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Right-nostril Dominance in Discrimination of Unfamiliar, but Not Familiar, Odours

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Abstract

In a recent PET study on processing of unfamiliar odours we observed that odour discrimination performance was superior during right compared with left nostril presentations, and that mainly the right cerebral hemisphere was activated. In the present study we investigated whether the asymmetric performance is present also during the processing of familiar odours. Seventy-one right-handed healthy subjects (age 21–49 years, 40 females) with normal nasal anatomy and olfactory thresholds participated. Forty pairs of odours (20 familiar and 20 unfamiliar) were presented in the same/different paradigm, alternating nostrils and balancing the order. The number of errors during the discrimination task was compared with respect to nostril and odour familiarity. The overall odour discrimination performance was superior on the right side. However, this difference was valid only for unfamiliar odours, whereas the performance for familiar odours was symmetrical. Familiar odours were easier to discriminate than unfamiliar ones. The present data are congruent with the idea of a semantic influence on odour processing. Odours seem to be processed with a right sided preponderance when not clearly familiar, and symmetrically when language becomes involved. Future studies on odour processing should therefore take into account odour familiarity and side of presentation.

Introduction

One effect of the specialization of cerebral function is the lateral asymmetry in the perception of complex stimuli (Fink *et al.*, 1997; Lechevallier, 1997; Kelley *et al.*, 1998). An example is the left hemispheric specialization of language-influenced information and perception (Kelley *et al.*, 1998). Another example is the right hemisphere dominance of the perception of visuospatial material and faces (Clark *et al.*, 1998; Martin *et al.*, 1996). Whereas extensive work has been carried out with hemispheric processing of auditory and visual stimuli, relatively few studies have been carried out on hemispheric processing of the olfactory modality. Moreover, available data are inconsistent. Toulose and Vaschide reported significant asymmetries in detection thresholds for camphor and ammonia (Toulose and Vaschide, 1900). Youngentop *et al.* reported that the right nostril was more sensitive in right handed subjects (Youngetob *et al.*, 1981), whereas Koelega, on the other hand, found no significant asymmetries in detection-thresholds for amyl acetate (Koelega, 1979).

Studies of olfactory function following brain lesions suggest that there might be some degree of specialization within the right hemisphere for certain types of odour processing; olfactory memory and discrimination are reported to be impaired in patients with partial epilepsy of mesial temporal lobe origin, especially if the epileptogenic region is right sided (Rausch and Serafetidines, 1975; Abraham and Mathai, 1983; Zatorre and Jones-Gotman, 1991; Jones-Gotman and Zatorre, 1993; Savic *et al.*, 1997). In recent monorhinal experiments we also observed that the impaired discrimination performance in right temporal lobe epilepsy patients was most pronounced when the odours were presented to the right nostril.

Interestingly, the only hitherto published study in normal subjects, addressing side differences in the ability to discriminate odour quality, clearly suggests a right nostril advantage, despite lack of significant asymmetries in detection thresholds for *n*-butanol (Zatorre and Jones-Gotman, 1990). Assuming that olfactory nerves project to the ipsilateral hemisphere, the authors interpreted this as a reflection of the right hemisphere dominance in normal processing of odour discrimination, which is compatible with the reported dysfunction in right-sided temporal lobe epilepsy.

The odours applied in the cited discrimination study were according to the tables presented both familiar and unfamiliar. This is of interest in the view of the current discussions of semantic influence on odour processing (Larsson, 1997). Odours are traditionally assumed to be

encoded perceptually as featureless stimuli (Engen and Ross, 1973; Lawless and Engen, 1977). More recent works, however, challenge this assumption, suggesting that specific odour knowledge is positively related to the episodic odour memory and that semantic or verbal factors play a role in more complex odour processing. For example, memory for familiar odours is reported to be better than memory for unfamiliar odours (Lyman and McDaniel, 1990), and Larsson and Bäckman even found a correlation between the rated familiarity and label quality, and recognition performance (Larsson and Bäckman, 1997).

When olfaction is considered, semantic influence refers to a subject's general knowledge of or experience with a specific odorant, and is usually expressed in odour identification and familiarity ratings (Schab, 1991). Because the sensation of familiarity is considered to involve retrieval from semantic memory (LaBarba and Kingsberg, 1990; Royet *et al.*, 1999), the question is whether familiar and unfamiliar odours are processed differently in general, as indicated by the recent study of Distel *et al.* (Distel *et al.*, 1999), and whether olfactory functions other than odour recognition memory are subjected to semantic influence.

Based on the cited observations, it is conceivable that processing of familiar odours may involve semantic networks and thereby the language-dominant cerebral hemisphere. It is also conceivable that such an engagement of the semantic networks could facilitate activation of the neighbouring left frontal operculum, which is also shown to be activated during discrimination of odour quality (Savic *et al.*, 2000). The activation of left frontal operculum may well be more prominent when the odour is presented to the nostril ipsilateral to the language-dominant hemisphere (assuming a predominantly ipsilateral olfactory nerve projection). In the present study we therefore investigated whether the previously reported right-nostril dominance in odour discrimination performance is attenuated when familiar odours are used. The following objectives were specifically addressed: (i) is the discrimination performance better for familiar compared with unfamiliar odours? (ii) Is the discrimination performance laterialized independently of odour familiarity?

Materials and methods

Subjects

Seventy-one right-handed, non-smoking subjects, (40 females) participated in the study. The mean age of females was 25 ± 4 years (range 21–40) and males 31 ± 7 years (range 21–49). The subjects were recruited mainly from graduate classes at the Karolinska Institute. The female subjects had 14.4 ± 1.3 years of education, the males, 15.4 ± 1.9 years. All were healthy and lacked heredity for neuropsychiatric disorders. All had normal otorhinological status, which was assessed prior to inclusion in the study. The subjects were free of nasal congestion at the time of the study. The study was approved by the local ethics committee.

Odours

Thirty familiar and 30 unfamiliar odours were used in the present study (Figure 1, Table 1). They were selected from a larger kit of odours rated prior to the study by another group (ten subjects). Odours rated at the two extreme ends of the visual analogue scale (VAS) (i.e. >80 mm or <20 mm; see below) with respect to intensity, irritability and pleasantness were excluded from the further study. Familiarity was defined as the ability to correctly categorize and/or verbally label the presented odour. Based on the preparatory study the odours were defined as familiar if the average rating score on the VAS scale (see procedure) was 70 mm or above and unfamiliar if it was 45 mm or below.

The two odours within a pair were matched for degree of familiarity (Figure 1, Table 1). The odour pairs were also scored for the degree of similarity, using a 1–4 scale, with 1 indicating that the two odours in the pair were judged as almost the same and 4 as completely dissimilar, (spontaneously judged to belong to completely different categories). The extremely similar and dissimilar pairs (category 1 and 4) were then excluded in the further study, to avoid ceiling effects.

Both odours of a pair were matched for approximately equal subjective intensity (see further). We also evaluated whether the odors caused significant trigeminal stimulation and trigeminal sensation by presenting the odours to two anosmic patients according to the method of Wysocki (Wysocki *et al.*, 1997). Both patients lateralized butanol, octane, red pepper, and methyl salicylate, but none of the other odours.

Procedure

Immediately prior to the discrimination test, all subjects were evaluated for odour detection thresholds in each nostril using solutions of *n*-butanol diluted in distilled water (Jones-Gotman and Zatorre, 1988). The odorants to be discriminated were presented in glass bottles with cotton wands in controlled, suprathresholded concentrations. Forty pairs of odours (20 familiar and 20 unfamiliar) were presented in a same/different paradigm. The two odorants in each trial consisted of the same odorant or different odorants, and were presented in succession with 20 s between the items in a pair, with 60 s between trials. Using this design, the second odour in a pair was assumed not to be adversely modified by sensory adaptation to the first. For presentation the odours were placed under the subject's nostril, alternating the side and balancing the order of odours presented to the right versus left side. Also, the order of nostrils tested was randomly assigned across trials. One nostril was tested on each trial by asking the subject to hold the other nostril closed with his/her finger and inhale only through the open nostril. The subjects were allowed to sniff

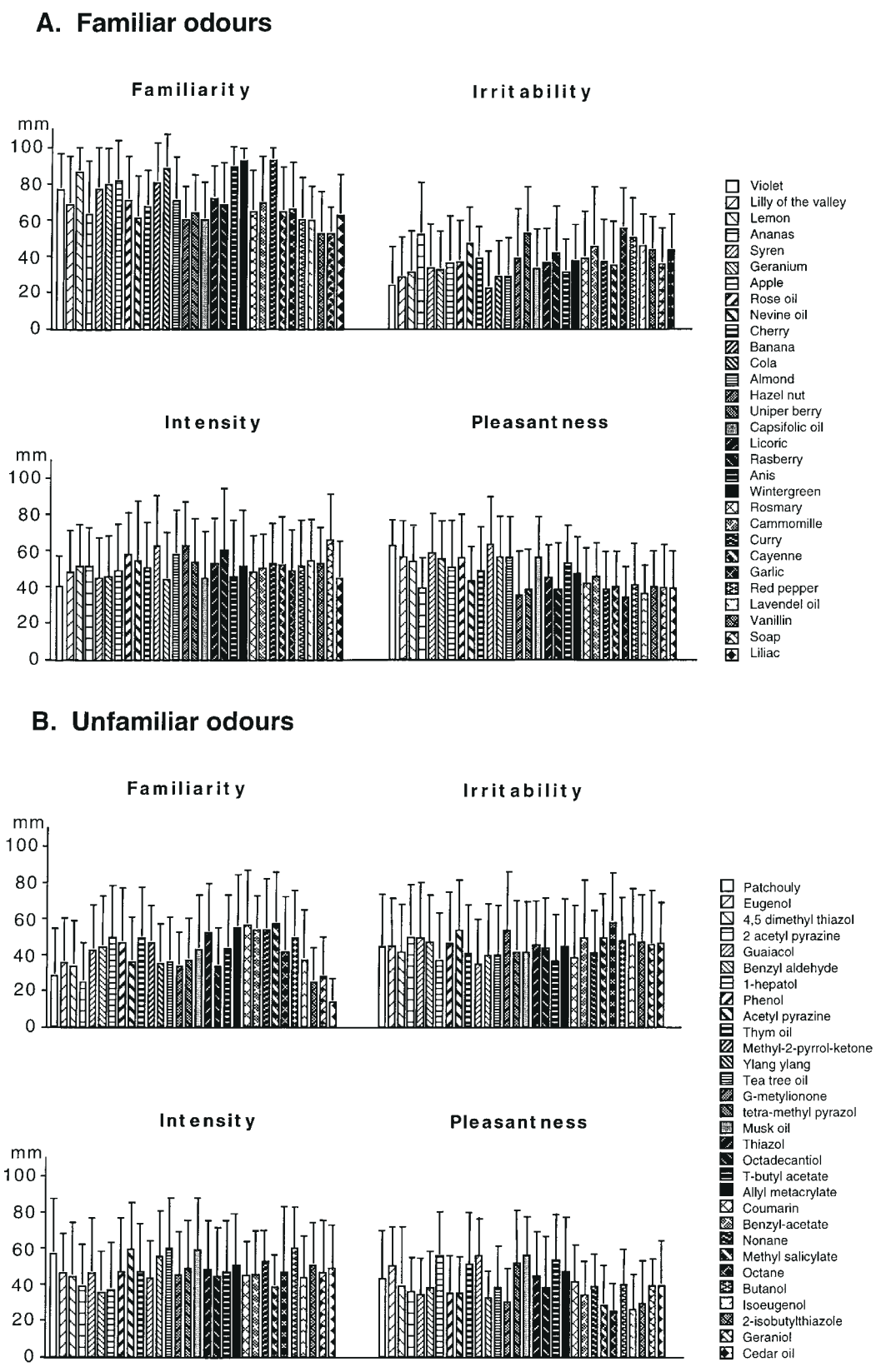

Figure 1 Rating of odours for familiarity, irritability, intensity and pleasantness. A visual-analogue scale (100 mm) was used. **(A)** Familiar odours; **(B)** unfamiliar odours. The vertical axis denotes mm on the VAS scale, the horizontal axis the odours. There was no statistically significant difference between the set of familiar and unfamiliar odours in the different rating variables, apart from familiarity.

Table 1 The odour pairs

Familiar		Unfamiliar	
1.Violet	lilly of the valley	1. 4,5-dimethyl thiazol	2-acetyl pyrazine[a]
2. Lemon	lemon	2. phenol[a]	thyme oil
3. Ananas	ananas	3. cedar oil	cedar oil
4. Syren	geranium	4. geraniol	thiazol[a]
5. Apple	rose oil	5. acetyl pyrazine	tetra-methyl pyrazol[a]
6. Nevine oil	nevine oil	6. 2-isobutyl thiazole	2-isobutyl thiazole[a]
7. Cherry	cherry	7. methyl-2-pyrrol-ketone	methyl-2-pyrrol-ketone[a]
8. Curry	cayenne	8. yilang	yilang
9. Garlic	red pepper	9. tea tree oil	octadecantiol[a]
10. Banana	banana	10. benzyl acetate	benzyl acetate[a]
11. Cola	cola	11. musk oil	musk oil
12. Almond	hazelnut	12. guaiacol	benzyl aldehyde[a]
13. Uniper berry	uniper berry	13. coumarin	coumarin
14. Vanillin	vanillin	14. nonane	nonane
15. Capsifolic oil	lilac	15. 1-heptanol	1-heptanol[a]
16. Soap	soap	16. T-butylacetate	allylmetacrylate[a]
17. Rasberry	lavender oil	17. butanol	butanol[a]
18. Resemary	camomille	18. patchouly	isoeugenol
19. Licoric	liquorice	19. eugenol	G-methyl ionone
20. Anis	wintergreen	20. methyl salycylate	octane[a]

Aliquots (2 ml) of each odour were dropped onto the cotton wand. The odours were manufactured by Nectarine Co. (Stockholm, Sweden) and Sigma-Aldrich Co. (St Louis, MO).

[a]Odors were given in 1–10% concentrations (diluted with distilled water, sometimes in addition to 0.1 ml methanol). The remaining odours were given in undiluted concentrations.

according to their preferred strategy, but only two sniffs per item presentation were permitted.

During the test the odorants were kept under an extraction hood, which prevented diffusion of odours into the testing room except during the presentation. After the discrimination tests, the odours were scored for familiarity, pleasantness, intensity and irritability, using a 100 mm bipolar VAS (Murphy *et al.*, 1991). The odour was defined as familiar if the subject could generate evocations about it and categorize it verbally, or associate a verbal label with its perception. To guide the familiarity ratings subjects were told that 0–33 mm signified a low familiarity score, 33–66 mm a medium score and 67–100 mm a high score. A low familiarity rating was defined as no, or only a very vague, perception of familiarity, a medium rating was given when the odour elicited meaningful associations or knowledge about the odour, and a high familiarity rating was given for specific knowledge of the odour, such as its name, or that it belonged to a specific category. With respect to intensity, 0–33 mm signified that the odour was perceived as weak and 67–100 mm as very strong. Likewise, 0–33 mm signified that the odour was judged as very unpleasant and 67–100 mm as very pleasant. Finally, 0–33 mm denoted a non-irritant and 67–100 a very irritant odour.

Statistics

We tested for possible asymmetries in olfactory thresholds between nostrils using repeated measures ANOVA. The obtained ratings of the respective odour qualities were analysed using an ANOVA with odour familiarity (i.e. familiar versus unfamiliar) as the between-subject factor and the respective rating score as the within-subject factor. The difference in familiarity ratings between the odours predefined as familiar versus unfamiliar was also tested with Mann–Whitney's *U*-test.

The overall number of errors in the discrimination task was compared between the right and the left nostril, and familiar–unfamiliar odours in a repeated measures ANOVA model with nostril as the within factor and familiarity class as the between factor. The ANOVA analysis was followed by contrasts as a post-hoc procedure to test for the influence of familiarity on the observed side difference. A P value of <0.05 was considered significant.

Results and discussion

The detection thresholds did not differ between right and left nostril; threshold on the right side was 2.5×10^{-4} M (SD 2.6×10^{-4}) and it was 1.9×10^{-4} M (SD 1.9×10^{-4}) on the left.

There was a significant overall difference in familiarity rating of odours which were predefined as familiar compared with unfamiliar (69 ± 25 versus 42 ± 27 mm; $P = 0.0007$). Ratings of irritability were similar between familiar (40 ± 25 mm) and unfamiliar odours (42 ± 26 mm), as

Table 2 Means and SDs of errors during the discrimination task

Gender	Familiar odours			Unfamiliar odours		
	Right nostril	Left nostril	Right and left	Right nostril	Left nostril	Right and left
Female	1.48 ± 1.24	1.58 ± 1.18	1.53 ± 1.20	2.14 ± 1.27	2,73 ± 1.47	2.43 ± 1.40
Male	1.58 ± 1.17	1.89 ± 1.37	1.73 ± 1.27	1.97 ± 1.19	2.53 ± 1.63	2.25 ± 1.45

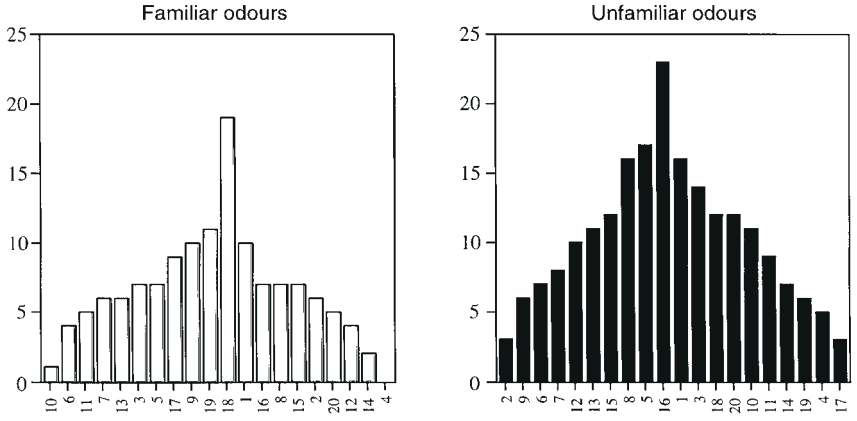

Figure 2 Frequency distribution of errors among the odour pairs. Familiar and unfamiliar odours had similar frequency patterns of errors. The vertical axis denotes the number of subjects who erroneously discriminated this specific pair. The numbers on the horizontal axis refers to the specific odour pair specified in Table 1.

were the ratings of intensity (47 ± 26 and 48 ± 27 mm, respectively) and pleasantness (47 ± 26 and 43 ± 24 mm, respectively).

The results from the discrimination tests are presented in Table 2 and Figure 2. The discrimination performance was found to be superior for familiar compared with unfamiliar odours (F = 16.04; P = 0.0001). The errors were similarly distributed across various pairs of odours (Figure 2).

The overall discrimination performance was superior on the right side (F = 6.39; P = 0.013). However, this effect was restricted to the unfamiliar odours (F = 7.84; P = 0.006), and was not valid for the familiar odours (F = 0.73; P = 0.39).

Thus, the major findings of the present study are that familiar odours are apparently more easily discriminated than unfamiliar ones, and that the right nostril advantage observed during the discrimination task was confined to unfamiliar odours. It may be argued that the results were biased by the fact that the stimulus material used had idiosyncratic properties, with a possible impact on the discrimination process other than the degree of familiarity. However, the odours were specially selected to be similar with respect to perceived odour qualities other than familiarity. Thus, the irritability, intensity and even pleasantness (although slightly higher for familiar odours) did not differ significantly between the two groups of odours. Several of the familiar odours were natural aromas, which usually are easier to discriminate then monosubstances. This cannot, however, explain the observed side difference with respect to nostril. Neither can the result be explained by a systematic difference in the degree of similarity in the familiar versus unfamiliar odour pairs, since this aspect was taken into consideration when choosing the test odours by excluding the extremely similar or dissimilar odour pairs.

The number of errors was relatively low, especially when testing the familiar odours. However, it is unlikely that the difference in performance with respect to odour familiarity was due to a possible ceiling effect for the familiar odours. In a recently conducted PET study during discrimination of unfamiliar odours, we found a right nostril advantage in spite of a hit rate of 0.9 ± 0.12 (Savic *et al.*, 2000). Likewise, in the study by the Montreal group, the right nostril advantage was present although the number of errors was similar to the presently obtained range for familiar odours (Zatorre and Jones-Gotman, 1990).

Our observation of a better performance when familiar odours are used is congruent with studies showing that memory for familiar and identifiable odours is better than for unfamiliar and unidentifiable odours (Rabin and Cain, 1984; Lyman and McDaniel, 1990; Schab, 1991; Jehl *et al.*, 1997).

The issue of lateralization in normal odour processing has only recently been addressed in brain imaging studies. The available data are, therefore, still anecdotal, and presently confined to cerebral activations during passive perception of odour stimuli. The majority of them suggest a right hemisphere dominance (Zatorre *et al.*, 1992; Simmonds *et al.*, 1997; Sobel *et al.*, 1998; Savic *et al.*, 2000), implicating that odours are processed mainly on the right side. However, the odours applied were both familiar and unfamiliar, and the issue about a difference with respect to odour familiarity was not addressed. Interestingly, in a recent PET study of cerebral activity during judgements of odour familiarity, a clear engagement of the left inferior frontal lobe was demonstrated (Royet *et al.*, 1999). One possible explanation for the lack of right nostril dominance during discrimination of familiar odours in our study may be that the right hemisphere dominance was balanced because information about familiar odours is transmitted more easily and quickly to the left hemisphere during presentations to the left nostril, leading to a better access to the language-processing centres of the left hemisphere. Notably, in contrast to the majority of studies on temporal lobe resected patients which show that odour recognition memory is dysfunctional after a right-sided resection (Abraham and Mattai, 1983; Zatorre and Jones-Gotman, 1991; Jones-Gotman and Zatorre, 1993), Eskenazi *et al.* found impaired olfactory memory irrespective of the side of surgical lesion, but only when the subjects were tested via the nostril ipsilateral to the temporal lobe lesion (Eskenazy *et al.*, 1986). They attributed this discrepancy to the fact that only familiar ('environmentally realistic stimuli') were used, whereas in the other reports both familiar and unfamiliar odours were applied. Another interesting observation is that Caroll *et al.* found that familiarity judgement was significantly impaired in left temporal lobe-damaged patients (Caroll *et al.*, 1993).

It remains to be established whether the presently observed difference in the performance of olfactory discrimination represents an isolated phenomenon in odour processing or if this might also be found with other types of olfactory tasks, thereby reflecting some more general aspect of olfactory function. It is worth mentioning that during two consecutive, yet anecdotal studies on cerebral activation with the familiar odour vanillin, a left-sided cerebral preponderance was found (Grodd *et al.*, 1997; Kettenmann *et al.*, 1997). In two recently conducted PET studies we also observed this left-sided dominance with vanillin (I. Savic *et al.*, unpublished data). Thus, perhaps different odours are processed by different regions, and areas mediating stimuli from familiar odours may be different from those processing the unfamiliar odours. This issue is of importance when designing specific tests of olfactory function, especially if they are to be used as a diagnostic tool in different populations of patients. For example, it is possible that when trying to detect a left hemisphere dysfunction the olfactory discrimination test should be based on familiar odours, whereas a suspected right hemisphere dysfunction may be easier to identify if unfamiliar odours are used. We therefore suggest that side of monorhinal presentation should be taken into account in future studies on olfactory processing.

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References

Abraham, A. and **Mathai, K.V.** (1983) *The effect of right temporal lobe lesions on matching of smells.* Neuropsychologia, 21, 277–281.

Caroll, B., Richardson, J. and **Thompson, P.** (1993) *Olfactory information processing and temporal lobe epilepsy.* Brain Cogn., 22, 220–243.

Clark, V.P., Maisog, J.M. and **Haxby, J.V.** (1998) *fMRI study of face perception and memory using random stimulus sequences.* J. Neurophysiol., 76,3257–65.

Distel, H., Ayabe-Kanamura, S., Martinez-Gomez, M., Schicker, I., Kobayakawa, T., Saito, S. and **Hudson, R.** (1999). *Perception of everyday odors—correlation between intensity, familiarity and strength of hedonic judgement.* Chem. Senses, 24, 191–9.

Engen, T. and **Ross, B.M.** (1973) *Long term memory for odors with and without verbal descriptions.* J. Exp. Psychol., 100, 221–227.

Eskenazi, B., Cain, W.S., Novelly, R.A. and **Mattson, R.** (1986) *Odor perception in temporal lobe epilepsy patients with and without temporal lobe ectomy.* Neuropsychologia, 24, 553–562.

Fink, G.R., Marshall, J.C., Halligan, R.W., Frith, C.D., Frackowiak, R.S. and **Dolan R.J.** (1997) *Hemispheric specialization for global and local processing: the effect of stimulus category.* Proc. R. Soc. Lond. Biol. Sci., 22, 487–494.

Grodd, W., Kettenmann, B., Erb, M., Pfister, M., Klusmann, A., Hulsmann, E., Klose, U. and **Kobal, G.** (1997) *fMRI of cerebral activation during olfactory stimulation.* Neuroimage, 5, S197.

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

Jones-Gotman, M. and **Zatorre, R.J.** (1988) *Olfactory identification deficits in patients with focal cerebral excision*. Neuropsychologia, 26, 387–400.

Jones-Gotman, M. and **Zatorre, R.J.** (1993) *Odor recognition memory in humans: role of right temporal and orbitofrontal regions*. Brain Cogn., 22, 182–198.

Kelley, W.M., Miezin, F.M., McDermott, K.B., Buckner, R.L., Raichle, M.E., Cohen, N.J., Ollinger, J.M., Akbudak, E., Conturo, T.E., Snyder, A.Z. and **Petersen, S.E.** (1998) *Hemispheric specialization in human dorsal frontal cortex and medial temporal lobe for verbal and nonverbal memory encoding*. Neuron, 20, 927–936.

Kettenmann, B., Hummel, C., Stefan, H. and **Kobal, G.** (1997) *Multiple olfactory activity in the human neocortex identified by magnetic source imaging*. Chem. Senses, 22, 493–502.

Koelega, H.S. (1979) *Olfaction and sensory asymmetry.* Chem. Senses Flav., 4, 89–95.

LaBarba, C. and **Kingsberg, S.A.** (1990) *Cerebral lateralization of familiar and unfamiliar music perception in nonmusicians: a dual task approach*. Cortex, 26, 567–574.

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

Larsson, M. and **Bäckman, L.** (1997) *Age-related differences in episodic odor recognition: the role of access to specific odor names*. Memory, 5, 361–378.

Lawless, H.T. and **Engen, T.** (1977) *Association to odors: interference, memories and verbal labelling.* J. Exp. Psychol., 3, 52–59.

Lechevallier, B. (1997) *Perception of musical sounds: contribution of positron emission tomography*. Bull. Acad. Natl Med., 181, 1191–1199.

Lyman, B.J. and **McDaniel, M.A.** (1990) *Memory for odors and odor names: modalities of elaboration and imagery.* J. Exp. Psychol., 16, 656–664.

Martin, A., Wiggs, C.L., Ungeleider, L.G. and **Haxby, J.V.** (1996) *Neural correlates of category-specific knowledge.* Nature, 379, 649–652.

Murphy, C., Cain, W.S., Gilmore, M.M. and **Skinner, R.B.** (1991) *Sensory and semantic factors in recognition memory for odors and graphic stimuli: elderly versus young persons*. Am. J. Psychol., 104, 161–192.

Rabin, M.D. and **Cain, W.S.** (1984) *Odor recognition: familiarity, identifiability and encoding consistency.* J. Exp. Psychol. Learn. Mem. Cogn., 10, 316–325.

Rausch, R. and **Serafetinides, E.A.** (1975) *Specific alterations of olfactory functions in humans with temporal lobe lesions*. Nature, 225, 557–558.

Royet, J.-P., Koenig, O., Gregoire, M.-C., Cinnoti, L., Lavenne, F., Le Bars, D., Costes, N., Vigouroux, M., Farget, V., Sicard, V., Holley, A., Mauguiére, F., Comar, D. and **Froment, J.-C.** (1999) *Functional anatomy of perceptual and semantic processing for odors.* J. Cogn. Neurosci., 11, 94–109.

Savic, I., Bookheimer, S., Fried, I. and **Engel, J. Jr** (1997) *Olfactory bed side test to identify and lateralize temporal lobe epilepsy.* Arch. Neurol., 54, 162–168.

Savic, I., Gulyas, B., Larsson, M. and **Roland, P.** (2000) *Olfactory functions are mediated by parallel and hierarchical processing.* Neuron, 26, 735–745.

Schab, F.R. (1991) *Odor memory: taking stock.* Psychol. Bull., 2, 242–251.

Simmonds, A. *et al.* (1997) *fMRI during 'pleasant' odor stimulations: normative data*. Neuroimage, 5, S196.

Sobel, N., Desmond, J.E., Glover, G.H., Goode, R.L., Sullivan, E.V. and **Gabrielli, J.D.** (1998) *Sniffing and smelling: separate subsystems in the human olfactory cortex.* Nature, 392, 282–286.

Toulouse, E. and **Vaschide, N.** (1900) *L'asymetrie sensorielle olfactive.* Rev. Philos., 49. 176–187.

Wysocki, C., Dalton, P., Brody, M.J. and **Lawley, H.** (1997) *Acetone odor and irritation thresholds obtained from acetone-exposed factory worrkers and from control (occupationally unexposed) subjects*. Am. Ind. Hyg. Assoc. J., 58, 704–712.

Youngentob, S.L., Kurtz, D.B., Leopold, D.A., Mozell, M.M. and **Hornung, D.E.** (1981) *Olfactory sensitivity: is there laterality?* Chem. Senses Flav., 6, 11–21.

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

Zatorre, R.J. and **Jones-Gotman, M.** (1991) *Human olfactory discrimination after unilateral frontal or temporal lobectomy*. Brain, 114, 71–84.

Zatorre, R.J., Jones-Gotman, M., Evans, A.C. and **Meyer, E.** (1992) *Functional localisation of human olfactory cortex*. Nature, 360, 339–341.

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