Just Noticeable Differences in Component Concentrations Modify the Odor Quality of a Blending Mixture

E. Le Berre^{1,2}, N. Béno¹, A. Ishii¹, C. Chabanet¹, P. Etiévant¹ and T. Thomas-Danguin¹

¹UMR1129 FLAVIC, ENESAD, INRA, Université de Bourgogne, 17 rue Sully, BP 86510, 21065 Dijon Cedex, France and ²James Cook University, Department of Psychology, PO Box 6811, Cairns QLD 4870, Australia

Correspondence to be sent to: Thierry Thomas-Danguin, UMR1129 FLAVIC, ENESAD, INRA, Université de Bourgogne, 17 rue Sully, BP 86510, 21065 Dijon Cedex, France. e-mail: thierry.thomas-danguin@dijon.inra.fr

Abstract

The odors we perceive are mainly the result of mixtures of odorants that, however, are commonly perceived as single undivided entities; nevertheless, the processes involved remain poorly explored. It has been recently reported that perceptual blending based on configural olfactory processing can cause odorant mixtures to give rise to an emergent odor not present in the components. The present study examined whether specific component proportions are required to elicit an emergent odor. Starting from the composition of a ternary target mixture in which an emergent pineapple odor was perceived, 4 concentration levels of each component were chosen to elicit just noticeable differences (JNDs). Each combination of levels was used to design sample mixtures. Fifteen subjects evaluated the intensity, typicality, and pleasantness of each sample mixture against the target mixture in a paired-comparison protocol. Statistical modeling showed that a variation of less than 1 JND in one of the components was sufficient to induce a significant decrease in pineapple odor typicality in the ternary mixture. This finding confirms previous findings on perceptual blending in simple odorant mixtures and underscores the human ability to discriminate between odor percepts induced by mixtures including very similar odorant proportions.

Key words: configural processing, discrimination, odor typicality, olfactory perception, ternary mixtures

Introduction

In our environment, mixtures of odorants are commonly perceived as single undivided entities (such as coffee or chocolate), the individual components of which are not generally identified (Livermore and Laing 1998). Several studies of such mixture perception reported our inability to identify more than 3 odorants in a mixture (Laing and Francis 1989). Laing and Glemarec (1992) tried but failed to improve this performance by focusing subjects' attention on only one component of a mixture. In another study, Livermore and Laing (1996) showed that neither training nor experience was able to increase identification performance beyond 3 or 4 components in a complex mixture. This failure in component identification may result from perceptual blending of individual component odors (Jinks and Laing 2001). Indeed, McBurney (1986) suggested that components of mixture may lose their individual odor identity through perceptual blending, which could even lead to the emergence of a new mixture-specific odor quality.

Several studies focused on the perception of a new emergent quality in odor mixtures. Kay et al. (2003) found that rats

trained to respond to a mixture of citronellal and octanal did not subsequently respond to either citronellal or octanal alone, showing that the components were perceived as different from the mixture. It was suggested that complete perceptual blending occurred in this mixture (Dreumont-Boudreau et al. 2006). Neural processing has been invoked in support of perceptual blending. Linster and Cleland (2004) demonstrated that the olfactory bulb output layer response to 2 perceptually similar odorants (A and B) was different from the response to the mixture (AB). At a cortical level, Zou and Buck (2006) demonstrated in rats that binary odorant mixtures can stimulate cortical neurons that are not stimulated by the individual component odorants. This result contributes to explaining why odorant mixtures can elicit novel odor percepts.

Inhumans, we have recently demonstrated perceptual blending with simple (e.g., ternary) odorant mixtures (Thomas-Danguin et al. 2007; Barkat S, Le Berre E, Thomas-Danguin T, Sicard G, unpublished data; Le Berre et al. forthcoming).

A mixture of specific proportions of ethyl isobutyrate (strawberry-like odor), ethylmaltol (caramel-like odor), and allyl-α-ionone (violet-like odor) was judged more typical of a pineapple odor than were the individual components. This observation led us to suggest that the pineapple odor arose from the mixture as a specific percept, through a perceptual blending phenomenon. Barkat (2005) showed that an optimum component concentration ratio was required to give rise to a pineapple odor. Testing 30 binary mixtures with different ratios of furaneol (caramel-like odor) and ethyl caproate (fruity-like odor) and asking a panel of subjects to rank samples from least to most pineapple like, only the sample comprising 65% furaneol and 35% ethyl caproate was ranked by every subject as smelling the most like pineapple. These findings suggested that perceptual odor blending occurred in this binary mixture and that a specific component proportion was required to elicit the emergent pineapple odor quality.

Beyond studies of mixtures that elicit novel odor percepts, many experiments demonstrated that odorants at a subthreshold concentration in a mixture could have an impact on the perceived intensity and quality of the mixture as a whole (Guadagni et al. 1963; Atanasova et al. 2005; Ito and Kubota 2005). It remains to be shown, however, whether very small variations in suprathreshold component proportions affect the perceived quality of an odor mixture. Bult et al. (2002) reported that adding odorants to a 7-component mixture reminiscent of an apple odor modified the "appleness" of the mixture. These findings, however, involved large changes in mixture composition and cannot be extrapolated to a potential effect of slight modifications. In the auditory modality, a chord can be considered as the equivalent of an odor mixture in terms of perceptual blending; Acker and Pastore (1996) demonstrated that very small frequency variations in 1 or 2 notes of a triad affected overall chord perception and that listeners were able to detect a slight change in the chord while being unable to say which note of the chord had been modified.

In the light of these findings, we investigated the importance of odorant proportions within mixtures in which perceptual blending occurs, testing the hypothesis that very small variations in component proportions may modify the perceived odor quality of a blending mixture. Specifically, we recorded variations in the perceived typicality of an emergent pineapple odor in a ternary mixture as component concentrations were slightly modified, using just noticeable differences (JNDs) in component concentration as variation units.

Materials and methods

Subjects

Fifteen volunteers (12 women and 3 men, ranging from 19 to 26 years old, with no self-reported olfactory problems or allergies) participated in the experiment. They were selected from a pool of 33 candidates for their olfactory capabilities: 1) European Test of Olfactory Capabilities olfactory test score

(Thomas-Danguin et al. 2003), 2) performance on evaluating the intensity of different concentrations of 1-butanol on a linear scale from "very slight" to "very strong," 3) classification of various concentrations of 1-butanol, and 4) odor description of model mixtures not included in the main experiment (cola, cherry, and carnation). Candidates also underwent a mental concentration test (Bourdon test, Lesschaeve 1997). We selected subjects whose total score to these different olfactory tests was the highest. The selected panelists signed an informed consent form, although the aim of the experiment was not explained to them. They were asked to avoid smoking, drinking, and eating at least 1 h before each session. Subjects were paid for their participation (\in 8.10/h).

Odorants

Three odorants entered into the composition of a pineapple model mixture (hereinafter called the "target" mixture): ethyl isobutyrate (ISO), ethylmaltol (EM), and allyl- α -ionone (AL). Table 1 shows the 5 concentration levels per component in the main experiment: the target mixture concentration (target) plus 2 levels above (JND+ and JND++) and 2 levels below the target concentration (JND- and JND--).

Each of the 125 possible ternary combinations was tested, as well as each individual odorant outside of the mixture at each level, plus 1 control (air only), that is a total of 141 stimuli tested.

 Table 1
 Odorant concentrations and variation levels for each component used in the experiment

Odorant	Concentration	JND
Ethyl isobutyrate	32.7 ppm	JND
	42.8 ppm	JND-
	46.6 ppm	Target
	49.8 ppm	JND+
	52.9 ppm	JND++
Ethylmaltol	0 ppb	JND
	0.49 ppb	JND-
	0.75 ppb	Target
	0.95 ppb	JND+
	0.96 ppb	JND++
Allyl-α-ionone	7.6 ppb	JND
	13.9 ppb	JND-
	18.5 ppb	Target
	21.8 ppb	JND+
	28.7 ppb	JND++

In bold are the concentrations of the 3 odorants in the target mixture. JND- and JND+ represent a difference of less than 1 JND, whereas JND-- and JND++ represent a difference of more than 1 JND.

Stimulus delivery hardware

An OM4/b olfactometer (Heinrich Burghart Elektro-und Feinmechanik GmbH, Wedel, Germany) was used throughout the experiment. Odorants were delivered through a cannula, onto which a funnel was fitted. Subjects had to put their nose above the funnel to smell the stimulus. Odor pulses were embedded in a constantly flowing humidified heated (37 °C) air stream. In our system, 2-4 air streams were directed toward the outlet of the olfactometer and mixed. One to 3 air streams contained 1 of the 3 odorants of the target mixture at a definite concentration, whereas the other contained odorless humidified air. Different odorant concentrations were generated by air dilution; hence, a preestablished, fully odorant-saturated air stream (odorant = O) was mixed with an odorless air stream (dilution = D). Although the sum of the air stream flow rates was held constant, different O:D ratios produced different odorant concentrations.

The concentration of each stimulus was measured at the outlet of the olfactometer using gas chromatography with a flame ionization detector and calibration curves.

Experimental procedure

Preliminary experiment: JNDs for each odorant

A preliminary experiment, with 4 persons working in the laboratory, established the 2 levels above and the 2 below the target mixture concentration of each odorant (data not shown). The subjects were not those included in the main experiment, so as to avoid preexposing the latter to the components of the mixture. Subjects received 3 series of 36 stimulus pairs, that is, 1 series per odorant. Each pair contained the target mixture and one of the variations in component concentration. Subjects were asked to determine which of the 2 samples in the pair was the more intense. Each sample was presented 4 times, twice as the first and twice as the second element in the pair. The presentation order of the 36 pairs was randomized within each series and that of the 3 series was randomized between subjects.

In order to calculate the JND of the whole group for 1 odorant, we first determined the percentages of answers "comparison sample more intense than target." These percentages were transformed into z scores under a normal probability curve. Least-square regression of z scores on concentrations was used to estimate concentrations corresponding to z values of -0.675 and +0.675 (z values of 25% and 75% more intense than the target). The target JND for the odor variation in question was estimated as half of the difference between these 2 concentration values (Köster et al. 2004).

The resulting JNDs for the 3 odorants were used as the unit of odorant variation in the main experiment. Thus, for each odorant, the JND defined the distance between the target and the comparison samples used in the main experiment (Table 1): JND- and JND+ represent a difference of less than 1 JND and JND-- and JND++ represent a difference of more than 1 JND.

Main experiment

The main experiment was divided into 5 sessions, held at 1week intervals. The first 4 sessions were dedicated to assessing the 141 stimuli. A paired-comparison method was used, with the target mixture presented against one of the other samples in each pair. The task was to sniff both odors and to choose one according to the question. Thirty-five stimuli (or 36 in the first session) were delivered 3 times per session. Stimulus presentation in these repeated paired-comparison tests was as follows: the first odor of the pair was delivered for 6 s and then odorless air was delivered from the olfactometer for 5 s, followed by the second odor of the pair for 6 s. There was a 25-s rest interval between pairs.

The first presentation was dedicated to assessing intensity. The question the subjects were to answer was "which of these 2 odors is the more intense?" (data not shown).

The second presentation concerned typicality. The question was "which of these 2 odors is the more typical of the pineapple odor?"

For the third presentation, subjects were asked to choose the preferred odor of the 2 (data not shown).

Each subject then attended a final session to evaluate their JNDs for each odorant (Table 2), so as to be able to correlate the panel's mean JND for each odorant to the typicality data. These JNDs were calculated following the same protocol as in the preliminary experiment.

Data presentation and acquisition were carried out using FIZZ software (Biosystèmes, Couternon, France).

Data analysis

All statistical analyses were conducted using SAS release 8.2. (SAS Institute Inc., Cary, NC). The generalized linear model for binary data was applied to model typicality as a function of odorant level (GENMOD procedure).

We investigated the influence of small variations (JND) in component concentrations on the pineapple odor typicality of the ternary mixture by generalized linear modeling for binary data. The model included the following factors: AL, AL², EM, EM², ISO, ISO², AL × EM, AL × ISO, EM × ISO, and AL × EM × ISO, where AL, EM, and ISO are the concentrations of allyl- α -ionone, ethylmaltol, and ethyl isobutyrate, respectively, expressed as JND multiples. AL,

Table 2 Means of the individual JNDs of each component used in theexperiment, calculated from the panels of the main experiment

Odorant	JND (ppb)
Ethyl isobutyrate	6654
Ethylmaltol	0.5
Allyl-α-ionone	5.8

EM, and ISO were considered as regressors. Under this model, "typicality" is the probability of the answer "sample perceived as more typical than the target." The model included the effects of JND variations for each odorant (AL, EM, and ISO) and their quadratic effects (AL², EM², and ISO²), which could account for optimum typicality as a function of concentration for each odorant. The interactions between the concentrations of each odorant were also included in the model. The model's ability to predict typicality was statistically significant (chi-square likelihood ratio statistic = 50.59 with 10 degrees of freedom, P < 0.0001).

Results

The JNDs estimated from the data of the whole group and used in the following are presented in Table 2. However, in order to give an idea of the interindividual variation in JNDs for each odorant, several descriptive statistics were calculated: allyl- α -ionone (min = 2.07, Q1 = 2.77, median = 3.63, Q3 = 5.67, max = 187), ethylmaltol (min = 0.16, Q1 = 0.18, median = 0.22, Q3 = 0.32, max = 1.12), and ethyl isobutyrate (min = 3173, Q1 = 3386, median = 3674, Q3 = 6756, max = 68969).

The modeling results showed a significant effect of ethylmaltol concentration ($\chi^2(1) = 23.1$, P < 0.0001) and of ethyl isobutyrate concentration ($\chi^2(1) = 13.4$, P = 0.0002) on the typicality of the pineapple odor, but no principal effect of allyl- α -ionone ($\chi^2(1) = 0.18$, P = 0.67), at least for the concentrations tested in this experiment. Nevertheless, the allyl- α -ionone concentration did have an effect on the typicality of the pineapple odor, depending on the level of ethylmaltol, with a significant AL × EM interaction ($\chi^2(1) = 6.18$, P =0.01). A significant quadratic effect of ethylmaltol concentration was also observed ($\chi^2(1) = 17.9$, P < 0.0001).

The influence of each concentration on mixture typicality was represented in 2 series of graphs, showing the variation in pineapple odor typicality when each odorant concentration varied by less than 1 JND (JND- or JND+) (first series: Figure 1) and more than 1 JND (JND-- or JND++) (second series: Figure 2).

Graphs A to C (Figure 1) and A to E (Figure 2) show increasing ethyl isobutyrate concentrations, and graphs G to A (Figure 1) and L to A (Figure 2) show increasing allyl- α -ion-one concentrations. The increase in ethylmaltol level is shown in each panel on the x axis.

One graph per level of ethyl isobutyrate and allyl- α -ionone was plotted. The increase in ethylmaltol level is shown in each panel on the x axis and the typicality responses on the y axis (with 1 meaning that 100% of the subjects found the sample mixture more typical of a pineapple odor than the target mixture and 0 that 100% of the subjects found the target more typical than the sample). In each graph, the values predicted from the previous model are represented (crosses) as well as the observed values (squares). Ninety-five percent confidence intervals, estimated from the model, are also represented for each estimated value. In each figure, chance level is for typicality 0.5, that is, that the typicality of the modified mixture (sample) was not different from the typicality of the target mixture. Conversely, when the response was below chance, the target mixture was perceived as more typical of the pineapple odor than the sample, and when the response was above chance, the sample was perceived as more typical of the pineapple odor than the target mixture.

Figure 1 shows no significant variation in pineapple odor typicality from target mixture values [panel E, circled point (0, 0, 0)] when the concentration of ISO was increased or decreased by less than its JND (panels F and D, respectively) and likewise for AL (panels H and B). However, increasing EM concentration by less than its JND (x axis) led to a significant decrease in pineapple odor typicality, whatever the level of the other 2 odorants (all panels in Figure 1, x axis).

For component concentration variations of more than 1 JND (Figure 2), a decrease in pineapple odor typicality could be observed. This was especially clear when the level of ethyl isobutyrate was decreased from target value [panel Q, circled point (0, 0, 0)] to that shown in panel H [circled point (ISO JND--, AL JND 0, EM JND 0)]. However, increasing or decreasing the level of allyl- α -ionone by more than 1 JND (panels C and N) did not have impact on the odor mixture typicality. An interaction between ethylmaltol and allyl-aionone was, however, observed, as illustrated in Figure 2, where some samples became significantly less typical than the target mixture when the levels of these 2 odorants were simultaneously modified (panels L to A, vertically). It seems that the more allyl- α -ionone there was in the mixture, the more ethylmaltol was needed to maintain pineapple odor typicality. Furthermore, both Figures 1 and 2 show curvature of the predicted typicality plot as a function of ethylmaltol level. This curve reflects the significant quadratic effect of EM ($\chi^2(1) = 17.9$, P < 0.0001), showing that pineapple odor typicality was optimal in a small range of ethylmaltol concentrations.

It is noteworthy that linear regressions between typicality and intensity on the one hand and typicality and hedonic value on the other indicated that the typicality results were poorly explained by the intensity differences between samples ($\beta = 0.09$, P = 0.0001, accounting for only 0.7% of the variance) or by hedonic differences ($\beta = 0.13$, P < 0.0001, accounting for only 1.8% of the variance).

Discussion

The present experiment was designed to test the hypothesis that small variations in component proportions modify the quality of the emergent odor in a blending mixture. We compared the perceived typicality of the pineapple odor elicited by a target mixture and several sample mixtures comprising slight variations in component concentration. The results showed that even less than JNDs in just 1 component's concentration were sufficient to significantly decrease the perceived odor typicality of the mixture.



Variation of less than 1 JND (JND- or JND+)

Figure 1 Perceived typicality of the pineapple odor according to a change of less than 1 JND in ethyl isobutyrate (ISO), ethylmaltol (EM), and allyl-α-ionone (AL) concentrations. The legend, the *x* axis, and the *y* axis are shown in full in panel E and apply to the other panels.

These results confirm previous findings on the perceptual blending phenomenon in simple odorant mixtures (Thomas-Danguin et al. 2007; Le Berre et al. forthcoming) and on the importance of component ratios for such perceptual blending to occur (Barkat 2005). These findings also highlighted the fact that, despite well-known interindividual differences in odor perception, the blending phenomenon, whereby a new quality emerges in mixture, requires very strict proportions of chemical compounds. These results give scientific support to the usual reports of perfumers and flavorists who design empirical recipes based on very precise proportions of ingredients (Butler 2000).

In the so-called pineapple mixture, allyl- α -ionone was the only component that did not have a main effect on typicality, at least in the range of concentrations tested. A previous study performed with these same odorants supports this finding. A binary mixture of ethyl isobutyrate and ethylmaltol, with no allyl- α -ionone, also induced the perception of a pineapple odor through a perceptual blending process (Thomas-

Danguin et al. 2007). In the present study, variations in allyl- α -ionone concentration had an impact on the perception of the pineapple odor of the mixtures only in interaction with variations in ethylmaltol concentration, suggesting an odor balance between these 2 components. Ethylmaltol seemed to be the critical component of the pineapple mixture as it showed a very narrow range of concentrations compatible with the emergence of a typical pineapple odor (<1 JND). Moreover, in the range of concentrations tested, it appeared that an optimal ethylmaltol proportion was associated with optimal pineapple odor typicality.

Odor perception starts with an interaction between a mixture of odorants and olfactory sensory neuron (OSN) receptors in the epithelium. Signals generated in these neurons induce a stereotyped map of olfactory receptors (Derby et al. 1991), which is further transmitted to the olfactory bulb and primary olfactory (piriform) cortex (Sullivan et al. 1995; Zou et al. 2001). At OSN level, the intensity coding of an odor depends on both the discharge frequency and the number



Figure 2 Perceived typicality of the pineapple odor according to a change of more than 1 JNDs in concentration of at least 1 of the following 3 odorants: ethyl isobutyrate (ISO), ethylmaltol (EM), and allyl-α-ionone (AL). The legend, the *x* axis, and the *y* axis are shown in full in panel E and apply to the other panels.

of OSNs activated at a given odorant concentration. This process implies that the combination of OSNs stimulated by an odorant will progressively be enriched with increasing concentration (Chastrette et al. 1998; Duchamp-Viret et al. 2003). In such a view, a change in odorant concentration would modify the odor's qualitative identity. In the case of odor blending, it is likely that a change in the concentration of 1 or several components modifies the spatial pattern activated by the specific proportions of each component in the mixture. This alteration of the stereotyped map could modify the perception (typicality) of the emergent odor in the mixture (e.g., pineapple). This hypothesis is supported by our present results as regards human perception. Interestingly, the modification of the stereotyped map seems to be effective even for JNDs in 1 odorant concentration. In the present case, this occurred especially with ethylmaltol. We suggest that this odorant may interact with quite specific olfactory receptors as the concentration used for this odorant is low (a few ppb, Table 1) as compared with the other odorants. It has been argued that some olfactory receptors are more specific and sensitive than others and may be activated by a restricted number of odorants and at very low concentrations (Holley 1996). It is conceivable that ethylmaltol activates specifically sensitive receptors, resulting in a more salient impact on the "pineapple neural pattern." This would explain how a very slight variation in the perceived intensity of this component modifies the emergent pineapple perception. It is also conceivable that ethylmaltol, with its caramel-like odor, determines the degree of perceived ripeness of the pineapple odor, according to the degree of activation of its specific receptor within the stereotyped map.

Perceptual blending is supported by configural olfactory processing of odor mixtures (Jinks and Laing 2001). This process limits our ability to identify more than 3 odorants in a complex mixture but allows us to identify a chemically complex mixture of odorants as a single entity (e.g., chocolate odor). The present study shows that subjects were able to discriminate slight variations in composition in such complex

mixtures. A similar observation was previously reported in honeybees, which are capable of using all the floral volatiles to discriminate subtle differences in scent (Wright et al. 2005). This ability could explain why we are able to discriminate between several states of maturity of a fruit (e.g., unripe and overripe). In the case of the pineapple ternary mixture, we previously suggested that ethylmaltol, with its caramel-like odor, may be an indicator of fruit ripeness. Thus, some variations in the proportion of ethylmaltol in the mixture would induce a modification of the emergent odor typicality. Subjects do not need to analyze the complex mixture to perform this discrimination but only to be sensitive to slight differences between close configurations, namely small variations in odorant composition in the case of mixtures. Most of the time, we are not aware of the origin of the difference—as in auditory perception, where listeners are able to tell that a chord has been modified but not which modification was made (Acker and Pastore 1996).

Taken together, the present results demonstrate our ability to discriminate between odor percepts induced by mixtures, including very close proportions of odorants.

Funding

This work was carried out with the financial support of the French National Institute for Agricultural Research and the Burgundy Regional Council.

Acknowledgements

The authors thank Anne-Sophie Nédellec for her participation in the experiment and the Centre Européen des Sciences du Goût for lending the olfactometer.

References

- Acker BE, Pastore RE. 1996. Perceptual integrality of major chord components. Percept Psychophys. 58(5):748–761.
- Atanasova B, Thomas-Danguin T, Langlois D, Nicklaus S, Chabanet C, Etievant P. 2005. Perception of wine fruity and woody notes: influence of peri-threshold odorants. Food Qual Prefer. 16(6):504–510.
- Barkat S. 2005. La qualité perçue des mélanges odorants: analyses psychophysiologiques. Lyon (France): Université Lumière Lyon 2.
- 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(6):485–594.
- Butler H. 2000. Poucher's perfumes, cosmetics and soaps. 10th ed. London: Kluwer Academic Publishers.
- Chastrette M, Thomas-Danguin T, Rallet E. 1998. Modelling the human olfactory stimulus-response function. Chem Senses. 23:181–196.
- Derby CD, Girardot M-N, Daniel PC. 1991 Jul. Responses of olfactory receptor cells of spiny lobsters to binary mixtures. II. Pattern mixture interactions. J Neurophysiol. 66(1):131–139.
- Dreumont-Boudreau SE, Dingle RN, Alcolado GM, LoLordo VM. 2006. An olfactory biconditional discrimination in the mouse. Physiol Behav. 87:634–640.
- Duchamp-Viret P, Duchamp P, Chaput MA. 2003. Single olfactory sensory neurons simultaneously integrate the components of an odour mixture. Eur J Neurosci. 18:2690–2696.

- Guadagni DG, Buttery RG, Okano S, Burr HK. 1963. Additive effect of subthreshold concentrations of some organic compounds associated with food aromas. Nature. 200:1288–1289.
- Holley A. 1996. Actualité des recherches sur la perception olfactive. Psychol Fr. 41(3):207–215.
- Ito Y, Kubota K. 2005. Sensory evaluation of the synergism among odorants present in concentrations below their odor threshold in a Chinese jasmine green tea infusion. Mol Nutr Food Res. 49(1):61–68.
- Jinks A, Laing DG. 2001. The analysis of odor mixtures by humans: evidence for a configurational process. Physiol Behav. 72(1–2):51–63.
- Kay LM, Lowry CA, Jacobs HA. 2003. Receptor contributions to configural and elemental odor mixture perception. Behav Neurosci. 117(5):1108– 1114.
- Köster MA, Prescott J, Köster EP. 2004. Incidental learning and memory for three basic tastes in food. Chem Senses. 29(5):441–453.
- 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.
- Le Berre E, Thomas-Danguin T, Béno N, Coureaud G, Etiévant P, Prescott J. Forthcoming. Perceptual processing strategy and exposure influence the perception of odor mixtures. Chem Senses.
- Lesschaeve I. 1997. Etude des performances de sujets effectuant l'analyse descriptive quantitative de l'odeur ou de l'arôme de produits alimentaires. Recherche de liens entre épreuves de sélection et épreuves de profil [Thèse de Doctorat]. [Dijon (France)]: Université de Bourgogne.
- Linster C, Cleland TA. 2004. Configurational and elemental odor mixture perception can arise from local inhibition. J Comput Neurosci. 16(1):39–47.
- Livermore A, Laing DG. 1996. Influence of training and experience on the perception of multicomponent odor mixtures. J Exp Psychol Hum Percept Perform. 22(2):267–277.
- Livermore A, Laing DG. 1998. The influence of chemical complexity on the perception of multicomponent odor mixtures. Percept Psychophys. 60(4):650–661.
- McBurney DH. 1986. Taste, smell, and flavor terminology: taking the confusion out of fusion. In: Meiselman HL, Rivlin RD, editors. Clinical measurement of taste and smell. New York: Macmillan. p. 117–125.
- Sullivan SL, Ressler KJ, Buck LB. 1995. Spatial patterning and information coding in the olfactory system. Curr Opin Genet Dev. 5:516–523.
- Thomas-Danguin T, Le Berre E, Barkat S, Coureaud G, Sicard G. 2007. Evidence for odor blending in odorant mixtures. Chem Senses. 32:A64.
- Thomas-Danguin T, Rouby C, Sicard G, Vigouroux M, Farget V, Johansson A, Bengtzon, A., Hall, G., Ormel, W., De Graaf, C. et al. 2003. Development of the ETOC: a European test of olfactory capabilities. Rhinology. 41: 142–151.
- Wright GA, Lutmerding A, Dudareva N, Smith BH. 2005. Intensity and the ratios of compounds in the scent of snapdragon flowers affect scent discrimination by honeybees (Apis mellifera). J Comp Physiol A. 191(2): 105–114.
- Zou Z, Buck L. 2006. Combinatorial effects of odorant mixes in olfactory cortex. Science. 311:1477–1481.
- Zou Z, Horowitz LF, Montmayeur J-P, Snapper S, Buck LB. 2001. Genetic tracing reveals a stereotyped sensory map in the olfactory cortex. Nature. 414:173–179.
- Accepted January 11, 2008