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Perceptual Blending in Odor Mixtures Depends on the Nature of Odorants and Human Olfactory Expertise

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Abstract

Our olfactory system is confronted with complex mixtures of odorants, often recognized as single entities due to odor blending (e.g., coffee). In contrast, we are also able to discriminate odors from complex mixtures (e.g., off-odors). Therefore, the olfactory system is able to engage either configural or elemental processes when confronted with mixtures. However, the rules that govern the involvement of these processes during odor perception remain poorly understood. In our first experiment, we examined whether simple odorant mixtures (binary/ternary) could elicit configural perception. Twenty untrained subjects were asked to evaluate the odor typicality of mixtures and their constituents. The results revealed a significant increase in odor typicality in some but not all mixtures as compared with the single components, which suggest that perceptual odor blending can occur only in specific mixtures (configural processing). In our second experiment, we tested the hypothesis that general olfactory expertise can improve elemental perception of mixtures. Thirty-two trained subjects evaluated the odor typicality of the stimuli presented during the first experiment, and their responses were compared with those obtained from the untrained panelists. The results support the idea that general training with odors increases the elemental perception of binary and ternary blending mixtures.

Key words: configural processing, expertise, odor mixtures, perceptual blending, quality, training, typicality

Introduction

The processing of complex stimuli by the olfactory system is a central issue in the understanding of odor perception in natural conditions because the odors we perceive come mostly from complex mixtures of odorants. The perception of single odorants and mixtures is a product of both interactions at the level of olfactory receptors and interactions during neural processing of olfactory information. In the case of a mixture of odorants, competition may occur at the olfactory receptors level as well as inhibitory interactions at the neural level. Therefore, the perception of an odorant mixture is not a simple sum of the percepts of the unmixed components (Laing and Jinks 2001).

Studies in animal models have investigated odor mixture processing and have mainly focused on odor discrimination (Derby et al. 1996; Deisig et al. 2006; Kay and Stopfer 2006; Coureaud et al. 2008). These studies have demonstrated that a binary mixture can be perceived in at least 2 ways. First,

each component of the mixture remains separate and identifiable. Such processing has been qualified as dissociative, analytical, or elemental (Derby et al. 1996). Second, the mixture is perceived as an entity, conveying a unique quality not present in its single components. This phenomenon has been called associative, synthetic, or configural processing (Derby et al. 1996). Kay et al. (2005) suggested that configural processing might be weak or robust, depending on whether the odor of the whole mixture partially smells similar to the odor of the mixture's constituents or does not smell at all like the constituents. These data support the idea that a mixture of odorants can elicit a novel odor percept through configural processing (i.e., perceptual odor blending). However, in humans, there is little scientific evidence for the perception of a specific quality carried by a mixture. According to Olsson (1994), a binary mixture percept does not form a quality that is dissimilar from the odorant quality of its chemical

components, but rather one that falls in between the 2. Nevertheless, it has been suggested that perceptual blending may happen in specific mixtures, especially those containing more than 4 components in which the odorants may lose their individuality and produce new odor sensations (Laing 1991, 1994; Jinks and Laing 2001). Recently, Le Berre, Thomas-Danguin, et al. (2008) showed that a binary and a ternary mixture could be perceived as more typical of a pineapple odor than their components. Moreover, recent results obtained in newborn rabbits with the same binary mixture as the one eliciting a pineapple odor in humans, have strongly suggested that this mixture is processed as a configuration (Coureaud et al. 2008, 2009, 2011). Taken together, these results are consistent with the idea that a mixture of odorants could induce an odor note different from the one carried by its components.

In spite of recent neurophysiological data showing that binary odorant mixtures can stimulate cortical neurons not stimulated by their individual components (Silbering and Galizia 2007; Grossman et al. 2008; Howard et al. 2009; Deisig et al. 2010), the rules that govern the involvement of either elemental or configural processes during odor perception remain poorly investigated. One possible explanation of this lack of investigation, especially in humans, could be the difficulty quantifying odor quality (Wise et al. 2000). Indeed, methods that address odor quality in mixtures of odorants need to be carefully selected, especially when perceptual interactions affect the mixture odor quality, which is likely the case when perceptual odor blending occurs. If components contribute to an odor blend, the main character descriptor of the odor can be used to measure the impact of the components on the perception of the blend (Bult et al. 2002). Therefore, to be able to describe odors with different degrees of blending, one can choose a detailed aroma-profiling task involving both single component descriptors and a main character descriptor. However, such a procedure engages panelists in an analytical perceptual processing strategy, which would decrease putative synthetic processing and consequently the blending effect (Le Berre, Thomas-Danguin, et al. 2008). Moreover, an aroma-profiling task requires an odor reference for each descriptor that needs to be presented at the beginning of the testing session. Such an exposition can also modulate the latter perception and evaluation of blending mixtures (Le Berre, Thomas-Danguin, et al. 2008). Thus, the choice of sensory method is a critical step in investigating blending processes in odor mixtures.

The creation of new odors is the common goal of perfumers and flavorists. These olfactory experts memorize and identify quantities of various odorant materials before creating new fragrances and aromas. One could ask if such experience and training with odors could affect their perception of odor mixtures. However, professionals who deal with odors daily (perfumers, flavorists, and oenologists) are not only exposed to a wide variety of odors but are also systematically confronted with descriptions and verbalizations of their olfactory perceptions. These abilities require both a perceptual and semantic knowledge of odors (Lawless 1984). Several studies have underlined that training and experience with odors do not improve olfactory discrimination, identification (Chambers and Smith 1993; Roberts and Vickers 1994; Livermore and Laing 1996), or detection thresholds (Parr et al. 2002), but other experiments have shown positive effects of training on olfactory performance (Clapperton and Piggott 1979; Rabin 1988). Bende and Nordin (1997) reported that expert oenologists did not achieve better performance than did untrained subjects during a detection task, but they had greater abilities to discriminate and identify specific odors. These findings suggest that experience and training could have an impact on mixture processing and perception. In a complementary way, Le Berre, Thomas-Danguin, et al. (2008) and Le Berre et al. (2010) reported that a pre-exposure of naïve subjects to out-of-mixture components could further influence blending mixture perception; however, it remains unknown whether general experience and extensive sensory training can modify the ways experts perceive mixtures in which perceptual blending occurs.

The aim of the present study was 2-fold. We first wanted to confirm, with an untrained (naïve) panel, that perceptual blending occurs in "chemically simple" odorant mixtures (2 or 3 odorants) and leads to an increase in mixture-induced odor character, using 2 different sensory tasks: a ranking task and a rating task. The second objective was to test the hypothesis that extensive training, namely olfactory expertise, alters the perception of mixtures in which perceptual blending occurs. To do so, we followed an experimental procedure that relied on odor typicality evaluations. This procedure prevents panelists from using an analytical perceptual processing strategy (Le Berre, Thomas-Danguin, et al. 2008; Le Berre et al. 2010). This task could be considered as a similarity rating between an actually sniffed odor and an internal representation. Thus, typicality should reflect the quality of the main character of the odor in the case of blending mixtures. We performed 2 separate experiments. In the first one, untrained panelists were asked to rate the odor quality of 2 binary and 1 ternary mixture formulated to elicit a pineapple odor. Through typicality ranking and rating tasks, the panelists were asked to evaluate the pineapple typicality of the mixtures, their components, and other pineapple odor references. The pineapple typicality of the mixtures was compared with that of the components to evidence the blending process. In the second experiment, a group of trained subjects (students in oenology) performed the same tasks with the same stimuli. A comparison of their results with those obtained by the naïve panel was performed to evaluate the impact of expertise on odor mixture perception.

Materials and methods

Both experiments relied on the same protocol, with the exception of different subjects.

Subjects

In the first experiment, 20 naïve students (10 women and 10 men, M = 23 years, standard deviation [SD] = 3 years) were involved. They were considered to be naïve subjects because they did not have any special expertise in olfaction or sensory analysis.

In the second experiment, the subjects included 32 oenology students (15 women and 17 men, M = 26 years, SD = 6 years) from the Oenology Faculty of Bordeaux (France). These subjects were considered to be expert subjects because they were trained in wine tasting and description of wines.

Stimuli

Ten odorous stimuli were tested (Table 1). A binary mixture designated F1 (ethyl isobutyrate + ethyl maltol), a ternary mixture designated F2 (ethyl isobutyrate + ethyl maltol + allyl-α-ionone), and another binary mixture designated F3 (ethyl caproate+ furaneol) were formulated by flavorists to produce a pineapple odor. The 5 components were also evaluated singly, as were 2 references that might produce a pineapple odor: a single odorant (allyl caproate) and an essential oil of pineapple designated HE (provided by Euracli). The 6 pure odorants were purchased from Sigma-Aldrich.

Ten strips of filter paper (1 × 16 cm, Granger-Veyron) were prepared 24 h before the sensory session. A total of 500 μL of each odorant solution (Table 1) was poured onto one end of each strip, and the strips were stored separately at the bottom of a closable 70 mL Pyrex test tube at ambient temperature.

Experimental procedures

The tests were conducted in a quiet well-ventilated room under daylight. Both groups of subjects were assigned 2 distinct tasks. First, the subjects had to smell each tube to sort the tubes from the most pineapple-like odor to the least pineapple-like odor, according to their resemblance to a pineapple odor (internal reference). The encoded tubes were presented to the subjects in a random order. The subjects were allowed to smell the stimuli as many times as they wanted until they were satisfied with their ranking. Subjects were instructed to close the tube after each evaluation to prevent odor dissemination in the room. Second, when the ranking was completed, the tubes were again shuffled and presented to the subjects. They were asked to smell each tube and rate, for each stimulus, first, the typicality of the pineapple odor on a dedicated labeled 9-point scale (from 1, "not typical at all" to 9, "extremely typical"). Second, they rated the edibility of the sample on another dedicated labeled 9-point scale (from 1, "not edible at all" to 9, "extremely edible"). Only the typicality scores are shown and discussed in this report.

Data analyses

All statistical analyses were conducted using SAS 9.1 release (SAS Institute Inc.).

For ranking data, the Kendall's coefficient of concordance (W) was calculated to evaluate the concordance between subjects on the samples' ranking. For ranking and rating data, a two-way analysis of variance (ANOVA) was performed ("Subject," "Odorant") with subjects as random factor using the SAS GLM procedure. Preplanned contrasts (no adjustment of alpha for multiple comparisons) between the typicality of the mixtures and their components were performed using least squares means comparisons. To compare the responses of the trained and untrained subjects ("Group" factor), a three-way ANOVA (Subject, Group, Odorant) with interactions was performed with Subject (nested in group) as random factor (SAS GLM procedure). Pearson correlation coefficients were calculated using the CORR procedure to compare typicality ratings and rankings. For all data analyses, the effects were considered to be significant when $P < 0.05$.

Table 1 The stimuli tested in the experiments: 2 binary mixtures, 1 ternary mixture, each of the individual components, and a pineapple-like odor reference

Type	Substances	Abbreviations	CAS #	Dilutions in ethylic alcohol (90°) (%)	Composition
Component	Allyl-α-ionone	AI	79-78-7	1	
Component	Ethyl caproate	CE	123-66-0	3.7	
Component	Ethyl isobutyrate	EI	97-62-1	10	
Component	Ethyl maltol	EM	4940-11-8	1	
Component	Furaneol	FU	3658-77-3	3.7	
Reference	Allyl caproate	CA	123-68-2	10	
Reference	Pineapple oil	HE		10	
Mixture	EI + EM	F1			30% EI + 70% EM
Mixture	EI + EM + AI	F2			20.5% EI + 50% EM + 29.5% AI
Mixture	CE + FU	F3			50% CE + 50% FU

Results

Naïve subjects

The aim of this experiment was to confirm that odor blending could occur in an odorant mixture and lead to an increase in the odor typicality of the mixture-specific odor. Thus, a group of naïve panelists performed rating and ranking tasks to evaluate the pineapple typicality of 10 samples.

In regard to the ranking task (Figure 1), Kendall's coefficient of concordance calculated on the scores was highly significant ($W = 0.38$, $P < 0.0001$), which indicated that the subjects agreed on the ranking of the samples. Allyl caproate (CA, Figure 1) was perceived as the most pineapple-like odor ($M = 9.01$, SD = 1.65). A two-way ANOVA (Subject, Odorant) on the typicality ranking scores indicated a significant effect of the Odorant factor ($F_{9,171} = 11.6$, $P < 0.0001$). Preplanned contrasts indicated that the F1 binary mixture was considered to be significantly more pineapple-like than its components EM ($P < 0.041$) and EI ($P < 0.0005$). Similar results were obtained for the F2 ternary mixture (EM $P < 0.050$, AI $P < 0.018$, and EI $P < 0.0006$). On the contrary, even if the F3 binary mixture was ranked as more typical than FU ($P < 0.0054$), its other component (CE) was ranked as more pineapple-like than the mixture ($P < 0.004$).

Regarding the results of the rating task (Figure 2), allyl caproate (CA) was rated the most typical of the pineapple odor ($M = 7.5$, SD = 2.0). A two-way ANOVA (Subject, Odorant) on the typicality scores indicated a significant effect of the Odorant factor ($F_{9,171} = 11.3$, $P < 0.0001$). Preplanned contrasts showed that the F3 binary mixture was perceived as more typical of the pineapple odor than its FU component ($P < 0.0002$) but significantly less typical than its CE component ($P < 0.042$). In contrast, the F1 and F2 mixtures were rated as significantly more typical of the pineapple odor than their components. Specifically,
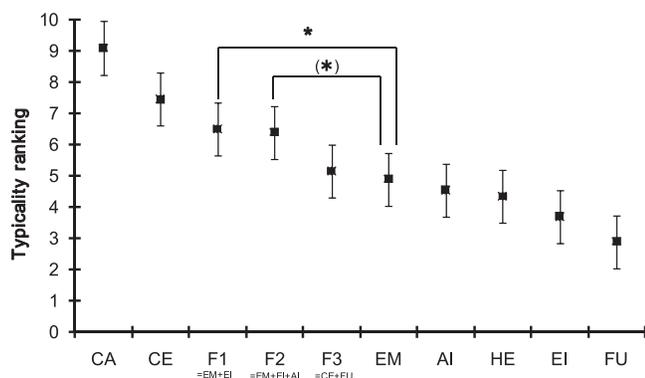
F1 was rated as more typical than EM ($P < 0.014$) and EI ($P < 0.008$). Similarly, F2 was rated as more typical than AI ($P < 0.024$), EM ($P < 0.011$), and EI ($P < 0.006$). Correlation analysis of the typicality ratings and rankings indicated that the more typical an odorant, the higher its rank ($r(198) = 0.31$, $P < 0.0001$). In other words, the results obtained in the rating analysis were in accordance with those obtained using the ranking methodology.

Expert subjects

The aim of the second experiment was to test the hypothesis that training and sensory olfactory expertise could influence the perception of odor blending mixtures. A panel of trained subjects evaluated the 10 stimuli presented in the previous experiment (with untrained subjects) by following exactly the same methodology. Such a strategy ensured that the only difference between the 2 experiments was the training level of the panelists.

Kendall's coefficient of concordance calculated from the ranking scores was highly significant ($W = 0.42$, $P < 0.0001$) and indicated a global agreement between the subjects. As with the naïve subjects, the trained subjects perceived allyl caproate (CA, Figure 3) as eliciting the most typical pineapple-like odor ($M = 8.6$, SD = 1.6). A two-way ANOVA (Subject, Odorant) on the typicality ranking scores indicated a significant effect of the Odorant factor ($F_{9,279} = 23.2$, $P < 0.0001$). Preplanned contrasts revealed that both F1 and F2 mixtures were perceived to be as pineapple-like as the EI component ($P > 0.3$). The F1 binary mixture obtained a higher typicality rank than EM ($P < 0.0006$), whereas the F2 ternary mixture obtained a higher typicality rank than EM ($P < 0.003$) and AI ($P < 0.0001$). The F3 binary mixture obtained a higher mean rank than FU ($P < 0.003$) but a lower mean rank than its CE component ($P < 0.0001$).
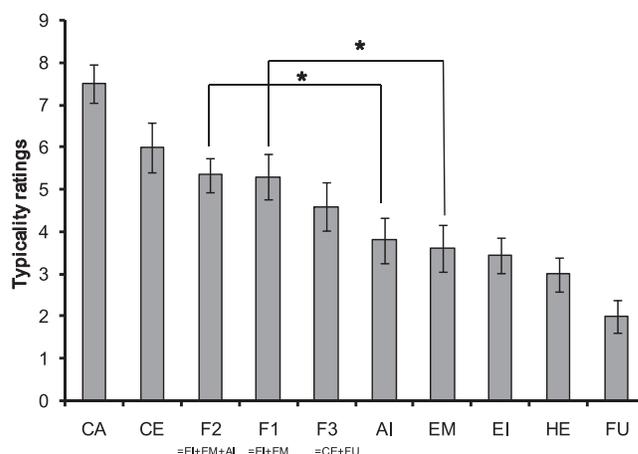

Figure 1   The means of the ranking scores of the stimuli sorted by the naïve subjects ($n = 20$) in the second experiment. CA (allyl caproate), CE (ethyl caproate), F1 (EI + EM), F2 (EI + EM + AI), F3 (CE + FU), EM (ethyl maltol), AI (allyl-α-ionone), HE (pineapple essential oil), EI (ethyl isobutyrate), and FU (furaneol). Asterisks indicate significant differences between 2 stimuli: (∗) = $P < 0.1$; ∗ = $P < 0.05$. Error bars represent 95% confidence interval on mean.

Figure 2   The means of the typicality ratings of the samples compared with those of a pineapple odor on a 9-point scale. The data were obtained with the "naïve" subjects ($n = 20$) in the second experiment. CA (allyl caproate), CE (ethyl caproate), F2 (EI + EM + AI), F1 (EI + EM), F3 (CE + FU), AI (allyl-α-ionone), EM (ethyl maltol), EI (ethyl isobutyrate), HE (pineapple essential oil), and FU (furaneol). Asterisks indicate significant differences between 2 stimuli: ∗ = $P < 0.05$. Error bars represent 95% confidence interval on mean.
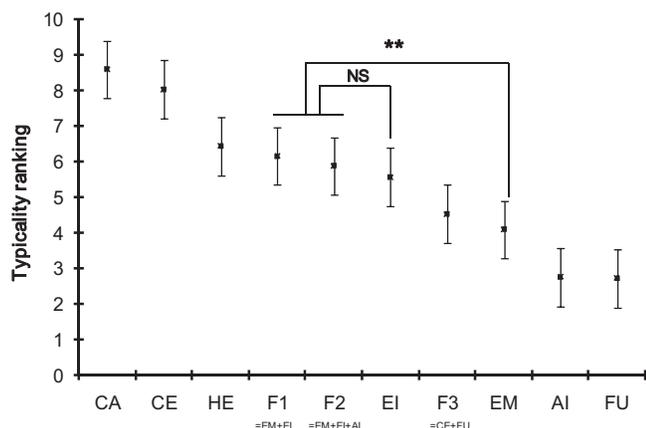
Figure 3 The means of the ranking scores of the stimuli sorted by the expert subjects ($n = 32$) in the third experiment. CA (allyl caproate), CE (ethyl caproate), HE (pineapple essential oil), F1 (EI + EM), F2 (EI + EM + AI), EI (ethyl isobutyrate), F3 (CE + FU), EM (ethyl maltol), AI (allyl-α-ionone), and FU (furaneol). Asterisks indicate significant differences between 2 stimuli: NS = Non-Significant; ** = $P < 0.01$. Error bars represent 95% confidence interval on mean.

Figure 4 The means of the typicality ratings of the samples compared with those of a pineapple odor on a 9-point scale performed by the expert subjects ($n = 32$) in the third experiment. CE (ethyl caproate), CA (allyl caproate), F1 (EI + EM), HE (pineapple essential oil), EI (ethyl isobutyrate), F2 (EI + EM + AI), F3 (CE + FU), EM (ethyl maltol), AI (allyl-α-ionone), and FU (furaneol). Asterisks indicate significant differences between 2 stimuli: NS = Non-Significant; ** = $P < 0.01$. Error bars represent 95% confidence interval on mean.

Regarding the results of the rating task, ethyl caproate (CE, Figure 4) and allyl caproate (CA) were rated as the most typical of the pineapple odor ($M = 7.3$, SD $= 1.7$ and $M = 7.2$, SD $= 2.1$, respectively). A two-way ANOVA (Subject, Odorant) on the typicality rating scores indicated a significant effect of the Odorant factor ($F_{9,277} = 24.9$, $P < 0.0001$). Preplanned contrasts showed that the F3 binary mixture was perceived to be more typical of the pineapple odor than its FU component ($P < 0.0001$) but significantly less typical than its CE component ($P < 0.0001$). The F1 and F2 mixtures were rated to be as typical of the pineapple odor as their EI component ($P > 0.2$). The F1 binary mixture was rated as more typical than EM ($P < 0.0001$), and the F2 ternary mixture was rated as more typical than AI ($P < 0.0001$) and EM ($P < 0.0001$). Moreover, a correlation calculated between the typicality ratings and rankings indicated that the more typical an odorant, the higher its rank ($r(316) = 0.75$, $P < 0.0001$). Again, the results obtained with the rating analysis were in accordance with those obtained with the ranking methodology.

To test the hypothesis that sensory expertise could influence the perception of odor blending mixtures, we compared the evaluations performed by trained and untrained subjects. We performed a three-way ANOVA (Subject, Group, and Odorant) for each task (ranking and rating); the factor Group represented the 2 different groups of subjects (naïve vs. trained). As expected, the results indicated a significant effect of Odorants on both tasks (ranking: $F_{9,450} = 29.1$, $P < 0.0001$; rating: $F_{9,448} = 29.5$, $P < 0.0001$). However, there was no significant effect of the Group factor on either task (ranking: $F_{1,50} = 1.6$, $P > 0.2$; rating: $F_{1,50} = 0.5$, $P > 0.5$). However, a significant interaction Group $\times$ Odorant was observed for both tasks (ranking: $F_{9,450} = 3.2$, $P < 0.002$; rating: $F_{9,448} = 3.7$, $P < 0.0003$). This result indicated that the
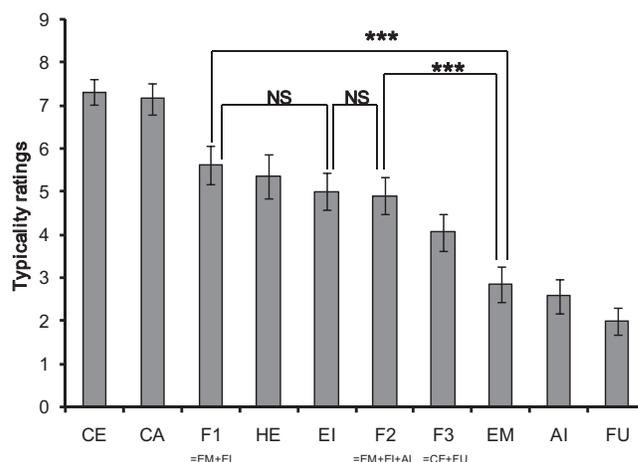
2 groups of subjects did not evaluate the pineapple odor typicality of some stimuli in the same way. Interestingly, differences between the 2 groups of subjects were observed for some mixtures and some components. The untrained subjects found the F1 and F2 mixtures to be more typical of the pineapple odor than all their components, whereas the trained subjects did not. An important difference was that the trained subjects rated ethyl isobutyrate (EI) as more typical of the pineapple odor compared with the naïve subjects (rating: $M = 5.0$ vs. 3.5, $P < 0.011$; ranking: $M = 5.6$ vs. 3.7, $P < 0.007$). Consequently, for the trained subjects, the differences between the F1 mixture and the EI component did not reach the level of significance.

Discussion

Our results confirmed, through distinct psychophysical procedures (rating and ranking), that, in human naïve subjects, certain mixtures of odorants could be judged as more typical of pineapple odor than each of their single components. Our findings also revealed differences in the perception of such mixtures between naïve subjects and experts who had received general sensory analytical training (oenology students).

The quantification of odor quality in humans, especially the comparison of the odor quality of a mixture with its components, suffers from several difficulties (Olsson and Cain 2000; Wise et al. 2000). It has been reported that in experimental investigations of mixture aroma quality, a single attribute describing the main character of the aroma cannot sufficiently reflect the contributions of all the components to the aroma (Bult et al. 2002). In particular, it has been argued that the use of a single attribute might obscure

perceptual interactions between odors. Indeed, the perceptual processing strategies engaged by subjects during odor mixture sensory testing could affect their perceptions and responses (Le Berre, Thomas-Danguin, et al. 2008). Panelists who were provided with specific descriptors that directed them in rating specific feature intensities were able to recognize the unique contribution of each manipulated component of a complex aroma mixture (Bult et al. 2002; Le Berre et al. 2010). In contrast, it has been shown that humans have great difficulty in deciding whether an odor is present, or not, in mixtures containing up to 3 or 4 odors. The limited capacity of such an identification process is as few as 3 or 4 components, regardless of the chemical complexity of the mixture (Laing and Francis 1989; Laing and Glemarec 1992; Livermore and Laing 1996).

In the present experiment, our objective was not to engage the panelists in any direct analytical strategy but rather to engage them in a synthetic strategy that might reflect a more natural way of perceiving everyday odors, especially food odors. We therefore postulate that the measurement of the odor typicality of a mixture compared with the typicality of its components relies on a holistic perception of odors and may thus reveal putative perceptual blending processes in odorant mixture perception. Rosch (1973) showed that color categories are structured along a typicality gradient from prototypes in that some exemplars were better and more representative than others. Prototypes, as representations, are stable within a subject's memory and are shared across a subject's memory as pieces of knowledge. Chrea et al. (2005) confirmed this theory with odors and demonstrated that odor categories were universally organized around some prototypes. Thus, we suggest that the typicality of an odor reflects the degree of qualitative similarity between the actual odor perception of a stimulus and the internal memorized representation of this odor. In a typicality rating task, subjects evaluate the perceptual distance between their actual perception of a stimulus and their memorized representation. It is likely that a higher odor typicality of a mixture, as compared with its components, reflects a better match between the mixture percept and the memorized odor representation. Namely, the mixing of components in definite proportions leads to the fusion of individual odors to create a combination with more specific odor quality characteristics. This fusion can be seen as a perceptual blending of individual odors in the mixture, this has also been proposed for the cross-modal interaction between spoken speech and the moving mouth (McGurk and MacDonald 1976) or during multisensory integration of the chemical senses in flavor perception (Veldhuizen et al. 2010).

In our data of untrained subjects, 2 of 3 mixtures were found to be more typical of pineapple odor than their individual components. Mixing the 2 odorants EI and EM, both slightly typical of pineapple odor, caused an increase in pineapple typicality of the mixture (F2) as compared with both individual components. Similar results were obtained with the F3 ternary mixture. These findings,

which were replicated in the present study using 2 different sensory tasks (rating and ranking), suggest that odor blending occurs but only in specific mixtures of odorants. One can argue that the F2 mixture could be more typical of pineapple than its unmixed components because it has 2 key odor notes of pineapple rather than that it becomes more similar to some main character of pineapple. Nevertheless, results obtained in newborn rabbits with this F2 mixture support also the idea that it is processed as a partial configuration (Coureaud et al. 2008, 2009, 2011). Moreover, when considering the results obtained for the third mixture (F3), the pineapple odor typicality was found to be lower than the typicality of one of its components (ethyl caproate; fruity note) and higher than the other (furaneol; caramel note). It is likely that the perception induced by this F3 binary mixture is in line with the rule proposed by Olsson (1994) that a binary mixture percept forms a quality positioned between the odorant qualities of its chemical components. This F3 mixture could thus carry the fruity and caramel notes, also carried, respectively, by EI and EM, but with no perceptual fusion; this suggestion could explain why pineapple typicality was not enhanced in this mixture. Taken together, these results are consistent with the idea that some odorant combinations are probably more inclined to elicit perceptual interactions, thus conferring an odor quality modification to the mixture. This theory is in agreement with previous findings that showed that blending was optimal for a specific ratio of odorants (Le Berre, Ishii, et al. 2008; Coureaud et al. 2011).

Several authors have suggested that the olfactory system could use both configural and elemental processes, according to the complexity of the mixture. Thus, it has been proposed that binary odorant mixtures could not produce configural effects in humans because a mixture of 2 components causes little loss of components' qualities and no emergent ones (Cain and Drexler 1974; Laing and Willcox 1983; Derby et al. 1996). However, for more complex mixtures (more than 3 components), evidence of configural effects could be produced by the subjects' poor ability to accurately discriminate and identify more than 3 components in a mixture (Laing and Francis 1989; Laing and Livermore 1992). In our case, perceptual blending occurred in binary and ternary mixtures, which may support a weak configural processing (Kay et al. 2005) of such chemically simple mixtures. Indeed, in our pineapple-like mixtures, the components were perceived as slightly typical of the pineapple odor. Therefore, the perception of a mixture as significantly more typical than its components could account only for an incomplete perceptual blending, which leads to an increase in the pineapple typicality. Here, incomplete perceptual blending occurred in 2 of the studied mixtures (F1 and F2). A similar conclusion has been drawn from studies with newborn rabbits exposed to the F2 mixture (Coureaud et al. 2008, 2009). In these studies, when the pups had learned the odor of the mixture, they responded to it and to the odor of the constituents. However, after they had learned one constituent's odor, they responded

to this odor but not to the mixture's odor (at least for a certain ratio of components; Coureaud et al. 2011). This result suggests that even though the mixture was perceived to be different from its components, information about the individual components remained perceptible in the mixture. This conclusion seems to be in accordance with a weak configural processing of the mixture, evidenced through an incomplete perceptual odor blending. This specificity of olfactory perception could correlate with neurobiological observations (Malnic et al. 1999; Duchamp-Viret et al. 2003).

Reports on the role of expertise in the perception of an odor mixture mainly focus on the capacity of discrimination and identification of odors in or out of mixtures. However, these results did not provide clear evidence of the impact of such specific training and exposure to odor discrimination and identification. Whereas several studies have demonstrated no effect of training and experience (Chambers and Smith 1993; Roberts and Vickers 1994; Livermore and Laing 1996), others have shown positive effects of training on olfactory performance (Clapperton and Piggott 1979; Rabin 1988). It has also been recognized that expertise, especially olfactory expertise such as that used by perfumers or oenologists, is based on 2 confounded cognitive abilities: perceptual and semantic learning (Holley 2002; Chollet et al. 2005). In fact, experts are exposed to odors daily and are confronted with the task of describing and verbalizing their olfactory perceptions. Our results shed light on the impact of such expertise on the perception of mixtures in which perceptual blending occurs. They suggest that trained analytical subjects ("experts") do not perceive these blending mixtures (the F1 and F2 mixtures) as significantly more typical than their components, in contrast to naïve subjects. In particular, the expert subjects perceived one of the mixtures' shared odorants (ethyl isobutyrate) as more typical of the pineapple odor than did the naïve subjects, leading to nonsignificant differences between both mixtures and this odorant. This result supports the idea that olfactory expertise can modify the configural perception of a mixture and lead the olfactory system to turn toward a more elemental perception. This finding is in agreement with a recent report from Le Berre et al. (2010) and with data from animal studies in which olfactory enrichment improved the recognition and discrimination of individual components in mixtures (Mandairon et al. 2006).

In all typicality rating tasks, even with expert subjects, the F1 and F2 mixtures were rated as moderately typical of the pineapple odor (the typicality mean scores were largely between 5 and 6). However, one of the components (ethyl isobutyrate) was rated as poorly typical of the pineapple odor by the naïve participants, whereas the expert subjects found this odorant to be more typical of the pineapple odor. This finding could also explain why the expert subjects did not show a difference in typicality ratings between the F1 and F2 mixtures and this component. One can argue that experts usually undergo specific training sessions in which they use odor references elicited by single chemical compounds. This training

could explain why the consistency between ranking and rating was much higher for the expert subjects than the naïve subjects (see correlation coefficients). Therefore, it could be assumed that the expert subjects were more accurate but also more likely to have a more sharply defined internal reference for the pineapple odor. Indeed, the expert subjects both rated and ranked the pineapple essential oil much higher than did the naïve subjects. Moreover, ethyl isobutyrate is often used as an example of a fruity odor during the training sessions undergone by the expert subjects. Thus, the members of the expert panel might have been quite familiar with the odor of ethyl isobutyrate and were thus more inclined to find a perceptual similarity between this component and the mixtures. Indeed, it is highly conceivable that odor typicality is linked to familiarity with the odor, even if there are counter examples that suggest that familiarity is not the only determinant of typicality (Chrea et al. 2005). In addition, Lawless et al. (1991) showed that odor category boundaries are often fuzzy and can vary depending on the context. In our study, such a context could be induced by the presentation of multiple odor quality exemplars. Indeed, as has been demonstrated for taste stimuli (O'Mahony 1991), the presentation of multiple quality exemplars serves to sharpen the fuzzy edges of taste quality classes and causes observers to be more decisively inclusive/exclusive of potential category members.

To conclude, our experiments emphasized that perceptual odor blending could occur in specific mixtures composed of 2 or 3 odorants; the results account for configural or weak configural processing of odor mixtures. Moreover, our data have shown that olfactory expertise, such as the one developed by perfumers, flavorists, and oenologists could affect mixture processing and, in some cases, prevent perceptual odor blending. Our results suggest that compared with the olfactory systems of naïve subjects, the specific training and exposure to odors experienced by expert subjects leads the olfactory system to engage more readily an elemental processing of odor mixtures.

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References

Bende M, Nordin S. 1997. Perceptual learning in olfaction: professional wine tasters versus controls. Physiol Behav. 62(5):1065–1070.

Bult JH, Schifferstein HN, Roozen JP, Boronat ED, Voragen AG, Kroeze JH. 2002. Sensory evaluation of character impact components in an apple model mixture. Chem Senses. 27:485–494.

Cain WS, Drexler M. 1974. Scope and evaluation of odor counteraction and masking. Ann N Y Acad Sci. 237:427–439.

Chambers E, Smith EA. 1993. Effects of testing experience on performance of trained sensory panelists. J Sens Stud. 8:155–166.

Chollet S, Valentin D, Abdi H. 2005. Do trained assessors generalize their knowledge to new stimuli. Food Qual Prefer. 16:13–23.

Chrea C, Valentin D, Sulmont-Rossé C, Nguyen DH, Abdi H. 2005. Semantic, typicality and odor representation: a cross-cultural study. Chem Senses. 30:37–49.

Clapperton JF, Piggott JR. 1979. Flavour characterization by trained and untrained assessors. J Inst Brew. 85:275–277.

Coureaud G, Gibaud D, Le Berre E, Schaal B, Thomas-Danguin T. 2011. Proportion of odorants impacts the configural versus elemental perception of a binary blending mixture in newborn rabbits. Chem Senses. 36:693–700.

Coureaud G, Hamdani Y, Schaal B, Thomas-Danguin T. 2009. Elemental and configural processing of odour mixtures in the newborn rabbit. J Exp Biol. 212:2525–2531.

Coureaud G, Thomas-Danguin T, Le Berre E, Schaal B. 2008. Perception of odor blending mixtures in the newborn rabbit. Physiol Behav. 95:194–199.

Deisig N, Giurfa M, Lachnit H, Sandoz JC. 2006. Neural representation of olfactory mixtures in the honeybee antennal lobe. Eur J Neurosci. 24:1161–1174.

Deisig N, Giurfa M, Sandoz JC. 2010. Antennal lobe processing increases separability of odor mixture representations in the honeybee. J Neurophysiol. 103:2185–2194.

Derby CD, Hutson M, Livermore BA, Lynn WH. 1996. Generalization among related complex odorant mixtures and their components: analysis of olfactory perception in the spiny lobster. Physiol Behav. 60:87–95.

Duchamp-Viret P, Duchamp A, Chaput MA. 2003. Single olfactory sensory neurons simultaneously integrate the components of an odor mixture. Eur J Neurosci. 18:2690–2696.

Grossman KJ, Mallik AK, Ross J, Kay LM, Issa NP. 2008. Glomerular activation patterns and the perception of odor mixtures. Eur J Neurosci. 27:2676–2685.

Holley A. 2002. Cognitive aspects of olfaction in perfumer practice. In: Rouby C, Schaal B, Dubois D, Gervais R, Holley A, editors. Olfaction, taste and cognition. Cambridge: Cambridge University Press. p. 16–26.

Howard JD, Plailly J, Grueschow M, Haynes JD, Gottfried JA. 2009. Odor quality coding and categorization in human posterior piriform cortex. Nat Neurosci. 12:932–939.

Jinks A, Laing DG. 2001. The analysis of odor mixtures by humans: evidence for a configurational process. Physiol Behav. 72:51–63.

Kay LM, Crk T, Thorngate J. 2005. A redefinition of odor mixture quality. Behav Neurosci. 119:726–733.

Kay LM, Stopfer M. 2006. Information processing in the olfactory systems of insects and vertebrates. Semin Cell Dev Biol. 17:433–442.

Laing DG. 1991. Perception of complex smells. In: Dulbecco R, editor. Encyclopedia of human biology. Vol. 6. 1st edn. New York: Academic Press. p. 759–767.

Laing DG. 1994. Perceptual odor interactions and objective mixture analysis. Food Qual Prefer. 5:75–80.

Laing DG, Francis GW. 1989. The capacity of humans to identify odors in mixtures. Physiol Behav. 46:809–814.

Laing DG, Glemarec A. 1992. Selective attention and the perceptual analysis of odor mixtures. Physiol Behav. 52:1047–1053.

Laing DG, Jinks AL. 2001. Psychophysical analysis of complex odor mixtures. Chimia. 55:413–420.

Laing DG, Livermore BA. 1992. Perceptual analysis of complex chemical signals by humans. In: Doty RL, Muller-Schwartz D, editors. Chemical signals in vertebrates VI. New York: Plenum Press. p. 587–593.

Laing DG, Willcox ME. 1983. Perception of components in binary odor mixtures. Chem Senses. 7:249–264.

Lawless H. 1984. Flavor description of white wine by 'expert' and non expert wine consumers. J Food Sci. 49:120.

Lawless H, Glatter S, Hohn C. 1991. Context-dependent changes in the perception of odor quality. Chem Senses. 16:349–360.

Le Berre E, Ishii A, Béno N, Chabanet C, Etiévant P, Thomas-Danguin T. 2008. Just noticeable differences in components concentrations modify the odor quality of a blending mixtures. Chem Senses. 33:389–395.

Le Berre E, Jarmuzek E, Béno N, Etiévant P, Prescott J, Thomas-Danguin T. 2010. Learning influences the perception of odor mixtures. Chemosens Percept. 3:156–166.

Le Berre E, Thomas-Danguin T, Beno N, Coureaud G, Etievant P, Prescott J. 2008. Perceptual processing strategy and exposure influence the perception of odor mixtures. Chem Senses. 33:193–199.

Livermore A, Laing DG. 1996. Influence of training and experience on the perception of multicomponent odor mixtures. J Exp Psychol Hum Percept Perform. 22:267–277.

Malnic B, Hirono J, Sato T, Bock LB. 1999. Combinatorial receptor codes for odors. Cell. 96:713–723.

Mandairon N, Stack C, Kiselycznyk C, Linster C. 2006. Olfactory enrichment improves the recognition of individual components in mixtures. Physiol Behav. 89:379–384.

McGurk H, MacDonald J. 1976. Hearing lips and seeing voices. Nature. 264:746–748.

Olsson MJ. 1994. An interaction model for odor quality and intensity. Percept Psychophys. 55:363–372.

Olsson MJ, Cain WS. 2000. Psychometrics of odor quality discrimination: method for threshold determination. Chem Senses. 25:493–499.

O'Mahony M. 1991. Descriptive analysis and concept alignment. In: Lawless HT, Klein BP, editors. Sensory science theory and applications in foods. New York: Marcel Dekker. p. 223–268.

Parr WV, Heatherbell D, White KG. 2002. Demystifying wine expertise: olfactory threshold, perceptual skill and semantic memory in expert and novice wine judges. Chem Senses. 27:747–755.

Rabin MD. 1988. Experience facilitates olfactory quality discrimination. Percept Psychophys. 44:532–540.

Roberts AK, Vickers ZM. 1994. A comparison of trained and untrained judges' evaluation of sensory attributes intensities and liking of Cheddar cheeses. J Sens Stud. 9:1–20.

Rosch E. 1973. On the internal structure of perceptual and semantic categories. In: Moore TE, editor. Cognitive development and the acquisition of language. New York: Academic Press. p. 110–144.

Silbering AF, Galizia CG. 2007. Processing of odor mixtures in the Drosophila antennal lobe reveals both global inhibition and glomerulus-specific interactions. J Neurosci. 27:11966–11977.

Veldhuizen MG, Shepard TG, Wang MF, Marks LE. 2010. Coactivation of gustatory and olfactory signals in flavor perception. Chem Senses. 35:121–133.

Wise PM, Olsson MJ, Cain WS. 2000. Quantification of odor quality. Chem Senses. 25:429–443.