol Sci*. 10:224–228.

*Accepted March 13, 2008*