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Hemispheric Lateralization in the Processing of Odor Pleasantness versus Odor Names

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Abstract

It is well established that for most people linguistic processing is primarily a left hemisphere activity, whereas recent evidence has shown that basic odor perception is more lateralized to the right hemisphere. Importantly, under certain conditions, emotional responding also shows right hemisphere laterality. Hedonic (pleasantness) assessments constitute basic level emotional responses. Given that olfaction is predominantly ipsilateral in function, it was hypothesized that odor pleasantness evaluations may be accentuated by right nostril perception and that odor naming would be superior with left nostril perception. To test this prediction we presented eight familiar neutral–mildly pleasant odors for subjects to sniff through the left and right nostrils. Subjects smelled each odor twice (once through each nostril) at two different sessions, separated by 1 week. At each session subjects provided pleasantness, arousal and naming responses to each odorant. Results revealed that odors were rated as more pleasant when sniffed through the right nostril and named more correctly when sniffed through the left. No effects for arousal were obtained. These findings are consistent with previously demonstrated neural laterality in the processing of olfaction, emotion and language, and suggest that a local and functional convergence may exist between olfaction and emotional processing.

Introduction

According to several theoretical accounts of affect, hedonic (pleasure–displeasure) responses represent the first level of emotional experience (Hoffman, 1986; Livesey, 1986). In olfactory perception, the primary response one has to an odor is an evaluation of how pleasant or unpleasant it smells. Thus, the fundamental reaction one has to an odor is emotional. Higher olfactory cognition is also distinguished by several emotional characteristics. Odors trigger memories that are more emotional than memories mediated through other modalities (Herz, 1996, 1998; Herz and Cupchik, 1995), and odors can readily influence moods and emotional states (Ehrlichman and Halpern, 1988; Schiffman *et al.*, 1995). Neuroanatomy offers a likely explanation for why this occurs. Projections from the lateral olfactory tract synapse directly into the amygdala–hippocampal complex, a neural area critically involved in the processing and experience of emotionally influenced memory (Cahill *et al.*, 1995; Cahill and McGaugh, 1998).

Olfactory function is bilateral and predominantly ipsilateral in projection. That is, odors transduced through receptors in the right nostril are projected to the right olfactory bulb and odors transduced through receptors in the left nostril are projected to the left olfactory bulb. However, more involved perceptual processing of odors appears to be dominated by right hemisphere function (Zucco and Tressoldi, 1988; Zatorre and Jones-Gotman, 1991; Kobal *et al.*, 1992; Jones-Gotman and Zatorre, 1993). Zattorre and Jones-Gotman presented eight pairs of odors to both nostrils in 99 subjects and found no nostril differences for odor detection thresholds, but discrimination performance was best when subjects smelled through the right nostril (Zattorre and Jones-Gotman, 1990). This right-nostril advantage did not vary as a function of sex or handedness and did not bear any relation to language lateralization. Recently, Yousem *et al.* (Yousem *et al.*, 1997) and Sobel *et al*. (Sobel *et al*., 1998) used functional magnetic resonance imaging during odor stimulation, and showed that neural activity in response to the odorants tested was greater in the right orbitofrontal cortex (the area primarily associated with olfactory experience) than in the left. These results and others (Zatorre *et al.*, 1992; Levy *et al.*, 1997), suggest that the right hemisphere is dominant for odor perception. By contrast, it has been well established that linguistic processing in most people is predominantly under the control of left hemisphere structures.

The current view on the hemispheric representation of emotion is mixed. Some researchers contend that emotional valence determines hemispheric laterality, with right hemisphere dominance for negative emotions and left dominance for positive emotions (Davidson, 1992). However, there is substantial evidence suggesting that the right hemisphere is dominant over the left for the processing of all emotions, at least under specific circumstances (Buck and Duffy, 1980; Joseph, 1992; Henry, 1993; Ross *et al.*, 1994). For example, a recent PET study revealed that in addition to other right hemisphere regions, the right amygdala–hippocampal complex was especially activated during recall of emotional autobiographical episodes (Fink *et al.*, 1997).

Following from the arguments above, we proposed that emotional evaluations of odors should be accentuated by right hemisphere activity, whereas, if odor naming is essentially a linguistic rather than perceptual task, odor naming should be superior with left hemisphere processing (Damasio *et al.*, 1996; Binder *et al.*, 1997). The purpose of the present research was to test this hypothesis by investigating subjects' ratings of odor pleasantness, arousal and their ability to name odors as a function of whether the odor was perceived through the right or left nostril. Following this test, we assessed whether potential laterality effects for pleasantness, arousal and naming could have been confounded by differential trigeminal activity elicited by the various odorants.

Main experiment

Method

Subjects

Thirty-two subjects participated in the main experiment. Subjects were male and female volunteers recruited from undergraduate psychology courses at the University of California, Irvine, and received extra course credit for their participation. Subjects were between 18 and 22 years of age, with self-reported normal sense of smell and were in good respiratory health when tested. Data for two subjects were later excluded due to experimental error in administering an odor, and data from another two subjects were omitted from analyses involving the emotion ratings, because they did not rate one of the odors. Statistical analyses were thus performed on 28 subjects (19 females, nine males). Handedness of subjects was not recorded at the time of the testing; however, we retrospectively believe that most if not all of the subjects were right-handed.

Procedure

Subjects were exposed to eight odors twice, at two sessions spaced 1 week apart. At the first session an odor was presented to either the right or left nostril and at the second session the same odor was presented to the opposite nostril. The order in which the odor stimuli were presented was counterbalanced in a Latin Square format, with eight possible arrangements. Assignment of each participant to a particular arrangement was partially randomized to accommodate each arrangement equally often. Half the participants received the first odor in their left nostril and half in their right nostril. Then for each consecutive odor the participant switched nostrils. Subjects were tested in groups of two. Each subject received the same treatments, one immediately after the other. Subjects were not permitted to communicate with each other during the sessions.

To sniff an odor, subjects held either their left or right nostril closed and inhaled for 2 s while the experimenter held an odor vial ~2 cm below the designated nostril. There was a 1 min inter-trial interval between each odor presentation, during which time the subjects provided their assessments of the odorant just smelled. At each session, this involved giving written responses for ratings of pleasantness and arousal on 11-point scales (–5 = highly unpleasant, 0 = neutral, +5 = highly pleasant; –5 = very calming relaxing, 0 = neutral, +5 = very exciting/agitating), and then trying to name/identify the odor. The scale scores for pleasantness and arousal were evaluated as the dependent measures of emotion. Naming ability was scored according to a strict criterion, with 0 = incorrect or no response and 1 = accurate description or accurate label (for example, 'caramelized sugar' or 'maple' for maple extract).

Odorants

Eight familiar, hedonically neutral–mildly pleasant odors were used as stimuli: pineapple, coconut, maple, vanilla, peppermint, almond, lemon and anise. The odors were commercially available liquid extracts manufactured by Schiller. Two milliliters of each odor extract (undiluted) were presented to subjects in unlabeled glass vials covered with masking tape to conceal the visual appearance of the liquid.

Results

Mean ratings for odor pleasantness and arousal by odorant for the right and left nostrils are shown in Table 1. Nonparametric sign tests were used to analyze the differences between right and left nostril ratings on the pleasantness and arousal scales. Naming ability was analyzed using a χ^2 test, as this measure yielded nominal data. Results revealed a significant difference between pleasantness ratings and subjects' ability to label the odors as a function of nostril. Specifically, odors were rated as more pleasant when sniffed through the right nostril than through the left nostril, $z(28) = 2.08$, $P < 0.05$. There were no differences between ratings of arousal as a function of nostril, $z(28) = 0.57$, (M right = 0.65, M left = 0.64). Table 2 presents the frequency and percentage of correct naming responses for each odor by nostril across subjects. A χ^2 test on the total accuracy score per nostril was computed for the naming data, and indicated that odors were more accurately named when sniffed through the left nostril than through the right (percentage correct right nostril = 52%, percentage correct left nostril = 61%), χ^2 (3) = 15.05, $P < 0.01$. A Pearson's bivariate (within-subject) correlational test was also used to

Table 1 Mean responses (± SEM) by odor for right and left nostril perception

Odor	Pleasantness[a]		Arousal[b]	
	Right nostril	Left nostril	Right nostril	Left nostril
Pineapple	1.32 ± 0.44	1.07 ± 0.40	–0.07 ± 0.37	0.36 ± 0.46
Coconut	2.11 ± 0.40	1.46 ± 0.47	0.04 ± 0.47	0.04 ± 0.47
Maple	1.97 ± 0.45	1.78 ± 0.49	1.18 ± 0.42	0.11 ± 0.40
Vanilla	0.64 ± 0.45	0.21 ± 0.45	0.61 ± 0.35	0.61 ± 0.35
Peppermint	1.61 ± 0.47	1.42 ± 0.46	1.14 ± 0.52	1.18 ± 0.51
Almond	1.21 ± 0.50	1.60 ± 0.38	0.21 ± 0.43	0.18 ± 0.44
Lemon	3.00 ± 0.27	2.50 ± 0.44	1.11 ± 0.46	1.46 ± 0.44
Anise	–0.21 ± 0.51	–0.82 ± 0.51	1.00 ± 0.45	1.64 ± 0.43

[a]Pleasantness scale: –5 = highly unpleasant; 0 = neutral; +5 = highly pleasant.

[b]Arousal scale: –5 = very calming/relaxing; 0 = neutral; +5 = very exciting/agitating.

determine the extent to which the mean of the absolute value pleasantness ratings (how far the ratings deviated from zero) correlated with odor naming ability. No significant correlation was found between these variables (r = 0.24). The sample of odorants were confirmed as neutral to mildly pleasant smelling. The overall mean pleasantness rating was 1.30 on an 11-point scale (–5 = highly unpleasant, 0 = neutral, +5 = highly pleasant).

Table 2 Correct odor naming by nostril and odor

Odor	Naming ability			
	Right nostril		Left nostril	
	Frequency[a]	Percentage[b]	Frequency	Percentage
Pineapple	7/28	25	9/28	32
Coconut	16/28	57	21/28	75
Maple	16/28	57	19/28	68
Vanilla	10/28	36	7/28	25
Peppermint	22/28	78	26/28	93
Almond	5/28	17	11/28	39
Lemon	22/28	78	26/28	93
Anise	18/28	64	18/28	64

[a]The number of correct identifications over all subjects (n = 28).

[b]Percentage conversions of the frequency data.

Trigeminal test of the odorants

To assess trigeminal activity elicited by the odorants in our experiment, we used a lateralization test following the methods of Wysocki *et al*. (Wysocki *et al*., 1992, 1999). Testing for trigeminal activity by assessing nasal lateralization is based on the early observation that individuals can not identify which side of the nose is receiving a pure olfactory stimulus, but they can readily do so when the stimulus elicits irritation (von Skramlik, 1925).

Subjects and odorants

Eight subjects from the Monell Chemical Senses Center (six females, two males, M age = 22.5 years) participated in a lateralization test of the eight odorants used in the main experiment. All subjects were right-handed, with a self-reported normal sense of smell, and were free from respiratory infections when they participated. Subjects were individually tested and received $10. Odorants were the same eight liquid flavor extracts used in the main experiment—pineapple, coconut, maple, vanilla, peppermint, almond, lemon and anise—manufactured by Schiller.

Method and results

Methods for lateralization testing were followed from Wysocki *et al*. (Wysocki *et al*., 1992, 1999). Ten milliliters of each of the extracts used in the main experiment were presented in clean, 280 ml glass bottles, which were capped with plastic screw-tops. Each top had two holes thorough which lengths of Teflon tubing were inserted. One tube, which provided access to room air in the bottle, penetrated the cap and terminated just above the liquid extract. The other tube extended from the cap and was topped with a Teflon nose-piece which the subject inserted into their nostril. It was through this nose-piece, and another positioned simultaneously in the other nostril that the subject sniffed the headspace over the odorant or blank (10 ml water). Subjects received each of the eight extract stimuli in 11 different random orders; each time compared with the blank. For half of the trials, the extract was presented to the right nostril and the blank to the left, and for the other half of trials this was reversed. Subjects placed both Teflon nose-pieces into their nostrils and inhaled. After removing the nose-pieces subjects indicated whether they thought the odor had been presented to the right or left nostril. The criterion for trigeminal activation was that subjects had to correctly identify which nostril the odorant had been presented to in 9/11 trials or better. This criterion was met by all subjects for all of the eight odorants. Therefore, all of the extracts used were trigeminally activating. This is most likely due to the fact that alcohol is the diluant in flavor extracts. With respect to the main experiment, these data indicate that the lateralization effects seen for the pleasantness and naming data were not confounded by trigeminal activation elicited by a subset of odors.

Discussion

The present study showed that hedonically neutral odors were experienced as smelling more pleasant when perceived through the right as compared to the left nostril, whereas naming ability was better when odors were perceived through the left nostril. These findings suggest the existence of hemispheric lateralization in the perception of olfactory hedonic value and olfactory naming ability consistent with evidence suggesting hemispheric specialization for olfaction (Zucco and Tressoldi, 1988; Zatorre and Jones-Gotman, 1991; Kobal *et al.*, 1992; Jones-Gotman and Zatorre, 1993), emotion (Buck and Duffy, 1980; Joseph, 1992; Henry, 1993; Ross *et al.*, 1994; Fink *et al.*, 1997) and language processing (Damasio *et al*., 1996; Binder *et al.*, 1997). Moreover, these results imply that evaluations of odor hedonic experience and odor naming access different neurological mechanisms; specifically, odor hedonic evaluations tap into perceptual/emotional aspects of neural processing, while odor naming is more of a linguistic than an olfactory sensory task (Herz and Engen, 1996).

In contrast to ratings of pleasantness, ratings of arousal in response to the odors were not lateralized. One reason for this may be that pleasantness and arousal are independent aspects of perceptual experience (Russell *et al.*, 1989), with independent neural substrates. Another possibility is that the arousal ratings obtained in the present experiment may have been related to perceived odor intensity more than to emotional arousal (calmness, excitation) *per se*. Kobal *et al*. (Kobal *et al*., 1989) have shown that subjects rated odorant intensity equally with the right and left nostrils. In the present study, odor intensity ratings were not independently assessed, thus it is currently not possible to resolve this issue. However, trigeminal activation for each of the odorants was determined, and all of them were found to be trigeminally stimulating. Trigeminally stimulating odors have been shown to produce bilateral brain activation (Youssem *et al.*, 1997). If the arousal ratings were, in fact, interpreted as intensity evaluations, then this may explain why no laterality effects were observed for arousal. Future research which considers odor intensity ratings with respect to arousal ratings will help to disentangle these issues.

None of the odors tested in this study were significantly unpleasant. Except for anise, all of the odors were rated in the neutral to mildly pleasant range. Dominance of the right hemisphere for pleasantness ratings corroborates evidence from previous brain imaging studies using pleasant odors (Zatorre *et al.*, 1992; Youssem *et al.*, 1997; D.H. Zald and J.V. Pardo, unpublished data). In a recent study which tested a highly unpleasant odor (a 'sulfide cocktail'), greater cerebral blood flow was seen in the left amygdala (Zald and Pardo, 1997). Accordingly, the authors speculated that the left amygdala may be more active in responding to highly unpleasant olfactory stimuli than the right amygdala. Consistent with this possibility, Kobal *et al.* (Kobal *et al.*, 1992) found that unpleasant odors induced chemosensory evoked potentials with shorter latencies and smaller amplitudes when perceived through the left nostril, whereas the one pleasant odor in their study (vanillin) consistently produced smaller amplitudes and shorter latencies when perceived through the right nostril. Research replicating the present experiment using both highly pleasant and unpleasant odors should be conducted to further investigate the role of odor hedonics in the laterality of olfactory processing.

Finally, although sex differences and certain complex interactions with handedness have been observed to affect odor perception (Gilbert *et al.*, 1989; Hummel *et al*., 1998), these issues were not a focus of the present research and thus were not addressed. Further investigations explicitly testing these variables, as well as issues of nasal patency, would be highly valuable.

In sum, our findings show that odors are perceived and processed differently as a function of which nostril is stimulated. Odors are experienced as smelling more pleasant when sniffed through the right nostril and are named more accurately when sniffed through the left. These results are consistent with neural laterality previously demonstrated for the processing of olfaction, emotion and language. We propose that these findings suggest that odor pleasantness perception and odor naming may be mediated by different neurological mechanisms, and that a local and functional convergence may exist between olfaction and emotional processing.

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