Chem. Senses 26: 1187–1192, 2001

Lateralization of Olfactory Cognitive Functions: Effects of Rhinal Side of Stimulation

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Abstract

This study investigated differences in olfactory cognitive functions, in 40 healthy young right-handed participants, with respect to side of rhinal stimulation. The targeted functions were: perceived familiarity, episodic recognition memory, free identification and repetition priming in identification. The results showed that odors presented to the right nostril were rated as more familiar than odors presented to the left nostril and also showed significant effects of repetition priming in identification. However, no differences were found between nostrils in episodic recognition memory or free identification. These latter results indicate a rather extensive inter-hemispheric interaction in higher-order cognitive functions.

Introduction

One characteristic feature of the anatomy of the olfactory system is the short and direct linkage between peripheral neurons and higher brain structures. Another feature is that the olfactory system seems to be mainly ipsilateral in that most receptor information from each nostril is projected, via the olfactory bulb, to the primary olfactory cortex in the same hemisphere. These facts have contributed to the interest in lateralization of olfactory functions and their relation to rhinal side of stimulation. For example, this has included the study of differences in absolute thresholds and discrimination between nostrils for odorous stimuli with varying results.

Differences in odor detection thresholds between nostrils have been reported, where left-handed participants were more sensitive in the left nostril and right-handed participants tended to be more sensitive in the right nostril (Youngentob *et al.*, 1982). However, another study (Cain and Gent, 1991) found right-nostril superiority in detection sensitivity irrespective of handedness. Conversely, there are studies that have failed to find differences in thresholds between nostrils (Koelega, 1979), regardless of handedness (Zatorre and Jones-Gotman, 1990; Betchen and Doty, 1998). Particularly noteworthy is the fact that the last two cited studies had the largest sample sizes and both used phenyl ethyl alcohol (PEA) as the stimulus, an odor without considerable trigeminal properties (Doty *et al.*, 1978).

Studies on odor quality discrimination indicate a right-nostril advantage, irrespective of handedness (Zatorre and Jones-Gotman, 1990). However, somewhat conflicting with that, another study (Hummel *et al.*, 1998) showed that left-handed participants had a left-nostril advantage for this task. A right-nostril superiority in quality discrimination was also found by Martinez and colleagues (Martinez *et al.*, 1993). Furthermore, a right-nostril advantage has been shown in an intensity categorization task, which also taps on memory functions, although these findings were statistically significant only for women (Pendense, 1987).

Studies of odor recognition memory have reported hemispheric differences in patient groups. Patients with right-temporal-lobe lesions perform more poorly than patients with left-temporal-lobe lesions in odor recognition tests, suggestive of a right-hemisphere superiority in odor recognition (Rausch *et al.*, 1977; Abraham and Mathai, 1983; Jones-Gotman and Zatorre, 1993). A right-side superiority in odor memory has also been shown in studies of healthy participants. It was found, in a cross-modal recognition task (odor–word, odor–picture) with the odor as the first stimulus presented birhinally, that the response time was faster when the second stimulus (word or picture) was presented to the right hemisphere compared to the left hemisphere (Zucco and Tressoldi, 1989). However, evidence for a right-nostril advantage in recognition memory was not found using either a single or multiple target test (Bromley and Doty, 1995). Additionally, Annett and associates (Annett *et al.*, 1996) reported no side differences in odor recognition without verbal elaboration from an experiment with a birhinal retrieval phase, although right nostril performance was poorer with verbal elaboration, which they suggested could be explained by cross-modality interference.

For odor identification there are findings showing that patients with surgically disconnected hemispheres are able to identify odors verbally when presented to the left but not the right nostril, which could be explained by a left-side lateralization for language (Gordon and Sperry, 1969). Interestingly, the patients were able to identify odors presented to the right nostril in non-verbal tests. However, there are indications of a left-hemisphere advantage in odor identification in patients with separated hemispheres, as performance for both verbal and non-verbal identification is superior in left-nostril stimulation. This might, though, have other explanations (e.g. hemispheric differences in cross-modal comparisons, verbal experimental settings) and may not necessarily indicate a left-side dominance in odor identification *per se* (Gordon, 1974). In contrast, other studies in patient groups with focal neuropathology or lobotomy have not shown side-related differences in odor identification (Eskenazi *et al.*, 1986; Carroll *et al.*, 1993). The fact that a side-related difference in odor identification was not demonstrated may be referred to the argument that olfactory information is transferred via the anterior commissure and corpus callosum (Gordon, 1974). In that perspective, findings of Herz and associates (Herz *et al.*, 1999) that odors presented to the left nostril are named more correctly than odors presented to the right nostril in healthy participants, are interesting but unexpected.

To conclude, the research on lateralization of olfactory functioning in neurologically normal participants tends to favor the right hemisphere for sensory functioning, particularly for quality discrimination. However, the lateralization of higher, cognitive functioning in this population has been scarcely investigated. The purpose of the present study was, therefore, to investigate differences in olfactory cognitive processing in healthy, young participants with respect to side of rhinal stimulation. The targeted functions were: perceived familiarity, episodic recognition, free identification and repetition priming in identification. As used here, repetition priming refers to differences in identification between odors presented both in an initial encoding phase and a final test phase, compared to odors presented in only the final test phase. Episodic recognition included measures of performance, response time and response confidence. Furthermore, it included memory experience in terms of ‘remember’ responses, reflecting memory recollection for a specific encoding episode, and ‘know’ responses, reflecting memory without episodic contextual information.

Materials and methods

Participants

Forty healthy persons, 20 men (20–29 years, mean 24.8) and 20 women (21–30 years, mean 24.7) participated. All participants were right-handed according to the Edinburgh Inventory (Oldfield, 1971) and were nonsmokers. Twenty participants reported superior patency in the left nostril and 20 in the right nostril, conceivably as a result of the nasal cycle. All participants were screened for loss in odor sensitivity, assessed separately in both nostrils (Cain, 1989).

Materials

The stimuli were 48 relatively common odors without significant trigeminal impact, many of which have been evaluated in an earlier study (Nordin *et al.*, 1998). The odors were: anise, apple, apricot, banana, cherry, chocolate, cinnamon, clove, juniper berry, lemon, lilac, orange, pine-needle, raspberry, strawberry, vanilla, violet (all from Stockholm Eter & Essensfabrik AB, Sweden), almond, grass, wood (Quest International), coconut, rose, (Interlam AB Malmö, Sweden), candle grease, caramel, cardamom, carrot, chlorine, coffee, dill, engine oil, garlic, ginger, honey, ketchup, mustard, nutmeg, oregano, peanut, pear, pineapple, soft soap, soy sauce, swedish turnip, baby powder, tar, tea, tobacco and yeast (all commercial products). The stimuli were placed in 80 ml opaque glass bottles with, when applicable, 5 ml liquid substances applied to a piece of tampon filled to reach saturation.

Procedure

The participants were tested one at a time by the same experimenter in a ventilated room and were given both written and verbal instructions. In an initial encoding phase, expected to provide relatively superficial encoding, the participants were presented with 24 stimuli and asked to rate perceived familiarity of the odor on a 160 mm bipolar visual analog scale (VAS) ranging from ‘not familiar’ to ‘very familiar’. The stimuli were presented for 2 s, during which the participant was instructed to take one natural sniff. All stimuli were presented monorhinally, alternating left- and right-nostril stimulation. The participant blocked the nostril not being stimulated by carefully placing the thumb to the opening. A 10 min break was given after the encoding phase, during which the participants filled out a questionnaire, including questions about their senses of smell and taste as well as handedness.

In a following retrieval phase, 48 stimuli were presented consisting of the 24 from the encoding phase and 24 new stimuli. The presentations were performed as in the encoding phase. The task was to report whether the stimulus had been presented in the encoding phase by responding ‘yes’ or ‘no’. The response time was measured by the experimenter from the start of the sniff to the response. Thereafter, the participants rated their confidence in the response on a 160 mm bipolar VAS ranging from ‘not certain’ to ‘completely certain’. If the participants reported that a stimulus was presented in the encoding phase they also made judgements about their recollective experience by responding either ‘remember’ or ‘know’. Thus, they reported whether they recollected the stimulus by conscious recollection of some aspect of the stimulus encountered in the study phase (‘remember’), or whether they just knew that the stimulus was presented previously in the absence of such recollection (‘know’) (Tulving, 1985; Gardiner and Java, 1991). Finally, before a new stimulus presentation, the participants were asked to freely identify the odor by veridical naming.

The entire session lasted 50–60 min and followed a double-blind procedure with respect to which stimuli that were presented in both phases. The stimulus set and presentation order was unique for each participant and randomized, with the exception that the same odor was always presented to the same nostril in both the encoding and retrieval phase.

Results

Mean values and standard deviations for familiarity, recognition memory and identification are presented in Table 1. The familiarity ratings were transformed to proportions (‘1’ corresponding to ‘very familiar’). Significantly higher familiarity ratings were found in right- compared to left-nostril stimulation according to a one-way analysis of variance (ANOVA) with repeated measures across nostrils [$F(1,39) = 6.39$, $P < 0.05$]. A Pearson correlation analysis across odors ($n = 48$) between lateralization (mean familiarity rating for an odor presented to the left nostril minus the mean when presented to the right nostril) and familiarity ratings (mean familiarity rating of an odor, irrespective of nostril) showed a significant positive correlation [$r = 0.42$, $P < 0.01$].

Performance (A') and response criterion (B'') for recognition memory were computed by the following equations (Donaldson, 1996):

$$A' = \tfrac{1}{2} + (\mathrm{HIT} - \mathrm{FA}) \times (1 + \mathrm{HIT} - \mathrm{FA}) / ((4 \times \mathrm{HIT}) \times (1 - \mathrm{FA})) \tag{1}$$

$$B'' = ((1 - \mathrm{HIT}) \times (1 - \mathrm{FA}) - \mathrm{HIT} \times \mathrm{FA}) / ((1 - \mathrm{HIT}) \times (1 - \mathrm{FA}) + \mathrm{HIT} \times \mathrm{FA}) \tag{2}$$

No significant differences between left- and right-nostril in either recognition performance [$F(1,39) = 0.04$, n.s.] or response criterion [$F(1,39) = 0.01$, n.s.] was shown in one-way ANOVAs with repeated measures. Neither did corresponding analysis of the confidence ratings (transformed to proportions such that ‘1’ corresponded to ‘completely certain’) show side differences [$F(1,39) = 0.65$, n.s.]. Furthermore, no side differences were found for response time (logarithmic units), hits [$F(1,39) = 1.79$, n.s.], correct rejections [$F(1,39) = 0.03$, n.s.], false alarms [$F(1,39) = 0.89$, n.s.], or misses [$F(1,39) = 0.86$, n.s.], according to one-way ANOVAs with repeated measures. A two-way ANOVA with repeated measures showed no significant difference between number of ‘remember’ and ‘know’ responses [$F(1,39) = 3.13$, $P < 0.10$], no overall difference between left- and right-nostril stimulation [$F(1,39) = 0.01$, n.s.] and, more importantly, no interaction between response type and stimulation side [$F(1,39) = 0.38$, n.s.].

Table 1 Mean values ± SDs for various measures of olfactory cognitive functions

	Left nostril	Right nostril
Familiarity rating (proportion)	0.54 ± 0.13	0.59 ± 0.10
Recognition memory		
Performance (A')	0.75 ± 0.13	0.76 ± 0.11
Response criterion (B'')	–0.36 ± 0.48	–0.35 ± 0.46
Confidence rating (proportion)	0.58 ± 0.10	0.59 ± 0.12
Response time (geometric means; s)		
Hit	4.35 ± 1.34	4.14 ± 1.10
Correct rejection	5.87 ± 2.01	5.88 ± 2.28
False alarm	5.48 ± 1.66	5.73 ± 2.22
Miss	6.73 ± 2.07	7.13 ± 2.71
Memory experience (*n*)		
‘Remember’ response	5.25 ± 2.50	5.05 ± 2.20
‘Know’ response	3.98 ± 2.68	4.15 ± 1.89
Identification (*n*)		
Old stimuli (encoding and retrieval phase)	2.75 ± 1.17	2.55 ± 1.58
New stimuli	1.98 ± 1.37	2.20 ± 1.02

In identification, no significant difference in performance between left- and right-nostril stimulation was shown for veridical naming in a two-way ANOVA with repeated measures [$F(1,39) = 0.00$, n.s.]. The same analysis did, however, show overall differences regarding repetition priming between odors presented in only the retrieval phase and odors presented in both the encoding and retrieval phase [$F(1,39) = 6.36$, $P < 0.05$], where odors presented in both phases were identified at a higher rate. Although the two-way ANOVA failed to confirm an interaction [$F(1,39) = 1.52$, n.s.], one-way ANOVAs (repeated measures) were computed for the separate nostrils, since previous studies have shown lateral differences in repetition priming (Olsson and Cain, 1995). These analyses showed that a difference due to priming was significant for left-nostril [$F(1,39) = 6.13$, $P < 0.05$], but not for right-nostril stimulation [$F(1,39) = 2.01$, $P = 0.16$].

Discussion

This study investigated differences in olfactory functions depending on side of rhinal stimulation and found that odors are rated as more familiar in right-nostril compared to left-nostril stimulation. This suggests the presence of a right-nostril advantage in perceived odor familiarity, which is seemingly in accordance with other studies that have shown a right-side advantage in functions related to odor perception, such as quality discrimination (Zatorre and Jones-Gotman, 1990; Martinez *et al.*, 1993) and intensity categorization (Pendense, 1987). Interestingly, the Pearson correlation analysis across odors between lateralization and familiarity ratings indicated that higher familiarity ratings in right-nostril stimulation compared to left-nostril stimulation were more strongly associated with low than high familiarity.

No differences between nostrils were found in episodic recognition in this study for any of the dependent measures; i.e. performance, response criterion, confidence, response time and memory experiences in terms of 'remember'/ 'know'. These results may at first sight seem different from findings in studies of neuropathological patients, which propose a right-hemisphere superiority in odor recognition (Abraham and Mathai, 1983; Jones-Gotman and Zatorre, 1993; Rausch *et al.*, 1977). However, the present results agree well with those of other authors (Bromley and Doty, 1995), who also investigated recognition memory in healthy subjects. An explanation that these authors proposed for the lack of a right-nostril superiority in odor recognition memory in healthy subjects, that does not contradict the neuropathological patient data, is that contralateral projections are sufficient to accommodate considerable higher-order neural processing in the opposite hemisphere. This explanation is also well supported by other studies that demonstrate inter-hemispheric interaction in olfactory functions (Gordon, 1974; Eskenazi *et al.*, 1988).

The present study showed no differences in odor identification between left- and right-nostril stimulation. This result is in accordance with studies in patient groups (Eskenazi *et al.*, 1986; Carroll *et al.*, 1993) and does not confirm the results of Herz and associates (Herz *et al.*, 1999) that odors presented to the left nostril are named more successfully.

This study also investigated effects of previous exposure on free identification, which in past research has been referred to as repetition priming (Graf and Schacter, 1985; Cave and Squire, 1992). Odors that previously had been rated for familiarity were better identified than odors that had not been previously presented. Because this effect tended to be more pronounced when tested via the left nostril, the results imply that left-nostril stimulation may be more sensitive to this type of priming effect compared to right-nostril stimulation. Similarly, it has been found that odors were identified more rapidly following previous exposure when tested via the left but not the right nostril (Olsson and Cain, 1995). Noteworthy in that study is also that left-side superiority in priming appeared irrespective of left- or right-nostril stimulation in the initial phase. The pattern of left-side superiority in priming effects for odor identification may be related to findings that indicate left-side neural underpinnings for conceptual priming (Schacter and Buckner, 1998). If so, it raises the question as to whether there is a right-side dominance for perceptual priming in olfaction, given that perceptual priming seems to be more right-side oriented. Accordingly, in the same vein as experiments in vision which indicate that right-hemisphere priming is more dependent on perceptual agreement between study and test than is left-hemisphere priming (Marsolek *et al.*, 1992; Marsolek, 1999), this pattern has been suggested to be valid also for olfactory priming (Olsson and Fridén, 2001).

To understand why odors are rated as more familiar when presented to the right nostril compared to the left nostril it is necessary to extend the discussion of odor familiarity in general. Murphy and colleagues (Murphy *et al.*, 1991) argued that familiarity for odors may involve semantic processing. In the case of high familiarity, it could be the knowledge of the identity. In the case of low familiarity, it could reflect vaguer meanings, such as whether an unidentifiable odor comes from a certain category, e.g. food, cleaning product, etc. It was further proposed that rated familiarity might reflect recognition memory for the stimulus in a person's past (Murphy *et al.*, 1991). Most likely, however, both perceptual and semantic processes are involved in tasks concerning odor familiarity. It might be fruitful to view odor familiarity on a continuum reaching from more perceptual, low-level functioning to more cognitive, high-level functioning (depending on aspects related to the stimulus, e.g. complexity, experience, category, distinctiveness, identity, etc.), instead of simply making a sharp low versus high level distinction. Moreover, given that familiarity ratings in the present study were higher following right-nostril presentations and that the literature points towards the right hemisphere as predominant in olfactory perceptual processing, it is possible that familiarity ratings to a large extent reflect clarity of perceptual processing.

Some research has also tied familiarity-based memory in episodic recognition to the fluency of processing. The processes could be either conceptual or perceptual (Rajaram, 1998), although perceptual fluency is most frequently discussed as the main source of familiarity in this context (Jacoby and Whitehouse, 1989; Rajaram, 1993). Furthermore, it is maintained that recollective experience in terms of 'remember'/'know' reflects the fluency of processing, in that 'remember' responses reflect a conceptual, or maybe rather a distinctive, component of recognition compared to 'know' responses that reflect recognition based on perceptual fluency (Blaxton and Theodore, 1997; Rajaram, 1998). Hence, 'know' responses in the current episodic recognition task should accordingly reflect the perceptual fluency with which odors were being processed. Although not statistically significant, episodic recognition via the right nostril had more 'know' responses and fewer 'remember' responses nominally than did odors recognized via the left nostril, which also agrees with the right-nostril advantage for the familiarity ratings. Interestingly, findings on recognition of visuospatial designs in unilateral temporal lobe epilepsy (TLE) patients indicated that left TLE patients give more 'know' than 'remember' responses, whereas right TLE patients show the opposite pattern (Blaxton and Theodore, 1997). Blaxton and Theodore concluded that these results suggest that neurological substrates of the left temporal lobe mediate distinctiveness processing (Rajaram, 1998), whereas the right temporal lobe structures subserve processes underlying perceptual fluency.

To conclude, the current study revealed a right-nostril advantage for perceived odor familiarity, possibly reflecting the differential functioning of the cerebral hemispheres and supporting the notion of a right-side advantage for tasks related to odor perception. No differences between right- and left-nostril stimulation were found in either episodic recognition or identification. A possible interpretation of this pattern of results is that the observed lateralization in the case of familiarity relates to relatively low-level functioning, possibly perceptual fluency, and that a more extensive inter-hemispheric interaction occurs in higher-order cognitive functions.

Acknowledgements

Supported by grants from the Bank of Sweden Tercentenary Foundation (1998-0270:01) and the Kempe Foundation. We are indebted to Dr Gregory Neely for valuable comments on the manuscript.

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Accepted August 6, 2001