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Startle Probe Reflex in Response to Lateralized Presentation of Pleasant, Neutral and Unpleasant Odors

by

Sandra Brown Kuhl

A dissertation submitted to the Graduate Faculty in Psychology
in partial fulfillment of the requirements for the degree of
Doctor of Philosophy.

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Abstract

Startle Probe Reflex in Response to Lateralized Presentation of Pleasant, Neutral and Unpleasant Odors

by

Sandra Brown Kuhl

Advisor: Professor Howard Ehrlichman

Many studies have supported the theory that the human startle reflex is modulated by affective stimuli, including two studies which used odors as affective stimuli. The present study was conducted to determine whether modulation of the startle reflex in response to lateralized presentations of odors was better predicted by the valence hypothesis, which postulates that the right hemisphere is specialized for processing of unpleasant stimuli and the left hemisphere is specialized for processing of pleasant or the right hemisphere hypothesis, which postulates that the right hemisphere is specialized for processing of both pleasant and unpleasant stimuli. A between subjects design was used wherein half of 80 right-handed participants were presented with pleasant and half with unpleasant odors. Startle reflexes to acoustic probes were measured as blink magnitudes (μV) while participants were monorhinically presented with valenced odors: coconut (pleasant), room air (neutral) and Limburger cheese (unpleasant). Heart rate responses, gender effects and verbal self-report of mood, arousal, hedonics and intensity to the odors also were measured.

As predicted, a startle modulation interaction was found. There was startle blink attenuation during pleasant odor presentation and augmentation during unpleasant odor exposure. Moods also were rated more positively during pleasant odor presentation and more negatively during unpleasant odor presentation. Compared to startle reflexes, heart rate did not as sensitively differentiate responses to valenced odors, as heart rate increased only during unpleasant odor exposure. With both startle and heart rate measures, females were more physiologically responsive to odors. Although the proposed startle interaction between laterality and valence of odors was not found, lending no support for either of the hemispheric hypotheses, an unexpected interaction of Nostril (left/right) X Valence (pleasant/unpleasant) X Breath Direction (inhalation/exhalation) was found. Left pleasant odor inhalations produced the smallest blink magnitudes and right unpleasant odor exhalations produced the largest blink magnitudes. These findings were most consistent with the valence hypothesis and were further discussed in terms of 1) Zajonc's vascular theory of emotional efference, regarding the hedonic effects of warmed and cooled air; and 2) inhalations and exhalations as behavioral correlates of approach and withdrawal.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Purpose of the Study

The idea that odors affect our mood has become an increasingly popular notion, which has been documented by increased sales of aromatherapy products and by the increasing frequency of advertisements for perfumes and colognes (Foderaro, 1988). There have also been recent efforts to examine the emotional effects of odors experimentally (e.g., Bastone & Ehrlichman, 1991; Ehrlichman and Bastone, 1992a; Ehrlichman, Brown, Zhu & Warrenburg, 1995; Miltner, Matjak, Braun, Diekmann & Brody, 1994; Baron, 1997; Knasko, 1992; Warm, Dember & Parasuraman, 1991). Ehrlichman and Bastone (1992a) have pointed out why it is of interest to examine odors as affectively valenced stimuli: odors can have extremely pleasant and unpleasant hedonic qualities; there are minimal cognitive demands related to the perception of this hedonic dimension; moreover, several brain regions have been implicated in mediating both olfaction as well as emotional processing.

It was proposed in this dissertation that examining lateralized effects of valenced odors could demonstrate hemispheric specialization of emotion. After over thirty years of neuropsychological investigations of hemispheric specialization of emotion utilizing brain-damaged and healthy subjects, different hypotheses have emerged to explain the valence aspects of emotion. Two hypotheses have been predominant: One states there is a right hemispheric specialization for all emotions regardless of valence (see reviews in Borod & Koff, 1984; Borod, Koff & Caron, 1983; Bryden & Ley, 1983); an alternative hypothesis endorses a right hemispheric dominance for negative emotions and a left hemispheric specialization for positive emotions (e.g., Davidson & Tomarken, 1989).

Many of the studies examining hemispheric specialization of emotion with normal healthy subjects have presented lateralized emotional stimuli using either dichotic listening or tachistoscopic techniques. In this dissertation the startle blink reflex was employed as the dependent variable for several reasons. First, the involuntary startle blink in response to sudden intense acoustic probes has been shown in a series of recent studies to be differentially affected by emotional stimuli, as its magnitude has been shown to be correlated to the emotional valence of pictorial slides and mental imagery (Bradley, Cuthbert, & Lang, 1990; Vrana & Lang, 1990). In general, these studies have found that startle eyeblink is largest while viewing aversive pictures or during unpleasant imagery and smallest during pleasant stimuli presentations. Second, two studies (Ehrlichman et al., 1995; Miltner et al., 1994) have found that startle blink responses are differentially affected by pleasant and unpleasant **olfactory** stimuli. Last, the startle reflex paradigm lends itself especially well to lateralized presentations of odors as emotional stimuli.

In general, affective stimuli have produced a difference in startle blink modulation between negative and neutral stimuli resulting in blink augmentation as well as between positive and neutral stimuli resulting in blink attenuation (e.g., Bradley et al., 1990). However, while olfactory stimuli have been found to produce a significant augmentation difference in startle blinks between unpleasant and neutral odors, a significant attenuation difference between the pleasant and neutral odors has not been found (Ehrlichman et al., 1995; Miltner et al., 1994). Several factors may have hampered the pleasant startle modulation effect in these experiments such as the negative odors carrying over their unpleasant effects and influencing the positive experience of the pleasant odors and utilization of a positive odor which was not sufficiently pleasant.

By presenting odors of different valence to each nostril, this study investigated whether according to the valence hypothesis of emotion there is hemispheric asymmetry for the processing of pleasant and unpleasant odors or whether according to right hemisphere hypothesis of emotion the processing of both pleasant and unpleasant odors was primarily performed by the right hemisphere. No other studies have used the startle probe reflex to examine these questions. Further, this study proposed to modify the methodology of previous startle probe odor studies which did not find a significant modulation difference between pleasant and neutral conditions, by using a highly rated pleasant odor and a between subjects design in which one group only received pleasant and neutral odors and another group only received unpleasant and neutral odors to avoid potential influence of the negative odors affecting the experience of the pleasant odors.

Laterality of Emotion

The notion that emotional processes may be lateralized in the brain is relatively new (past three decades) compared to the long standing (over a century) assumption that cognitive processes are lateralized. Despite the relative infancy of the concept of emotional lateralization, there is an impressive and substantial amount of research on the topic in the neuropsychological literature. Of the many different lateralization hypotheses which have been generated from this work, two have become the most prominent and will be discussed below.

Right Hemisphere Hypothesis. A popular perspective is that the right hemisphere is specialized for the processing of all emotion and affect. Several reviews (e.g., Borod, 1992; Borod et al., 1983; Bryden & Ley, 1983; Heilman & Bowers, 1990; Heilman, Bowers, & Valentstein, 1985; Ross, 1985) refer to a substantial amount of research with unilateral brain damaged and normal populations which support this contention.

Why the right hemisphere may be superior for emotional processing was discussed by Borod and colleagues (Borod, 1992; Borod, Bloom & Santchi-Haywood, 1998), who cite several types of evidence (i.e., psychological, neurological, and arousal) to support this proposition. For instance, psychologically, the right hemisphere performs strategies (i.e., nonverbal, holistic, and integrative) and functions (i.e., visuospatial organization, pattern perception, and visual imaging) which may be related to emotional processing. Neurologically, there is evidence of a greater white to grey matter density and a greater electroencephalogram coherence in the right hemisphere compared to the left hemisphere. These findings imply greater neuronal interconnectivity and thus integrative ability for the right hemisphere which Borod contends is important for emotional processing. Lastly, enhanced arousal has been associated with heightened emotional processing and it has been suggested there is greater right hemisphere involvement with subcortical regions which control arousal and attention. In support of this notion, Borod discusses evidence that right hemisphere damage has resulted in greater amounts of unilateral neglect and abnormal patterns of autonomic nervous system functioning shown by measures of both heart rate and skin conductance.

Valence Hypothesis. Many investigators have challenged the empirical findings which suggest that the right hemisphere is predominantly responsible for the processing of affect and endorse a valence hypothesis of emotion. This hypothesis postulates right hemisphere dominance for negative emotions and left hemisphere dominance for positive emotions (e.g, Silberman & Weingartner, 1986).

Another version of the valence hypothesis takes into consideration different emotional processing modes and postulates differential (left/right) hemispheric specialization for **experiential feeling** of emotion as a function of valence, while the right hemisphere is specialized for the **perception and expression** of emotion, regardless of valence (Bryden, 1982; Davidson, 1984; Ehrlichman, 1987; Sackeim et al., 1982).

In a review of the literature, Davidson (1984) concluded that many findings in emotion research exhibiting hemispheric asymmetries for affective processes supported the valence hypothesis. For example, he cited research that has demonstrated the differential effects of unilateral cerebral lesions and unilateral injections of sodium amytal on emotional processes, and lateralized dysfunctions in affective disorders. Additionally, in response to stimuli with different affective valence Davidson cited studies showing lateral gaze shifts, visual field asymmetries, and lateralized electrophysiological hemispheric activation. Davidson also suggested the normal and clinical data indicate the frontal lobes and possibly the temporal lobes exhibit asymmetric processing of affective information. Specifically, he contended that the frontal brain regions appear to demonstrate lateralized emotional hemispheric specialization for **experienced** emotional stimuli that differ in valence, and the posterior brain regions process **perceptual** emotional information which is more cognitive in nature in the right hemisphere.

Why there might be differential hemispheric specialization for positive and negative emotions has been investigated by several researchers. For instance, one suggestion endorsed by Davidson and colleagues (Davidson, 1984, 1992, 1993; Davidson, Ekman, Saron, Senulis, & Friesen, 1990; Fox, 1991) involves the concept of approach and withdrawal. These researchers asserted that the right hemisphere is specialized for undifferentiated gross automatic movement which subserves withdrawal behavior, while the left hemisphere is specialized for sequentially rendered movements such as fine motor behavior which is more important for approach behavior.

Alternatively, it has been suggested (Borod, 1992; Borod, Koff, & Buck, 1986) that differential hemispheric processing for different emotions has evolved because unpleasant and pleasant emotions require qualitatively different types of decision making which may be best subserved by different hemispheres. For example, the decision made in a negative emotional situation (presumably linked to survival and danger) requires a multi-modal system which is responsive to a range of inputs which offer quick responses to scan and survey the situation. The right hemisphere appears to possess these qualities, as it is specialized for Gestalt and synthetic processing. In contrast, Borod, Caron, and Koff (1981) proposed positive emotions frequently are "more linguistic and communicative than emotional and reactive," and therefore may be best mediated via the left hemisphere which is specialized for those attributes.

Laterality during Perception, Expression, and Experience of Affective Information. The two major differences of opinion expressed in the above hypotheses are whether the brain hemispheres vary in their amount of processing of emotional information or whether the two hemispheres process qualitatively dissimilar emotions.

Levy (1990) has sought to temper the differences in hemispheric specialization of emotion with the suggestion that right brain superiority in processing regardless of valence is more probable when social communication or nonverbal processing are entailed, while differential processing as a function of valence may occur when a mood state has been created. Others have also suggested the perception and expression of emotional information is specialized by the right hemisphere, regardless of hedonic valence, whereas the experience of emotion may be differentially processed by both of the hemispheres depending on the hedonic valence of the emotion (Bryden, 1982; Davidson, 1984, Davidson & Tomarken, 1989; Ehrlichman, 1987). This model calls into question whether the right hemisphere subserves all emotional experience. As Ehrlichman (1987) suggested, perceiving or appraising emotional stimuli is different from actually experiencing the emotion, and it has been clinically observed in brain-damaged patients that even though they may appear to exhibit one emotion, they may be feeling a completely different emotion (e.g, Gainotti, 1983; Ross, 1984; Sakeim et al., 1982). Thus, the manner in which an emotional stimulus is evaluated is important to consider when comparing laterality studies. Because this proposal is concerned with the hemispheric lateralization of experienced emotional stimuli with normal subjects, a brief discussion will follow regarding findings from emotional laterality studies of perception, expression, and experience involving primarily normal subjects.

Hemispheric Specialization of Emotional Perception. Findings from empirical studies with normal subjects have been largely supportive of a right hemispheric superiority for perception of emotion (Borod & Koff, 1989; Bryden, 1982). The most frequently used methodologies include differences elicited by dichotic presentations of affectively toned auditory information and visual field differences elicited by tachistoscopic presentation of facial expressions. It is assumed that laterality effects occur in dichotic listening studies and divided visual field studies because one hemisphere is more specialized than the other in processing certain types of information. Because of the central nervous system's mainly contralateral innervation (Brodal, 1981) a left ear or visual field advantage suggests dominance of the right hemisphere.

Dichotic listening studies usually involve presenting two sentences or vocalizations with affective overtones and discerning whether they are the same as well as identifying the type of affect heard. Another technique is to present sentences with an affective tone with neutral content or filter the speech so that the utterances are veiled but the affective quality remains. In general, the literature (i.e., see Borod & Koff, 1989; Bryden, 1982) has demonstrated these types of dichotic listening studies show a left-ear advantage/right hemisphere superiority for processing the affective tone of nonverbal vocalizations, normal speech, and musical passages.

The divided visual field technique often involves deciding whether facial expressions projected to the right or left visual field show the same affect as a target facial expression retained in memory or spontaneously presented. In a review of this literature in normals, Ley and Strauss (1986) found a left visual field/right hemisphere superiority for processing both positive and negative facial expressions in 11 studies. The right hemisphere superiority was seen with photographs of real people or cartoons, with reaction-time or accuracy dependent variables, with cartoons compared with photographs, and with facial expressions compared with words. Additionally, the left visual field advantage appeared to be separate from the left visual-field superiority for visuospatial perception (McKeever & Dixon, 1981) and for face recognition (Ley & Bryden, 1979; Suberi & McKeever, 1977). Likewise, during free-field viewing of chimeric faces, a left-hemispace advantage for emotional processing has been increasingly implicated (for reviews see Borod, Vingiano, & Cytryn, 1989; Heller, 1990).

Hemispheric Specialization of Emotional Expression. Behavioral studies of emotional expression in normal subjects primarily examine facial asymmetry. Borod and colleagues (Borod, 1993; Borod, Santchi-Haywood, & Koff, 1997) reviewed 47 studies in the facial asymmetry literature which evaluated spontaneous and posed expressions. Borod explained that for posed expressions the face is thought to be innervated by cortical structures contralaterally for the lower face and bilaterally for the upper face, whereas for spontaneous expression the innervation is more complex in that bilateral subcortical structures have been suggested, although cortical and unilateral innervation have also been implicated. Additionally, there is no consensus regarding the manner the upper and lower face are innervated. Due to the way the face is innervated, Borod only reviewed studies which included evaluation of the lower or entire face. Findings from these studies suggested that for both spontaneous and posed expressions, the left side of the face was judged to show greater intensity and demonstrated greater movement indicating greater right hemisphere processing. Although some valence effects were noted (left-sided facial asymmetry was stronger for negative emotions (100%) than for positive emotions (76%), and right-sided asymmetries were greater for positive (24%) than for negative (0%) expressions), Borod's overall findings are consistent with others who have examined the literature on facial expressive asymmetry and find it generally suggests the left side of the face is more expressive than the right (e.g., Borod, Koff & White, 1983; Cambell, 1978; Sackeim & Gur, 1978).

Because a right hemisphere superiority for emotional expression has not been replicated in every study, and the literature reviews suggest that studies are hampered by different portrayal of types of expression, incomparable emotional expressions and inconsistent analysis techniques, Skinner and Mullen (1991) conducted a meta-analysis of 65 hypothesis tests in 14 studies of laterality in the facial expression of emotion to address these issues. These authors' meta-analysis supported a highly significant although small effect such that the left side of the face is generally judged to be more expressive than the right. Additionally, these authors found the asymmetry was greater for emotional than neutral facial expressions. Therefore, these results also support the dominance of the right hemisphere in the generation of emotional expression.

Hemispheric Specialization of Emotional Experience. The above findings suggest that the right hemisphere has been implicated in predominantly processing perceptual emotional information as well as the appraisal of emotional expressions. However, as has been mentioned previously, perceiving or making judgements about emotional information is very different from actually experiencing an emotion, and the right and left hemispheres have been differentially implicated in processing different hedonically valenced experienced emotions. Studies which have examined affective experience in unilaterally brain lesioned patients have indicated that lesions of the left anterior region have a greater likelihood in resulting in depressive symptomatology than similarly right hemisphere lesioned patients (i.e., Gainotti, 1972; Robinson, Kubos, Starr, Rao, & Price, 1984). Likewise, Sackeim et al. (1982) reviewed the literature on unilaterally lesioned patients with pathological crying and laughter, and found greater right hemisphere specialization for crying and greater left hemisphere specialization for laughter. Consistent with these studies, Davidson and colleagues using EEG, have also found a similar pattern of hemispheric specialization in the prefrontal regions of the hemispheres in normal subjects during emotional experience (i.e., Davidson, 1984; Davidson & Tomarken, 1989). Likewise, other researchers using EEG have found that the anterior area of the right hemisphere shows more activation during negative compared to positive emotion (e.g., Ahern & Schwartz, 1985; Tucker, Stenslie, Roth & Shearer, 1981).

In Davidson's and colleagues EEG studies with normal adults and infants, they often evaluated the activity of the brain during an actual experience of an emotion by examining the EEG corresponding to the production of emotional facial expressions (for methodological details, see Davidson, 1988), because facial expression is considered by many emotional theorists to represent affective experience (i.e., Adelmann & Zajonc, 1989; Ekman & Oster, 1979). In one such study (Davidson et al., 1990), subjects watched happy and disgusting films clips. The artifact free EEG during facial expressions of happiness and disgust was examined and the results supported the valence hypothesis of emotion, in that greater relative right hemisphere activation in anterior regions was found during facial expressions of disgust compared to facial expressions of happiness. Indeed this effect appears to be becoming well established, as Davidson (1993) has noted that at least five independent laboratories have demonstrated that negative affect such as disgust and fear elicit more relative right hemisphere frontal activation than positive affects of similar intensity. Likewise, Heller (1990) has reviewed other studies which are consistent with these findings using different behavioral and physiological methodologies.

These effects have not only been demonstrated in adults, but in infants as well. For instance, Fox (1991) presented EEG evidence that in infants there are brain asymmetries in the frontal region favoring the valence hypothesis that are associated with the production of emotion. In an early study (Davidson & Fox, 1982), examination of whole epoch EEG's of 10-month old infants who watched a video tape of an actress laughing or in distress indicated that the positive laughter condition generated greater left-sided frontal activation than with the negative distressed condition. To determine if this asymmetry was present at birth, Fox and Davidson (1986) examined EEG in neonates who were given tastes with different hedonic valence. They found facial signs of disgust to unpleasant tastes elicited greater right-hemisphere activation than tastes which generated greater positive facial signs. However, at this age, the asymmetry was found in both frontal and parietal conditions. Likewise, in agreement with the approach and avoidance concept incorporated in the valence hypothesis, Fox and Davidson (1988) demonstrated that infants generated relative left-hemisphere activation with approach behavior, as measured by expressions of joy and anger, and right-anterior activation during withdrawal behavior as measured by expressions of disgust and distress.

Utilizing psychophysiological techniques such as EEG and PET scans, Davidson and colleagues have also found a relationship between neural activity in the left and right sides of the prefrontal lobes and people's moods (for reviews of studies see Davidson & Tomarken, 1989; Davidson, 1993). In these studies of individual differences in asymmetry and their relation to affective reactivity, EEG activity is measured during a short period while subjects are sitting quietly. Davidson reports the typical finding is that people with relatively more activity in the left prefrontal area report more positive emotions and endorse greater pleasure from daily activities, feeling more enthusiastic, energetic and alert in general than do those who have more activity on the right side (Goleman, 1996). Although most of Davidson's work was conducted with normal subjects, when Davidson and colleagues examined the EEG activity of depressed subjects compared to non-depressed subjects, they found the depressed subjects elicited less relative left hemisphere frontal activation at rest (Schaffer, Davidson & Saron, 1983; Davidson, Chapman & Chapman, 1987). Similarly, Davidson's claims were supported by a functional imaging study (cited in Goleman, 1996) in which positron emission tomography (PET) was utilized to evaluate the brains of 25 clinically depressed patients. Davidson found these patients to have relatively greater right prefrontal cerebral blood flow implying greater activity in this region of the brain. This difference was related to these patients endorsing greater agitation, nervousness, distress, and worries.

Taken together, the laterality studies from the above sections lead to different conclusions regarding the roles of the hemispheres in processing emotional information. These differences are likely related to the manner in which the emotional stimuli are examined (perceived, expressed, or experienced) as well as the methods used to elicit and measure emotions. Davidson (1993) aptly points out that methodological and conceptual differences in the emotion literature are primarily due to "the failure to distinguish between the perception and production of emotion, the failure to carefully distinguish between spontaneous and more controlled or posed facial expressions, and the assumption that lesions in particular cortical regions were sufficient to produce an alteration of emotion or mood" (p. 470). Due to these types of inconsistencies, the evidence is inconclusive regarding the roles the left and right hemispheres in affective experience and continues to be an unresolved issue in emotion research. Odors could be beneficial in resolving some of these issues. The use of odors to elicit positive and negative affective experiences may help to establish whether the hemispheres differentially process pleasant and unpleasant information. In order to better justify this contention, it is necessary to consider the relationship between odors and affective experience. The following section will discuss research which supports the notion odors can produce affective experiential states.

Odor, Hedonics and Affect

In considering how odors can produce affective states, first the hedonic aspect of affective experience will be discussed, next the hedonic nature of odors will be considered, then studies supporting the involvement of odors in producing affective states will be discussed, and finally anatomical relationships between olfaction and emotional processing will be presented.

Emotion and Hedonics. Moods are emotional states that involve both feelings and cognitions. In considering the nature of the core feeling state which accompanies the cognitions in moods, Ehrlichman and Bastone (1992a) suggested the core experience of affective states to be the hedonic valence, which is the feeling of pleasure or displeasure. Most emotion theorists agree that at least to some degree that hedonics are an aspect of affective experience. Several of these emotional theorists (e.g., Adelmann & Zajonc, 1989; Frijda, 1986; Ortony, Lore & Collins, 1988) refer to how the hedonic nature of emotion makes evolutionary sense. These theorists usually describe how it is adaptively important for an organism's survival to approach stimuli which enhance survival (i.e., food) and avoid or distance themselves from stimuli which could compromise their survival. Instances of such valenced approach and withdrawal actions have been found in all organisms. Ehrlichman and Bastone (1992a) suggested that in simpler organisms these actions are automatic while in higher order organisms, it is probable that "experiential representations" of pleasurable and displeasurable feelings have evolved. These representations are adaptive because they exemplify the organisms present circumstance as well as signal and motivate the behavior of the organism.

Odors and Hedonics. Not all emotion theorists make reference to the involvement of odors when discussing the hedonics of affective experience. However, some have specified pleasant and unpleasant odors to be examples of a primary level of affect which is directly experienced and essentially noncognitive (Hoffman, 1986; Livesey, 1986). Others (Ortony et al., 1988) have suggested odors may be reacted to affectively, as other kinds of stimuli.

One property of odors is that they are usually experienced as either pleasant or unpleasant. This property of odors is also in accordance with the olfactory system's evolved predominant function of approaching or avoiding advantageous or detrimental substances. Studies examining the hedonic nature of odors via self-report and physiologically are somewhat limited but supportive of this contention.

Judgements of odor similarities in multidimensional scaling and factor analytic studies invariably discover a prominent pleasant-unpleasant dimension (e.g., Wright & Michaels, 1964; Yoshida, 1979). Ehrlichman and Bastone (1992b) suggested odors may have more hedonic salience than other stimuli because the pleasantness or unpleasantness of an odor is an intrinsic part of the sensory experience, whereas a sensory experience evoked by a visual stimulus is usually interpreted more cognitively as a judgement about an object. These authors tested this theory by asking students to produce lists of the first five things that came to mind which did not include their present experiences, but were related to experiences they had heard, seen, smelled, tasted, and touched. Of the five senses recalled, olfactory stimuli were rated as the most hedonically laden (although not significantly different from visual stimuli).

When investigating the hedonic ratings of odors, it has also been demonstrated that context can influence sensory-affective experiences. Moskowitz (1979) found that labeling a fragrance with or without a brand name made a difference in ratings of preference and sweetness. Additionally, Zellner and Kautz (1990) found that if identical food odors were displayed in a clouded liquid verses a clear liquid, the odors were rated as more intense in the clouded liquid. Therefore, even though odor hedonics may be in part intrinsic, expectancies may also influence olfactory responses.

Kobal and Hummel (1992) lent physiological evidence to the notion of hedonics being inherent in olfaction. These authors found differences in latencies and amplitudes of an early component of ERPs for odorants with differently rated hedonic qualities (i.e., hydrogen sulfide was rated negatively and vanillin was rated positively). Others have also reported differential brainwave patterns in response to pleasant and unpleasant odors (Brauchi, Ruegg, Etzweiler & Zeier, 1995; Kobal, Hummel & Van Toller, 1992; Kobal, Van Toller & Hummel, 1989; Pauli, Hummel & Kobal, 1992; Saito, Yamamoto & Kanamura, 1991; Yoshida, Saito, Iida, Yamamura & Kanamura, 1989). These authors reported different patterns for pleasant and unpleasant odors using fluctuations of alpha frequency waves measured by spectral densities, olfactory evoked potentials, and ERPs.

Besides their hedonic quality odors have other properties which make them useful for eliciting affective experience. The following properties of odors were emphasized by Ehrlichman and Bastone (1992a): 1) Odors are experienced via a basic primitive neural circuitry, with absence of symbolic interpretation, with minimal or no cognitive mediation or associated cognitions about the self; 2) It is easy to administer and induce positive and negative experiences, whereas other methods of inducing these experiences have incorporated within them other attributes besides the pure hedonic state.

Influence of Odor on Affective States. The idea that odors can change one's feelings or state of mind has become increasingly popular with the advent of aromatherapy. Aromatherapists' claims and related research on odors effect on moods are generally limited to the stimulating and relaxing effects. Because the hedonic effects of odors is more relevant to this proposal than the arousing effects, only a brief discussion will follow.

EEG is a common method used to examine odorants or fragrances for various arousing effects (for reviews see Lorig, 1989; Jellinek, 1994). Some studies (i.e., Van Toller, 1988; Van Toller & Kendal-Reed, 1989) purport to show that certain odorants influence alpha activity. It is generally assumed in a less aroused state there is greater alpha EEG activity, while in an excited state beta activity predominates. Other studies (i.e., Kanamura et al., 1989; Sugano, 1989, 1992; Torii et al., 1988) have used other physiological measures besides EEG, such as PET and contingent negative variation (CNV) with fragrances to examine their relaxing and arousing effects. All these studies taken together are very supportive of the idea that odorants change physiological states. In general, a decrease in alpha wave activity, olfactory evoked potential and an increase in CNV are signals of arousing effects in odors. However, disagreement about interpretations have arisen with CNV as it is also responsive to expectations of qualities of odors and it is responsive to both arousal and distraction (e.g., Lorig and Roberts, 1990; Tecce, Saviganano-Bowman & Meinbresse, 1976; Lorig & Schwartz, 1988).

Besides the many articles recently promoting the healthful aspects of aromatherapy, negative effects of odors are also being increasingly reported. For instance, odors have been implicated in the exacerbation or creation of conditions in people with chemical sensitivities, as well as playing a role in "sick building syndrome" (Bell, 1987; Doty, Deems, Frye, Pelberg & Shapiro, 1988).

Facial expressiveness holds great interest as a possible way of inferring affective states (Adelmann & Zajonc, 1989). Additional support for the idea that odors elicit positive and negative feeling states has come from studies of facial responsiveness. Steiner (1974) found that facial responses of infants which were rated by adults, showed pleasure or displeasure in response to tastes and odors, although the evidence for tastes appeared more reliable than for odors (see Van Toller, Hotson & Kendal-Reed, 1992). Others have found that judges who examined facial expressions could more readily distinguish when people were smelling unpleasant odors compared to pleasant odors (Kraut, 1982; Gilbert, Fridlund & Sabini, 1987). In these two studies, spontaneous facial expressions were often not produced as the subjects smelled the odors, although when Gilbert et al. (1987) instructed subjects to deliberately pose a facial expression reflecting their experience of the odors, they found judges often could correctly distinguish the hedonic valence of the odor. Therefore, even though spontaneous facial expressions to odorants in these studies are limited, results suggested that posed facial expressions can accurately convey the hedonic nature of the odor, lending further credence to the notion odors are affective.

Studies that investigate the effects of odor on mood ratings are limited, but generally indicate that odors can affect mood in negative and positive ways. For instance, North Carolinians who live down wind of pig farms were reported by Schiffman (cited in Angier, 1995) to be depressed and anxious. Conversely, reports of intensive care unit hospital patients who were exposed to pleasant odors reflected greater improvement in positive mood than those not exposed to the pleasant odors (Dunn, Sleep & Collet, 1995). Similarly, Baron (1997) found that shopping mall patrons who were near pleasant ambient odors (e.g., roasted coffee, baked pastries and cookies) reported greater levels of positive affect than people in areas of the mall without pleasant odors (e.g., clothing and shoe stores).

Experimental laboratory studies also have shown odors' effects on moods. After smelling odors in a bottle, subjects who smelled a malodor reported feeling less pleasure, dominance, and arousal than control subjects (Rotton, 1983). Ehrlichman and Bastone (1992a) have shown differences in mood ratings depending on the pleasantness or unpleasantness of odors. Subjects exposed for 20 minutes to pleasant, unpleasant, or no-odor conditions showed significant differences in their ratings of positive and negative moods related to pleasant and unpleasant odor conditions, respectively. Odor main effects were found for annoyed-pleased, disgusted-delighted and tense-relaxed scales, but not for sleepy-alert or depressed-elated scales. The no-odor group showed minimal changes in mood from pre-odor baseline levels, whereas the pleasant and unpleasant odor groups reported changes in mood ratings 1 minute after smelling the odorant, with the annoyed-pleased scale showing the greatest change. The unpleasant odor-induced mood change persisted throughout the experiment (28 minutes), while the effects of the pleasant did not persist. The authors suggested that habituation to the pleasant odors over the course of the study occurred.

Baron (1990) found that positive ambient odors in a room positively influenced work performance compared to the work performance which occurred in an unscented room. Pleasant fragrance was influential in setting greater monetary goals and utilizing an efficient strategy (making more concessions and stating a greater preference for less confrontational approaches). It was also found that exposure to pleasant odors resulted in increased helping behavior to the same degree as receiving a small, unexpected present (Baron and Thomley, 1994). In these studies the findings were attributed to mood changes elicited by the pleasant odor, because the participant's self-reported affects were more pleasant and positive than the participants in a no-odor control condition.

Knasko (1992) found that the health reports differed for subjects who were exposed to low to moderate ambient levels of odorants depending on the hedonic quality of the odorant. Significant reductions in reported health-impairment symptoms were found while exposed to a lemon odorant, whereas nonsignificant increases in symptoms were found in the presence of dimethyl sulfide.

In contrast to the majority of studies which have found mood effects related to odors there is at least one study which has not found changes in reported mood when exposed to pleasant, neutral or unpleasant ambient odors (Cann & Ross, 1989).

Knasko, Gilbert and Sabini (1990) demonstrated that demand characteristics may influence subjective reports. These authors told subjects to expect a pleasant or unpleasant ambient odor, when there was actually no difference in the ambient odor. When subjects were told there was a malodor present, they generally endorsed more negative health symptoms than when told that there existed a neutral or pleasant odor. It therefore seems important to make efforts to minimize potential demand characteristics in this type of odor research.

Ehrlichman and Bastone (1992a) suggested that not only are emotions and odors interrelated, but "that the experience of odors may have effects on people that are 'functionally equivalent' to effects of emotion; especially mood states" (p. 143). These authors examined how odors may act in similar ways to mood states to influence certain cognitions and behaviors. Their research indicated that odors are more likely to influence cognitive processes which are automatic (unconscious and spontaneous) than controlled (conscious and deliberate). They found that for certain behaviors which had previously been demonstrated to be influenced by moods, pleasant odors created enhanced evaluations of words and pictures of people, increased creative performance, and evoked a greater number of happy memories. The authors proposed that these tasks included automatic processes which allowed for the influence of affective states without mood associated cognitions. In contrast, on other tasks which also are affected by moods, such as judgements regarding the probability of risk taking and helping other people, the odors were not influential. The authors speculated that these less automated and more cognitively controlled tasks were not influenced by mood states but rather by the thoughts which exist with the mood states. Because the odors have greater hedonic than cognitive salience they also did not influence these types of tasks.

Taken together, most of the studies leave little question that pleasant and unpleasant odors can induce changes in affective experience.

Olfactory and Limbic System Associations. A close association between olfaction and emotion is not only suggested by the literature which shows odors elicit strong feelings of pleasure or displeasure, produce relaxation or alertness and influence mood, but also by their common central nervous system pathways. In fact, the limbic system, primarily concerned with emotional functioning and feeling states, was originally named the rhinencephalon. It was therefore initially thought to be specialized for the perception of smell (Van Toller, 1988). Indeed, neuroanatomical studies have shown that the olfactory system has direct afferent and efferent connections with the diffuse limbic systems (see Brodal, 1981).

The olfactory tract's close proximity and connections with the limbic system has been proposed as a possible mechanism for mood changes elicited by odors (King, 1988); however, there is to date little research which has attempted to investigate this possibility (Lorig, 1992). Neural signals produced by odors are relayed initially to the limbic region, as most of the olfactory reflexes are mediated through subcortical structures (Brodal, 1981). These signals then travel to the cerebral cortex which governs the conscious perceptions of odors. Therefore, in humans limbic as well as cortical processing of odors occurs. Warren and Warrenburg suggest (1993) that limbic control of olfactory information occurs in humans but not to the same extent as in nonhuman mammals in which processing of olfactory information is intimately related to sexual and emotional behaviors.

Lateralization and Olfaction

Lateralized Anatomy of Olfactory System. How does the brain recognize and interpret various scents? Mammals recognize odors via approximately 1000 receptors in the nerve tissue of the nasal cavity. These receptors change shape when they bind with an odor molecule. This change in configuration prompts the nerve to fire a signal back to the brain via transmission from the olfactory bulb. Brodal (1981) points out that in addition to fibers from the olfactory receptors, the olfactory bulb receives afferents from the contralateral bulb and the olfactory cortex, thalamus, limbic system, hypothalamus and pituitary gland. There also appears to be feedback connections to the olfactory bulb from most of the regions to which it projects.

An important aspect of the anatomy of the olfactory system for this study, besides its relationship with the limbic system, is that it is lateralized. Even though some fibers interconnect to the opposite olfactory bulb via the anterior commissure, anatomical and functional evidence from studies of olfactory fatigue (see Brodal, 1981) indicate that the majority of afferent impulses from the olfactory bulb are transmitted to the ipsilateral half of the brain. Olfactory fatigue occurs when a subject can no longer perceive an odor after being subjected to it for some time. It is considered a central process because an increase in fatigue occurs after central lesions which have not affected the olfactory bulb or tracts. When the olfactory bulbs or tracts are lesioned, decreases are found in olfactory acuity without increases in olfactory fatigue. The olfactory fatigue seen in central lesions is ipsilateral to the side of the lesion. This finding is consistent with knowledge of the olfactory pathways which indicates the majority of the afferent impulses from the olfactory bulb are transmitted to the ipsilateral half of the brain.

Commissurotomy studies have found human olfactory perception may be confined to a single hemisphere when only the ipsilateral nostril is stimulated with an odorant (Gordon & Sperry, 1969; Gordon, 1974). In right-handed subjects whose cerebral hemispheres had been surgically disconnected to alleviate severe epileptic seizures, it was found that odors were only named after left but not right nostril stimulation and right (non-verbal) hemisphere recognition of right nostril odors was demonstrated utilizing non-verbal recognition tests. On tasks involving cross-modal olfacto-tactal matchings, subjects correctly identified the tactual and olfactory stimuli presented to the same hemisphere but not to opposite hemispheres.

Hemispheric Specialization in Olfaction. Given that the olfactory system is lateralized in the brain, it would be reasonable to explore whether or not there is hemispheric specialization for the processing of olfactory information. However, in contrast to the extensive neuropsychological literature on the visual and auditory modalities, only limited studies have examined lateral asymmetries in the olfactory modality.

Early studies examining olfactory asymmetries are contradictory. For instance, one group of investigators using 19 subjects found detection thresholds of n-butanol was differentially more sensitive in the right nostril if the subject was right-handed, whereas if the subject was left-handed greater sensitivity was found in the left nostril (Youngentob, Kurtz, Leopold, Mozell & Hornung, 1981). Pendse (1987) also demonstrated a greater right nostril sensitivity in an intensity scaling procedure, although only in only in right-handed females. In contrast, Koelega (1979), using 40 right handed subjects, did not report any differences in detection thresholds for amyl acetate.

More recent studies have implicated a right hemisphere advantage in tasks of odor discrimination. While Zatorre and Jones-Gotman (1991) did not find a lateralization in the detection of n-butanol in a group of normal right-handed subjects, they did find a significant right-nostril advantage in odor discrimination ability. These authors also found that unilateral cortical excisions affected the right nostril advantage, such that left temporal lobe lesions produced an enhanced effect while right temporal lobe lesions resulted in an attenuated effect. These authors reported bilateral impairments in odor discrimination when the right frontal lobe was lesioned and it was suggested that this finding further implicated right hemisphere involvement in odor discrimination. Zatorre and Jones-Gotman (1990) replicated the right nostril asymmetry in odor discrimination in another study in which they studied odor discrimination in 99 subjects with close to equal numbers of right and left handers as well as both sexes. Odor discrimination was enhanced for odors presented to the right nostril compared to the left nostril, whereas no asymmetry was demonstrated in detection thresholds. The right nostril advantage was not related to sex, handedness or the hemisphere of presumed language representation (measured by a dichotic listening task).

Generally consistent with the previously mentioned discrimination studies, evidence for dominant right orbitofrontal functioning in olfaction was reported in a (PET) study (Zatorre, Jones-Gotman, Evans & Meyer, 1992). Cerebral blood flow changes during bilateral olfactory stimulation showed increases in the brain bilaterally in the region which connects the inferior frontal and temporal lobes and coincides with the piriform cortex, and unilaterally in the right orbitofrontal area.

Some support for specialization of the right hemisphere for certain olfactory processing comes from neuropsychological studies of brain-lesioned subjects. Odor matching tasks and recognition tasks have been associated with greater deficits resulting from right orbitofrontal or temporal-lobe lesions than similar lesions in the left hemisphere (Abraham & Mathai, 1983; Jones-Gotman & Zatorre, 1988a; Rausch, Serafetinides & Crandall, 1977). However, the hemispheric specialization only appeared in tasks requiring discrimination; other olfactory tasks have not been found to show asymmetric performance as a function of the side of lesion (i.e., Eskenazi, Cain, Novelly & Friend, 1983; Eskenazi, Cain, Novelly & Mattson, 1986; Jones-Gotman & Zatorre, 1988b).

Regarding the possibility of hemispheric differences in olfactory processing, Zatorre and Jones-Gotman (1990) suggested that both hemispheres are probably involved, but to a different extent, because most studies in which an olfactory region was lesioned have shown olfactory deficits regardless of the hemisphere lesioned. Likewise, Gordon and Sperry's (1969) study of olfactory matching in patients with sectioned corpus callosums demonstrated that these patients were able to perform the matching task with odors presented to either nostril, albeit the right nostril matchings required a nonverbal response.

Trigeminal Versus Olfactory Odor Stimulation. Research on lateralized responses to odors is compromised by the fact that many studies use odors that not only stimulate the olfactory nerves but the trigeminal nerves as well. Because trigeminal and olfactory innervation is quite different (e.g., olfactory innervation is ipsilateral while trigeminal is contralateral) the lateralized studies that do not use pure olfactory stimuli are confounded by the trigeminal effects of the odors and thus make interpretation of the results difficult. Thus it is important in this type of research to ascertain whether the odor has trigeminal sensory components. An interesting phenomenon regarding lateralized presentations of odorants is the ability to differentiate odors which are exclusively olfactory and odors which have trigeminal sensory components. Several authors (Ehrlichman, 1987; Kobal, Hummel, & Pauli, 1989a; Schneider & Schmidt, 1967) have reported that subjects monorhinically stimulated with an odorant could not recognize which nostril was stimulated, except when the odorant produced trigeminal effects. In contrast, only one group of investigators (Bellas, Novelly & Eskenazi, 1989) found with unilateral and double simultaneous stimulation (different odorants delivered to each nostril) that normal subjects could recognize above chance the stimulated nostril with both trigeminal and olfactory odorants. These authors also reported that right hemisphere lesioned subjects were unable to accurately localize the olfactory odorants and could only localize the monorhinically presented trigeminal odorants. Except for this latter study, the ability to distinguish between trigeminal odors and nontrigeminal odors using nostril localization appears quite robust. In the present study it was important to establish that the odorants used were olfactory because it is only concerned with lateralization effects of olfactory stimulation. Therefore, the odorants were tested monorhinically in a pilot study to ensure absence of trigeminal stimulation effects (localization of stimulated nostril above chance).

In sum, studies concerned with the lateralization of the olfactory system indicate that anatomically, the olfactory system primarily projects to the ipsilateral hemisphere. These findings generally also have been confirmed in behavioral studies. At present, a hemispheric specialization for olfactory processing has only been suggested for tasks requiring olfactory discrimination. Taken together, these findings support the use of odorants to investigate affective hemispheric specialization because 1) the odorants can be presented monorhinically for ipsilateral processing, 2) hemispheric specialization of certain olfactory tasks has been previously found, and 3) the odorants can be chosen that do not show trigeminal nostril localization effects and are therefore assumed to be solely olfactory in nature.

Lateralization of Odors and Hedonics. Very few studies have investigated differences in affective ratings of odors depending on the side of stimulus presentation (right or left nostril). Ehrlichman (1987) was one of the first to show this effect. He found that when the right nostril was presented with unpleasant odors, the odors were rated as more unpleasant than when presented to the left nostril. With presentation of pleasant odors to either nostril; however, no differences in hedonic ratings were found. As has been previously discussed, the olfactory nerves make ipsilateral projections to the hemispheres. Ehrlichman interpreted these results to suggest right hemispheric dominance for the processing of negative affective experience, while there may be no dominance for the processing of positive affective experience.

Kobal and Hummel (1992) reviewed several of their prior studies (Kobal et al., 1992; Kobal et al., 1989a; Pauli et al., 1992) to examine whether the hedonic (pleasant or unpleasant) aspects of an odorant correlated with physiological changes in the brain as evidenced by olfactory evoked potentials (OEPs) in right-handed subjects. These authors found changes in amplitudes and latencies of the OEPs which were related to the hedonic component of the odorants. For instance, odors rated as pleasant (vanillin, phenylethyl alcohol, or low concentrations of acetaldehyde) elicited greater amplitudes and longer response latencies (period between stimulus onset and response) when presented to the left nostril compared to the right nostril. In contrast, presentation of odorants rated as unpleasant (hydrogen sulphide, carbon dioxide, or high concentrations of acetaldehyde) or given mixed ratings (menthol) evoked smaller amplitudes and shorter latencies with left nostril stimulation. The authors contended that it was the emotional hedonic component of the odorants which elicited the differential latency and amplitude effects, especially because the different concentrations of acetaldehyde were given different hedonic ratings which corresponded to different latency and amplitude effects. The lateralized physiological differences in OEPs were suggested to be in accord with the valence hypothesis, which holds that pleasant emotions are predominantly processed by the left hemisphere, and unpleasant emotions are more greatly processed by the right.

Two other studies examining whether differential brain responses for pleasant and unpleasant odors exist also have shown valence effects. Yoshida et al. (1989) reported pleasant and unpleasant odors were differentially associated with variation of fluctuations of alpha EEG activity and Saito et al. (1991) found with ERPs that lemon oil was responded to greater by the left hemisphere and isovaleric acid elicited enhanced responses by the right hemisphere.

The results of the few studies which examined hemispheric processing of the hedonic qualities of odors appear consistent with specialized roles for the hemispheres such that the left hemisphere showed dominant processing of pleasant odorants and the right hemisphere showed enhanced processing of unpleasant odorants. However, given the limited number of studies on this topic, these interpretations are still tentative.

Odors are particularly interesting to study as a function of lateralized stimulation because, as mentioned previously, there can be minimal cognitive processing involved when odors are experienced affectively. As Ehrlichman and Bastone (1992a) point out, "when stimuli such as films, faces or sentences are used to evoke affective responses there is always the danger that lateralized cognitive processes are coming into play. Further, since moods and emotions are complex states, involving both feelings and thoughts, it is important to specify exactly what aspect of affective experience is lateralized" (p. 158). These authors contend that using odors to evoke positive and negative affective experiences may be useful in establishing whether the two hemispheres of the brain are specialized for different hedonic processes.

Sex Differences Related to Laterality, Emotional Procedures in the Laboratory and Olfactory Stimulation

Given that the present study was concerned with lateralized emotional responses to odors, gender was considered an important variable to investigate because there have been notable sex differences found in research related to the laterality of cognitive functions, in response to emotional procedures in the laboratory and in sensitivity to olfactory stimulation, as will be discussed below.

There is an abundance of evidence that male's cognitive functions are more lateralized than female's. For instance, greater right hemisphere lateralization for spatial cognitive functions have been found for males (e.g., McGee, 1979). Pennebaker and Roberts (1992) also noted further evidence to suggest that female's brains are less lateralized that male's. Specifically, neuroanatomically, females have a relatively larger corpus callosum (Springer & Deutsch, 1989), which has been suggested to permit greater integration of information between the hemispheres (De La Coste-Utamsing & Holloway, 1982). Differences in lateralization in men in woman have been suggested to originate from maturational differences (e.g., Waber, 1976) as well as by evolutionary means (e.g., Levy, 1978).

In terms of emotional procedures in the laboratory, a number of mood induction, facial EMG, and heart rate studies indicate that females are more emotionally physiologically responsive than males. For instance, Liotto and Tucker (1992) used mood induction procedures to induce elation or depression, and examined reaction times to stimuli presented to the left or right visual field in both sexes. These authors reported that only females who were in the depressed mood showed slowed reaction times during uncued presentations of stimuli in the left visual field. Similarly, Rothkopf and Blaney (1991) used mood induction procedures and only found a mood-congruent memory effect in women. Females also have demonstrated enhanced facial responsiveness (measured by EMG) to emotionally valenced stimuli while viewing affectively laden slides (Dimberg & Lundquist, 1990; Brown-Kuhl & Bruder, 1997; Grossman & Wood, 1993; Lang, Greenwald, Bradley & Hamm, 1993), during emotional imagery (Schwartz, Brown & Ahern, 1980) and while exposed to loud noises (Dimberg, 1990). Consistent with these findings, other studies have found females to have increased heart rates compared to men in aversive situations, such as during a 3 minute surprise speech (Baldwin & Clevenger, 1980), in a shock avoidance discrimination learning task (Graham, Cohen & Shavonian, 1966) and during unpleasant relaxation imagery (Gautier & Cook, 1997).

In the odor literature, females are often reported to demonstrate enhanced sensitivity compared to men. For instance, females have shown greater sensitivity to odors in olfactory tests (Koelega & Koster, 1974; Doty, Snyder, Huggins & Lowry, 1981; Cain, 1982). Physiological investigations of odors have also shown larger olfactory evoked potential amplitudes in females compared to males (Evans, Cui, & Starr, 1995; Becker et al., 1993).

In summary, while males have been found to have greater lateralized hemispheric cognitive functioning, females have shown enhanced physiological emotional responsivity as well as increased sensitivity to odors. Based on these findings, it was expected that females would be more physiologically responsive than males if sex differences emerged in the present study.

Startle Probe Reflex

The startle probe reflex is a physiological measure that on theoretical and empirical grounds differentiates the hedonics of affective stimuli. Recently, investigators have begun examining how valenced odorants modulate the startle probe reflex and the results have been generally consistent with the way other affectively valenced stimuli influence this response (Ehrlichman et al., 1995; Miltner, et al., 1994). However, the startle probe reflex has never been used to examine the effects of lateralized affective stimuli, including odors. As will be discussed below, it holds great promise in this area of investigation because of its demonstrated relationship to hedonics. A brief summary of the startle probe reflex and its modulation by emotional stimuli will follow.

What is the Startle Probe Reflex? When suddenly presented with a burst of bright light or a loud noise, animals and humans usually respond with an involuntary startle reflex. In animals, the reflex often causes the whole body to move. In humans, the eyeblink response is the most easily observed and considered the most reliable manifestation of the startle reflex, although the reflex may continue as a general flexion causing a wavelike motion throughout the torso of the body. Various secondary behaviors which appear to be voluntary avoidance behaviors may follow the primary flexion as well.

Various methods have been used to measure the eyeblink response in humans to a startle probe; however, the usual technique is to measure the electromyographic (EMG) activity from the orbicularis oculi muscles in close proximity to the lower eyelids. EMG activity is measured in terms of the latency and amplitude of the eyeblink response to the startle probe. The eyeblink reflex usually occurs between 30 and 50 ms after the onset of an abrupt acoustic stimuli. For acoustic stimulation, a stimulus of 90 dB with a rise time of 10 to 12 ms produces a reliable startle blink. The involuntary aspect of the startle reflex, as well as the fact that the subjects are usually instructed to ignore the noise or light probes allows this technique, compared to some other psychophysiological measures, to be more resistant to extraneous influences such as subject's attention, systematic processing, or cognitive interpretations.

Modulation of Startle Probe Reflex with Emotional Stimuli. For many years the startle probe reflex has been used to investigate classical fear conditioning, arousal and attention. However, recently Lang and his colleagues have studied its capacity to distinguish positively and negatively valenced stimuli (Bradley et al., 1990; Lang, Bradley & Cuthbert, 1990, 1992; Vrana, Spence & Lang, 1988). When subjects experience negative, neutral or positive foreground stimuli, the startle blink modulates in a linear manner such that it is potentiated, intermediate or attenuated, respectively. Lang and his colleagues have postulated that the magnitude of the startle reflex reflects the affective/motivational state of the organism, either positive (approach, appetitive) or negative (avoidance, defensive). When an organism is experiencing a negative affective state, its efferent system (which includes exteroceptive reflexes) is primed for a defensive reaction, and a startle response (which is considered to be a defensive response to an aversive stimulus) will be enhanced. During positive motivational experiences the organism's system is primed for approach behaviors, and its response to the startle probe, which is aversive, will be attenuated.

Many studies support the theory that the startle reflex is differentially modulated by the valence of affective stimuli. For example, this modulatory pattern was demonstrated during the presentation of slides (Bradley et al., 1990; Lang et al., 1990; 1992; Vrana et al., 1988) which were either pleasant (e.g., romantic couples, cuddly animals, appetizing food), neutral (e.g., books, shoes, hair dryers) or aversive (e.g., snakes, bloody body wounds or burns, medical injections). A similar modulatory pattern was also demonstrated during pleasant and unpleasant mental imagery (Cook, Hawk, Davis & Stevenson, 1991), during rehearsal of neutral and unpleasant sentences (Vrana & Lang, 1990) and during the anticipation of electric shock (Greenwald, Hamm, Bradley, & Lang, 1991).

The replication of this pattern of modulation of the startle reflex response to emotional stimuli also was attempted using odorants as affective stimuli (Ehrlichman et al., 1995; Miltner et al., 1994). As expected, in both studies, the startle probe response was potentiated by unpleasant odors; however, the expected attenuation by pleasant odors compared to the neutral no-odor condition was not confirmed in either study. Ehrlichman et al. used a within subjects design in which subjects randomly inhaled unpleasant, neutral no-odor, and pleasant odors. Because subjects were presented with both pleasant and unpleasant odors, they may have found the entire experience unpleasant, thus compromising the positive effects of the pleasant stimuli. Miltner et al. also used a within subjects design; however, the subjects were presented with an unpleasant odor and a pleasant odor during different sessions and they were presented neutral air during both sessions. These authors speculated that their pleasant odor was not pleasant enough to produce the desired effect.

This study employed a modification of the methodology used in the previous study by Ehrlichman et al. (1995) to maximize the impact of the pleasant odor on startle probe magnitude. To avoid the possibility of the unpleasant odor interfering with the processing of the pleasant odor, a between-subjects design, in which different subjects inhaled pleasant and unpleasant odorants (and all subjects inhaled neutral air) was used.

To maximize differences in the experiences produced by the odorants and the neutral conditions, only the 2 odorants which were previously rated as extremely pleasant and unpleasant and produced the greatest attenuation and augmentation in the Ehrlichman et al. (1995) study were used in this study (i.e., coconut and Limburger cheese).

Startle Reflex and Laterality. The primary purpose of this study was to examine whether there was hemispheric specialization for the modulation of the blink reflex in response to the lateralized presentation of pleasant and unpleasant odors. Recent studies support the view that the startle reflex may be a useful technique in the study of laterality of emotion (Bradley, Cuthbert & Lang, 1991, 1996). These studies examined the effects of startle probe modulation by lateralizing the startle probes as subjects viewed pleasant, neutral and unpleasant slides. Significant modulation was demonstrated when acoustic probes were presented to the left ear but not to the right ear using either blocked monaural presentations or mixed presentations (Bradley et al., 1991; 1996). Because acoustic information is primarily processed by the contralateral hemisphere (approximately two thirds of the neural connections), the authors suggested that these data supported a right hemispheric specialization for emotional processing. In another study, Hawk and Cook (1997) reasoned that the haptic system is more lateralized than the acoustic system. They utilized a similar hedonic slide procedure and found the same pattern of startle modulation with tactile probes (i.e., an air puff to the side of the face). Although these studies are consistent with a right hemispheric superiority, the results are only suggestive. In all these lateralized probe studies, although modulatory effects of valence were significant on the left (right hemisphere processing) and not on the right side, there was no interaction between slide valence and probe side. However, when Grillon and Davis (1995) utilized the threat of shock as an aversive condition stimulus verses no threat, they found a different pattern of acoustic reflex modulation. These authors found that effects were larger for probes presented to the right ear. Given these inconsistencies, a right hemispheric modulatory superiority for lateralized presentations of startle probes is somewhat tenuous.

Unlike the above studies which lateralized the background startle probe (acoustic or tactile), this study is the first to examine the startle probe reflex response during lateralized presentations of **emotional foreground stimuli**.

Statement of Hypotheses

Using the acoustic startle probe reflex in response to lateralized presentations of odorants, the major prediction was that there would be a significant hemispheric modulation effect for emotional processing of pleasant and unpleasant odorants compared to their corresponding no-odor conditions favoring either the right hemisphere hypothesis or the valence hypothesis. Notably, the following predictions are based on findings that during pleasant stimuli presentation there is startle blink magnitude attenuation and during unpleasant stimuli presentation there is startle blink magnitude augmentation as well as the findings that olfactory hemispheric projections are primarily ipsilateral.

For the **pleasant** odorant, it was predicted that if the right hemisphere hypothesis was supported, **right** nostril presentation of the odorant would have shown the greatest attenuation of eyeblink responses when compared to its corresponding neutral no-odor condition. However, if the valence hypothesis was implicated, the pleasant odorant presented to the **left** nostril would have evoked the smallest eyeblink response when compared to its corresponding neutral no-odor condition.

For the **unpleasant** odorant, if either the right hemisphere hypothesis or the valence hypothesis was upheld, **right** nostril presentation of the odorant would have resulted in the greatest augmentation of the eyeblink response when compared to its neutral no-odor condition.

METHOD

Participants

The data from 80 participants (40 males and 40 females) were studied, with 40 participants in each of two odorant (pleasant and unpleasant) groups. All the participants were nonsmokers between the ages of 18 and 36 and were screened for right-handedness according to the Edinburgh inventory (Oldfield, 1971), anosmia, absence of facial neuromuscular problems, strong sensitivities to odors and conditions that may interfere with the smelling of odors (e.g., a deviated septum, a cold).

Odorants

Participants were monorhinically presented with two odor stimuli: the neutral no-odor, and either the pleasant or unpleasant odor. The two odorants which were determined in the study by Ehrlichman et al, (1995) to have the highest hedonic (pleasant and unpleasant) ratings and greatest startle modulation were used. The unpleasant odorant was Limburger cheese (4 grams) and the pleasant odorant was IFF pure coconut saturated in polyethylene interflo pellets. Each of the 4 oz. bottles containing the stimuli were filled with cotton and covered on the outside to insure that their contents were not visible.

Some odorants induce trigeminal as well as olfactory stimulation. Trigeminal innervation is quite different from olfactory innervation. Because this study was only concerned with lateralization effects during olfactory stimulation, the odorants were tested in a pilot study to ensure they did not produce trigeminal stimulation effects (See Appendix A).

Acoustic Startle Probe and Breath Monitoring

The acoustic startle probe was delivered via stereo headphones (Radio Shack Titanium Pro 25) and consisted of a 100 DB 50 ms burst of white noise (measured at the earphones with a Bruel & Kjaer Model 2203 sound level meter) with an instantaneous rise time generated by a Med noise generator and audio amplifier. Breathing was detected by a Grass ONT2 thermocouple attached to a rod 4 mm in diameter that was snapped into position above each bottle prior to being sniffed. The signals from the thermocouple were amplified 10,000 times and filtered (1-300 Hz) by a Grass Model 12 Neurodata Acquisition System. Signals were sampled on-line at 60 Hz using an IBM AT and average values were obtained every 10 samples. Inhalations and exhalations were detected as a shift halfway between the increasing or decreasing values. Presentation and timing of acoustic probes were controlled by an IBM AT. Heart rate signals were amplified 5,000 times and filtered via a Grass Model 12 Neurodata Acquisition System with high and low cutoffs set at .3 Hz and 300 Hz, respectively. Heart rate signals were sampled on-line at 80 Hz and stored and examined off-line using a Turbo basic program which visually indicated the presence of a cardiac R-wave.

Physiological Data Collection and Reduction

EMG activity was recorded from two Beckman Ag-AgCl miniature electrodes on the orbicularis oculi muscles beneath the left eye using the placement recommended by Lang et al. (1990). A ground electrode was placed on the center of the forehead. Recording sites were prepared with rubbing alcohol and a mild skin abrasive. Resistance of the electrodes did not exceed 5,000 Ohms.

The raw EMG signal was amplified by a factor of 10,000 with a 100-1000 Hz bandpass filter using a Grass Model 12 Neurodata Acquisition System and displayed on a Tektronix 5111 oscilloscope. Digital sampling at 1000 Hz began at the onset of the acoustic probe and continued for 250 ms. The startle data was stored and examined off-line using a Turbo Basic program. The first 90 samples of each trial were rectified and smoothed using a software procedure that utilizes an IIR low-pass digital filter and a 20 ms time constant. Several other studies have demonstrated baseline differences among conditions (e.g., Bradley et al., 1990,1991; Ehrlichman et al., 1995). Because it has been suggested that significant effects for both startle blink magnitude and baseline EMG could indicate that the EMG baseline effects biased the startle results (Ehrlichman et al., 1995), change scores were computed to rule out this possibility. The change scores comprised the measure of startle magnitude on each trial and were computed by measuring the peak startle response from the transformed data on each trial and subtracting it from baseline orbicularis oculi tension, calculated as the average of the first 20 rectified samples prior to reflex onset.

Prior to statistical analysis, EMG for each trial was examined graphically on the computer screen for visual inspection. Information about the odor trials was not provided during this inspection. Trials were eliminated when the baseline was unstable, the waveform was too unstable for peak response to be accurately measured, experimenter error occurred or equipment error occurred.

Heart rate activity was recorded from two Beckman Ag-AgCl standard electrodes. One electrode was applied to the middle of the right collarbone and the other was attached to the left ankle. The number of heart-beats per 10 second trial was calculated and averaged off-line to beats per minute.

Procedure

When the participants arrived at the laboratory, written informed consent was obtained, and electrodes were attached. All aspects of electrode placement took place in a room separate from the experimental chamber. Participants were told that the study involved "brain responses" to odors. In an attempt to draw attention away from eye blinks, two extra "dummy" electrodes were attached to the forehead supposedly to measure EEG. In the experimental chamber, participants were seated in an adjustable chair and given instructions (see below). Participants were also told that loud noises heard over the headphones (acoustic startle probes) were used to "calibrate" the brainwave recordings and should be ignored.

There were two groups of participants. One group was presented with an unpleasant odorant; the other group was presented with a pleasant odorant. Both groups were also presented with a neutral no-odor. During each of 8 blocks, the participants inhaled with the right or left nostril either an odorant or a no-odor. The four schedules of block orders of nostril and odor presentations are shown below. In each schedule there were 2 parts, where Part 2 was the reverse order of the blocks from Part 1. It was considered important to have two parts to provide counter balancing for the strong habituation of startle responses which occurs over time and to provide enough data to analyze. Each participant was randomly assigned to one of the 4 schedules of block presentations until an equal number of participants was in each schedule order.

	Part 1				Part 2			
Block #:	1	2	3	4	5	6	7	8
Schedule								
1	LN	LO	RN	RO	RO	RN	LO	LN
2	RN	RO	LN	LO	LO	LN	RO	RN
3	LO	LN	RO	RN	RN	RO	LN	LO
4	RO	RN	LO	LN	LN	LO	RN	RO

Where L=Left Nostril, R=Right Nostril, N=Neutral No-Odor, and O = Odorant.

Participants were given the following instructions: "Focus your attention only on the odor as you are smelling it, even if you do not smell an odor, and reflect upon how you experience it or how it makes you feel." To limit possible visual distractions, participants were instructed to keep their eyes open and to focus on a black dot (1 cm diameter) in front of them (1 meter distance). Immediately preceding each block, one nostril was completely covered with gel foam tape to ensure that air was unable to enter the nostril. The experimenter then opened a bottle, placed it in a holder, and moved the thermocouple into position 4 mm above the bottle. The bottle holder and chin rest were adjusted so that the participant's nostrils were approximately 0.5 cm directly above the thermocouple. The contents of the bottle were then breathed for the entire block (approximately 80 seconds).

Within each block, 8 probe trials were presented. Although Ehrlichman et al. (1995) administered startle probes only during inhalations in order to ensure the participants were experiencing the odors, studies examining the effects of smelling odorants usually do not hold constant when a participant is inhaling or exhaling. Therefore, 4 probes were presented during inhalations and 4 probes were presented during exhalations within each block to guarantee every participant received the same smell experience with each odorant. To increase the unpredictability of the probe presentations during inhalations and exhalations, it was also considered important to present probes randomly during every trial with an interstimulus interval varying between 5 and 10 seconds. The participants were asked to breathe at their usual intensity and two soft tones (one high, one low) were used to signal when to inhale and exhale. A practice trial was given prior to the experimental trials, in which 2 probes were delivered to ensure that the participants understood the procedure.

Participants were administered two Likert scales that assessed their current affective experiences on the 2 dimensions of arousal and valence. These scales were given before the electrodes were applied, between blocks of startle trials, and after the electrodes were removed. Both scales were numbered from 1 to 9. The participants were asked to visually inspect the scales and verbally indicate a number corresponding to their experience. The valence scale included descriptors where 1 was "Feeling Bad, 5 was "Neutral", and 9 was "Feeling Good". The arousal scale included the descriptors where 1 was "Drowsy", 5 was "Neutral", and 9 was "Alert". Between Part 1 and Part 2 of the experiment, participants completed the Edinburgh handedness questionnaire for approximately 5 to 10 minutes. Following the last block, participants gave hedonic ratings of the odors. They were instructed to rate the degree that they liked or disliked the odors, using a visually presented Likert scale ranging from -100 (extremely unpleasant) to +100 (extremely pleasant). Instructions emphasized that ratings should be used to report hedonic quality, not odor intensity. Then a similar scale was presented for the participants to rate the intensity of the odors. Next, the participants were administered the valence and mood scales they received after each block of trials; however, instead of assessing their current affective experience, they were instructed to rate their overall experience of the entire experiment. Finally, participants were given a brief test for anosmia, which required recognition of 5 common odors, each from a list of 4 possibilities. The data of participants who failed to recognize 2 or more odors was eliminated from the analysis.

RESULTS

Startle Blink Effects

Startle blink magnitude responses were analyzed using a 5-way MANOVA, with 2 between group measures, Valence Group (positive odor with corresponding neutral no-odor vs. negative odor with corresponding neutral no-odor) and Sex (male vs. female); and three within group measures, Nostril (right vs. left), Odor/No-Odor (presence of odor vs. absence of odor) and Breath Direction (inhalation vs. exhalation). The results are presented so that the laterality and odor interactions of primary relevance to the dissertation are presented first, gender effects are presented next, and Breath Direction effects are presented last.

<u>Laterality and Odor Effects</u>. From the 5-way MANOVA the interactions most relevant to the dissertation hypotheses were 1) a 3-way Valence Group X Odor/No-Odor X Nostril interaction to determine whether the findings supported the right hemisphere or valence hypotheses and 2) a 2-way Valence Group X Odor/No-Odor interaction to find out whether odors of different valence elicited different startle blink modulation effects.

The significant effects presented from the startle blink magnitude analysis are shown in the startle column of Table 1. No main effects were found involving Nostril, Valence Group or Odor/No-Odor. The 3-way Valence Group X Odor/No-Odor X Nostril interaction was also not significant. Therefore, the findings did not support either the right hemisphere or valence hypotheses.

However, as is shown in Table 1, there was a significant 2-way interaction which

Table 1. Main Effects and Significant Interactions from MANOVA Analyses for Measures of Startle Blink Magnitudes, Baseline EMG Responses, Heart Rate Responses, Mood Ratings and Arousal Ratings.

	Measure														
	Startle			**Baseline**			**Mood**			**Arousal**			**Heart Rate**		
Main Effects	**df**	**F**	**p**	**df**	**F**	**p**	**df**	**F**	**p**	**df**	**F**	**p**	**df**	**F**	**p**
Nostril (N)															
Odor/No Odor (O/NO)															
Valence (V)				1,76	4.26	.042	1,76	9.63	.003						
Sex (S)				1,76	4.31	.041									
Breath Direction (B)	1,76	8.53	.005												
Interactions															
V x O/NO	1,76	9.75	.003				1,76	37.41	.000				1,76	4.25	.043
S x O/NO										1,76	4.56	.036			
V x N x B	1,76	4.52	.037												
S x V x O/NO	1,76	4.25	.043										1,76	4.25	.043

involved Valence Group and Odor/No-Odor. It was predicted that this interaction would show startle blink modulation effects related to the hedonic nature of the odors, such that the smallest blink magnitudes would be elicited with pleasant odor blocks and the largest responses would be exhibited with unpleasant odor blocks. As shown in Figure 1, the pleasant and unpleasant odor blocks differentially induced changes in startle modulation in the expected directions. Consistent with previous findings (Ehrlichman et al., 1995; Miltner et al., 1994), paired t-tests confirmed startle blink magnitudes were augmented ($p = .066$) with the unpleasant odor blocks compared to the no-odor blocks. Additionally, as expected because of improved methodology but previously not found, startle magnitudes were attenuated ($p =.02$) during the pleasant odor blocks compared to the no-odor blocks.

Gender Effects. No main effects for gender were found (see startle column in Table 1). However, compounding the above mentioned 2-way Valence Group X Odor/No-Odor interaction, there was a significant 3-way Sex X Valence Group X Odor/No-Odor interaction. This interaction is illustrated in Figure 2. Additional 2 X 2 Valence Group X Odor/No-Odor analyses were performed independently for each sex to better understand the significance of the 3-way interaction. These analyses showed that the Valence Group X Odor/No-Odor interaction was significant for females [$F(1, 38) = 10.69$, $p = .002$)] but not for males [$F(1, 38) = .76$, $p = .390$)]. Paired t-tests between the odors of different valence and their no-odor counterparts confirmed there were significant modulation effects in the directions predicted only for females, such that compared to no-odors, startle blink magnitudes were augmented by unpleasant odors (p

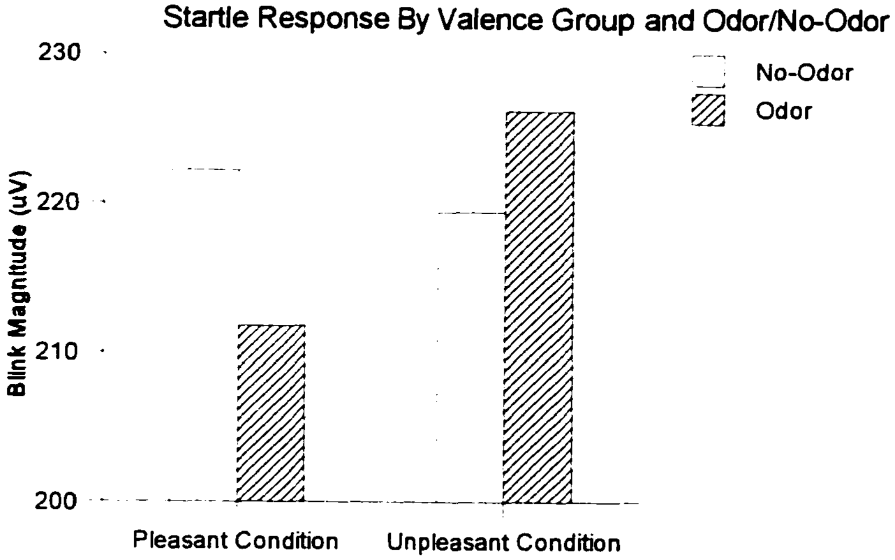


Figure 1. Interaction of Mean Startle Magnitudes as a Function of Valence Group and Odor/No-Odor.

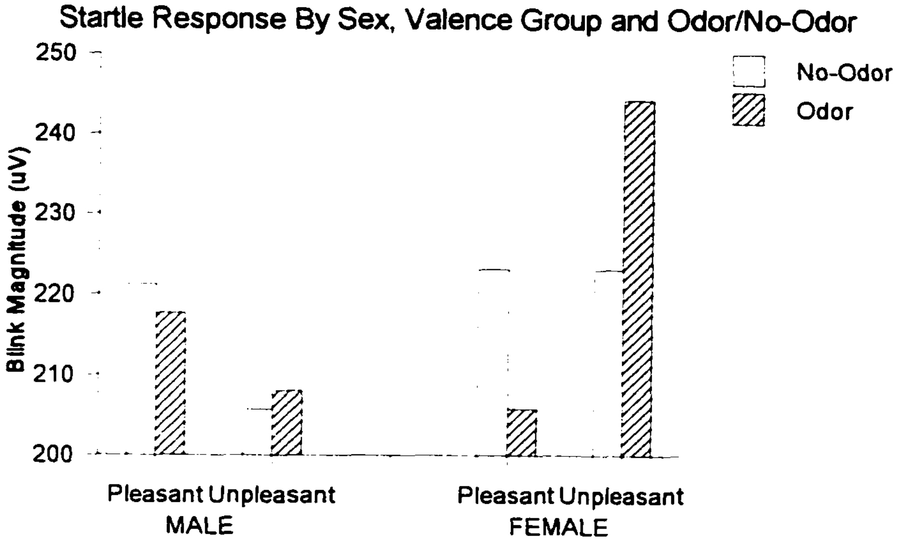


Figure 2. Interaction of Mean Startle Blink Magnitudes as a Function of Sex, Valence Group and Odor/No-Odor.

= .018) and attenuated by pleasant odors (p = .059). The males showed a similar but nonsignificant pattern of startle blink modulation (pleasant odor compared with no-odor, p = .601, unpleasant odor compared with no-odor, p = .499). This finding supports research which shows facial muscles of females are more physiologically reactive to emotional stimuli as compared to males (Schwartz et al., 1980; Dimberg & Lundquist, 1990; Brown-Kuhl & Bruder, 1997; Grossman & Wood, 1993; Lang et al., 1993; Dimberg, 1990). However, the results do not necessarily indicate that males did not show startle blink modulation in response to the pleasant and unpleasant odors, given that the statistical power was reduced by the analysis and that the patterns of startle blink responses of the males were in the expected directions.

Breath Direction Effects. Recall that in each block there was an equal number of probes presented during inhalations and exhalations. It was expected that maximum smelling experience would occur during inhalations so it seemed important to present probes while inhaling. Although there was no particular interest in exhalations, probes were also presented equally during exhalations to insure unpredictability of the startle probes. The within group factor of Breath Direction (inhalation vs. exhalation) was therefore exploratory to investigate whether there was a Breath Direction effect.

As is shown in the startle column in Table 1, there was a significant main effect found for Breath Direction, such that startle blink magnitudes during inhalations were reduced (M = 243.10, sd = 139.28) relative to those during exhalations (M = 249.98, sd = 142.56). Although this Breath Direction effect was not expected, there are two theoretical implications of these findings which will be elaborated upon in the Discussion:

1) Zajonc's vascular theory of emotional efference (Zajonc, Murphy & Inglehart, 1989), regarding the hedonic effects of warmed and cooled air; and 2) inhalations and exhalations considered in terms of emotional behavioral indicators of approach and avoidance.

There was also an unexpected laterality interaction which involved Breath Direction. This 3-way Valence Group X Nostril X Breath Direction interaction is illustrated in Figure 3. Additional 2 X 2 Valence Group X Nostril simple effects analyses were performed independently for inhalations and exhalations in an attempt to gain a better understanding of the 3-way interaction. These analyses showed only a Valence Group X Nostril interaction trend during inhalations [F(1, 78) = 3.09, p = .083)] but not during exhalations [F(1, 78) = .32, p = .575]. As is depicted in Figure 3, the smallest startle blink magnitudes occurred in the pleasant Valence Group during left nostril inhalations (M = 206.54, sd = 119.48). Paired t-tests confirmed that the left nostril inhalation blink responses were significantly attenuated compared to right nostril inhalations (M = 218.70, sd = 127.48), (p = .034). However, none of the other paired t-tests examining left/right differences for the pleasant or unpleasant conditions during inhalations or exhalations were significant, although the largest augmentation of startle blink magnitudes was found in the presence of the unpleasant Valence Group during right nostril exhalations (M = 229.65, sd = 148.80). T-tests were also used to compare differences in startle blink magnitudes during inhalations and exhalations. Decreased startle blink magnitudes occurred in the pleasant Valence Group with left nostril presentations during inhalations compared to exhalations (p = .003), and increased startle

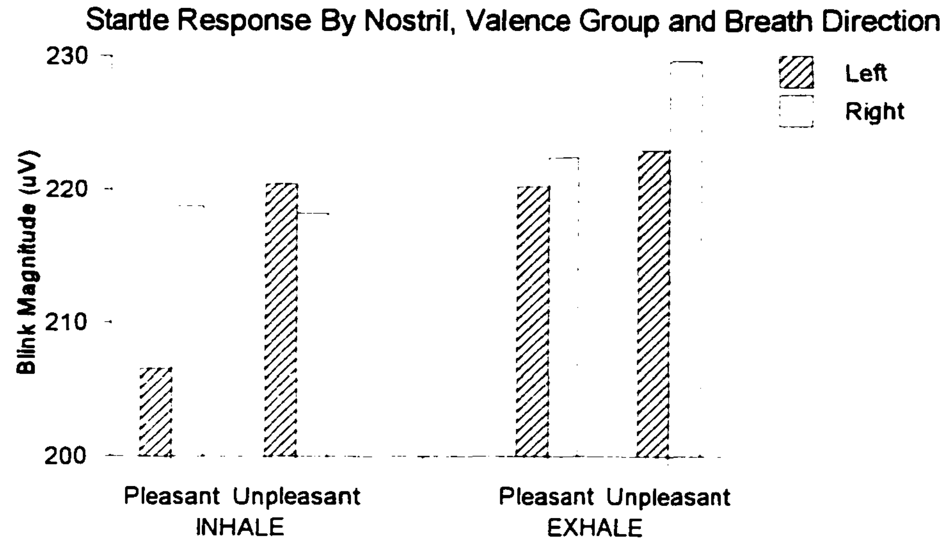


Figure 3. Interaction of Mean Startle Blink Magnitudes as a Function of Nostril, Valence Group and Breath Direction.

Note: This analysis collapses across the Odor/No-Odor factor blink magnitudes occurred in the unpleasant Valence Group with right nostril presentations during exhalations compared to inhalations (p=.029).

In summary, one of the hypotheses of this study was that startle blink magnitudes elicited during lateralized presentations of odors of different valence would produce significant modulation patterns favoring either the right hemisphere hypothesis or the valence hypothesis. Unexpectedly, the only lateralized effect found in this study involved the above mentioned effect of Breath Direction, wherein the smallest eyeblink magnitudes were found in the **pleasant** Valence Group with **left** nostril **inhalations** and the largest eyeblink magnitudes were found in the **unpleasant** Valence Group with **right** nostril **exhalations**.

Baseline EMG

Startle blink magnitudes were calculated by subtracting a pre-startle baseline EMG from peak startle EMG. Given that startle probe studies have reported differences in resting baseline EMG responses amongst affective conditions of valenced pictures (e.g. Bradley et al., 1990, 1991) and odors (Ehrlichman et al., 1995), it is prudent to check for baseline differences during presentation of affective stimuli. If startle magnitude was measured without subtracting the baseline, differential baseline activity elicited by valenced stimuli could influence measurement of the peak startle. In order to determine whether the baseline EMG responses were influenced by the valenced odors, the baseline EMG responses were compared across the same conditions and subjected to the same analyses as the startle responses (5-way Valence Group X Odor/No-Odor X Sex X Nostril X Breath Direction MANOVA). The results of this analysis are presented in the baseline column of Table 1.

Unlike the startle data, no significant interactions were found with the baseline EMG data which would suggest modulation responses between the valenced odor blocks and the no-odor blocks, nor were there any significant Breath Direction effects. However, there was a significant main effect of Valence Group (see baseline EMG column in Table 1), wherein the presence of the unpleasant odor (and its no-odor) blocks elicited larger mean baseline EMG responses (M = 9.10, SD = 2.66) then the presence of the pleasant odor (and its no-odor) blocks (M = 7.98, SD = 2.56). These findings are similar to the results found by Ehrlichman et al. (1995) in which greater EMG activity was found with unpleasant odors than with pleasant or neutral odors.

As is shown in the baseline column of Table 1, the only significant effect involving gender was a main effect of Sex, in which females exhibited significantly greater baseline EMG responses (M = 9.10, SD = 2.45) than males (M = 7.97, SD = 2.47).

Odor Ratings

All of the odors (coconut, no-odor, Limburger cheese) were rated for hedonic and intensity qualities at the end of the experiment. In order to examine the effects of odors on the ratings, the hedonic and intensity ratings were each examined by a Valence Group X Odor/No-Odor MANOVA.

For the analysis involving hedonic ratings, there was a main effect which involved Valence Group [$F(1, 78) = 639.69$, $p < .001$] wherein the unpleasant Valence Group odor and no-odor produced a substantially decreased hedonic rating compared to the pleasant Valence Group odor and no-odor. Notably, as is depicted in Figure 4, the main effect is related to the expected and highly significant Valence Group X Odor/No-Odor interaction, F(1, 78) = 658.76, $p < .001$ for the hedonic ratings of the odors. Figure 4 illustrates the mean ratings of the valenced odors and no-odors individually and clearly shows that the main effect is due to the hedonic ratings of the unpleasant and pleasant odors and not their corresponding neutral no-odors which were given neutral hedonic ratings. As expected from this interaction, t-test comparisons revealed that all the odor conditions were rated significantly different from each other, such that the pleasant odor was rated as more pleasant than unpleasant odor ($p < .001$) and both the pleasant and unpleasant odors were rated as more pleasant and unpleasant, respectively, than their corresponding neutral odors (both t-tests, $p < .001$).

Similarly, the results of the intensity analysis were as expected. There was a highly significant main effect for Odor/No-Odor [F(1, 78) = 1174.57, $p < .001$] in which the valenced odors were found to be more intense (M = 70.85, sd = 18.49) then the neutral no-odor (M = 1.00, sd = 3.12).

Further analyses were conducted comparing just the pleasant and unpleasant odors to determine whether they were comparable in respect to hedonic magnitude as well as in intensity. T-tests conducted between the absolute values of the hedonic ratings of the pleasant (M = 65.70, sd = 17.73) and unpleasant odors (M = 61.68, sd = 25.81) were not significantly different from each other [t (78) = .81, p = .419], suggesting that both odors exhibited equal but opposite levels of hedonic qualities. Likewise, intensity ratings of the pleasant (M = 73.25, sd = 16.76) and unpleasant odors (M = 68.45, sd =

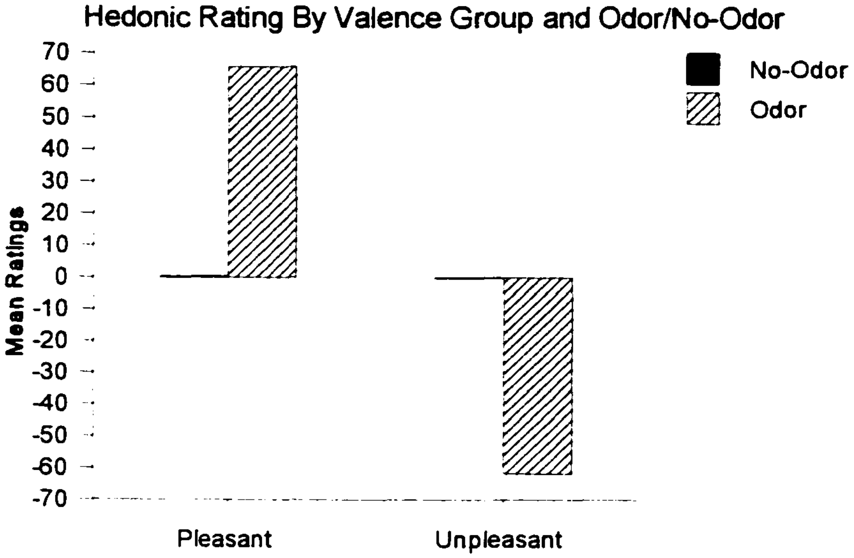


Figure 4. Interaction of Mean Hedonic Ratings as a Function of Valence Group and Odor/No-Odor.

20.00) were not significantly different from each other [t(78) = 1.16, p = .248], indicating that both odors were also matched for intensity.

When gender effects were analyzed via an additional 2x2x2 MANOVA (Sex, Valence Group and Odor/No-Odor), no significant gender main effects or interactions were found for either the hedonic or the intensity ratings.

Mood and Arousal Ratings

In order to assess the emotional experience of the participants during the experiment, mood and arousal ratings were compared across the same conditions and subjected to the same analysis as the startle blink magnitude responses (with the exception of Breath), i.e., a 4-way (Sex X Valence Group X Nostril X Odor/No-Odor) MANOVA. The significant effects are presented in Table 1 under the columns of Mood and Arousal.

As is seen in the mood column of Table 1, there was a significant main effect of Valence Group. The pleasant Valence Group odor and no-odor blocks were rated as inducing a significantly better mood (M = 6.39, sd = 1.22) than the unpleasant Valence Group odor and no-odor blocks (M = 5.06, sd = 1.05). There was also a highly significant interaction between Valence Group and Odor/No-Odor (see Table 1 and Figure 5). T-tests confirmed that moods were rated significantly better [t (39) = -4.41, p < .001] in response to the pleasant odor blocks (M = 6.74, sd = 1.17) compared to the no-odor blocks (M = 6.04, sd = 1.41). In contrast, worse moods were associated with unpleasant odor blocks (M = 5.03, sd =1.45) then with the no-odor blocks (M = 6.18, sd = 1.23), [t (39) = 4.40, p < .001]. Additionally (and not unexpectedly), between group

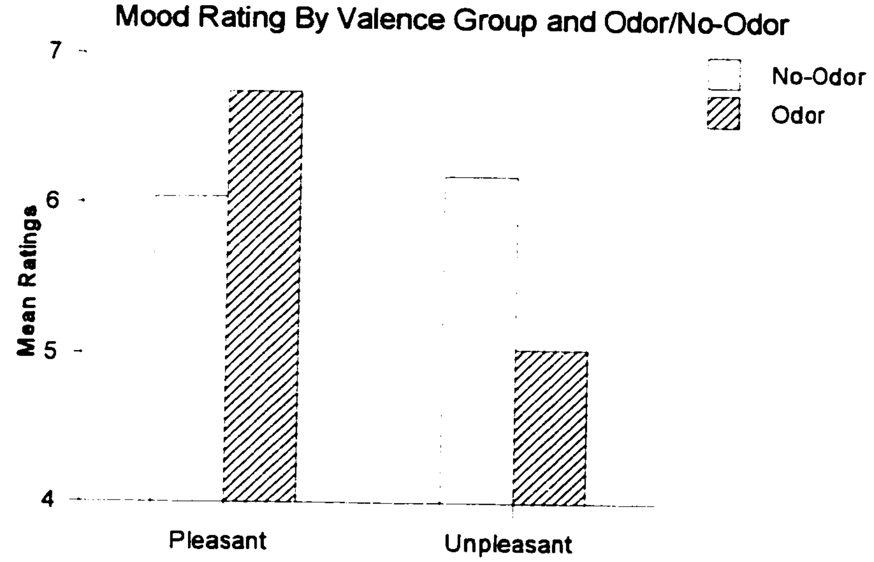


Figure 5. Interaction of Mean Mood Ratings as a Function of Valence Group and Odor/No-Odor.

t-tests revealed that the pleasant odor blocks were rated as producing significantly better moods than unpleasant odor blocks [t (78) = 5.82, p < .001]. No significant gender effects regarding mood were found.

The only significant finding in the overall analysis of arousal ratings was a Sex by Odor/No-Odor interaction (see arousal column of Table 1). As is depicted in Figure 6, and confirmed by t-tests, only males showed a tendency to be more aroused by odor blocks, both pleasant and unpleasant (M = 6.62, SD = 1.48) then no-odor blocks (M = 6.39, SD = 1.52), t (39) = -1.65, p = .107). Females showed no significant arousal difference [t (39) = 1.35, p = .185] between the no-odor blocks (M = 6.56, SD = 1.39) and the odor blocks (M = 6.39, SD = 1.50).

Additional MANOVAs were conducted for both mood and arousal to examine whether there was change from pre-experimental ratings to post-experimental ratings of overall experience of the experiment. Significant changes were not found for arousal ratings but there were significant changes in mood. In the pleasant Valence Group, ratings of moods significantly increased to a positive degree [F(1,39) = 6.30, p = .016] and conversely, in the unpleasant Valence Group, ratings of moods significantly decreased to a negative degree [F(1,39) = 16.62, p < .001].

Heart Rate Effects

<u>Heart Rate Modulation</u>. A common physiological measure used in emotional studies is the heart rate response. Therefore, in order to better understand emotional physiological responses during lateralized presentation of valenced odors, this study not only examined startle reflex eyeblink magnitudes but also heart rate responses. Heart

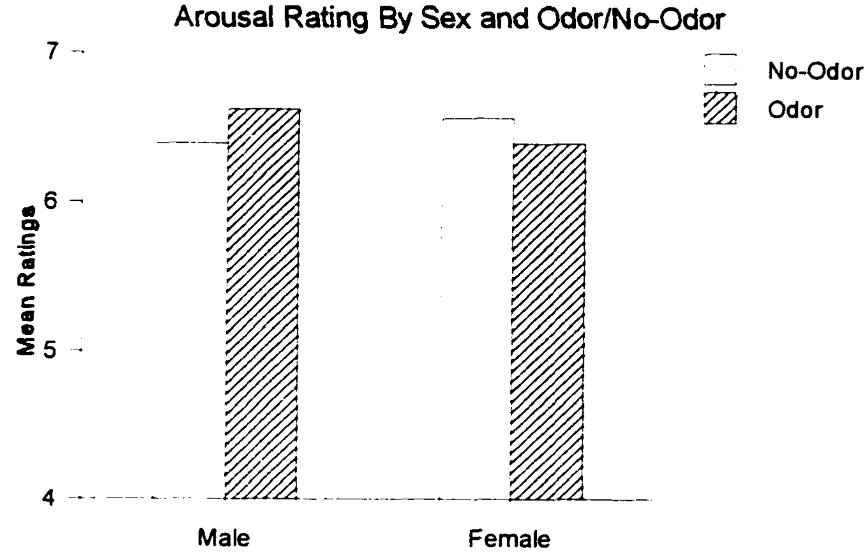


Figure 6. Interaction of Mean Arousal Ratings as a Function of Sex and Odor/No-Odor.

rate responses were subjected to a 2 X 2 X 2 X 2 MANOVA, with the between group variables consisting of Valence Group (positive odor with corresponding no-odor vs. negative odor with corresponding no-odor) and Sex (males vs. females) and the within group variables consisting of Nostril (right vs. left) and Odor/No-Odor (presence vs. absence of odor). As is seen in the heart rate column of Table 1, no significant main effects or interactions regarding Nostril were found, but there was a significant Valence Group X Odor/No-Odor interaction. Figure 7 illustrates that heart rate modulation was only apparent in response to unpleasant odorants such that there was heart rate acceleration in response to the unpleasant odor compared to the no-odor. T-tests confirmed that heart rates increased in response to the unpleasant odor blocks (M = 74.80, sd = 10.42) compared to the neutral no-odor blocks (M = 73.68, sd = 9.55), (p = .002). However, no significant differences in heart rate responses were found between the pleasant odor (M =75.66, sd = 11.02) and no-odor blocks (M =75.71, sd = 11.78), [t(39) = .12, p = .096].

Heart Rate Gender Effects. The only significant gender effect found was a 3-way Valence Group X Odor/No-Odor X Sex interaction (see heart rate column of Table 1 and Figure 8). T-tests revealed that significant modulation effects were only seen for females in the unpleasant Valence Group. The heart rates of females increased significantly in response to unpleasant odor blocks compared to no-odors (p = .004), whereas the heart rates of males showed the same pattern of response although it was nonsignificant (p = .199). Moreover, females showed an overall tendency to elicit greater heart rate responses to unpleasant odor blocks compared to males (p = .067).

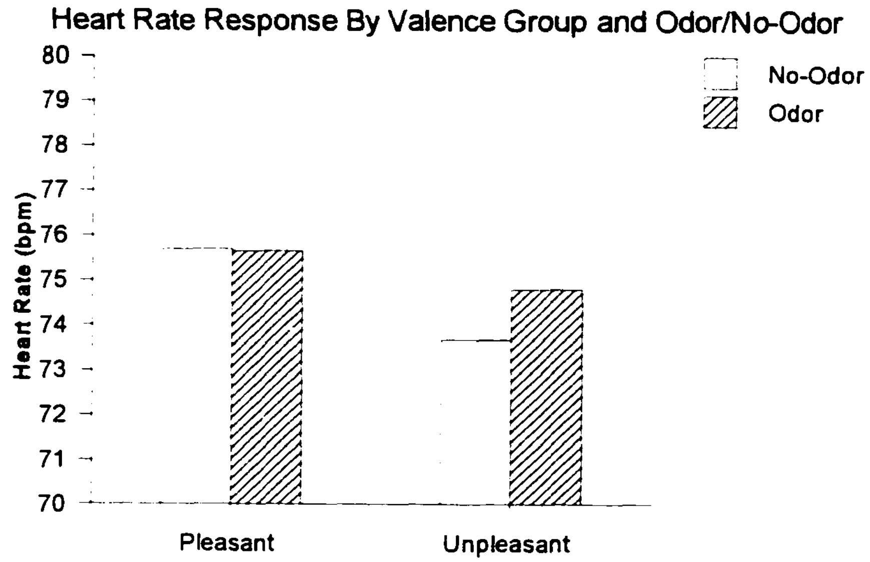


Figure 7. Interaction of Mean Heart Rate Responses as a Function of Valence Group and Odor/No-Odor.

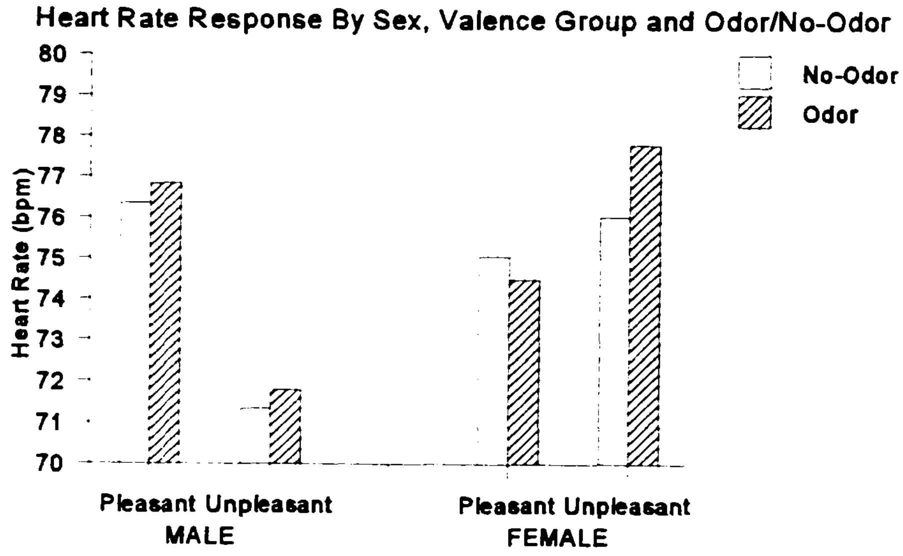


Figure 8. Interaction of Mean Heart Rate Response as a Function of Sex, Valence Group and Odor/No-Odor.

These findings suggest that although both males and females demonstrate acceleration of heart rate to unpleasant odors, females show an enhanced response.

DISCUSSION

Summary of major findings

The chief findings in this study were as follows: 1) the valenced odors were effective in altering moods such that moods were more positive in the presence of the pleasant odor and more negative in the presence of the unpleasant odor; 2) as predicted, pleasant odor exposure resulted in attenuated startle blinks and unpleasant odor presentation resulted in enhanced startle blinks; 3) heart rate responses were increased only in response to the unpleasant odor and 4) females were more physiologically responsive to odors in both startle blink magnitude and heart rate measures. Finally, while the expected startle blink laterality interaction Valence Group X Odor/No-Odor X Nostril was not found, a startle blink laterality interaction of Valence Group X Nostril X Breath Direction was found. This interaction was consistent with the valence hypothesis when considered in context of the startle-attenuating effects of inhaling the pleasant odor and the startle-augmenting effects of exhaling the unpleasant odors.

Laterality Effects of Startle Blink Modulation

One of the primary purposes of this study was to investigate which neuropsychological emotion hypothesis, right hemisphere or valence, would be supported by lateralized presentations of valenced odors as indexed by startle blink magnitudes. It was predicted that a 3-way interaction between Valence Group (pleasant odor plus no-odor vs. unpleasant odor plus no-odor), Odor/No-Odor (presence vs. absence of odor), and Nostril (left vs. right) would support one hypothesis or the other. If the valence hypothesis was supported, the greatest enhancement of startle blink magnitudes would be observed in response to right nostril presentations of the unpleasant odor and the greatest attenuation of startle blink magnitudes would be observed in response to left nostril presentations of the pleasant odor. If the right hemisphere hypothesis was supported, both the pleasant and unpleasant odors presented to the right nostril would show the greatest attenuation and augmentation, respectively, of startle blink responses. This interaction was not significant; hence neither hypothesis was supported. However, when the startle data were analyzed including the additional variable of Breath Direction (inhaling vs. exhaling), not only was there a main effect of Breath Direction, wherein inhalations produced attenuated startle blink magnitudes compared to exhalations, but the key finding was that there was also a laterality interaction of Valence Group X Nostril X Breath Direction.

Influence of Breath. The unexpected Breath Direction findings raise several questions. Why did inhalations and exhalations differentially affect startle responses? Two possible explanations are proposed: 1) Zajonc's vascular theory of emotional efference (Zajonc et al, 1989), regarding the hedonic effects of warmed and cooled air; and 2) inhalations and exhalations as behavioral indicators of approach and withdrawal.

Zajonc's vascular theory of emotional efference (Zajonc et al, 1989) postulates that facial muscular movement mechanically affects the cavernous sinus which may then impede the venous blood flow which in turn may influence the cooling of the arterial blood flow to the brain, especially the hypothalamus. Different brain temperatures may lead to differential release or blocking of neurotransmitters which may influence emotional subjective states. In support of this theory, Zajonc et al. demonstrated that phonetic utterances which resembled emotional facial displays produced different hedonic experiences and generated corresponding changes in forehead temperature. In the case of utterances which acted on the facial muscles used in negative emotions, it was thought that the facial muscles restricted the venous blood supply and the nasal passages, which then impeded the cooling of the cavernous sinus and ultimately resulted in forehead warming. The opposite effect was said to occur with utterances which acted on facial muscles used in positive affective experience. Additionally, when cool air was introduced into the nasal cavity it was rated as pleasant, while warm air was rated as unpleasant. Following this line of reasoning, it is possible that the hedonic effects of cooled and warmed air may have affected the startle blink responses in the present study. Perhaps the inhalation of odorants, which brought cooler air into the nasal cavity produced a positive emotional experience and startle blink attenuation; conversely, exhalation of odorants may have caused a relative warming of the nasal cavity and produced a less pleasant emotional experience resulting in startle blink augmentation.

Another proposed explanation for the Breath Direction effect which takes laterality theories is based on the theory that emotional behaviors can be understood in terms of primitive underpinnings of functionally opposite approach and withdrawal reactions with inhalations experienced emotionally as approach behavior and exhalations as withdrawal. An evolutionary biological conceptualization was proposed by Schneirla (1959): "In general, what we shall term the A-type of mechanism, underlying approach, favors adjustments such as food-getting, shelter-getting, and mating; the W-type, underlying withdrawal, favors adjustments such as defense, huddling, flight, and other protective reactions. Also, through evolution, higher psychological levels have arisen in which through ontogeny such mechanisms can produce new and qualitatively advanced types of adjustment to environmental conditions " (p.4). Lang et al. (1990) also theorized that emotions are organized biphasically and that the emotional state of an organism is governed by appetitive (approach, attachment or consummatory) or by defensive (withdrawal, defensive aggression, avoidance, escape) behaviors. These authors suggested that startle attenuation or augmentation results from a mismatch or match with the current emotional state of the organism. Therefore, if a startle probe is presented in the presence of an appetitive stimulus, there is a mismatch between the two responses and the resultant defensive startle response is attenuated; however, if the probe is presented during an aversive stimulus there is match between the responses which results in an augmented startle reflex. This approach/withdrawal theory could explain why there was startle attenuation during inhalations of the pleasant odor and augmentation during exhalations of the unpleasant odor in the present study.

The possibility that inhalations and exhalations may be related to approach and withdrawal behaviors resulting in differential hedonic responses is consistent with findings from studies examining affective responses to other approach and withdrawal motoric behaviors (Forster & Strack, 1996; Cacioppo, Priester & Berntson, 1993). Cacioppo et al. reported that neutral stimuli (Chinese ideographs) produced more positive hedonic effects (increased preference ratings) following an approach behavior of arm flexion (pressing the arm upward against a table) than an avoidance behavior of arm extension (pressing the arm downward on a table). Forster and Strack also found that the motoric movements of head nodding or head shaking during encoding of positive and negative adjectives differentially influenced the recognition of the valenced adjectives. Head nodding resulted in greater recognition of positive words and head shaking resulted in greater recognition of negative words.

Both of the above suggestions for the Breath Direction effect are speculative. Of the two proposals, Zajonc's theory related to Breath Direction may be more plausible given that it has been shown that cool air in the nasal cavity is considered pleasant and warm air is found to be unpleasant (Zajonc et al., 1989). While there are presently no known data to support the hypothesis that inhalation is an approach behavior and exhalation is a withdrawal behavior, the suggestion does have some face validity and it also has some merit because differential affective responses have been reported in response to other approach and withdrawal motoric behaviors (Forster & Strack, 1996; Cacioppo et al., 1993).

Valence Hypothesis in Conjunction with Zajonc's Theory or Approach / Withdrawal Theory. Is the Breath Direction finding concerning the 3-way interaction involving Valence Group X Nostril X Breath Direction better explained in terms of the right hemisphere or valence hypotheses? Table 2 outlines the predicted outcomes of the startle responses based on these hypotheses. The findings show that greatest attenuation of startle blink magnitudes occurred during **pleasant left** nostril **inhalations** and the greatest augmentation of startle blink magnitudes occurred during **unpleasant right** nostril **exhalations.** As is shown in Table 2, of the two hypotheses, these effects are more consistent with the valence hypothesis. This hypothesis postulates that the **left**

Table 2. Predicted startle blink changes as a function of Breath Direction, Odor Valence, Valence Hypothesis and Right Hemisphere (RH) Hypothesis (< = startle blink attenuation, > = startle blink augmentation and - = no predicted effect).

Note: The predicted startle augmentation or attenuation attributable to Breath Direction, Odor Valence and the Hemispheric Hypotheses are additive and the combined effects are represented in the Total Effect columns (Valence or Right Hemisphere).

			Breath Direction	Odor Valence	Valence Hypothesis	Total Effect (Valence)	Right Hemisphere Hypothesis	Total Effect (RH)
INHALE	PLEASANT	*LEFT*	<	<	<	<<<	-	<<
		RIGHT	<	<	-	<<	<	<<<
	UNPLEASANT	*LEFT*	<	>	-	-	-	-
		RIGHT	<	>	>	>>	>	>>
EXHALE	PLEASANT	*LEFT*	>	<	<	<	-	-
		RIGHT	>	<	-	-	<	<
	UNPLEASANT	*LEFT*	>	>	-	>>	-	>>
		RIGHT	>	>	>	>>>	>	>>>

hemisphere is specialized for **pleasant** and the **right** hemisphere for **unpleasant** affective stimuli. In light of the Breath Direction effect (startle attenuation during left inhaling and augmentation during right exhaling), the valence hypothesis receives more support.

The laterality interaction may be explained in terms of a combination of the valence hypothesis and Zajonc's theory. Because startle attenuation is associated with positive emotional experience and startle augmentation is related to unpleasant emotional experience, it is possible that the cooling effect of inhalation may have produced an additive pleasant effect to both pleasant and unpleasant olfactory stimuli. Thus, during **left** positive presentations, the significant attenuation of inhalations may reflect an even greater positive physiological response to the pleasant odorant because of additive pleasant cooling. Furthermore, according to the valence hypothesis, the greatest attenuated startle blink response resulted during left-sided presentations because of left hemisphere specialization for pleasant affective processing. In contrast, during **right** unpleasant presentations, the significant startle potentiation during exhalation may suggest that increased warming during exhalations produced additive negative affect which resulted in startle blink augmentation.

On the other hand, the interaction of Valence Group X Nostril X Breath Direction can also be understood considering inhalation and exhalation as indications of approach and avoidance behaviors, respectively. That the valence hypothesis is associated with approach and avoidance behaviors has been previously suggested by Davidson and his colleagues (Davidson, 1984, 1992, 1993; Davidson et al., 1990; Fox, 1991) who postulated that the right hemisphere is specialized for withdrawal behavior and the left hemisphere is specialized for approach. In support of this contention, Fox and Davidson (1988) measured EEG activity in infants and found relative left-hemisphere activation was generated with approach behavior (measured by expressions of joy and anger), as well as relative right-anterior activation during withdrawal behavior (measured by expressions of disgust and distress).

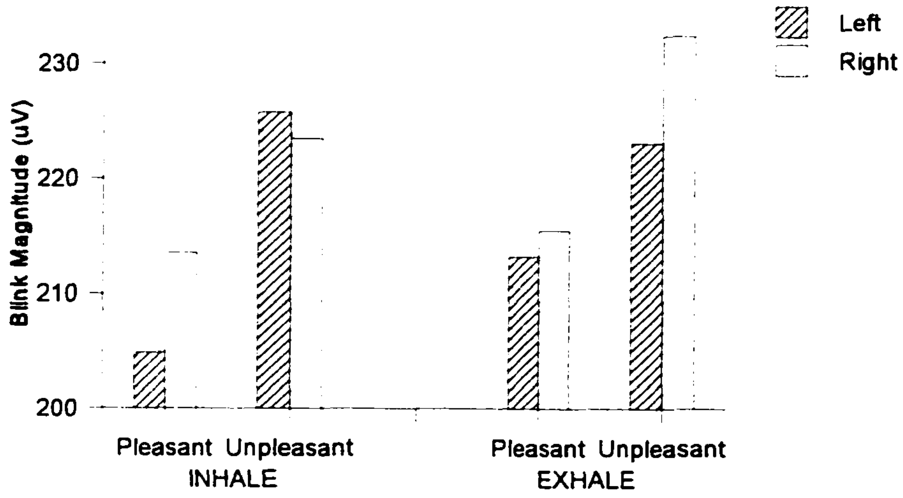
To better understand how the valence model of approach and withdrawal may explain the Valence Group X Nostril X Breath Direction interaction, it is useful to consider how inhalation and exhalation would be expected to affect startle blink response in the absence of valenced odors. If the left hemisphere is specialized for approach behavior and the right hemisphere is specialized for withdrawal, and if inhalation is an approach behavior and exhalation is a withdrawal, it follows that left-sided inhalations should produce the greatest startle attenuation and right-sided exhalations should produce the greatest startle augmentation. When the valence effect of the odors is added to the Breath Direction effect, this is precisely what was found in the significant laterality interaction and is listed in the total effects column of the Valence Hypothesis in Table 2. Therefore, the final effect can be explained by **left** sided presentations of pleasant odors resulting in attenuation as well as attenuation by the inhalation-related approach. In contrast, the augmentation of startle blinks during **right** sided presentations of unpleasant odors resulted in startle attenuation by unpleasant odors and further enhanced by exhalation-related withdrawal.

Notably, the laterality interaction involved only the Valence Group, Nostril and Breath Direction variables. The Odor/No-Odor variable was collapsed in the interaction and thus the dependent variables were the startle blink means for pleasant odors combined with their corresponding neutral odors and means for unpleasant odors combined with their corresponding neutral odors. To understand the degree to which each odor contributed to the Valence Group effect, 2 separate Valence Group X Nostril X Breath Direction MANOVAs were performed for valenced odors and neutral odors.

The 3-way analysis of startle blinks under valenced odor conditions revealed no significant effects although the Valence Group X Nostril X Breath Direction interaction did approach significance [F(1, 78) = 2.62, p = .110]. As can be seen in Figure 9A the pattern of pleasant and unpleasant startle responses was very similar to the pattern of responses seen in the significant interaction in Figure 3 and the Total Effects column of the Valence Hypothesis in Table 2. The Valence Group X Nostril X Breath Direction analysis of startle blinks under neutral odor conditions also did not reveal a significant 3-way interaction [F(1, 78) = 1.63, p = .205]; however, as is illustrated in Figure 9B the pattern of startle blink responses was remarkably similar to the significant interaction in Figure 3. Therefore, it appears that the interaction in Figure 3 reached significance because it pooled the similar albeit nonsignificant effects from the neutral and the valenced odors.

The neutral no-odor 3-way analysis also revealed a significant main effect of Breath Direction [F(1, 78) = 11.41, p > .001], wherein inhalations produced startle blink attenuation and exhalations produced startle argumentation. This finding was interesting because the no-odor had essentially no inherent hedonic qualities (mean hedonic rating = .063 ± 3.13), and therefore the Breath Direction effect may have been related to just the

A) Startle Responses of Pleasant and Unpleasant Odors



B) Startle Responses of Neutral No-Odor

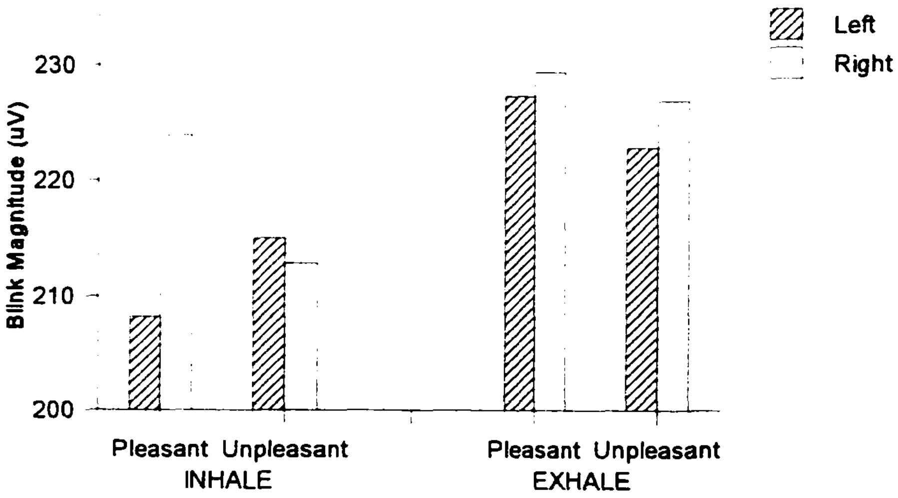


Figure 9. Mean Startle Blink Magnitudes as a Function of Nostril, Valence Group and Breath Direction for A) the Valenced Odors and B) the Neutral No-Odor.

pleasant and unpleasant experience associated with inhaling and exhaling, respectively. To gain further insight into the relationship between hedonics and Breath Direction, the no-odor startle magnitudes where examined in terms of the hemispheric hypotheses. Therefore, as was discussed previously and diagramed in Table 2, if **inhaling** air is **pleasant or an approach behavior**, then the valence hypothesis predicts that **left** nostril presentations of the no-odor should show the most **attenuation** of startle blink magnitudes and conversely if **exhaling** warmer air is experienced as more **negative or a withdrawal behavior**, then **right** nostril presentations of the no-odor should demonstrate the greatest **enhancement** of startle blink magnitudes. The pattern of no-odor startle blink responses was in accordance with these predictions, because the greatest attenuation of startle blink magnitudes occurred during left nostril inhalations (M = 211.63, sd = 128.19) and the greatest augmentation occurred during right nostril exhalations (M = 228.13, sd = 138.05), and t-tests confirmed that they were significantly different from each other (p = .003). This finding lends further credence to the notion that inhaling and exhaling may have had a hedonic effect.

In sum, in trying to understand why the predicted Valance Group X Odor/No-Odor X Nostril interaction was not significant but the Valence Group X Nostril X Breath Direction interaction was significant, it appears that the effect of Breath Direction additionally enhanced or reduced startle blink responses under pleasant and unpleasant conditions in a valenced manner. Even though the hedonic qualities of individual odors did appear to modulate the startle blink magnitudes, their impact was not sufficient to demonstrate significant lateralized hemispheric specialization without the added Breath

Direction effect.

Influence of Odors on Affective Experience

This study sought to examine whether odors of different valence influence affective experience differently as a function of hemispheric laterality. The emotional influence of odors was examined by investigating their effects on two physiological measures of emotion, i.e., startle blink magnitudes and heart rates, and on subjective verbal reports of mood.

Startle Blink Modulation. As predicted, this study replicated previous findings in which the unpleasant odor enhanced startle blink magnitudes compared to the neutral odor (Ehrlichman et al., 1995, Miltner et al., 1994). The effect of unpleasant odors on startle blink responses appears to be reliable and the effects are consistent with startle modulation effects of other negative affective stimuli such as pictorial slides, mental imagery and tactile stimuli (e.g., Bradley et al., 1990; Vrana et al., 1988; Cook et al., 1991; Hawk & Cook, 1997).

Additionally, as predicted, the pleasant odor decreased startle blink responses compared to the neutral no-odor. This finding is consistent with results of studies using positively valenced pictorial stimuli, but it has not previously been reported for pleasant odors. The inconsistency in findings between the present study and the two other previous studies examining startle modulation in the presence of pleasant odors (Miltner et al., 1994; Ehrlichman et al., 1995) may have been due to improved methodology. In the study by Ehrlichman et al. (1995), a within subjects design was used with random presentations of pleasant and unpleasant odorants. The strong aversive effect of the unpleasant odors may have resulted in participants perceiving the entire experiment as unpleasant and this could have compromised the positive effects of the pleasant odors. Although the Miltner et al. (1994) study was not hampered by the odors influencing each other, because the odors of different valence were presented during different sessions, the study used a pleasant odor that was rated as only mildly pleasant and the authors speculated that it was not pleasant enough to cause significant attenuation of the startle blink magnitudes.

To avoid the potential influence of one odor on another, in contrast to Ehrlichman et al.'s (1995) within subjects design, a between subjects design was used in which one group was exposed to only the pleasant odor and other group was presented with only the unpleasant odor. To optimize the effects of the valenced odorants only Limburger cheese and coconut were used because they produced the highest hedonic ratings and the greatest augmentation and attenuation of startle blink magnitudes in the Ehrlichman et al. (1995) study. In contrast to Miltner et al.'s (1994) study, both the odors were sufficiently hedonically strong (between moderate to very strong) and intense (between moderate to very intense).

Heart Rate Responses. Unlike startle blink magnitudes, heart rate changes were found during exposure to the unpleasant but not the pleasant odors. While Miltner et al. (1994) did not report any differences in heart rate responses to any odors (pleasant, neutral or unpleasant), the present study and the study by Harver, Katkin, Bott, Ehrlichman & Warrenburg, (1989) found acceleration of heart rate in response to an unpleasant odor. This finding is also in keeping with the notion that heart rate acceleration may be a defensive response (Lang et al, 1993), as has been reported in fearful subjects in response to pictures related to their phobias. For instance, mutilation phobics showed heart rate acceleration in response to mutilation pictures (Klorman, Wiessberg & Wiesenfeld, 1977) as did small-animal and blood phobics in response to their phobia related pictures (Hamm, Globisch, Cuthbert & Vaitl, 1991).

Mood Ratings. Pleasant and unpleasant odors not only differentially affected the physiological measures of startle blink and heart rate but also differentially affected self-reported mood. Mood was rated to be more positive during exposure to the pleasant odor and more negative during presentation of the unpleasant odor. Furthermore, moods also changed from the beginning to the end of the experiment, such that the pleasant Valence Group moods improved and the unpleasant Valence Group moods became worse. Therefore, these findings support the limited but growing literature which have found that the hedonic qualities of odors can influence mood (e.g., Bastone & Ehrlichman, 1991; Ehrlichman and Bastone, 1992a; Rotton, 1983; Dunn et al., 1995).

Gender Differences

Startle Blink Modulation. Females showed increased startle potentiation in response to unpleasant odor and greater startle attenuation to pleasant odor. While the males also showed this pattern, it was not significant. Why were the females more responsive?

Perhaps the females in this study were more sensitive to the odors than the males and this resulted in the greater startle blink modulating effects. This possibility is consistent with better performance of females often reported in olfactory tests (Koelega

& Koster, 1974; Doty et al., 1981; Cain, 1982) and larger olfactory evoked potential amplitudes in females compared to males (Evans et al., 1995; Becker et al., 1993).

Evans et al. (1995) have suggested that gender differences in olfaction may be hormonally based. These authors cite many studies which showed that hormones such as estradiol and estrogen affected neurons and cells concerned with olfaction. For instance, there are findings which suggest that estrogens are involved with olfactory epithelium and that these effects are mediated by autonomic control of secretory and vascular structures involved with patency of nasal passages and mucous composition. Likewise, neuroanatomical differences related to olfactory functioning may also contribute to gender differences. For instance, Hines, Allen & Gorski, (1992) cite several lines of evidence showing sex differences in subcortical regions of the rat brain [e.g, the medial nucleus of the amygdala and the bed nucleus of the stria terminalis (BNST)] which are associated with the regulation of several sexually dimorphic functions including aggression, sexual behavior and gonadotropin secretion, as well as the integration of olfactory information. These sexually dimorphic anatomically connected nuclei have been found to differ in volume and amount of neurochemical innervation (cholecystokinin, substance P, vasopressin). Additionally, these subcortical nuclei are involved in a neural circuit which relays olfactory information to hypothalamus regions which regulate reproduction and other sexually dimorphic functions, such as male copulatory behavior, ovulation, and chemoinvestigation. While all of these attributes have been found for the rat, little research on sexual dimorphism and concomitant olfactory function has been reported in other species including humans; however, the encapsulated portion of the

BNST has been found to be sexually dimorphic in the guinea pig, as well as in a similarly darkly staining region of the human brain.

Another reason why females showed greater startle modulation may be greater responsiveness to the acoustic probes, demonstrated for example by gender differences in physiological measures of acoustic responsivity such as auditory brain-stem potentials (Don, Ponton, Eggermont, & Masuda, 1993; Elkind-Hirsch, Wallace, Malinak & Jerger, 1994). These studies showed that there were larger amplitudes in females and shorter latencies in males. The authors suggested that these differences were associated with estrogen or testosterone levels and also provided evidence that these differences may be at least partially related to anatomical sex differences in the cochlea.

Finally, females may have shown greater startle modulation because their facial muscles (orbicularis oculi) may have been more responsive to the odor hedonics. This contention is consistent with previously observed enhanced facial responses (corrugator and/or zygomatic EMG tension) in females to affective stimuli such as emotional imagery (Schwartz et al., 1980) affectively charged slides (Dimberg & Lundquist, 1990; Brown-Kuhl & Bruder, 1997; Grossman & Wood, 1993; Lang et al., 1993) and 95 dB tones (Dimberg, 1990). It has been postulated that the gender differences in facial EMG studies may be related to enhanced communication patterns in woman (Lang et al., 1993) and increased facial expressiveness in women (Dimberg, 1990). Moreover, the influence of the hedonics of odors on facial muscles has been considered a general component of the emotional response (Dimberg, 1990) and is consistent with emotion theories with Darwinian derivations such as differential theory (Ekman & Oster, 1979;

Izard, 1977; Tomkins, 1962). Further evidence of a link to emotion has been provided by research which demonstrates that facial expressions are biologically pre-wired and associated with emotional activity (Dimberg, 1990).

Baseline EMG. Females showed greater baseline orbicularis oculi EMG responses than males. Likewise, Grossman & Wood (1993) found women showed greater baseline EMG responsiveness of the corrugator muscle (although they found this effect only during negative affective slide presentations). Their findings are also in accordance with a general tendency for woman to exhibit greater facial responsiveness (e.g., Dimberg, 1990).

Heart Rate. Heart rates were found to be significantly accelerated in response to the unpleasant odor. There was a gender difference for this effect as well, wherein only the heart rates of females increased significantly in response to the unpleasant odor. Although the heart rates of males exhibited the same pattern of response, it was nonsignificant. Additionally, female's heart rates in response to the unpleasant odor were greater than the heart rates of the males. This finding is consistent with other studies which have shown women to increase heart rate in response aversive situations. For example, women responded with elevated heart rate levels compared to men during aversive versus relaxation imagery (Gautier & Cook, 1997) in a shock avoidance discrimination learning task (Graham et al., 1966) and during a 3 minute impromptu speech (Baldwin & Clevenger, 1980).

Arousal Ratings. Only males reported greater arousal by both the pleasant and unpleasant odors than the neutral odor. A physiological measure of arousal is skin conductance. Consistent with male's arousal reports in the present study, skin conductance has been shown to vary for males in other studies, such that valenced stimuli (pleasant or unpleasant) but not neutral stimuli have been reported to produce greater skin conductance responses as well as arousal ratings. For instance, in studies using perceptual or imagined affective stimuli, a direct relationship was found in reports of arousal and skin conductance regardless of the valence of the reported experience (Bradley, Cuthbert, & Lang, 1990; Cook, Hawk, Davis, & Stevenson, 1991; Greenwald, Cook, & Lang, 1989; Winton, Putnam , & Krauss, 1984). Gender differences also have been reported in which a greater concordance between arousal reports and skin conductance magnitudes were found in males than in females (Lang et al., 1993). Other researchers have also found similar gender-specific skin conductance results (O'Gorman, 1983; Graham et al., 1966). Lang et al. (1993) have cautioned that this gender difference may reflect a difference in arousal levels or it may be due to differences in peripheral sweat gland distributions. It would have been interesting to have also measured skin conductance in this study to determine whether it also would have shown a greater correlation with arousal ratings of the odors in males, as was found in the aforementioned studies which used other affective stimuli.

Odors Induce Gender Differences in Physiological Responses but not in Verbal Report. While women were found to be more physiologically responsive to odors (i.e., increased startle blink modulation, increased heart rate response and increased baseline orbicularis oculi EMG), no gender differences were found for self-reported affective ratings. This finding is in accordance with reports of no gender differences in affective ratings when exposed to food odors (Baron, 1997).

In a different kind of emotion study (Liotto & Tucker, 1992), which also showed a gender disparity between responses and self ratings, reaction times to stimuli presented in the left or right visual field while participants received either depression or elation mood suggestions were slowed only for females during uncued presentations of stimuli in the left visual field in the depressed mood condition. The authors suggested that even though the men reported similar mood induced depression as the women, they "may have been less open to the behavioral/physiological consequences of a depressed mood. Thus, the mood induction might have been less effective for the men, even though this was not shown by the mood state scales" (pp. 149). This rationale could also be used to interpret the results in the present study. Odors may have been less effective in evoking emotions in males which in turn resulted in less physiological responses.

In order to explain physiological gender differences, other authors have also proposed that women and men experience and respond to emotions differently. For example, in another mood induction study, a mood-congruent memory effect was found only among women (Rothkopf & Blaney, 1991). It was proposed that while men in a depressive state attempt to mentally and behaviorally distract themselves from their mood, depressive women conversely, are inclined to ruminate about the causes of their mood (Nolen-Hoeksema, 1987). Additionally, because of evidence showing woman to be more reactive to emotional stimuli, Ladavas, Nicoletti, Umilta & Rizzolatti (1984) used only woman in a study of normal depression induction.

Unlike the present study, many studies have found females to report greater emotional responsiveness verbally. For instance, Grossman and Wood (1993) cite many studies which have found women to report more intense experience of emotions, intense expression of emotion, comfort with emotional experiences and likelihood to seek out emotional experiences. These authors also cite instances of females giving higher self-reports of positive feelings (i.e., overall warmth, emotional expressiveness, comfort to others, happiness and life satisfaction) and negative feelings (i.e., negative affect, depression, fear and sadness) except anger, which is more consistently reported by males. In other studies, women have reported more extreme emotional ratings than men to both positive and negative affective stimuli such as valenced pictures (Lang et al, 1993, Grossman & Wood, 1993). Grossman and Wood suggest that the different social roles of men and women are responsible for the sex differences in emotion studies. For instance, these authors contend that the gender roles likely "generate sex differences in social behavior because sex-differentiated roles form the basis for general beliefs of social stereotypes about the likely and expected behavior of men and women" (pg. 1010). It is possible that in the present study, food odors are not the typical affective stimuli which would elicit sex role differentiated self-report. Not finding a concordance between self-report and physiological responsiveness is not uncommon and it has been suggested that a direct relationship between the two is probably restricted to discrete emotions and certain physiological measures (Grossman and Wood, 1993). Unlike the present study, the general finding in past research has been sex differences in self-reported intensity of emotional experience on questionnaires, but not a gender difference in physiological reaction during emotional events (LaFrance & Banaji, 1992). The inability to find physiological differences in those studies may have been due to the physiological measure not being sufficiently associated with the investigated emotion. Thus, any sex differences related to the emotion will not be measured by the physiological measure. Some physiological indicators are not directly related to verbal reports, and even inverse relationships sometimes are found. For example, increased skin conductance in men compared to women has been suggested to be related with the proclivity of men to show suppression of emotional expression (Manstead, 1992). In sum, when associating self-reports with physiological measures complex patterns are likely to be revealed which are probably influenced by the physiological measures, the specific emotions examined, the ability to elicit those emotions, an inclination for women to be responsive and males to be suppressive according to social role theorists and biological differences between the sexes.

Conclusions and Future Directions

While physiological and self-report findings from this study lend support for odors influencing affective experience, support for neither of the predominant hemispheric hypotheses of emotional processing, right hemisphere or valence, was initially found. However, when the Breath Direction variable was entered into the analysis, the findings were explainable by the valence hypothesis in conjunction with the startle-attenuating effects of inhaling and the startle-augmenting effect of exhaling. These unexpected results have raised interesting questions concerning the emotional processing of not only valenced odors but of Breath Direction.

Why was the predicted laterality interaction not significant, and instead a laterality interaction involving Breath Direction was significant? The hemispheric hypotheses used to examine the laterality effects of odors concerned only cortical processing of valenced affective stimuli. Because there are complicated interactions between the cortical and subcortical structures in olfactory and emotional processing and because the startle reflex itself has been implicated in being subserved by the subcortical amygdala (Davis, 1997; Rosen & Davis, 1988, 1990; Hitchcock & Davis, 1986) perhaps a cortical model of emotional processing may not be sufficient to explain the emotional processing of odors using the startle probe reflex without the added influence of the Breath Direction effect.

It may be more useful for future research to focus more precisely on the interrelationships of hemispheric and subcortical involvement in the emotional processing of valenced odors. For instance, ongoing research is presently examining the evoked potentials from depth electrodes implanted close to the amygdala in the brains of temporal lobe epilepsy (TLE) patients while they view valenced pictures and preliminary reports haven shown a valence discrimination between negative and neutral stimuli (Bradley, 1997). This type of procedure would also be interesting to use with valenced odors to examine the effects of subcortical processing. This could also be accomplished by examining the startle probe response to valenced odors in temporal lobectomy patients who have had their right or left amygdala removed.

Alternatively, it is possible that the context of the odor presentation was not adequately arousing to induce sufficient lateralized hemispheric emotional processing without the effect of Breath Direction. This possibility is consistent with the proposition by Lang et al. (1992) who proposed that startle modulation requires motivational states which include sufficient arousal as well as the pleasant-unpleasant dimension. As Ehrlichman et al. (1995) suggest, it is possible that the arousing effects of odors are different in different contexts. These authors proposed that although hedonic ratings may be equivalent, the emotional/motivational impact of smelling coconut in a laboratory versus on a tropical beach may differ. In the case of Limburger cheese, all participants in the present study were informed that they would be smelling cheese. After smelling the foul odor, spontaneous self-report of many of the participants reflected relief in knowing that they were just smelling cheese. Thus, it is likely that knowing the origins of the offensive scent created less arousal in the participants than it would have otherwise. It would be worthwhile to replicate the present study using odors with contextual cues to enhance the arousing effects of the odors to determine whether lateralized hemispheric emotional processing is affected.

The unexpected finding that Breath Direction produced significant startle attenuation and augmentation was considered in terms of findings from Zajonc's facial efference theory as well as of approach and withdrawal behavior. According to the findings of Zajonc, inhaling may have caused cooling of the nasal passages resulting in a positive experience, while exhaling may have caused warming of the nasal passages and a negative experience. Alternatively, inhaling could be considered an approach behavior and exhaling a withdrawal behavior. Although it was not significant, the pattern of startle blink responses even in the neutral condition during inhalations and exhalations were very consistent with hemispheric processing according to the valence hypothesis.

To better understand these effects, future studies could examine startle blink magnitudes during experimental manipulation of cooled and warmed neutral air introduced into the nasal passages. Additionally, EEG studies could be conducted with inhalations and exhalations to examine whether there is differential activation of the hemispheres which coincides with the valence hypothesis or approach/withdrawal behaviors. It also would be important to replicate the present inhalation and exhalation findings because if this is a robust effect, it would then be an important variable to control as it could bias the results in any startle probe study examining affective stimuli.

This study showed that the startle blink paradigm was useful in examining lateralized effects of odors. No other studies have examined the startle modulation effects of lateralized presentations of affective stimuli . This would indicate that the startle reflex paradigm holds promise in further elucidating the role of the hemispheres in the processing of different emotional stimuli in different modalities such as visual, auditory and tactile stimuli.

It was also found that the startle paradigm was useful in physiologically distinguishing pleasant and unpleasant odors. Although the unpleasant odor augmentation of startle blink magnitudes replicated that found in previous studies, improved methodology in this study also showed that the pleasant odor produced startle blink attenuation. These results are consistent with findings of startle blink modulation during presentations of pleasant and unpleasant affective stimuli in other modalities. In order to investigate the generality of this finding, future studies should examine the effects of other types of pleasant and unpleasant odors. However, heart rate was not found to be as sensitive a measure to the emotional effects of pleasant and unpleasant odors as startle blink responses. No laterality effects emerged and it served only to physiologically distinguish the unpleasant from the neutral odor. Future studies can employ other physiological measures which lend themselves to lateralized presentations of valenced odors such as EEG or functional imaging to help provide further information about the hemispheric processing of odors.

Additionally, results of this study emphasize that subject parameters such as gender are a source of variability. For instance, while there was no difference in self-report measures of emotion, in general physiological responses of females were typically enhanced compared to males. Males on the other hand, tended to report more arousal by the valenced odors. Future research can also explore how other sources of variability such as personality differences or cognitive style may interact with affective reports and physiological reactivity.

APPENDIX

Piloting procedures used to identify whether odorants produced trigeminal stimulation

Participants

Ten right-handed volunteer nonsmokers (5 females, 5 males) between the ages of 23 and 35 (M = 30.20, s.d. = 4.44) participated in the pilot study. The participants were screened for right-handedness, anosmia, and absence of strong sensitivities to odors and conditions that might interfere with the perception of odors (e.g., deviated septum, rhinoviral infection).

Odorants

Four odor stimuli were presented: neutral air, coconut (IFF pure coconut saturated in polyethylene interflo pellets), Limburger cheese and peppermint extract (saturated in polyethylene interflo pellets).

Method and Procedure

This study utilized a procedure similar to that by Ehrlichman (1987), in which it was found that participants who were simultaneously presented with an odorant and neutral air in separate nostrils were unable to distinguish above chance levels the nostril that was delivered the odorant, as long as the odorant did not produce trigeminal effects. However, participants were able to make this distinction above chance levels when an odorant did produce trigeminal stimulation (e.g. peppermint).

The apparatus which delivered the odorants held two plastic squeeze bottles (one containing odorant and one containing neutral air). The bottle nozzles were inserted in the nostrils and as the blindfolded participant inhaled, the bottles were compressed by the participant with a lever on the apparatus which ensured that both stimuli were simultaneously delivered with equal air flow. Each odorant, paired with neutral air, was presented in blocks of ten trials quasi-randomly (i.e., 5 trials per nostril per odorant). The first block contained the coconut, the second block contained the Limburger cheese, and the third block contained the peppermint extract with known trigeminal effects. A forced-choice procedure was used, wherein after each trial the participants were required to choose which nostril was presented with the odorant.

Results

Chi-square analyses were performed on data from each block. Odorants were considered undetectable by the trigeminal nerve if the odorant was not correctly localized in the nostril to which it was presented at above chance levels (Bellas et al., 1989). As expected, coconut and Limburger cheese were not accurately localized but peppermint, which has known trigeminal effects, was able to be localized. Coconut was identified in the correct nostril in 49% of the trials [not significantly different from chance (50%, X^2 (1) = .04, P = 0.841] and Limburger cheese was identified in the correct nostril in 42% of the trials [not significantly different from chance (50%, X^2 (1) = 2.56, P = 0.110]. Peppermint, however, was identified in the correct nostril in 81% of the trials [significantly different from chance (50%, X^2 (1) = 38.44, P < .001]. Thus, coconut and Limburger cheese were considered to have only olfactory effects, and therefore were used in the major study.

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IMAGE EVALUATION
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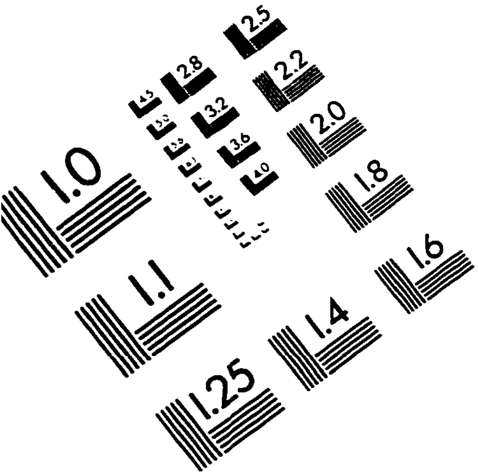

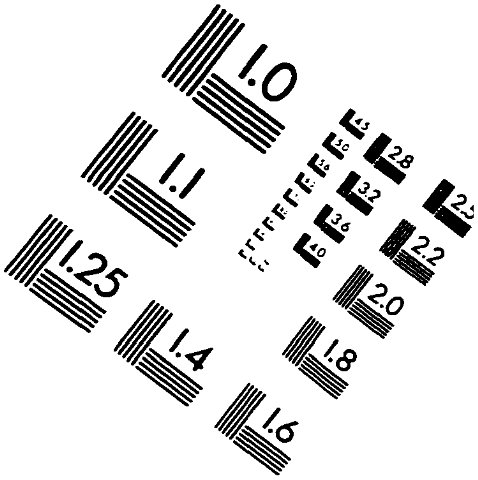

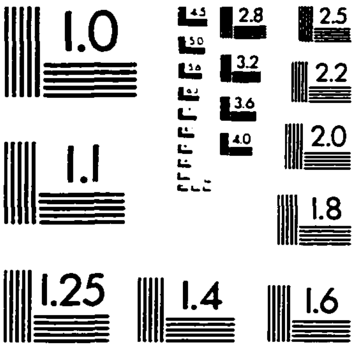

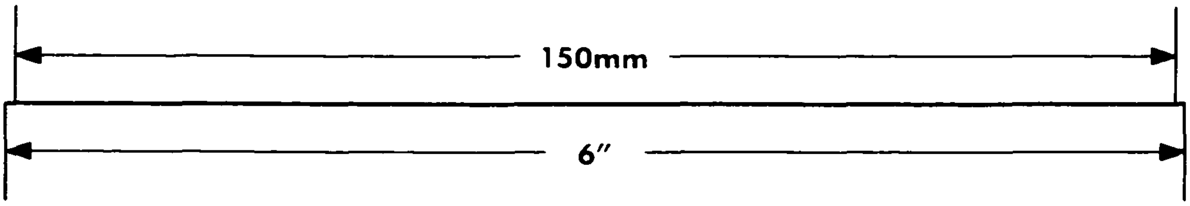

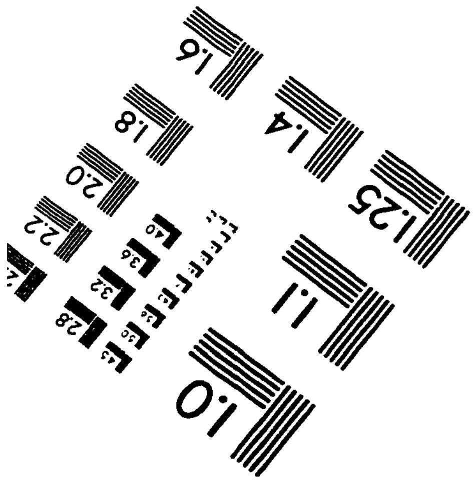

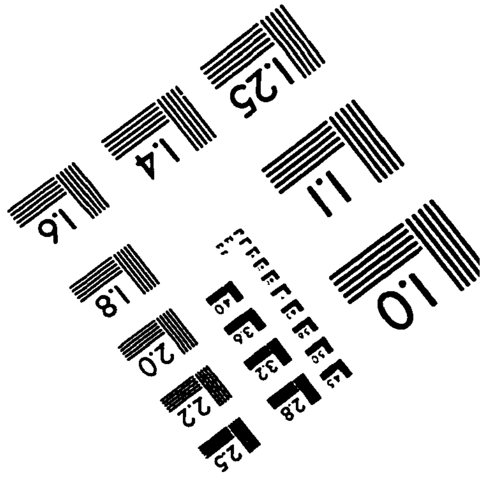

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