SCENTS AND SENSIBILITY: EFFECTS OF AROMAS ON EMOTION AND DECISION-MAKING

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Grace S. Tang
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Abstract

Aromas offer many advantages over traditional methods of manipulating emotion and influencing behavior, especially in the context of studying the mechanisms of decision-making. Many of the brain areas that are activated when perceiving aromas are also known to be involved in emotion, judgment, and decision-making. Pleasantness in particular has been highlighted as an important dimension of olfaction that influences affect and behavior. However, given the richness and diversity of aroma types and qualities, other qualities of aroma percepts likely influence decision processes as well. The goals of this dissertation were 1) to assess the practicality of using aromas as affective stimuli, 2) to expand work on the dimensionality and structure of olfactory space beyond pleasantness, and 3) to determine mechanisms by which aroma-induced affect can influence decisions. To this end, I first gathered ratings along two dimensions commonly used in affective science, pleasantness and intensity, and found that aromas are organized on the affective circumplex along two main axes corresponding to approach and avoidance tendencies. The reliability of the affective properties of aromas across time and between individuals was found to be high. This result confirmed that aromas are useful as affect induction tools for research, and I report affective ratings for a collection of aromas. In the second study, a dimensionality reduction approach was used to discover dimensions that contribute to perceived aroma pleasantness. Finally, using aromas identified in the first study to elicit affective responses, I tested influences of pleasantness and intensity on decision-making, focusing on decisions involving risk and ambiguity. We found that aroma-induced valence and arousal were able to influence risk-aversion, and the effect of aroma intensity was mediated by activity in the anterior insula.

Overall, I demonstrate that aromas are potent affect-inducing stimuli that give rise to multi-dimensional percepts, with correspondingly diverse effects on decision-making.

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Chapter 1

Introduction

Despite being one of the more underappreciated senses (Jones & Rog, 1998), olfaction has a wide range of influences on our lives, shaping behaviors as diverse as social interactions (Baron, 1983, 1997; Hirsch, 2008), consumer preferences (Turley & Milliman, 2000), reaction time (Ilmberger et al., 2001; Millot, Brand, & Morand, 2002), impulsivity (X. Li, 2008), and moral judgment (Schnall, Haidt, Clore, & Jordan, 2008).

As a tool for research on emotion and decision-making, aromas offer several advantages. Scents can be presented subliminally and passively (X. Li, 2008; Millot et al., 2002; Millot & Brand, 2001), so that they can be delivered without interfering with performance on other tasks, or even during sleep (Arzi et al., 2012; Carskadon & Herz, 2004; Rasch, Büchel, Gais, & Born, 2007). The olfactory system is also closely linked to emotion and memory (Herz, Eliassen, Beland, & Souza, 2004; Herz & Engen, 1996), requiring little cognitive elaboration (Ehrlichman & Halpern, 1988; Orth & Bourrain, 2008) to elicit viscerally arousing responses (Ditto, Pizarro, Epstein, Jacobson, & MacDonald, 2006). Consonant with the close association between olfaction, emotions, and memory, many of the brain areas involved in aroma perception are also implicated in decision-making (see sections 1.2 and 1.4 and below). In this dissertation, I posit that understanding how the brain represents and parses olfactory stimuli will ultimately lead to a greater understanding of how aromas influence emotions and interact with high-level cognitive processes to influence behavior. This improved understanding will in turn provide insight into the behavioral and neural mechanisms of decision-making. To demonstrate the utility of scents for affective and decision neuroscience, I first review the literature on perception of aromas, emotional qualities of aromas, links to learning and memory, and how behavioral and neural data have informed the debate on how to organize aromas categorically or along dimensions in olfactory space. I then review theories on mechanisms underlying decisions involving risk and ambiguity, and propose how we can study these using aromas.

The remainder of the dissertation focuses on three experiments that sequentially examine affective responses to aromas and consequent effects on behavior. Chapter 2 assesses the utility of aromas as tools for emotion manipulation, and constructs a library of naturalistic aromas along with information about their affective properties. Following this, I analyze how perceptual features of aromas are summed together in the brain to construct pleasantness (Chapter 3). Finally, I demonstrate a use of aromas in studying the influence of emotion on decision-making, as well as associated neural mechanisms, by showing that aromas affect preferences for risk and ambiguity, and that these influences are mediated by the anterior insula (Chapter 4).

1.1 Structure of the olfactory percept

In order to understand the neural mechanisms underlying the effects of aromas on emotion and behavior, we first need to understand the structure of the olfactory percept. While there is relative agreement on properties of basic olfactory function (Jones & Rog, 1998), there is substantial debate on how the qualities of aroma percepts are parsed. Multiple viewpoints exist that broadly either deconstruct aroma percepts along fundamental dimensions, or into discrete categories. Dimensional models describe aromas in quantitative terms, assigning scores on a usually small number of fundamental dimensions. On one extreme, an influential model states that the aroma percept is one-dimensional, with pleasantness as the main dimension of importance (Khan et al., 2007; Schiffman, Robinson, & Erickson, 1977; Yeshurun & Sobel, 2010). There are a number of pieces of evidence in support of this theory: People in general have trouble describing aromas except in terms of pleasantness (Yeshurun & Sobel, 2010), and various dimensionality reduction techniques show that pleasantness captures the most variance among aromas. For example, applying multi-dimensional scaling to similarity judgments across aromas identified a primary dimension that was closely related to subjective pleasantness (Berglund, Berglund, Engen, & Ekman, 1973; Schiffman et al., 1977). Similarly, principal components analysis was used to reduce a 146-dimensional space (160 aromas were rated on 146 descriptor terms) to one with four significant dimensions, and the dimension which captured the most variance among the 160 aromas used in the study was associated with pleasantness (Khan et al., 2007). The pleasantness of an aroma is also thought to be responsible for the majority of known effects of aromas on affect and behavior, ranging from prosocial tendencies to the pitch of one's voice (Baron & Kalsher, 1998; Baron, 1983, 1997; Bone & Ellen, 1999; Herz, 2009; Hirsch, 2008; Millot & Brand, 2001). Clearly, the pleasantness of an aroma is important in perceptually and behaviorally meaningful ways.

However, the one-dimensional view of olfaction may not be sufficient to fully describe an aroma object. Though Khan et al. focused on the first dimension in his PCA analysis, his analysis resulted in 3 other significant principal component dimensions.

Unlike the first dimension, which was fortuitously easily linked to pleasantness, the other three had no natural label and therefore did not receive as much attention, but nonetheless show that aroma space has more than one dimension. Furthermore, while pleasantness has been suggested to be responsible for many effects of aromas, in some studies, different pleasant smells have been observed to drive effects in opposite directions (Eghil et al., 2010). This suggests that other factors or dimensions that contribute to influencing behavior could have been neglected.

Affective science commonly describes stimuli in terms of a second dimension – arousal (Bradley, Codispoti, Cuthbert, & Lang, 2001). For olfaction, intensity is defined as the perceived strength of an aroma, and has been used as a proxy for arousal because of the strong correlation between aroma intensity and subjective and physiological indicators of arousal (Anderson et al., 2003; Bensafi et al., 2002). Many olfaction studies neglect to take intensity/arousal into consideration, either because only a single aroma is used, intensity ratings are not obtained, or multiple aromas are intensity-matched, eliminating variability in this potentially important dimension (e.g. Khan et al., 2007). However, in studies where aroma intensity has been manipulated or allowed to vary, interesting behavioral and neural results have been found (Anderson et al., 2003; Winston, Gottfried, Kilner, & Dolan, 2005).

The circumplex model of affect posits that pleasantness (valence) and intensity (arousal) interact to produce two motivational axes, approach and avoidance (Bradley et al., 2001; Mehrabian & Russell, 1974). When combined with pleasantness ratings, intensity ratings can be used to calculate positive and negative arousal scores that are thought to drive approach and avoidance behaviors. This corresponds to rotating the pleasantness-intensity dimensions by 45 degrees (Knutson, Taylor, Kaufman, Peterson, & Glover, 2005; Watson, Wiese, Vaidya, & Tellegen, 1999), such that approach tendencies increase as arousal increases for pleasant stimuli, and conversely, avoidance tendencies increase with increasing arousal for unpleasant stimuli. Various studies have identified regions of the brain where activity correlates with some combination of pleasantness and arousal (see section 1.2 below).

While dimensional models have been useful in describing aroma characteristics, they do not capture the more nuanced qualitative properties of aromas. Patterns of brain activity distinguish aromas from different categories with matched pleasantness and intensity, suggesting that the olfactory percept is more fine-grained than a one, two, or even three-dimensional representation suggests (Howard, Plailly, Grueschow, Haynes, & Gottfried, 2009). Discrete models take a more categorical approach to describing stimuli that capture these aroma properties – the subject of debate with respect to discrete models is which categories describe the tremendous diversity of olfactory stimuli encountered in the environment (Delplanque et al., 2012).

Attempts have been made to associate aromas with basic emotions such as joy, surprise, anger, disgust, fear, and sadness. Aromas are powerful evokers of autobiographical memories (Herz & Cupchik, 1995; Herz et al., 2004; Herz & Schooler, 2002; Herz, 1998). When examining autobiographical memories elicited by aromas, using basic emotional terms like “anger” and “sadness” is appropriate. However, outside the context of autobiographical memories, these basic emotional terms might not be very suited to aromas. An exception may be the basic emotion of disgust, which I discuss further below. The Geneva Emotion and Odor Scale (GEOS) (Chrea et al., 2009) was developed to construct a set of affective descriptors that was more suitable for aromas (Delplanque et al., 2012). The terms of this scale include pleasant feeling, unpleasant feeling, relaxation, refreshment, sensuality, and sensory pleasure (although different terms have been included in various cultural versions of the scale). Various studies have used other discrete terms and aroma properties, some of which are context-dependent, such as congruity (Bone & Ellen, 1999), or have biological significance, such as comestibility (Royet et al., 1999). Frequently, the sets of terms used will be determined by the specific hypotheses in question.

One reason discrete models are preferred to dimensional models is that the latter assume that pleasantness is a unitary construct. Instead, it is reasonable to suspect that there may actually be multiple aroma qualities, each with their own associated pleasantness, that contribute to an overall pleasantness judgment. One way to bring discrete and (uni)dimensional models closer together is to discover aroma qualities that contribute to pleasantness. Drivers of liking studies are common for flavor studies, aimed at determining what factors determine preference for specific types of foods. For example, factor analysis techniques like Partial Least Squares (PLS) have been used to determine the factors that drive liking across different types of Swiss cheese (Liggett, Drake, & Delwiche, 2008). These techniques can conceivably be adapted to determine what factors drive perceived pleasantness over a much wider set of diverse aromas. In Chapter 3, I use PLS on neural (fMRI) responses to aromas in lieu of subjective ratings to investigate perceptual features that contribute to perceived pleasantness of aromas, and their associated neural patterns of activation.

1.2 Neural correlates of olfactory perception

The olfactory system differs on the neuronal level from other sensory modalities in a number of ways. The olfactory system, being one of the evolutionarily oldest senses (Philpott, Bennett, & Murty, 2008), has relatively direct projections to limbic areas, including the amygdala, which is separated from the olfactory nerve by two synapses, and the hippocampus, which is separated by three synapses (Herz & Engen, 1996). The olfactory epithelium is also only separated from the orbitofrontal cortex (OFC) by three synapses (Powell, Cowan, & Raisman, 1965). The fact that olfactory signals can bypass processing in the thalamus contributes to the observed low degree of separation. In contrast, signals in other sensory systems must pass through a thalamic relay to cortical association areas, and only then travel to the limbic areas and OFC. The direct pathway for olfactory signals to areas important for processing of memory, emotion, and decision-making, without the need to first pass through the thalamus and cortex, may be why aromas have been found to be powerful evokers of emotions and emotional memories, while requiring little cognitive elaboration (Ehrlichman & Halpern, 1988).

The olfactory system varies in other ways, such as the fact that olfactory neurons project ipsilaterally, compared to the usual contralateral projections of many other systems (Herz & Engen, 1996). The olfactory system is also slow – olfactory detection takes almost ten times as long as visual detection, and olfactory sensations persist longer than sensations in other modalities. This makes evolutionary sense in light of the fact that odorant molecules travel at a rate much slower than light and sound, and thus there was no need to evolve a system that could detect olfactory changes in the environment quickly. A recent study took advantage of the slow time-course of the olfactory response to study perceptual decision-making using fMRI (Gottfried & Zelano, 2011). fMRI has roughly the same temporal resolution (on the order of seconds) as the evolving sensory percepts in this study.

fMRI studies have also begun to tease apart the neural representation of the olfactory percept. The presence of aromas (i.e. when air entering the nostril carries a smell, as opposed to unscented air) has been found to activate the piriform cortex (also called the primary olfactory cortex), the orbitofrontal cortex (the secondary olfactory cortex), the anterior cingulate cortex (ACC), and parts of the limbic system, such as the amygdala, hippocampus, thalamus, and peri-insular regions (Gottfried, Deichmann, Winston, & Dolan, 2002; Howard et al., 2009; Hudry, Ryvlin, Royet, & Mauguière, 2001; Savic & Berglund, 2004; Sobel & Prabhakaran, 1998; Suzuki et al., 2001; Yousem et al., 1999; Zelano et al., 2005).

Beyond mere presence of aromas, work has also been conducted to determine the neural correlates associated with various properties of aromas. Most fMRI studies have adopted the dimensional view, employing a more traditional General Linear Model (GLM) analysis approach to study dimensions like pleasantness and intensity. Neurally, odor pleasantness has been shown to activate areas of the brain associated with affect and decision-making: Several studies have found that medial orbitofrontal cortex (mOFC) activity correlates with aroma pleasantness, while lateral orbitofrontal cortex (lOFC) activity correlates with odor unpleasantness (Anderson et al., 2003; Gottfried et al., 2002; Rolls, Kringelbach, & de Araujo, 2003; Zald & Pardo, 1997). Royet et al. found that the piriform, amygdala, and insula were more active in response to unpleasant than pleasant aromas (Royet, Plailly, Delon-Martin, Kareken, & Segebarth, 2003). Intensity, on the other hand, has been found to correlate with the amplitude of activity in the amygdala, piriform cortex, anterior entorhinal cortices, as well as the ACC (Anderson et al., 2003; Rolls et al., 2003).

There is evidence that activity in some brain regions more closely tracks the motivational value of an aroma – that is, the level of approach or avoidance that aroma elicits (approach and avoidance dimensions are rotated 45° from pleasantness and intensity, see above, as well as Figure 2-1). For example, amygdala activity has been found to correlate with intensity, but only for valenced (pleasant or unpleasant) aromas, not neutral ones (Winston et al., 2005; Zald & Pardo, 1997). There is evidence that the anterior piriform cortex shows a similar pattern of activity, responding most strongly to the extremes of hedonic intensity, regardless of valence (Gottfried et al., 2002). There might therefore be some biological basis to support the use of approach and avoidance as dimensions for classifying aromas.

Other studies have investigated aroma properties using the categorical approach instead of relying on quantitative variation along particular dimensions. A number of studies show that the brain encodes aroma quality and identity. Using Multivariate Pattern Analysis (MVPA) methods, Howard et al. (2009) demonstrated that similarity of patterns of activation in the piriform cortex was related to the subjective similarity of aromas, and was capable of distinguishing between aroma categories. A second study (Veldhuizen, Nachtigal, Teulings, Gitelman, & Small, 2010) found that the insula responded differently to aroma sweetness depending on whether or not it was a food or non-food aroma, suggesting that the insula codes taste-like aspects of food aromas. Evidence for odor quality coding comes from lesion studies as well: OFC, temporal, and thalamic lesions produce deficiencies in the ability to discriminate qualitatively different aromas (Eichenbaum, Morton, Potter, & Corkin, 1983; Potter & Butters, 1980; Zatorre & Jones-Gotman, 1991). Patients with OFC lesions are even more impaired at aroma identification than are temporal lobectomy patients (Jones-Gotman & Zatorre, 1988). In a case of "blind smell," aroma-induced changes in brain activity were measured with fMRI in an right OFC lesion patient even though he could not detect the presented aromas (W. Li et al., 2010). It therefore appears that distributed regions of the brain contribute to the conscious and unconscious coding of distinct aspects of aroma quality, suggesting that a categorical approach may also be useful in studying neural activity associated with olfaction.

1.3 Aromas and memory

The categorical approach to studying the relationship between affect and olfaction has been used to study discrete emotions evoked by aromas and their associated autobiographical memories. As mentioned previously, aromas are powerful evokers of emotional memories, which may be unsurprising in light of the fact that olfactory information has a relatively direct pathway to brain areas involved in memory and emotion (Herz & Engen, 1996). Odor perception is also dependent on having an intact memory system (Wilson & Stevenson, 2003) – Korsakoff's patients show significant memory deficits, and are also impaired on odor detection and discrimination tasks (Potter & Butters, 1980). Medial temporal lobe (MTL) lesion patients, including the famed H.M., are not able to discriminate between qualitatively different aromas when intensity cues are removed (Eichenbaum et al., 1983).

Familiar aromas are processed differently from unfamiliar aromas. Familiar aromas are easier to distinguish, and though there is a right hemisphere bias for the processing of olfactory stimuli, at least for unfamiliar stimuli, neural activation towards familiar aromas is more symmetrical, suggesting semantic influence (Savic & Berglund, 2000). Memory for familiar aromas or those associated with labels was better than for unfamiliar or incorrectly identified aromas (Lyman & McDaniel, 1986; Rabin & Cain, 1984), and there is evidence that memory for aromas might be verbally mediated (Herz & Engen, 1996). Neurally, familiar aromas activate left frontal cortex (Brodmann's area 44, 45, and 47, implicated in language), right parahippocampal cortex, and left parietal cortex including the precuneus. Right parahippocampal and left frontal cortex activity correlate with familiarity ratings. More evidence for the role of MTL in olfactory perception comes from studying epileptic patients: frontal regions of left mesial temporal lobe epilepsy patients are not activated by familiar aromas, and these patients report aromas as less familiar than controls (Ciumas, Lindström, Aoun, & Savic, 2008). These findings suggest that memory and language systems are preferentially activated by familiar odors (Savic & Berglund, 2004). I return to these findings in Chapter 3.

Perception of aromas can be altered with repeated exposures. The ability to discriminate between aromas can be improved with experience (Rabin, 1988). Even enantiomers (molecules that are identical chemically, except that they are mirror images of each other) that are at first indistinguishable can be distinguished after aversive conditioning, and patterns of activation in the piriform cortex towards the two diverge (W. Li, Howard, Parrish, & Gottfried, 2008).

In addition to altering sensitivity to and discrimination of aromas, experience with an aroma can also alter preferences. While there is evidence for some innate preferences for the other chemical sense (i.e. gustation; Rozin & Vollmecke, 1986), there is no strong evidence for innate preferences in olfaction, and it appears that young children have no aversion to disgusting aromas like feces and decay (Petó, 1936; Rozin & Fallon, 1987). This suggests that all affective responses to aromas are learned. In fact, pleasantness has been repeatedly found to be correlated with familiarity (Bensafi et al., 2002; Distel et al., 1999; Royet et al., 1999). Female newborns develop a preference for an aroma that they are exposed to within the first day after birth (Balogh & Porter, 1986), and this preference persists for two weeks postpartum (Davis & Porter, 1991). These changes in preference could be explained by the mere exposure effect, which states that repeated exposure to a stimulus increases liking or preference for it (Zajonc, 1968). There is also a possibility that perceptual fluency plays a role in increased liking of familiar aromas, a theory which is supported by activation of neural circuits involved in semantic processing after repeated exposures of stimuli (Bornstein & D'Agostino, 1994). However, in the short term, repeated exposure might cause affective habituation – in one study it was found that a period of intensive exposure reduced subsequent valence so that pleasant aromas were rated less pleasant after 30 minutes of exposure, and similarly, unpleasant aromas were perceived as less unpleasant (Cain & Johnson, 1978). Changes in preference might depend on initial hedonic quality: Delplanque et al. (2008) point out that the positive correlation between pleasantness and familiarity is specific to the pleasant aromas, and does not apply to unpleasant aromas. Evolutionarily, this may reflect novelty-aversion that may protect organisms from contact with or ingestion of potentially dangerous new stimuli, until repeated exposures allow the organism to know that the stimulus is safe.

Increased familiarity may not occur towards unpleasant stimuli because organisms avoid them, thus never accumulating repeated exposures to them. In Chapter 3, I show that familiarity is associated with a pattern of brain activity that contributes to perceived pleasantness in a set of 12 varied aromas.

In addition to having a unique relationship with the memory system, aromas and emotion are similarly closely related. As previously stated, the olfactory system is closely linked to brain areas involved in emotion and memory (Herz & Engen, 1996), which may be why aromas are particularly effective at evoking emotional memories. Pleasant aromas tend to evoke more happy memories than unpleasant aromas (Ehrlichman & Halpern, 1988), though there is an overall bias for nostalgia to be associated with positive memories and emotions (Baumgartner, Sujan, & Bettman, 1992; Holak & Havlena, 1998). Aromas are powerful evokers of autobiographical memories (Herz & Cupchik, 1995; Herz et al., 2004; Herz & Schooler, 2002; Herz, 1998). There is evidence that aromas are more evocative memory cues than are cues in other sensory modalities, and aroma-cued memories are more emotional than memories cued by other sensory stimuli, as measured by self-report and physiological measures like heart rate (Herz & Cupchik, 1995; Herz & Schooler, 2002; Herz, 1998). Personally significant aromas (perfumes which elicited a pleasant memory of a person, place, or event) activate the amygdala and hippocampus (Herz et al., 2004). It has been proposed that aroma-evoked nostalgic memories might drive increased risk-taking in consumers by increasing sensation-seeking (Orth & Bourrain, 2008).

1.4 Using aromas to study decision-making

Aromas have the potential to be useful tools in the study of decision-making. In this section, I review mechanisms hypothesized to underlie decision-making involving risk and ambiguity, and propose how aromas can be used to test these hypotheses.

1.4.1 Risk

Preferences for risk (as opposed to certainty) vary widely between individuals. In addition to personality differences, whether or not one chooses to take a risk has also been shown to depend on situational factors, such as emotional and mood state (Isen & Patrick, 1983; J S Lerner & Keltner, 2001; Yuen & Lee, 2003), peer influence (Gardner & Steinberg, 2005), arousal (Ariely & Loewenstein, 2006), history of substance use (Lane, Cherek, Pietras, & Tcheremissine, 2004; Lane, Cherek, Tcheremissine, Lieving, & Pietras, 2005), and ambient incidental aromas (Hirsch, 1995; Orth, Bourrain, & Lyon, 2005; Orth & Bourrain, 2008).

Multiple theories have been proposed to explain how we make decisions involving risk, and how external influences on risk preferences arise. An influential theory known as risk-as-feelings (Loewenstein, Weber, Welch, & Hsee, 2001) states that emotional reactions to situations, and not just cognitive evaluations, affect our preference for risk. The somatic marker hypothesis is a related theory that states that bodily (somatic) responses to stimuli rapidly signal the potential outcomes of our behaviors, and thus help guide our decisions (Bechara & Damasio, 2005). Both of these theories predict that incidental stimuli (unrelated to the decision) might affect decisions through the emotional responses that they evoke.

Several studies have demonstrated that pleasant visceral cues such as food or erotica influence willingness to accept risk. For example, the sight and smell of cookies (compared to a verbal description of cookies) made people more willing to make a risky choice for the chance to win cookies, while sexual arousal in response to erotic images or self-stimulation increased the reported tendency to engage in certain risky sexual behaviors (Ariely & Loewenstein, 2006; Ditto et al., 2006). Incidental emotional stimuli are also able to exert an out-of-domain influence on risk preference. For example, it was found that the anticipation of viewing rewarding stimuli (erotic pictures) increased financial risk-taking (Knutson, Wimmer, Kuhnen, & Winkielman, 2008). It has been proposed that such visceral cues put a person in a "hot", emotionally aroused state, (Loewenstein, 1996), altering perception of potential rewards (Knutson et al., 2008). In the context of the somatic marker hypothesis, physiological responses to these rewarding visceral cues signal the potential rewards of the risky action, increasing our tendency towards risk.

1.4.2. Ambiguity

While much research has been conducted on the mechanisms behind risk preferences, there has been relatively less work investigating ambiguity. Ambiguity, though closely related to risk, differs in terms of the amount of information available about the probabilities of potential outcomes of decisions. While the exact probabilities of potential outcomes are known with risk, these probabilities are not known with ambiguity (Ellsberg, 1961). Ambiguity has been found to elicit higher physiological responses (anticipatory skin conductance response) than risk (Bechara & Damasio, 2005).

1.4.3. Neural correlates of decisions involving risk and ambiguity

Because most work has focused on risk, more is known about the neural correlates of risk compared to ambiguity. Two regions that are commonly found to be associated with risk are the striatum and the anterior insula (Kuhnen & Knutson, 2005). The nucleus accumbens and caudate were found to be active preceding a risky choice (Kuhnen & Knutson, 2005; Matthews, Simmons, Lane, & Paulus, 2004). Consistent with the observation that insula activity precedes risk-averse choices (Helfinstein et al., 2014; Kuhnen & Knutson, 2005), insula activity has been hypothesized to signal the potential aversive consequences of a gamble, so that greater anterior insula activity steers people away from risk (Paulus, Rogalsky, Simmons, Feinstein, & Stein, 2003).

Studies of risk and ambiguity have uncovered several structures that underlie both risk and ambiguity processing, such as parts of the lateral prefrontal cortex, parietal cortex, basal ganglia, and thalamus (Huettel, Stowe, Gordon, Warner, & Platt, 2006). However, neural processes involved in the processing of risk and ambiguity have been shown to differ in important ways. While activity in the lateral prefrontal cortex was found to correlate with ambiguity preferences, risk preferences were associated with activation in the posterior parietal cortex (Huettel et al., 2006). Moreover, activity in the posterior inferior frontal sulcus, the amygdala, anterior insula, posterior parietal cortex, and the OFC are more active when choices involve ambiguity, whereas the dorsal striatum was more active for choices involving risk (Hsu, Bhatt, Adolphs, Tranel, & Camerer, 2005; Huettel et al., 2006).

1.4.4. Using aromas to study decisions involving risk and ambiguity

Aromas have been used to affect risky decisions in a few studies. In a casino setting, it was found that an ambient pleasant aroma increased gambling compared to an unpleasant aroma or absence of aroma (Hirsch, 1995). Aromas were also found to increase risk preferences among consumers (Orth et al., 2005; Orth & Bourrain, 2008). In these studies, the observed effects on risk preference in a consumer context were interpreted as being driven by aroma pleasantness or intensity, or by aroma-evoked nostalgic memories. By using aroma stimuli that vary along the dimensions of pleasantness, intensity, and familiarity, we can study these proposed mechanisms in a controlled lab setting using standard decision tasks (as opposed to field studies in casinos or surveys framed to target consumer risk-taking), as well as extend the investigation to include ambiguity.

In addition to testing these hypotheses behaviorally, mechanisms of decision-making can be inferred from neural patterns of activity, using what we know about various regions of the brain. For example, activity in the caudate was observed to be lower in response to ambiguous compared to risky stimuli, and because of the role of the caudate in reward valuation, this was interpreted to mean that ambiguity decreased the subjective value of the stimulus compared to risk, where more information about the payoff structure is known (Hsu et al., 2005). Similarly, the relationship between harm avoidance and the insula's response to risk was the basis for asserting that the insula likely signals potential harms associated with risky decisions (Paulus et al., 2003).

In a similar fashion, we can use neural responses to test various hypotheses regarding aroma effects on risk. For example, to test the theory that aroma pleasantness influences the perceived value of a risky (or ambiguous) reward, we might expect aromas to interact with structures related to reward evaluation, such as the striatum, ventromedial prefrontal cortex (vmPFC), or the OFC. On the other hand, emotionally arousing aromas might activate the anterior insula (activity in this regions has been found to predict risk-averse choices ; see above), leading to decreased risk-taking. If familiarity and nostalgia affect risk preferences, we might look for differential activation in structures involved in autobiographical memory such as the hippocampus (Cabeza & St Jacques, 2007). Furthermore, since neural responses to risk and ambiguity differ in regions that are also involved in olfactory processing, it is possible that aromas affect risk and ambiguity decisions in different ways. In Chapter 4, I report effects of aromas and associated patterns of brain activity related to the impact of aromas on decisions involving risk versus ambiguity.

1.5 Methodological considerations

Before beginning, it is worth discussing some broad challenges faced when studying olfaction. First, people are notoriously poor at being able to name the identity of an aroma, or describe its properties (Cain, De Wijk, Lulejian, Schiet, & See, 1998). Despite the paucity of details in conscious olfactory percepts, hedonic judgments are known to be robust (Yeshurun & Sobel, 2010). People are able to make nuanced hedonic judgments related to aroma quality, and I show in Chapter 2 that these ratings are reliable. Given these considerations, in this dissertation, I intentionally avoid components of olfactory percept that are troublesome from a psychological perspective – such as aroma identity, similarity of aromas, etc. – to focus on their affective features.

Purported roles of different brain regions and interpretation of results are likely to vary across studies simply due to the chosen analysis methods or models. An example that illustrates this well is the role of the insula. In studies that took a categorical approach, the insula was found to encode sweetness and to distinguish between food and non-food smells. With a dimensional approach, insula activity was found to correlate with pleasantness and intensity, leading to different conclusions. A second example is the role of the piriform cortex. With GLM analysis, the piriform was found to respond to higher intensity valenced scents, but with MVPA approaches, it was revealed that the piriform might perform much finer categorical encoding. This demonstrates how different types of analysis can complement each other to incrementally reveal neural mechanisms of aroma processing and their effects on behavior.

For *a priori* analyses, the importance of having multiple sets of hypothesized models is captured in the comparison between the pleasantness-intensity and approach-avoidance dimensional analyses. It can be hard to understand why two such similar representations of olfactory space are necessary. However, intensity is often correlated with stronger valence (Bradley et al., 2001; Royet et al., 1999), and unpleasant aromas are usually more salient or biologically significant than pleasant aromas. Certain regions are responsive to all salient (high-arousal valenced) aromas, regardless of valence, as mentioned above. If we had only considered the pleasantness-intensity dimensions, we might found that these regions were more active towards unpleasant aromas simply due to the fact that the unpleasant aromas in those particular studies were more arousing than the pleasant stimuli.

Great care must be exercised in selecting aromas for experiments, and generalizing conclusions beyond these aromas. If an aroma is selected as representative of a particular dimension or category, it is quite possible that observed effects of the aroma are really due to other qualities of the aroma, rather than the selected dimension or category. Take for example a disgusting aroma that is picked as a representative "unpleasant" aroma. If we find that the insula reacts to this aroma, we might conclude that the insula reacts to all unpleasant aromas, whereas in reality it might actually react to disgusting aromas. Similarly, for pleasant aromas, if a lemon aroma is used to represent "pleasant", for example, we need to consider that it is food related. These examples are meant to illustrate that care has to be taken in selecting an aroma or set of aromas to represent terms like "disgusting", or axes like "pleasantness", and when generalizing beyond the specific aromas used in each study.

As mentioned above, olfaction is unique among the senses in that it is slow. Timing and length of exposure to an aroma will therefore be longer than for other stimulus modalities, and is an important factor to consider. Furthermore, adaptation effects need to be kept in mind for longer exposure times. During longer exposures (e.g. a minute), it has been found that different parts of the brain like the primary olfactory cortex (including piriform and amygdala), hippocampus, and anterior insula habituated sooner, while other regions like the OFC remained active the entire time the aroma is present (Poellinger et al., 2001; Sobel et al., 2001). This was used to explain why early olfaction studies that employed long block designs found activity in the secondary but not primary olfactory cortex.

There is some evidence pointing to right side dominance in olfactory processing. Presentation to the right nostril leads to superior performance on an aroma discrimination task (Savic & Berglund, 2000). Since projections are ipsilateral in the olfactory system, this behavioral result would lead to the prediction of a neural right side bias. Indeed, right OFC was found to be more active in olfaction than left OFC (Zatorre, Jones-Gotman, Evans, & Meyer, 1992), and right OFC lesions led to birhinal impairments in discrimination (Zatorre & Jones-Gotman, 1991). For tests of aroma recognition memory, only right side lesions of temporal and OFC led to impairments (Jones-Gotman & Zatorre, 1993), and right but not left temporal lobe epilepsy patients demonstrate deficits in aroma identification tests (Kohler et al., 2001). A right-side bias in neural activation was also found by Savic & Berglund (2000), but only for unfamiliar aromas; they hypothesize that with familiar aromas, the left hemisphere is also activated because of semantic influences (Savic & Berglund, 2000). There is also one study which shows that there is more left side activation towards pleasant aromas, and right side bias for unpleasant aromas, both for real and imagined aromas (Henkin & Levy, 2001). This might be due to pleasant aromas being in general more familiar (Bensafi et al., 2002; Distel et al., 1999; Royet et al., 1999). Royet et al. (1999) found a left side dominance when subjects were asked to assess the emotional quality of an odor, possibly due to the semantic demands of the task, and this laterality was flipped in left-handed subjects (Royet et al., 2003). Relevant to the work in this dissertation, a right side bias for activation in the insula is found in the study conducted in Chapter 4.

Finally, in order to be used to study behavior and decision-making, aromas should be able to reliably induce emotional states over time and across people. In the following chapter, I construct a library of aromas and catalogue their affective properties so that they can be used to research mechanisms of judgment and decision-making.

Chapter 2

Aromas as affective stimuli

2.1 Introduction

The ability to manipulate emotion is a powerful tool in health, marketing, and research. Especially with use in the latter field, it is crucial to be able to elicit emotional responses in a controlled and reliable manner. To this end, libraries of stimuli in a number of domains have been compiled, such as for pictures (Lang, Bradley, & Cuthbert, 1997), sounds (Bradley, Lang, Margaret, & Peter, 2007), words (Bradley & Lang, 1999), faces (Ekman & Friesen, 1971), and films (Gross & Levenson, 1995). By mapping a variety of stimuli from each modality in affective space, these stimuli have been shown to be organized around appetitive (approach) and defensive (withdrawal) motivational systems (Bradley et al., 2001) – when stimuli are mapped along the axes of hedonic valence and arousal, the further in valence a stimulus is from neutral, the higher arousal tends to be, resulting in a characteristic 'V' shape often observed in affective mapping (Figure 2-1).

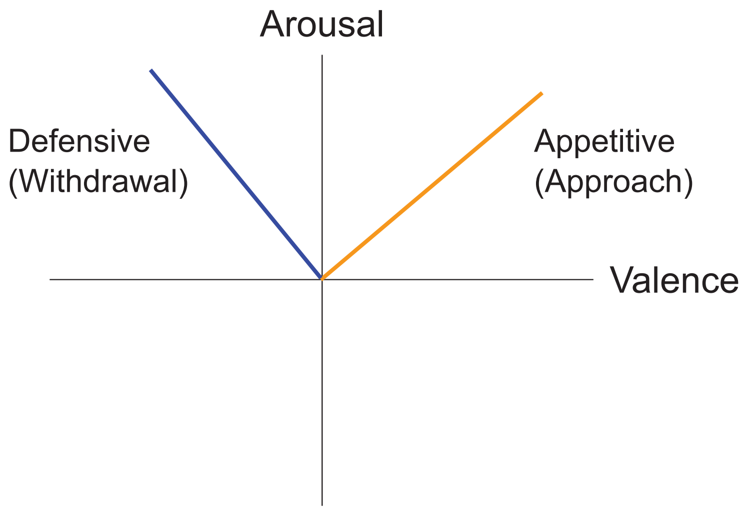

Figure 2-1. Appetitive and defensive motivational systems on the affective circumplex. When mapped on the affective circumplex, stimuli from various modalities typically fall along two main arms, one corresponding to appetitive, or approach, motivations, and the other to defensive, or withdrawal, motivations. The further away a stimulus is from neutral arousal, the higher its absolute valence tends to be, resulting in a 'V'-shaped plot. Note that for negative stimuli, valence increases faster for each unit increase in arousal, resulting in a steeper slope for the defensive motivational arm.

Perhaps owing to the potential difficulty in eliciting constant judgments both between and within subjects, and also the complex nature of olfactory stimuli and technical difficulty associated with delivery, less attention has been given to the study of the affective properties of naturalistic smells than to stimuli from other sensory domains. Despite these challenges, aromas have certain advantages over other modalities. They are highly emotionally evocative (Herz et al., 2004; Herz, 2009), and can be presented subliminally (W. Li, Moallem, Paller, & Gottfried, 2007), in a non-distracting manner, simultaneously with other stimuli (Baron & Kalsher, 1998; Lehrner, Marwinski, Lehr, Johren, & Deecke, 2005), even during sleep (Rasch et al., 2007). They are therefore potentially powerful tools in a behavioral psychologist's arsenal.

In order to be useful as emotion manipulation tools, however, it is important to determine if affective properties of aromas are similar to stimuli in other domains that are currently used to elicit emotion, and if these properties are suitably reliable within and between raters. It has yet to be determined if aromas arrange themselves on the affective circumplex in a similar fashion to other sensory modalities, with stimuli distributed along both the dimensions of valence and arousal. Several studies have argued that pleasantness is the sole dimension of aroma space (Khan et al., 2007; Schiffman et al., 1977; Yeshurun & Sobel, 2010). However, aroma stimuli used in these studies were intensity-matched, thus ignoring an important affective dimension. Neural evidence supports the importance of the intensity/arousal dimension. While activity in the medial and lateral orbitofrontal cortices were shown to correlate with valence of aromas, the amygdala was shown to reflect information about intensity, or an interaction of pleasantness and intensity (Anderson et al., 2003; Winston et al., 2005). While some behavioral studies have investigated the effects of both intensity and pleasantness of odors, one of these studies (Moskowitz, Dravnieks, & Klarman, 1976) was carried out on chemicals that are not frequently encountered in the environment (e.g. cyclohexene and butyl-acetate). Furthermore, aromas used in these studies were also mostly neutral or unpleasant. Another study collected ratings for naturalistic aromas in order to find suitable stimuli for a subsequent PET study (Royet et al., 1999), but no attempts were made to assess the reliability of these ratings, nor was it their intention to publish information about the ratings for use by other groups.

The goal of the current study is to assess the suitability of aromas as a method of emotion-induction, and to investigate and publish the affective properties of a variety of naturalistic aromas to make them available for use in future studies. In the current study, we collect subjective ratings of aromas along a number of dimensions to determine if aromas are organized around the motivational axes of approach and avoidance, like other modalities (or if they are unidimensional), as well as to assess inter-rater and test-retest reliability.

2.2 Methods

Participants

Participants were 52 students (30 female) in Stanford University's introductory psychology course, participating as part of a course requirement.

Materials and Procedure

Aromas and aroma delivery. 47 aromas were chosen to span a wide range of odor space (see Table 2-1 for concentrations and solvents). In an effort to include a diverse set of aromas, we included aromas spanning several qualitatively distinct dimensions, including common (e.g. strawberry) and uncommon (patchouli), edible (beef) and inedible (fuel), pleasant (lemon) and unpleasant (overripe), and complex mixtures (oatmeal cookie) and single chemicals (isovaleric acid). Aromas were delivered using a 30-channel olfactometer (Givaudan Flavors Corporation), and subjects positioned their faces on a chin rest such that both nostrils were directly in front of a glass nosepiece. Flow rate of aroma was adjusted to 10ml/min. Aroma delivery and ratings were self-paced. Subjects were prompted to press a button to indicate when they were ready to receive each aroma. The aroma was then presented for six seconds, after which subjects were prompted to press a button to indicate that they were ready to rate the delivered aroma. To prevent carryover effects and allow for washout of aromas between trials, aroma presentations were separated by at least one minute.

Subjects rated one of two sets of 30 aromas, set A (25 participants, 15 female) or set B (27 participants, 15 female). Set A and set B shared 11 aromas in common (see Table 2-1); the remaining aromas were unique. 37 subjects (20 from set A, 12 female, and 17 from set B, 12 female) returned for a second session 14 days after the first session, in which they rated the same aromas a second time. The second session was scheduled at the same time of day as the first session.

Ratings. A 9-point Self Assessment Manikin scale was used to obtain ratings of valence and arousal, mirroring methods used to measure emotional responses to a number of other stimulus modalities, such as words, pictures, and sounds (Bradley et al., 2001; Bradley & Lang, 1994). Though dominance is less relevant to olfactory stimuli as it is to modalities such as pictures or words, in order to be consistent with earlier studies of affective stimuli in other modalities, the Self Assessment Manikin was also used to collect ratings of dominance. The extremes of the scales had the following labels: “Happy” to “Unhappy” for valence, “Excited” to “Calm” for arousal, and “Controlled” to “In control” for dominance. Nine-point Likert scales were used to obtain ratings for pleasantness (Extremes were labeled “Very pleasant” and “Very unpleasant”, midpoint labeled “Neutral”), intensity (“Very intense” to “Undetectable”, midpoint labeled “Moderate intensity”), and craving (“Strong cravings” and “Turned me off food”, midpoint labeled “Neutral”). Additionally, as a measure of familiarity of the aroma, participants were asked to guess the identity of the aroma, and rate their confidence in their guess (Homewood & Stevenson, 2001; Jehl, Royet, & Holley, 1995) (“Extremely confident" to "Purely guessing", midpoint labeled "Moderately confident"). The starting value of the cursor for pleasantness, valence, dominance, and craving scales was the center of the scale, while the default value for intensity, arousal, and familiarity was the right extreme (least intense or familiar). All ratings were reverse-scored such that increasing value corresponded to increasing levels of the dimension the scale was named after, e.g. pleasantness scale reflected increasing pleasantness. Pleasantness scores were shifted to a -4 to 4 scale, such that -4 reflected maximum unpleasantness. Intensity, craving, and familiarity ratings were adjusted to a 0 to 8 scale, with 0 reflecting the lowest intensity, craving, or familiarity.

Pleasantness and intensity ratings were very similar to valence and arousal scales, but were phrased to target properties of the aromas themselves, as opposed to emotions elicited by the aromas. Valence and pleasantness have been used synonymously, as have intensity and arousal, with the assumption that these dimensions are highly correlated and can therefore serve as a proxy for each other. To explicitly check if this assumption is correct, we conducted a correlation test between pleasantness and valence, and between intensity and arousal.

Reliability. In order to measure test-retest reliability, Pearson's correlation coefficients were calculated between session 1 and session 2 ratings for each of the thirty aromas. To determine inter-rater reliability, intra-class correlations (ICC2k in CRAN psych package) were calculated for session 1 and session 2 separately, for each rating dimension. Split-half coefficients have also been used as a measure of inter-rater reliability in previous analyses of affective stimuli in other modalities (Lang et al., 1997). We therefore calculated split-half coefficients for each rating dimension by splitting the subject pool in half, then computing the degree of correlation between mean ratings of each aroma (from session 1) from each half.

Procedure. Upon arriving in lab, participants were given instructions modeled after those from Bradley & Lang (Lang et al., 1997), modified for olfactory stimuli, and with four additional dimensions added – pleasantness, intensity, craving, and familiarity (see Ratings section). After the participants read the instructions and indicated that they understood, they were given three practice trials, during which they rated sulfury cheese, orange, and cucumber for set A, and toasted almond, animalic acid, and green tea for set B. Ratings from the practice trials were not included in subsequent analyses.

Thirty aromas were then presented to the participants (Table 2-1). Each aroma was rated according to the rating schemes detailed above in “Ratings”.

Set A	Concentration	Solvent
Almond, toasted	100%	NA
Animalic	100%	NA
Bacon	100%	NA
Chai	100%	NA
Cheese	5%	Miglyol
Cinnamon roll	100%	NA
Fishy (tri-methyl-amine)	0.01%	Miglyol
Fuel (Benzothiazole)	25%	Miglyol
Green tea	100%	NA
Hibiscus	100%	NA
Hickory liquid smoke	25%	PG
Lavender	100%	NA
Lemon	100%	NA
Mango	100%	NA
Overripe/trash (Methylthiobutyrate)	0.5%	Miglyol
Onion oil	10%	Miglyol
Patchouli	30%	Miglyol
Peanut butter	50%	Water
Pear	100%	NA
Pepper	10%	Miglyol
Peppermint	10%	PG
Rose Oil	5.0%	Miglyol
Sandalwood oil	100%	NA
Seaweed	100%	NA
Strawberry	100%	NA
Sweaty/onion (P-Mentha 8-thiol-3-one)	0.50%	Ethanol
Taco	100%	NA
Vanilla ice cream	100%	NA
Violet Leaf	100%	NA
Practice:		
Cheese, sulfury	1%	Miglyol
Orange	100%	NA
Cucumber	100%	NA

Set B	Concentration	Solvent
Beef	100%	NA
Chai	100%	NA
Champagne	100%	NA
Cheese, sulfury	1%	Miglyol

Cherry	100%	NA
Chocolate	100%	NA
Coffee	100%	NA
Cucumber	100%	NA
Fishy (tri-methyl-amine)	0.01%	Miglyol
Fried flavor	100%	NA
Fuel (Benzothiazole)	25%	Miglyol
Grape	100%	NA
Hickory liquid smoke	25%	PG
Isovaleric acid	10%	Miglyol
Key Lime Pie	100%	NA
Lemon	100%	NA
Mango	100%	NA
Mangosteen	100%	NA
Menthol	27%	Miglyol
Overripe/trash (Methylthiobutyrate)	0.5%	Miglyol
Oatmeal cookie	100%	NA
Onion oil	10%	Miglyol
Orange	100%	NA
Pear	100%	NA
Peppermint	10%	PG
Rose oil turkey	5%	Miglyol
Strawberry Jam	100%	NA
Vanilla	100%	NA
Violet leaf	100%	NA
Practice:		
Almond, toasted	100%	NA
Animalic	100%	NA
Green tea	100%	NA

Table 2-1. Aroma concentrations and solvents. Single molecule aromas are in bold font.

2.3 Results

Ratings for trials where aromas were not detected (rated “undetectable” for intensity) were excluded from analysis. Across all subjects, aromas from 2.8% of trials were not detected in session 1, and 4.0% in session 2. Means and standard deviations for ratings for each aroma along each dimension are summarized in Table 2-2. Aromas were found to span a wide range within each dimension.

		Pleasantness		Intensity		Valence		Arousal		Dominance		Craving		Confidence	
Aroma	Number of raters	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Almond, toasted	25	0.46	1.72	3.75	1.7	5.46	1.77	4.17	1.66	4.96	1.23	4.04	1.68	1.75	1.48
Animalic acid	25	-2.5	1.18	4.5	1.69	2.79	1.25	5.46	1.59	5.75	1.82	1.08	1.32	2.33	1.71
Bacon	25	0.48	2.43	4.88	1.96	5.36	2.2	5.04	2.28	4.76	1.92	4.04	1.99	4.16	2.19
Beef	27	0.15	1.89	3.58	1.53	5.04	1.78	4.5	1.98	5.15	1.52	4.04	1.78	2.62	1.94
Chai	52	2.04	1.37	4.12	1.63	6.88	1.35	4.71	2.11	4.04	1.49	5.42	1.43	3.67	2.14
Champagne	27	-0.85	1.78	4.12	1.73	4.12	1.53	4.69	1.91	5.92	1.81	3.42	1.72	2.81	2.21
Cheese	25	-2.68	1.7	5.32	1.57	3.08	1.8	5.6	1.35	6	1.94	1.6	2	2.64	2.53
Cheese sulfury	27	-2.78	1.25	5.44	2.01	2.3	1.41	4.7	2.77	6.85	1.66	1.11	1.37	1.89	1.95
Cherry	27	1.74	1.65	4.74	1.4	6.59	1.74	4.22	2.01	4.52	1.5	4.78	1.42	3.41	2.17
Chocolate	27	0.27	2.38	4.27	1.73	5.38	2.23	5.08	2.02	5.35	1.55	3.77	2.07	2.19	1.9
Cinnamon roll	25	2.12	1.62	4.28	1.4	7.04	1.43	4.4	2.24	4.28	1.65	5.68	1.8	3.76	2.28
Coffee	27	1.59	1.67	4.52	1.81	6.56	1.48	5.33	2.17	4.89	1.65	4.63	1.55	3.89	2.26
Cucumber	27	0.81	2.22	3.63	2.08	5.37	2	3.67	1.84	4.81	1.67	4.04	2.07	2.89	2.58
Fishy	52	-2.47	1.38	4.3	1.97	2.96	1.49	5.17	1.86	6.13	1.84	1.26	1.37	2.09	1.99
Fried flavor	27	-3.04	1.45	5.96	1.85	2.19	1.36	5.63	2.57	7	1.64	0.7	1.32	2.48	2.19
Fuel	52	-1.77	1.41	4.54	1.8	3.42	1.59	5.02	1.94	6.17	1.64	1.73	1.55	2.25	1.94
Grape	27	1.15	1.71	4.27	1.73	5.92	1.76	5.04	2.25	4.88	1.56	4.42	1.65	3.38	2.3
Green tea	25	-0.47	1.35	2.47	1.54	4.58	1.39	3.95	1.84	5	1.41	3.21	1.51	1.16	1.54
Hibiscus	25	-0.44	2.52	4.24	1.98	4.68	2.34	5.28	1.97	5.04	1.86	3.2	2.33	2.4	2.42
Hickory liquid smoke	52	-1.5	2	5.06	2.04	3.85	1.95	5.71	1.79	5.67	1.81	2.37	2.19	2.38	2.34
Isovaleric acid	27	-2	1.79	4.42	2.27	3.42	1.75	4.81	2.47	6.08	1.76	2	2.12	1.85	1.76
Key lime pie	27	0.88	1.4	3.62	1.63	5.85	1.29	4.54	1.88	4.96	1.48	4.31	1.44	2	1.94
Lavendar	25	1.5	1.18	3.46	1.79	6.42	1.06	3.67	1.83	4.63	1.21	4.04	0.91	2.67	2.12
Lemon	52	1.71	1.39	3.98	1.9	6.63	1.33	4.27	1.93	4.43	1.55	4.73	1.31	3.39	2.42
Mango	52	2.08	1.53	4.96	1.55	7.06	1.18	5.44	2.03	4.15	1.36	5.42	1.45	3.31	1.94
Mangosteen	27	1	1.77	4.15	1.87	6.08	1.6	4.46	2.1	4.73	1.37	4.27	1.69	2.62	2.14
Menthol	27	-0.62	1.72	3.05	2.04	4.38	1.72	4.62	2.29	5.38	1.53	3.43	1.63	1.95	2.01

Oatmeal cookie	27	1.33	1.96	4.74	1.56	6.15	1.97	4.74	1.83	4.26	1.79	4.85	1.83	3.44	2.1
Onion oil	52	-1.65	1.81	5.35	1.93	3.52	1.64	5.6	1.91	6.04	1.63	2.27	1.89	3.1	2.58
Orange	27	2.56	0.85	5.26	1.48	7.48	1.19	5.48	1.99	3.89	1.5	5.85	0.91	4.96	2.16
Overripe	52	-2.39	1.41	4.29	2.1	2.76	1.49	4.98	1.81	6.29	1.51	1.35	1.49	1.69	1.56
Patchouli	25	-0.76	1.83	4.24	1.79	4.48	1.96	5	2	5.16	1.57	2.84	1.7	1.88	2.11
Peanut butter	25	-0.83	1.71	2.92	1.89	4.54	1.25	3.92	1.79	5.21	1.18	3.13	1.78	1.83	2.3
Pear	52	1.1	1.54	4.46	1.54	6.15	1.45	4.9	1.91	4.71	1.42	4.23	1.71	2.71	2.24
Pepper	25	-0.08	1.5	3.56	1.76	5.16	0.99	4.48	2.12	5.16	1.4	3.48	1.64	1.84	2.27
Peppermint	52	1.68	1.5	3.22	1.63	6.46	1.51	4.4	2.22	4.36	1.43	4.9	1.34	3.26	2.58
Rose oil turkey	27	1.41	2.31	4.52	1.63	6.41	2.32	4.04	2.26	4.48	2.08	4.22	1.93	3.07	2.7
Rose oil	25	0.24	1.85	4.36	1.68	5.56	1.76	4.48	1.66	4.92	1.47	3.2	1.71	2.36	2.04
Sandalwood	25	-1.33	1.33	3	1.14	4.11	1.02	4	1.65	5.61	0.7	2.06	1.43	0.94	1.47
Seaweed	25	-0.92	1.63	3.76	2.18	4.52	1.29	4.48	1.5	5.48	1.36	2.84	1.72	1.12	1.64
Strawberry	25	2.16	1.25	4.48	1.78	7.16	1.28	4.8	2.02	4.36	1.6	5.36	1.32	3.32	2.17
Strawberry jam	27	2.67	1.04	4.26	1.43	7.63	1.08	4.81	2.22	3.7	1.44	5.63	1.52	3.56	2.19
Sweaty / onion	25	-1.04	1.81	3.8	1.98	4.28	1.81	4.84	2.03	5.24	1.36	2.84	1.84	1.56	1.71
Taco	25	-0.4	2.1	5.28	1.7	4.72	2.03	5.56	1.69	5.76	1.71	3.6	2.42	2.6	2
Methylthiobutyrate	52	-2.84	1.35	5.27	2.09	2.37	1.47	5.84	2.07	6.55	1.91	1.12	1.38	2.12	2.12
Vanilla	27	1.58	1.5	3.77	1.86	6.54	1.42	5	2.38	4.31	1.29	4.81	1.65	2.65	1.98
Vanilla ice cream	25	1.92	1.28	4	1.5	6.83	1.43	4.63	1.69	4.21	1.44	5.29	1.37	3.75	2.35
Violet leaf	52	-1.31	2.02	5.06	1.71	3.9	1.86	4.79	2	5.98	1.7	2.44	1.91	2.13	2.32

Table 2-2. Ratings for 47 aromas. Means and standard deviations (SD) are shown.

Valence and pleasantness are often used interchangeably, as are intensity and arousal (Anderson et al., 2003). In an earlier study, it was found for six aromas that intensity was highly correlated with arousal (Bensafi et al., 2002). We wished to extend this finding to a wider range of aromas, as well as confirm that pleasantness and valence are highly correlated as well. In the current study, the correlation between mean valence and pleasantness for each aroma was found to be high ($r = 0.995$, $p < 0.001$, Figure 2-2a). The correlation between mean intensity and arousal ratings was not as high, but was still highly significant ($r = 0.735$, $p < 0.001$, Figure 2-2b). Because of the high correlation between pleasantness/intensity and valence/arousal, we concluded that pleasantness and intensity were suitable proxies for valence and arousal. All subsequent analyses were conducted using pleasantness and intensity to avoid redundancy, using pleasantness and intensity because pleasantness/intensity ratings were also found to be more reliable within and across subjects (see below).

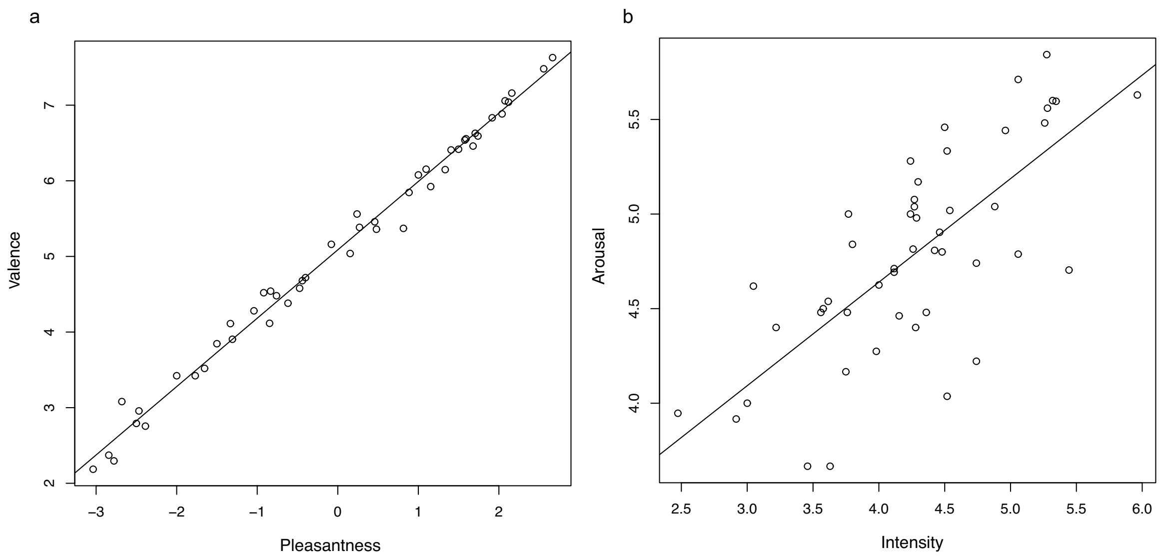

Figure 2-2. Correlations between pleasantness/intensity and valence/arousal ratings. (a) A high correlation was observed between pleasantness and valence ($r = 0.995$, $p < 0.001$), and (b) for intensity and arousal ($r = 0.735$, $p < 0.001$).

Our next goal was to determine whether aroma percepts are distributed on the affective circumplex in a manner similar to other sensory modalities. To this end, mean pleasantness and intensity scores for each aroma were plotted against each other. A significant quadratic effect was found between pleasantness and intensity ($p = 0.00738$), similar to findings in other modalities (Lang, Greenwald, Bradley, & Hamm, 1993; Royet et al., 1999). Aromas were observed to arrange themselves into two motivational arms corresponding to approach and withdrawal (Figure 2-3). Correlations between pleasantness and intensity were carried out for aromas on either side of neutral pleasantness. Similar to other domains, it was found that there was a higher correlation between pleasantness and intensity for unpleasant stimuli in the defensive arm (negative aromas, mean pleasantness < 0) (e.g. Lang et al., 1997) compared to the appetitive arm (positive aromas, mean pleasantness > 0) ($r = -0.601$, $p = 0.00309$ for negative aromas, versus a non-significant correlation of r = 0.288, for positive aromas)., and the gradient for the defensive arm was steeper than the appetitive arm (defensive arm gradient was -0.634, versus 0.204 for the appetitive arm).

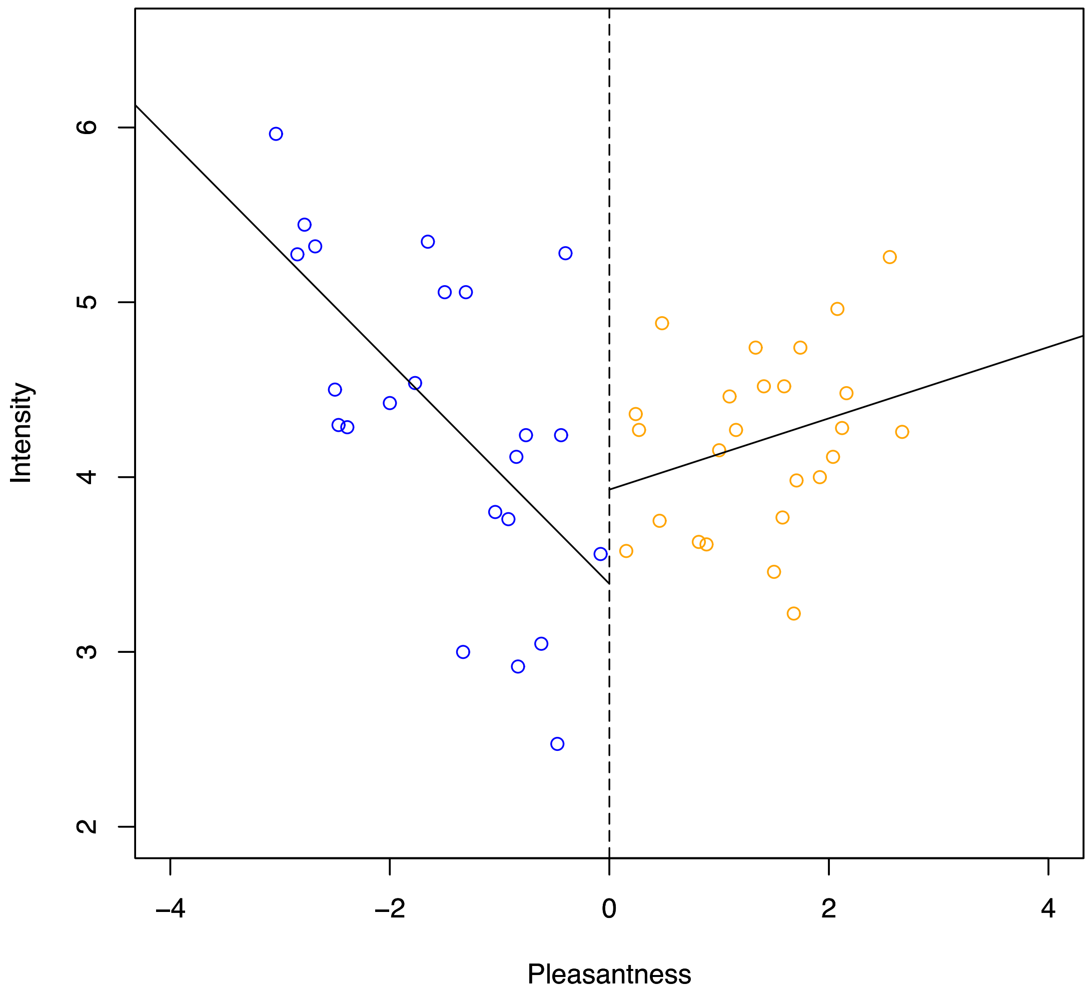

Figure 2-3. Correlations between pleasantness and intensity for negative and positive aromas. The correlation for the negative aromas (mean pleasantness < 0, r = -0.601, p = 0.00309) was higher than for positive aromas (mean pleasantness > 0, r = 0.288, n.s.).

To determine if ratings were stable over time, test-retest reliability (Pearson's correlation coefficients between mean ratings for each aroma in sessions 1 and 2) for each dimension was computed. Reliability for most dimensions was found to be high (Arousal was an exception at $r = 0.661$, see discussion). Results are summarized in Table 2-3.

Rating dimension	Pearson's correlation coefficient
Pleasantness	0.960
Intensity	0.865
Valence	0.957
Arousal	0.661
Dominance	0.894
Craving	0.950
Familiarity	0.855

Table 2-3. Test-retest reliability for aroma ratings. Pearson's correlation coefficients between mean ratings for each aroma in sessions 1 and 2 are shown. All correlations were significant at $p < 0.001$.

Furthermore, aromas should elicit reasonably similar reactions across participants in order to be useful as an emotion manipulation tool. All 52 subjects rated 11 aromas in common. Intra-class correlation (ICC) values for each dimension were calculated for each rating dimension within set A, set B, and for the 11 aromas in common, and were summarized in Table 2-4. In previous analyses of stimuli in other modalities, split-half coefficients were obtained as a measure of inter-rater reliability (Lang et al., 1997). Split-half coefficients for the current aroma set are shown in Table 2-5. All results for both sets of analyses were significant at $p < 0.001$.

Set	Number of scents	Number of raters	Pleasantness	Intensity	Valence	Arousal	Dominance	Craving	Familiarity
A	30	25	0.960	0.838	0.954	0.660	0.800	0.943	0.859
B	30	27	0.963	0.802	0.960	0.510	0.895	0.951	0.709
AB common	11	52	0.986	0.857	0.984	0.698	0.942	0.980	0.798

Table 2-4. Inter-rater reliability for aroma ratings. Intraclass correlations for each rating dimension are shown. Values are from session 1. ICC values for pleasantness and intensity were slightly higher for pleasantness/intensity than valence/arousal. All results were significant at $p < 0.001$

Rating dimension	Pearson's correlation coefficient
Pleasantness	0.844
Intensity	0.628
Valence	0.834
Arousal	0.319
Dominance	0.614
Craving	0.842
Familiarity	0.344

Table 2-5. Split-half coefficients for aroma ratings. Split-half coefficients for each dimension. All correlations were significant at $p < 0.001$, except arousal ($p = 0.0289$) and familiarity ($p = 0.0183$).

2.4 Discussion

Words, pictures, and sounds have been shown to be effective and reliable tools for eliciting emotion. Because aromas offer certain advantages over these existing methods, our goal was to determine the suitability of aromas as an emotion manipulation tool. We constructed a library of 47 aromas that varied along several ecologically relevant dimensions, and collected affective ratings for each. We investigated the distribution of aromas on the affective circumplex, and assessed the reliability of subjective ratings across raters and across time.

When plotted on the affective circumplex, aromas were arranged in a 'V'-shaped pattern with a significant quadratic component, where the negative arm was steeper than the positive arm, similar to other sensory modalities. (Bradley et al., 2001; Lang et al., 1993). This shows that aromas are able to elicit emotions in a similar manner to existing stimuli in other domains, and confirms that aromas do not vary solely along the dimension of pleasantness (Yeshurun & Sobel, 2010).

We also assessed the reliability of subjective ratings. Test-retest reliability and intra-rater reliability were found to be high for most dimensions (reliability of arousal and familiarity was relatively low, see below). Rating variances were comparable to other modalities (Bradley et al., 2007; Bradley & Lang, 1999). These findings indicate that aromas can be used to reliably elicit emotional responses across time and across individuals, which is a prerequisite for their utility as research tools. However, given that familiarity ratings do vary to some degree across subjects, aroma ratings should ideally be obtained for every subject.

Pleasantness/intensity and valence/arousal are conceptually very similar, and are often used interchangeably. The subtle difference between the two is that pleasantness/intensity pertain to the properties of the aromas themselves, while valence/arousal refers to the emotional response elicited by the aromas. In this study, it was found that pleasantness/intensity were highly correlated with valence/arousal, as expected. However, the test-retest and inter-rater reliability of pleasantness/intensity was found to be higher than valence/arousal. This might be because raters attempt to be more objective when asked to rate properties of aromas compared to when the ratings targeted their subjective emotions.

In the current study, all our participants were Bay Area college students, which represents a central caveat in our study. Given the vast cultural differences in aroma experiences (Ayabe-Kanamura et al., 1998; Ferdenzi et al., 2011), cross-cultural studies are needed before these results can be generalized beyond this population. Although we did not collect ethnicity information for the subjects in this study, future studies might want to consider ethnic differences in their analyses. Another factor that might affect emotional responses to aromas is age – all our subjects were college-aged young adults, and odor perception has been shown to vary with age (Evans, Cui, & Starr, 1995; Kobal et al., 2000).

Even within our population, the inter-rater reliability of familiarity was low compared to other dimensions that we collected ratings for. This is not too surprising, as familiarity is highly dependent on individual experience. However, the low inter-rater reliability of aroma familiarity highlights the importance of collecting individual ratings of familiarity from each participant, instead of assuming that aromas will be equally familiar to two individuals from the same cultural background. The test-retest reliability of familiarity of aromas was reasonably high, indicating that at least within an individual, aroma familiarity remains stable.

In summary, this study shows that aromas have affective properties that are similar to stimuli in other sensory domains. Furthermore, subjective ratings of aromas are reasonably reliable for a number of important dimensions, both between and within subjects over time. Aromas are therefore a potentially powerful way to elicit and study the effects of emotion.

Chapter 3

A computational neuroscience approach to identifying features underlying pleasantness of olfactory stimuli

3.1 Introduction

Overall assessments of the pleasantness (or subjective value) of a stimulus have been hypothesized to be computed by combining signals related to values assigned to independent sensory features or attributes (Figure 3-1; Lim, O'Doherty, & Rangel, 2013; Rangel, 2013). Evidence from various sensory modalities supports this theory: for example, the pleasantness of musical excerpts is well described as a weighted combination of the pleasantness values independently associated with timbre, pitch, rhythm, and melodic contour (Makris & Mullet, 2003), while the pleasantness of geometric shapes depends on factors such as symmetry and complexity (Jacobsen, Schubotz, Höfel, & Cramon, 2006).

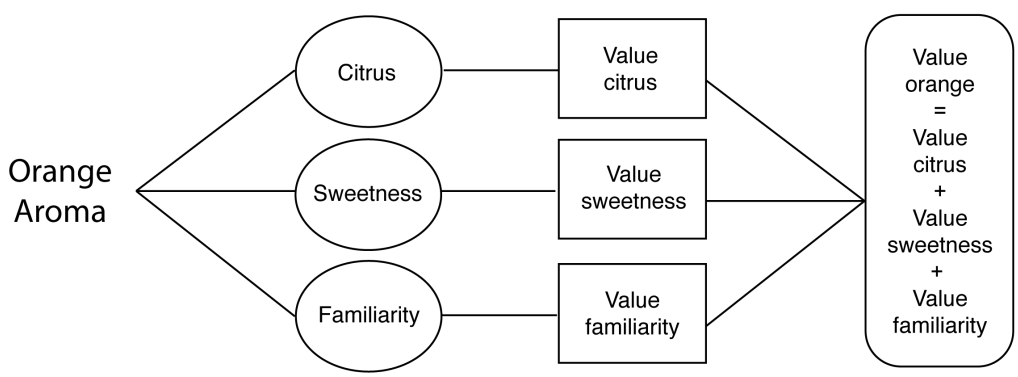

Figure 3-1. Construction of overall subjective value in aromas. The overall pleasantness or subjective value of an aroma is hypothesized to be computed by integrating the values of the aroma's component features. An aroma is composed of a mixture of various perceptual features (e.g. an orange may smell citrusy, sweet, familiar, and so on). Each feature is associated with a certain subjective value, based on the

individual's unique experience and preferences. Overall value is then determined by the summed feature values (Adapted from Rangel, 2013)**.**

In the current study, our goal was to determine the main perceptual features that contribute to aroma pleasantness across a range of aromas. Perceptual features are articulable for many sensory modalities. For example, people generally have little trouble describing visual stimuli in terms of color or shape, and tactile stimuli in terms of smoothness or softness. However, when aromas are presented without contextual cues to their identity, they are notoriously difficult to describe or discriminate except in terms of overall pleasantness (e.g. Berglund, Berglund, Engen, & Ekman, 1973). This phenomenon mirrors the results of numerous attempts at determining the basic perceptual features of aromas using subjective ratings. Various forms of factor analysis have been conducted to reduce a large number of dimensions for which subjective ratings have been collected to a smaller number of key discriminatory features (Ferdenzi et al., 2013; Khan et al., 2007; Schiffman et al., 1977). The primary conclusion from these analyses was that the main dimension of olfactory space is pleasantness. Unfortunately, these findings provide no further insight into the perceptual components which contribute to perceived pleasantness of aromas, and has even led to the argument that pleasantness itself is the sole dimension in aroma perception (Yeshurun & Sobel, 2010).

Because analyses that utilize subjective descriptors have not been able to detect perceptual features contributing to pleasantness, in our current investigation, we employed a factor analysis method which allowed us to determine factors underlying perceived pleasantness using only subjective pleasantness ratings and neural responses to aromas. This way, we reduced dependance on subjective ratings to the one dimension, pleasantness, that we are trying to deconstruct, and that has been found over multiple studies to be a dimension we can measure reliably. Neural responses served as more objective measures of reaction to each stimulus. Based on previous work on preference and value judgment, we hypothesized that patterns of activity across the brain reflect diverse component features that give rise to perceived pleasantness, and that values for these features are integrated in a separate part of the brain (Hare, Camerer, & Rangel, 2009; Lim et al., 2013). Like the studies above, the factor analytics approach we used assumes that factors are linear and independent (Ferdenzi et al., 2013; Khan et al., 2007; Schiffman et al., 1977).

We first sought to validate that this factor analysis method would be able to recover unobservable factors related to pleasantness. We did so by first constructing a neural network model in which several independent (but unknown) perceptual features contribute to pleasantness. Each perceptual feature was associated with a unique pattern of activity across an array of neural units, and was activated to varying degrees by different input stimuli. To make the model more ecologically valid, we set the subjective pleasantness of each feature in an idiosyncratic manner across individuals, to reflect the fact that individuals may find different scent qualities pleasant to varying degrees (Lundström, Seven, Olsson, Schaal, & Hummel, 2006). We show that we can recover the assumed features that contribute to pleasantness using factor analysis on the covariance between brain activity and pleasantness ratings – a partial least squares (PLS) approach.

In the second half of this chapter, we apply the same analysis approach used in model simulations to a functional magnetic resonance imaging (fMRI) data set in which participants were repeatedly exposed to a diverse set of aromas. We identify four significant latent factors related to pleasantness judgments. One of these factors is associated with neural activity in the orbitofrontal (OFC) and ventromedial prefrontal cortex (vmPFC). We relate this factor to a unit in our neural network model that integrates the diverse contributors of pleasantness to form an overall pleasantness judgment (cf. Rangel & Hare, 2010). Additionally, we find a factor that is closely related to aroma familiarity, highlighting the role of familiarity in the computation of pleasantness for aromas in our set, and potentially indicating the neural pathway by which familiarity relates to the perception of pleasantness.

Our approach offers several advantages over traditional methods, both in terms of discovering perceptual features underlying subjective value, as well as imaging neural responses associated with each perceptual feature. Firstly, as previously stated, our use of neural responses in our factor analysis decreases our reliance on subjective ratings. In this approach, we first determine perceptual features independent of subjective ratings (with the exception of pleasantness), *then* attempt to describe these features by comparing them with subjective ratings in dimensions previously hypothesized to be related to pleasantness. Secondly, this approach allows us to determine the neural responses associated with each perceptual feature, which is not possible with only the use of subjective ratings. With respect to this latter point, PLS methods are not only inherently more powerful than General Linear Model (GLM) methods at detecting neural patterns of response (McIntosh, Chau, & Protzner, 2004), but more importantly, without being able to *a priori* identify the component features of aroma pleasantness behaviorally, it is impossible to use standard approaches (GLM, multiple linear regression) to parse associated brain structures. Taken together, the PLS approach allows us to discover the patterns of activity across the brain that reflect diverse component features that give rise to perceived pleasantness.

3.2 Methods

Neural network model of drivers of perceived pleasantness

We started by constructing a neural network model that describes how basic aroma features may combine to produce summary judgments of pleasantness and brain activity. The goal of this initial analysis is to demonstrate the suitability of PLS as a method to identify aroma features that underlie pleasantness judgments. The PLS approach that we employ here identifies perceptual components of pleasantness in terms of their associated patterns of brain activity, and uses only recorded whole brain activity and subjective reports of overall pleasantness.

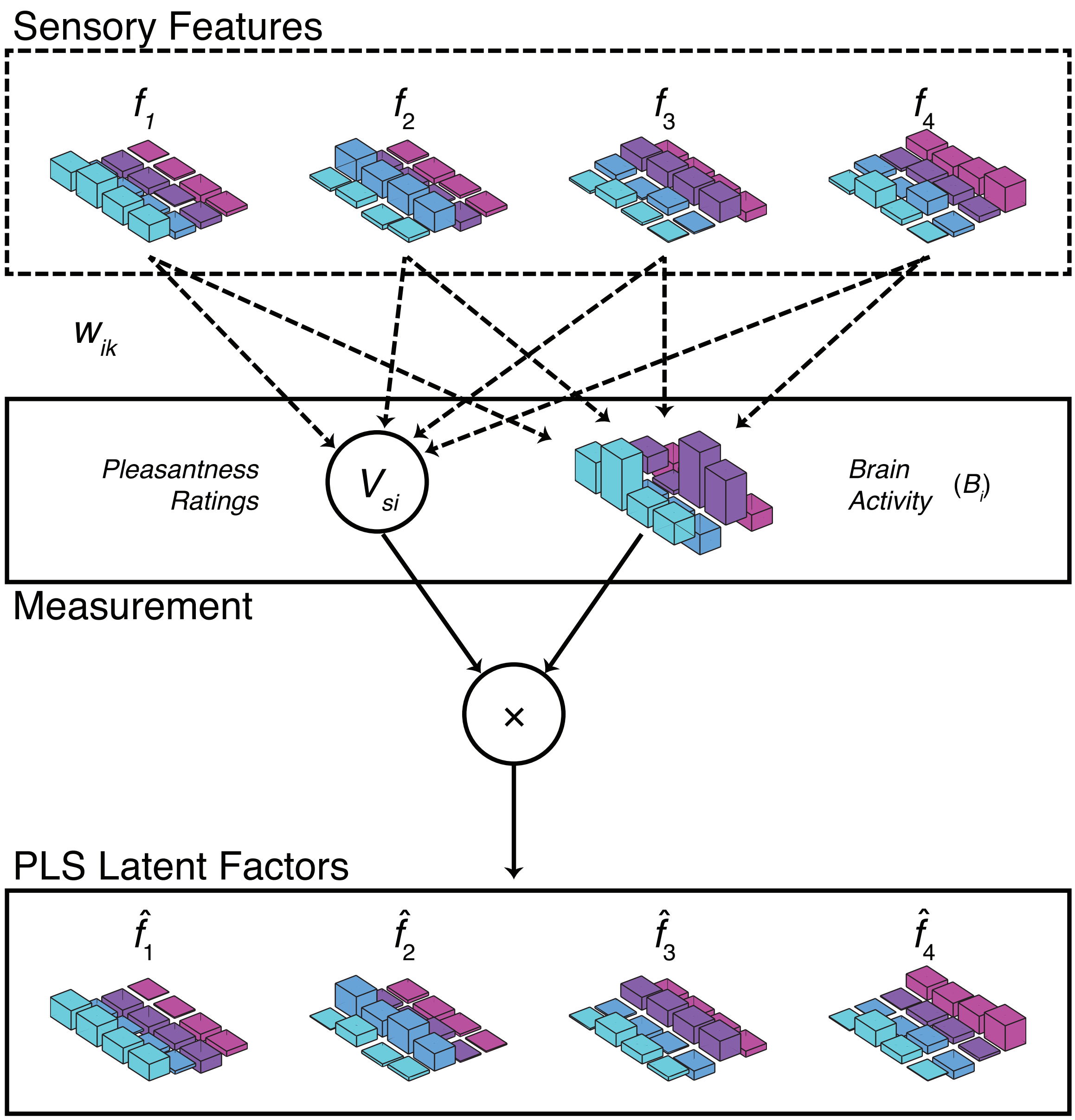

Figure 3-2. A neural network model showing the recovery of hidden perceptual features using only overall pleasantness and patterns of brain activity in response to exposure to one aroma. The top row illustrates 4 independent, unobservable features that contribute to overall pleasantness and brain activity (second row). Using only the observable quantities in the second row (V_{si} and B_i), factor analysis on the covariance between preferences and brain activity (PLS) is able to recover the hidden perceptual features. The height of each box represents activity in that unit for this representative instance of the model.

The neural network model is illustrated in Figure 3-2. In the model, we assumed that aromas may be described as linear combinations of separate perceptual features. For our model, we remain agnostic about the nature of these features, and refer to them generically as f_1, f_2, f_3, etc. An aroma (indexed by i) may therefore be described by a set of weights on each of these features:

$$A_i = \{w_{i1}, w_{i2}, w_{i3}, \ldots\}. \qquad \text{(Equation 1)}$$

The combination of features associated with each aroma contributes both to (1) the pattern of brain activity measured when subjects are presented with the aroma and (2) subjective reports of pleasantness. We considered how these two measures are associated with the component features in turn. First, for brain activity, it was assumed that the different perceptual features (f_k) are each associated with unique patterns of brain activity, b_k (where k indexes the different features). We assumed that these neural responses are independent so that the total brain activity elicited by an aroma may be expressed as

$$B_i = \Sigma_k\, w_{ik}\, b_k + \eta_b. \qquad \text{(Equation 2)}$$

The η_b term is noise associated with measures of brain activity and w_{ik} is the amount of feature k in aroma i.

A similar relationship was assumed to exist between component features and empirical measures of subjective pleasantness. In this case, to reflect real world differences in preferences for various perceptual components, we assumed that the pleasantness of each feature differs across subjects (indexed by s). We describe this relationship by v_{sk}. Each subject's reported pleasantness of an aroma (V_{si}) is then given by

$$V_{si} = \Sigma_k \, w_{ik} \, v_{sk} + \eta_v. \qquad \text{(Equation 3)}$$

As before, we let η_v capture noise in reports of subjective value.

We can directly measure total brain activity related to the presentation of a specific aroma (B_i) and subjective pleasantness (V_{si}), but mirroring the difficulty people face in describing perceptual features of aromas, it is difficult to isolate the unobservable features (f_k) that underlie the singular measures of overall pleasantness (V_{si}), as well as the neural basis of these features (i.e. b_k). We constructed a neural network model in order to determine if these hidden features can be recovered given summary brain activity and overall perceived pleasantness alone.

For the model, we simulated 4 basic aroma features that contribute to overall pleasantness (although a competent tool should be able to recover any number of features). Whole brain activity was simulated in 17 neural units. Each of the 4 latent features was associated with a random pattern of activity across 16 of these neural units (b_k). (The 17th unit is described below.) For illustrative purposes, we represent the 16-dimensional perceptual features that underlie pleasantness (b_k) as 4×4 arrays in Figure 3-1 where each b_k has higher values for each consecutive row of four units. b_1 therefore has higher values for the first row of four units compared to the other 12 units in the remaining 3 rows, b_2 has higher values in the second set of four units, and so on. This distinction across unit weights was done purely to make it visually apparent which patterns of activity are related to which perceptual feature, and does not influence our subsequent analyses. We then simulated an experiment with 20 subjects (indexed by s) with distinct random values of v_{sk} (values drawn from a normal distribution with mean zero and standard deviation 1). We simulated neural responses to 15 aromas (B_i) as a weighted sum of neural responses to each feature, constructed of randomly distributed weights (w_{ik} drawn from a normal distribution with mean 0 and s.d. 1) associated with distinct patterns of brain activity for each basic feature (b_k). Gaussian noise was randomly added to each neural unit (η_b, mean 0 and standard deviation 0.1). Finally, we assumed that overall perceived pleasantness was integrated in the brain from component features. The neural network therefore contained a 17th unit with activity equal to a noisy (η_b, Gaussian noise with mean 0, s.d. 0.1) version of subjective value (V_{si}, see above; also with random noise η_v with mean 0, s.d. 0.1), based on previous work that suggests vmPFC activity correlates with subjective value (Chib, Rangel, Shimojo, & O'Doherty, 2009; Rangel & Hare, 2010). Overall, our goal was to determine whether we could deduce assumed values of b_k and v_{sk} using only B_i and V_{si} generated by the model.

As will be shown in Results, we found that PLS was able to identify factors associated with each of the simulated contributory perceptual features using only modeled neural activity and subjective pleasantness values. PLS was run on 100 independently generated random models. For each iteration, we calculated the correlation between the original neural patterns associated with each feature, b_k, and the patterns of activity associated with the first four factors ($\hat{f}_k$) extracted from PLS, yielding four sets of four correlation coefficients. If an original feature matched one of the extracted PLS factors and was therefore "recovered," then the correlation between the neural activation from the original feature and matching extracted latent factor should be significantly higher than the correlation with the other features. Furthermore, the matches should be unique – activation patterns from each original feature should match exactly one extracted factor. To confirm this, we plotted the mean correlation coefficients in a matrix, with a row for each original feature and one column for each recovered factor (Figure 3-3). If recovered features match unique original features, a diagonal matrix should be observed. We tested if there was a significant difference between the best matching correlation and the second highest correlation (or best "non-matching" feature) for each factor across the 100 model iterations.

Aromas and aroma delivery

Twelve aromas spanning a range of pleasantness scores were selected based on ratings collected in an earlier study (Chapter 2) for use in the fMRI session (Table 3-1). Aromas were presented one at a time using a custom-built, 30-channel olfactometer (MiniVirtual Aroma Synthesizer^{TM}, MiniVAS; Givaudan Flavors Corp.). Briefly, 1-ml flavor aliquots were pipetted into glass vials previously filled with a proprietary, inert absorbent material. The vials were capped and shaken with a vortex mixer for 1 minute to distribute the liquid evenly throughout the absorbent material, which was then transferred to 6-inch long HDPE carrier tubes and placed into the olfactometer. Subjects were exposed to the air from the headspace above a given concentration of aroma dissolved in water, polyethylene glycol or miglyol (see Table 3-1 for flavor concentrations and solvents). A programmable valve controlled with customized software regulated the onset, duration, and concentration of aromas by precisely varying the amount of carrier air exposed to the aroma headspace. Aromas were delivered into the scanner through a waveguide using PTFE microbore tubing (Cole-Parmer). The microbore tubing was connected, at one end, to the olfactometer outlet and, at the other end, to a glass nosepiece positioned at the anterior nares of each subject. A constant flow of air ensured that aromas were rapidly washed out after each presentation. Instructions and other visual cues were presented on a screen that was viewed through a mirror set above a subject's eyes as they lay in the scanner bore.

			Pleasantness		Intensity		Valence		Arousal		Dominance		Craving		Familiarity	
Odorant	Concentration	Solvent	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Bacon	100%	NA	-0.143	2.032	4.048	2.061	-0.048	1.658	3.286	2.348	0.381	1.962	-0.190	2.015	3.143	2.373
Fishy (tri-methyl-amine)	0.01%	Miglyol	-1.952	1.830	4.571	2.561	-1.905	1.758	3.667	2.153	0.381	2.224	-2.238	1.814	3.048	2.539
Fried flavor	100%	NA	-0.143	1.621	2.810	1.887	-0.190	1.365	2.238	1.610	-0.095	1.480	-0.905	1.921	2.143	2.265
Lemon	100%	NA	1.905	1.729	4.333	2.352	1.857	1.315	3.000	2.302	-0.762	1.671	1.000	1.761	4.286	3.019
Mango	100%	NA	1.476	1.470	4.286	1.821	1.571	1.248	3.143	1.982	-0.524	1.662	0.333	1.155	2.952	2.519
Onion oil	10%	Miglyol	-2.000	1.844	4.952	2.133	-0.857	2.197	3.619	1.830	0.333	1.880	-1.524	2.442	3.143	2.351
Patchouli	30%	Miglyol	0.429	1.121	3.286	1.617	0.381	1.596	2.429	2.014	0.143	1.682	-0.571	1.076	1.714	2.004
Pear	100%	NA	0.714	2.239	4.857	1.824	0.619	1.910	3.619	2.224	0.095	1.841	-0.143	1.769	2.905	2.386
Peppermint	10%	Polyethylene Glycol	1.714	1.617	4.000	1.703	1.810	1.401	3.429	1.938	-0.667	1.683	0.952	1.746	4.333	2.352
Rose oil	5%	Miglyol	0.905	1.998	3.905	1.921	0.857	1.852	2.524	1.778	-0.190	2.089	-0.571	1.568	2.714	2.305
Strawberry	100%	NA	2.143	1.389	3.571	1.938	2.143	1.276	2.952	1.884	-0.524	1.834	1.238	1.136	3.333	1.932
Vanilla ice cream	100%	NA	1.429	1.777	3.714	1.617	1.191	1.601	3.095	1.998	-0.571	1.777	0.524	1.861	3.095	2.166

Table 3-1. Concentrations, solvents, and affective ratings for 12 aromas used in fMRI session.

fMRI data acquisition and preprocessing

21 participants (10 female) were recruited from the community surrounding Stanford University to participate in the fMRI study. Two participants (GST and SMM) were authors of this paper.

Each session consisted of 10 runs, with each aroma in the set of 12 presented once per run in random order, resulting in a total of 120 trials (2 participants had to exit the scanner before the session was complete, resulting in one subject having 6 runs and another with 8). Participants were cued to the onset of each trial three seconds before aroma delivery, and were told to inhale when the screen displayed the word 'Inhale'. Participants were instructed to indicate when they detected an aroma via a response box. Onset of the aroma began with the appearance of the inhale cue, and both cue and aroma lasted for 6 seconds. The inter-trial interval (ITI) was 9 seconds, for a total of 12 seconds between the offset of the current aroma and the onset of the next. Although ITIs for presentations of olfactory stimuli are typically longer than for other sensory modalities, a relatively short ITI was necessary to keep the total time in scanner manageable. Intervals of the length we employed have been used in other studies involving aromas (Savic & Berglund, 2000, 2004; Veldhuizen et al., 2010; Veldhuizen & Small, 2011). Additionally, there was an interval of at least 2 minutes between runs. Because each aroma was presented only once per run, repeated presentations of each aroma were never less than 2 minutes apart.

Magnetic resonance imaging was performed with a 3.0T General Electric scanner with a Nova 32 channel whole-brain coil. Head movement was minimized using foam padding. High-resolution T1-weighted fast spin-echo structural images (BRAVO) were acquired for anatomical reference (TR = 8.2ms, TE = 3.2ms, flip angle = 12°, slice thickness = 1.0mm, FOV = 24cm, 256×256). T2*-sensitive gradient echo spiral in/out pulse sequences (Glover & Lai, 1998; Glover & Law, 2001) were used for functional imaging (33 oblique axial slices parallel to the AC-PC, slice thickness = 4mm, no gap, TR = 2000ms, TE = 30, TE2 = 30.5, flip angle = 77°, FOV = 20cm, 64×64). Spiral in/out methods have been shown to reduce signal loss in regions compromised by susceptibility-induced field gradients generated near air-tissue interfaces such as ventral PFC (Glover & Law, 2001; Preston, Thomason, Ochsner, Cooper, & Glover, 2004).

Data were analyzed using Analysis of Functional Neural Images (AFNI) software (Cox, 1996) and the Partial Least Squares Analysis Software Package (McIntosh & Lobaugh, 2004). For preprocessing, retrospective correction for physiological motion effects was first performed on images with Retroicor, using respiration data recorded with respiratory bellows during the task (Glover, Li, & Ress, 2000). Images were then slice-time corrected, deobliqued, realigned to the last image for motion-correction, co-registered to each subject's anatomical image, z-scored, and high-pass filtered. For group analyses, images were spatially normalized to a Montreal Neurological Institute (MNI) template image, and spatially smoothed with a 8mm kernel for PLS.

A General Linear Model (GLM) analysis was carried out to determine the main effects of pleasantness. Separate GLMs were carried out with familiarity, and pleasantness and intensity as parametric regressors (see following section on Ratings procedure). Regressors of non-interest included 6 regressors for residual motion, and a regressor for trials where the subject did not indicate that they detected an aroma.

AlphaSim was used to calculate the appropriate cluster size for a corrected significance threshold of $p < 0.05$ (1000 Monte Carlo simulations). A minimum cluster size of 64 was required with a voxel-wise threshold of $p < 0.005$ given the smoothness of our preprocessed data.

Ratings procedure

Following the 10 scanning runs, participants were asked to rate the aromas along several dimensions. These dimensions were selected either because they were previously identified as important in emotion research that employs a dimensional view (valence/pleasantness, arousal/intensity, and dominance) (Bradley & Lang, 1994; Russell & Mehrabian, 1977), or if they are known to be related to pleasantness (craving, familiarity). Ratings were collected after the scanning portion of the experiment because affective judgments have been shown to modify neural responses to aromas, and we wished to avoid this confound during aroma perception (Rolls, Grabenhorst, Margot, da Silva, & Velazco, 2008). Although no scanner data was collected during ratings, participants were asked to remain in scanner so that ratings would be obtained in the same environment as the scanning portion of the study. Participants initiated the delivery of each aroma with a button press. A 9-point Self Assessment Manikin scale was used to obtain ratings of valence, arousal, and dominance, mirroring methods used in a number of other stimulus modalities such as words, pictures, and sounds to obtain emotional responses (Bradley et al., 2001; Bradley & Lang, 1994). The extremes of the scales had the following labels: “Happy” to “Unhappy” for valence, “Excited” to “Calm” for arousal, and “Controlled” to “In control” for dominance. Nine-point Likert scales were used to obtain ratings for pleasantness (Extremes were labeled “Very pleasant” and “Very unpleasant", midpoint labeled "Neutral"), intensity ("Very intense" to "Undetectable", midpoint labeled "Moderate intensity"), and craving ("Strong cravings" and "Turned me off food", midpoint labeled "Neutral"). Pleasantness and intensity ratings were very similar to valence and arousal scales, but were phrased to target properties of the aromas themselves, as opposed to emotions elicited by the aromas. Additionally, as a measure of familiarity of the aroma, participants were asked to guess the identity of the aroma, and rate their confidence in their guess (Jehl et al., 1995) ("Extremely confident" to "Purely guessing", midpoint labeled "Moderately confident"). The starting value of the cursor for pleasantness, valence, dominance and craving scales was the center of the scale, while the default value for intensity, arousal, and familiarity was the right extreme (least intense or familiar). All ratings were reverse-scored such that increasing value corresponded to increasing levels of the dimension the scale was named after, e.g. pleasantness scale reflected increasing pleasantness. Pleasantness scores were shifted to a -4 to 4 scale, such that -4 reflected maximum unpleasantness. Intensity and familiarity ratings were adjusted to a 0 to 8 scale, with 0 reflecting the lowest intensity or familiarity.

In each of the analyses reported below, results replicated qualitatively when using valence and arousal instead of pleasantness and intensity. Intensity ratings were found to be more reliable than arousal ratings within and between raters in an earlier study (Chapter 2). For these reasons, we exclude discussion of valence and arousal results for the remainder of the paper.

Partial least squares analysis on fMRI data

With the neural network model described above, we confirmed that PLS was a suitable technique for recovering factors associated with hidden features that determine pleasantness (see Results below). We therefore carried out a multivariate PLS analysis on our fMRI data (McIntosh & Lobaugh, 2004). A 16-second temporal window (i.e. 8 TRs) was specified for each event to account for lag in the hemodynamic response after the 6-second aroma exposure. Briefly, for each aroma, neural data (21 subjects * 10 trials × 33*64*64 voxels * 8 time points) was first correlated with behavioral ratings of pleasantness and intensity (2 rating dimensions × 21 subjects * 10 trials). Both pleasantness and intensity ratings were included so that the effect of pleasantness independent of intensity could be observed. The resulting matrices for each condition were stacked to yield a single covariance matrix. Singular value decomposition was then applied to this covariance matrix to yield a set of orthogonal factors, which corresponded to the hidden features in the model above, and account for the most covariance between subjective pleasantness and total brain activity. Each factor was associated with two corresponding sets of saliences – behavioral saliences, which in the current study represents how much the subjective scores of each aroma contribute to each factor, and brain saliences, or how much each voxel is related to each factor.

Statistical significance of each factor was determined by permutation test with 500 permutations. Briefly, in each iteration of the permutation test, the order of aroma conditions was randomly resampled without replacement, and the PLS analysis was recalculated on the new permuted values. The p-value was equal to the proportion of times the permuted singular values exceeded the observed singular values. To measure the stability of each voxel's contribution to each factor, the data set was resampled within condition for each voxel, and the PLS procedure was repeated on the new data set. The bootstrap procedure was repeated 100 times to calculate the standard error of the salience scores. The reliability of the saliences was then measured by taking the ratio of each salience score from the original data set over the standard error (McIntosh & Lobaugh, 2004).

Conjunction analysis

A conjunction analysis was performed by finding the intersection between voxels which were significant at $p < 0.05$ (corrected for multiple comparisons) in the GLM and PLS analyses.

3.3 Results

Neural network model

In this study, we aimed to discover perceptual features that contribute to perceived pleasantness of aromas (Figure 3-1). Using a neural network model in which latent perceptual features are associated with distinct patterns of brain activity and pleasantness evaluations (Figure 3-2), we first aimed to demonstrate that PLS factor analysis is capable of identifying the perceptual features that underlie pleasantness from measured brain activity during aroma perception and subjective reports of pleasantness.

Figure 3-2 schematizes the model and PLS analysis method, and includes unit activity from a single run of the model related to the presentation of one aroma. The top row of Figure 3-2 shows the simulated patterns of activity associated with each perceptual feature (b_k), and the dashed arrows indicate the computations (multiplication by weights) that give rise separately to measured brain activity (B_i) and subjective value (V_{si}). Brain activity associated with any given aroma is a linear combination of neural activity associated with each component sensory feature. Likewise, to reflect individual variability in preferences for various aromatic features, we determined pleasantness ratings for each aroma from a weighted combination of subject-specific evaluations of the underlying sensory features.

PLS analysis entails identifying latent factors in the covariance between neural activity and pleasantness. The bottom panel of Figure 3-2 shows the output of PLS factor analysis performed on the model simulations of brain activity and associated pleasantness judgments. The latent factors identified by this analysis approximately recapture the features that determine subjective value and brain activity. This can be observed in our representative single run shown in Figure 3-2, where the factors recovered with PLS in the bottom row are similar to the perceptual features in the top row. The model analysis therefore demonstrates that PLS serves as a means to identify perceptual features and their accompanying neural patterns that underlie preference.

Our full neural network model included a 17th "integrator" unit. The activity of this 17th unit was set to (noisily) track overall pleasantness, and thereby represent a putative brain region that integrates signals from various parts of the brain to arrive at an overall pleasantness signal (Rangel & Hare, 2010). PLS performed on the full 17-unit network model returned one factor with a high salience of the 17th unit (Figure 3-5b), demonstrating that an integrated subjective pleasantness signal can be found as an independent feature with PLS.

In order to confirm that this relationship between perceptual features and extracted neural factors holds generally, we next ran 100 random iterations of the model, each with four preference-related features. We then tested whether the relationship between patterns of activation across neural units associated with the original features and the best matching extracted ("recovered") factors was one-to-one. To do so, we tested whether, for each PLS factor, the highest correlation with assumed perceptual features was significantly greater than the second highest correlation. We performed a paired t-test on the correlation coefficients and found that there was a one-to-one relationship between recovered PLS factors and simulated pleasantness-related perceptual features ($p < 0.01$). The mean correlation coefficients for original versus extracted features are shown in Figure 3-3. The one-to-one mapping that generally results from PLS is clearly evident in this plot. Specifically, the correlation matrix is approximately diagonal, indicating that original features and recovered factors generally matched in a one-to-one manner.

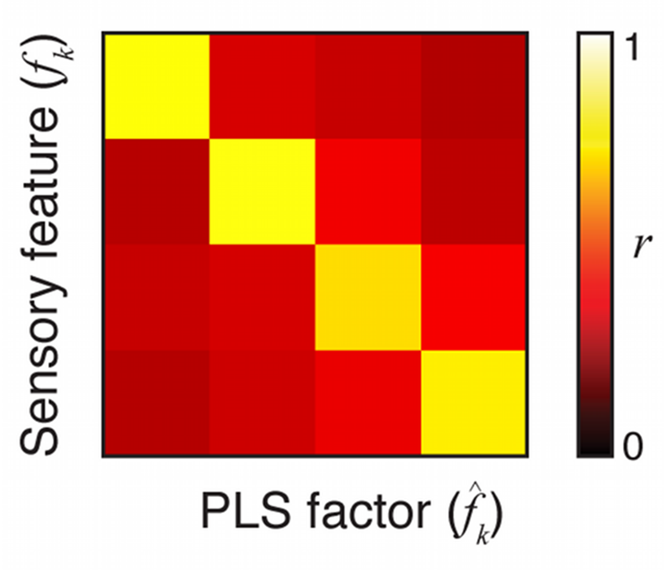

Figure 3-3. Mean correlation coefficients for original features versus extracted factors across 100 runs of the model. The correlation matrix is approximately diagonal, indicating that there is generally a one-to-one mapping between the original perceptual features (f_k) and the factors recovered by PLS ($\hat{f}_k$).

PLS analysis on fMRI data

Given the utility of PLS in our model simulations, we next aimed to identify latent neural factors that underlie perceived pleasantness in people. We therefore collected brain activity and pleasantness judgments from participants as they were exposed to an array of 12 different aromas.

The PLS analysis on fMRI data identified four significant latent factors. The first four factors accounted for 23.61% ($p < 10^{-3}$), 10.78% ($p = 0.002$), 8.47% ($p = 0.010$), and 7.28% ($p = 0.028$) of the covariance between brain activity and pleasantness ratings, respectively. The fifth factor was marginally significant ($p = 0.078$), accounting for 5.85% of the covariance.

As with all dimensionality reduction techniques, it is often difficult to assign meaning to the dimensions identified with PLS. However, PLS yields behavioral and brain saliences for each factor that indicates the degree to which each aroma and activity in each voxel, respectively, is associated with that factor. We used these saliences to infer the likely psychological basis of each identified factor.

We began by analyzing the first factor, and found that behavioral saliences for this factor across aromas correlated significantly with subjects' ratings of familiarity ($r = 0.618$, $p = 0.0324$, Figure 3-4b). The relationship between familiarity and pleasantness has been demonstrated behaviorally before (Delplanque et al., 2008; Royet et al., 1999). Figure 3-4a illustrates the associated neural saliences. Voxels are highlighted according to the magnitude of the stability of their contribution, restricted so that only voxels for which saliences are significantly different from zero at $p < 0.005$ are shown. Widespread regions contribute to the first factor, including the hippocampus, anterior insula, dorsal striatum, and regions throughout the middle frontal gyrus. Overall, this suggests that a factor closely related to familiarity has an independent effect on determining pleasantness ratings that is mediated by a widely distributed network of brain areas associated with memory and reward. With a GLM approach, no brain region was found where activity significantly covaried with familiarity at our corrected significance threshold. The difference between the PLS and GLM results is likely due to the fact that PLS combines information across voxels to achieve higher statistical power than GLM (McIntosh et al., 2004).

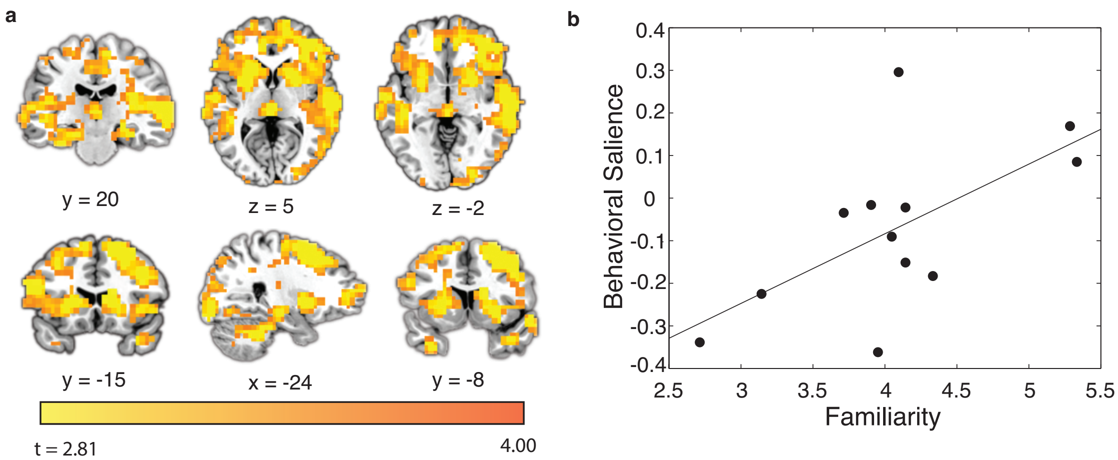

Figure 3-4. The first factor recovered with PLS, and its relationship with aroma familiarity. (**a**) Neural saliences for the first factor included areas of the hippocampus, anterior insula, striatum, and regions throughout the middle frontal gyrus. Voxels in the brain images are highlighted according to the magnitude of the stability of their contribution to each factor, determined by 100 bootstrap samples (McIntosh & Lobaugh, 2004). The values shown come from 6 seconds after event onset to account for hemodynamic lag. Absolute values of bootstrap ratios ($p < 0.005$) are shown. (**b**) Familiarity ratings correlated significantly with behavioral saliences on the first recovered factor.

For the second factor, behavioral weights for individual aromas correlated significantly with reports of pleasantness ($r = 0.705$, $p = 0.0105$). This result is reminiscent of the subjective pleasantness feature found in the neural network simulation above, which was most strongly associated with the neural unit whose value tracked overall subjective pleasantness, as indicted by the saliences for that feature (Figure 3-5b). Brain areas associated with this factor included medial and lateral OFC and vmPFC (Figure 3-5c), confirming and extending previous studies that explicitly tested for pleasantness as a mediator of neural activity (Anderson et al., 2003; Rolls et al., 2003; Winston et al., 2005). Additionally, we carried out a conjunction analysis to determine if these OFC regions overlapped with regions from a GLM analysis explicitly testing for brain regions that correlated with pleasantness. Overlapping areas were found in the vmPFC and mOFC (Figure 3-5e).

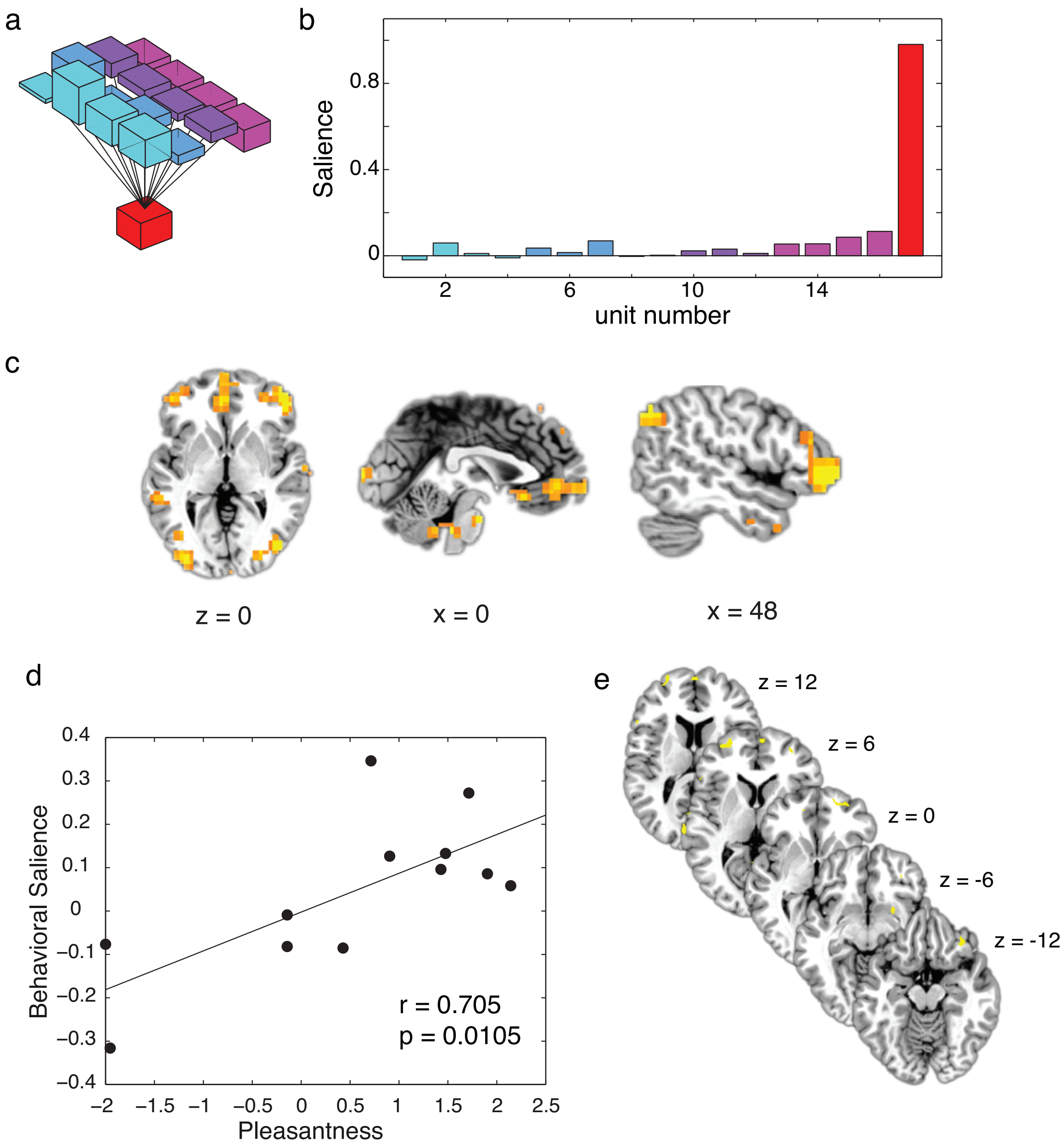

Figure 3-5. The second recovered factor is associated with subjective pleasantness. (**a**) A 17th unit in the neural network model tracked subjective pleasantness values. (**b**) Saliences for a feature returned by PLS analysis on the 17-unit model was highest for the unit that tracked overall pleasantness, indicating that this factor was most strongly associated with overall subjective pleasantness. (**c**) Factor saliences correlated with subjective pleasantness ratings. (**d**) Regions associated with this factor include the mOFC

and lOFC, as well as mPFC. (**e**) Results of a conjunction analysis between regions identified with PLS and the regions returned by a GLM analysis with subjective pleasantness ratings as parametric regressors revealed overlapping areas in the vmPFC and mOFC.

The brain regions contributing to the third and fourth factors are frequently implicated in studies of memory, emotion, and decision-making. Regions associated with the third factor included the hippocampus, superior temporal gyrus bordering the insula, and a region of the mPFC extending above the supraorbital sulcus to the anterior part of the superior frontal gyrus (Figure 3-6a). The mammillary bodies were found to contribute reliably to the fourth factor (Figure 3-6b). This structure has been identified as important in memory and emotion, and damage to this area has been associated with an impaired sense of smell (Dusoir, Kapur, Byrnes, Mckinstry, & Hoare, 1990; Mair, Capra, McEntee, & Engen, 1980). Saliences on these final two factors did not correlate with any of the behavioral ratings that we collected (all Ps > 0.3). Identifying these factors indicates that at least two additional neural systems contribute independently to pleasantness ratings in a manner that escapes the perceptual descriptions that we captured in subjective reports.

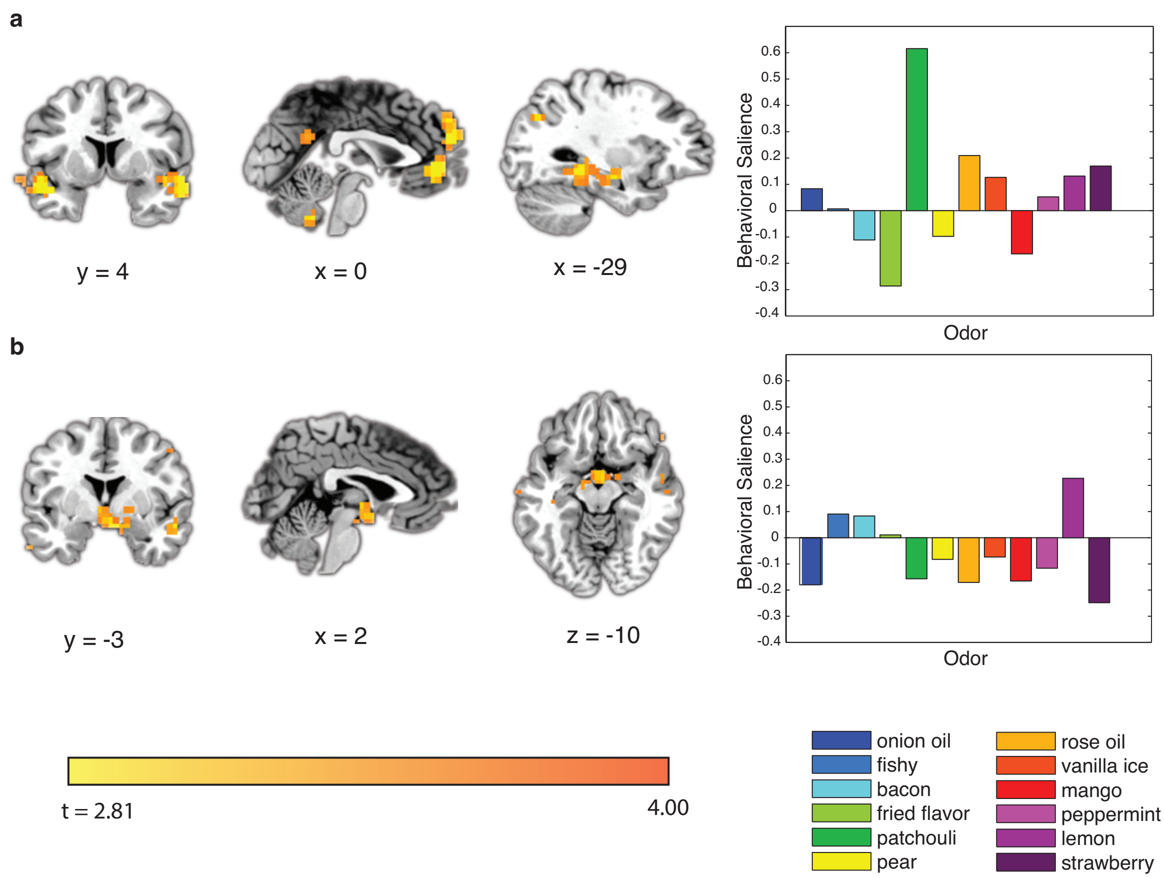

Figure 3-6. PLS neural and behavioral saliences for third and fourth factors. (**a**) A third factor was associated with activity in the hippocampus, mPFC, and superior temporal gyrus. (**b**) The fourth factor was associated with focal activity in the mammillary bodies.

3.4 Discussion

In this study, we aimed to identify component perceptual features that underlie pleasantness judgments, as well as patterns of brain activity associated with these factors. Tackling this problem required demonstrating that PLS factor analysis was able to extract these factors, based solely on total neural activity and subjective pleasantness. We believe that this is an promising new use of PLS that may allow for more precise, or at least independent, analyses of the components of subjective value for sensory stimuli.

General linear models can be used to uncover neural activity associated with basic aroma features, but only if the identities of the features are known beforehand. PLS, on the other hand, is a model-free, data-driven technique, and has the benefit of being able to discover features we may not have previously known about or predicted. Furthermore, it identifies the degree to which each of these features contributes to overall pleasantness. These advantages of PLS are particularly critical for the analysis of olfactory stimuli given the lack of detail available to the conscious perception of scents.

Using this PLS approach, a factor related to familiarity appears to be a primary determinant of the relationship between whole brain activity and subjective pleasantness. This finding is interesting in light of the fact that subjective pleasantness is highly dependent on experience and cross-cultural differences in the commonness of certain smells (Heuberger, Hongratanaworakit, & Buchbauer, 2006). This finding might also be related to phenomena such as the mere exposure effect, where liking increases with the number of exposures to a stimulus (Birch & Marlin, 1982; Rozin & Vollmecke, 1986; Zajonc, 1968). Neural activity associated with familiarity spanned a large number of brain areas. It will require additional work to determine how familiarity comes to influence preference through its influence on these neural structures.

The second factor identified in our analysis correlated with overall subjective pleasantness, similar to a feature in our neural network model that was designed to signal aggregate subjective value. Neurally, this dimension was associated with regions of the

OFC and vmPFC. Studies of the OFC and surrounding regions in the vmPFC suggest that these areas mediate a common route through which diverse stimuli are reported as valuable or pleasant, potentially by integrating the multiple influences that impinge on these judgments (e.g. Bartra, McGuire, & Kable, 2013). Specifically, Small et al. have argued that the OFC integrates perceptual features in determining the reward value of a food (Small et al., 2007). Damasio and Bechara have long speculated that the vmPFC integrates signals important for valuation and decision-making (A Bechara, Damasio, Damasio, & Lee, 1999; Damasio, 1994). Rangel and colleagues have similarly shown that the vmPFC and OFC integrate diverse influences to produce a value signal that predicts preferences (Rangel & Hare, 2010). We therefore believe that the OFC integrates diverse percepts that contribute to overall ratings of pleasantness. The relationship of these areas to pleasantness is further supported by the conjunction analysis, which showed that similar areas in the mOFC and vmPFC were found in both model-free (PLS) and model-driven (GLM) analytic approaches.

We collected ratings for features we hypothesized from previous research to be related to pleasantness, and attempted to assign meaning to factors by their correlation to these subjective ratings. However, we were not able to find relationships with subjective reports for every factor recovered through the PLS method. We found two additional novel contributors to pleasantness that are associated with independent networks of brain areas, but which were unrelated to the behavioral ratings we collected for each aroma. This indicates the exciting possibility that other factors contribute to olfactory perception and pleasantness than may have been intuited and tested behaviorally. The nature of many of these higher dimensions just remains to be better described behaviorally and cognitively.

In this study, like many prior attempts at reducing the dimensionality of olfactory space, we assumed linear, independent perceptual features. However, the actual construction of aroma subjective value is likely to be much more complicated, involving non-linear, non-independent relationships between perceptual features. Unfortunately, accounting for these types of relationships is complex and computationally demanding. We suspect that linearity is reasonable to assume for many of the perceptual features that contribute to pleasantness. It remains for future studies to identify non-linear interactions among features.

This study was a first demonstration that PLS can be used to uncover basic features of aromas that are integrated in the brain to arrive at pleasantness judgments. By showing that PLS is capable of identifying basic components of pleasantness and their associated neural patterns of activity, we have laid the groundwork for future studies with larger sets of different aromas, to determine if these results extend beyond the 12 aromas we used in this study. With new insight into the various factors that contribute to perceived pleasantness of an aroma, we can begin to explain the varying effects of aroma pleasantness on behavior, olfactory perception, and associated neural activity.

Chapter 4

Effects of aromas on decisions involving risk and ambiguity

4.1 Introduction

People often rely on feelings to make decisions involving risk, with factors such as physiological arousal, vividness of imagined outcomes, and background emotions and moods playing a role in determining a course of action (Loewenstein et al., 2001). We might experience sweaty palms or gut feelings when deciding whether or not to make a risky gamble; feelings and physiological responses such as these might signal the potential rewards or adverse consequences of a risky action, thus steering us towards or away from risk. Manipulating emotions has been demonstrated to influence perceived risk and risk-taking behavior, and both positive and negative incidental affect have been shown to affect risk preferences (Bruyneel, Dewitte, Franses, & Dekimpe, 2009; Knutson et al., 2008; Jennifer S. Lerner, Gonzalez, Small, & Fischhoff, 2003).

While numerous studies have been conducted on the influence of emotion on risk, less work has examined the role of emotions in ambiguity. As mentioned in Chapter 1, risk and ambiguity differ in the amount of knowledge available about the likelihood of possible outcomes. With risk, each outcome occurs with a known probability. Under ambiguity, however, the exact probabilities are unknown (Ellsberg, 1961). People mostly prefer more knowledge over less, and therefore generally prefer risk over ambiguity (Becker & Brownson, 1964; Huettel et al., 2006). Ambiguity has been found to elicit higher physiological responses (anticipatory skin conductance response) than risk (Bechara & Damasio, 2005).

In neuroscience studies that have examined ambiguity in addition to risk, several structures in the brain have been commonly found to be active when evaluating both types of choice, including parts of the lateral prefrontal cortex, parietal cortex, basal ganglia, and thalamus (Huettel et al., 2006). However, several differences have been found as well. While activity in the lateral prefrontal cortex was found to correlate with ambiguity preferences, risk preferences were associated with activation in the posterior parietal cortex (Huettel et al., 2006). Moreover, activity in the posterior inferior frontal sulcus, the amygdala, anterior insula, posterior parietal cortex, and the OFC are more active when choices involve ambiguity, whereas the dorsal striatum was more active for choices involving risk (Hsu et al., 2005; Huettel et al., 2006).

Of these, one region of particular interest is the anterior insula (Kuhnen & Knutson, 2005). Consistent with the observation that insula activity precedes risk-averse choices (Helfinstein et al., 2014; Kuhnen & Knutson, 2005), insula activity has been hypothesized to signal the potential aversive consequences of a gamble, so that greater anterior insula activity steers people away from risk (Paulus et al., 2003). The insula is also thought to be the region where emotional, physiological, and external sensory signals are integrated with cognitive evaluations of uncertainty (Chang, Yarkoni, Khaw, & Sanfey, 2013; Singer, Critchley, & Preuschoff, 2009).

Given the observed behavioral, physiological, and neural differences between ambiguity and risk, the goal of the current study was to compare the role of emotions in decision processes involving each type of uncertainty. To accomplish this, we used a paradigm adapted from Huettel et al. (2006) to investigate the effects of emotions on decisions involving risk and ambiguity, using aromas to induce affect. Aroma intensity has been shown to correlate with measures of physiological arousal (Bensafi et al., 2002), as well as insula activity (Anderson et al., 2003). We therefore hypothesize that aroma intensity will drive affective signals which in turn cause decreases in risk and ambiguity preferences. Additionally, we hypothesize that these influences will be reflected by activity in areas of the brain related to integration of sensory signals and value judgments, such as the anterior insula (Chang et al., 2013; Singer et al., 2009).

4.2 Methods

Subjects

The experiment consisted of two parts – a behavior-only study and a neuroimaging study. Subjects were recruited from the community surrounding Stanford University. 22 subjects (11 female) participated in the behavior-only study and received \$7, while 25 participants (10 female) took part in the fMRI study and received \$20. Subjects also received the outcome of one gambling task trial.

Aromas and aroma delivery

Six aromas, two intense pleasant (vanilla ice cream, lemon), two intense unpleasant (Methylthiobutyrate, onion oil), and two low-intensity neutral aromas (green tea, air), were selected during an earlier study (Chapter 2) based on their affective properties for use in the current study (concentrations and solvents are listed in Table 4-1). Subjective pleasantness and intensity of aromas were found to be closely related to induced levels of valence and arousal in the earlier study (Chapter 2).

Aroma	Concentration	Solvent
Onion oil	10%	Miglyol
Methylthiobutyrate	0.5%	Miglyol
Vanilla ice cream	100%	N.A.
Lemon	100%	N.A.
Green tea	100%	N.A.
Control (air)	N.A.	N.A.

Table 4-1. Aromas used to induce affective states.

Aromas were presented one at a time from a custom-built, 30-channel olfactometer (MiniVirtual Aroma Synthesizer^{TM}, MiniVAS; Givaudan Flavors Corp.). Briefly, 1-ml flavor aliquots were pipetted into glass vials previously filled with a proprietary, inert absorbent material. The vials were capped and shaken with a vortex mixer for 1 minute to distribute the liquid evenly throughout the absorbent material, which was then transferred to 6-inch long HDPE carrier tubes and placed into the olfactometer. Subjects were exposed to the air from the headspace above a given concentration of aroma (pure or dissolved in miglyol, see Table 4-1 for concentrations and solvents). A programmable valve controlled with customized software regulated the onset, duration, and concentration of aromas by precisely varying the amount of carrier air exposed to the aroma headspace. A constant flow of air ensured that aromas were rapidly washed out after each presentation. For behavior-only sessions, subjects rested their chins on a chin rest such that their nose was positioned in front of a glass nosepiece. Instructions and other visual cues were presented on a screen in front of the chin rest. For scanner sessions, aromas were delivered into the scanner through a waveguide using PTFE microbore tubing (Cole-Parmer). The microbore tubing was connected, at one end, to the olfactometer outlet and at the other end, to a glass nosepiece positioned at the anterior nares of each subject. Instructions and other visual cues were presented on a screen that was viewed through a mirror set above a subject's eyes as they lay in the scanner bore.

Gambling task

Each session consisted of 4 runs of 30 trials, for a total of 120 trials. The gambling task and stimuli were adapted from a previous study by Huettel et al. (Huettel et al., 2006). In each trial (Figure 4-1a), subjects were exposed to one of the six aromas. The word "INHALE" was presented on screen on aroma onset, prompting subjects to inhale. Six seconds after aroma onset, subjects were then presented with a pair of options, where each option was one of three types with varying degrees of outcome uncertainty – certain, risky, and ambiguous (Figure 4-1b). Four pairings of option types were presented with equal frequency: Ambiguous/Certain (AC), Ambiguous/Risky (AR), Risky/Certain (RC), and Risky/Risky (RR). The four choice types were paired with aromas in a counter-balanced manner. Certain options consisted of a uniformly colored circle with one monetary value. If a subject selected this option, the outcome of that trial would be equal to the displayed monetary value. Risky options were presented as pie charts with two different-colored sections, each associated with a different monetary value. The size of each pie section indicated the probability that the corresponding monetary value would be selected as the outcome for that trial. Probabilities ranged from 0.25 to 0.75 in 0.25 increments. Ambiguous options, like risky options, were associated with two monetary values. However, the probabilities of each value were not known. To reflect the unknown probabilities, the center of the option was a uniform grey. Furthermore, unlike risky options, one of the two values was always \$0. Participants were instructed that actual (but unknown) outcome probabilities ranged from 0 to 1 in 0.25 increments. Expected values for the certain and risky gambles ranged from $5 to $25 (mean of $14), and expected value was matched within 20% for all pairs of options.

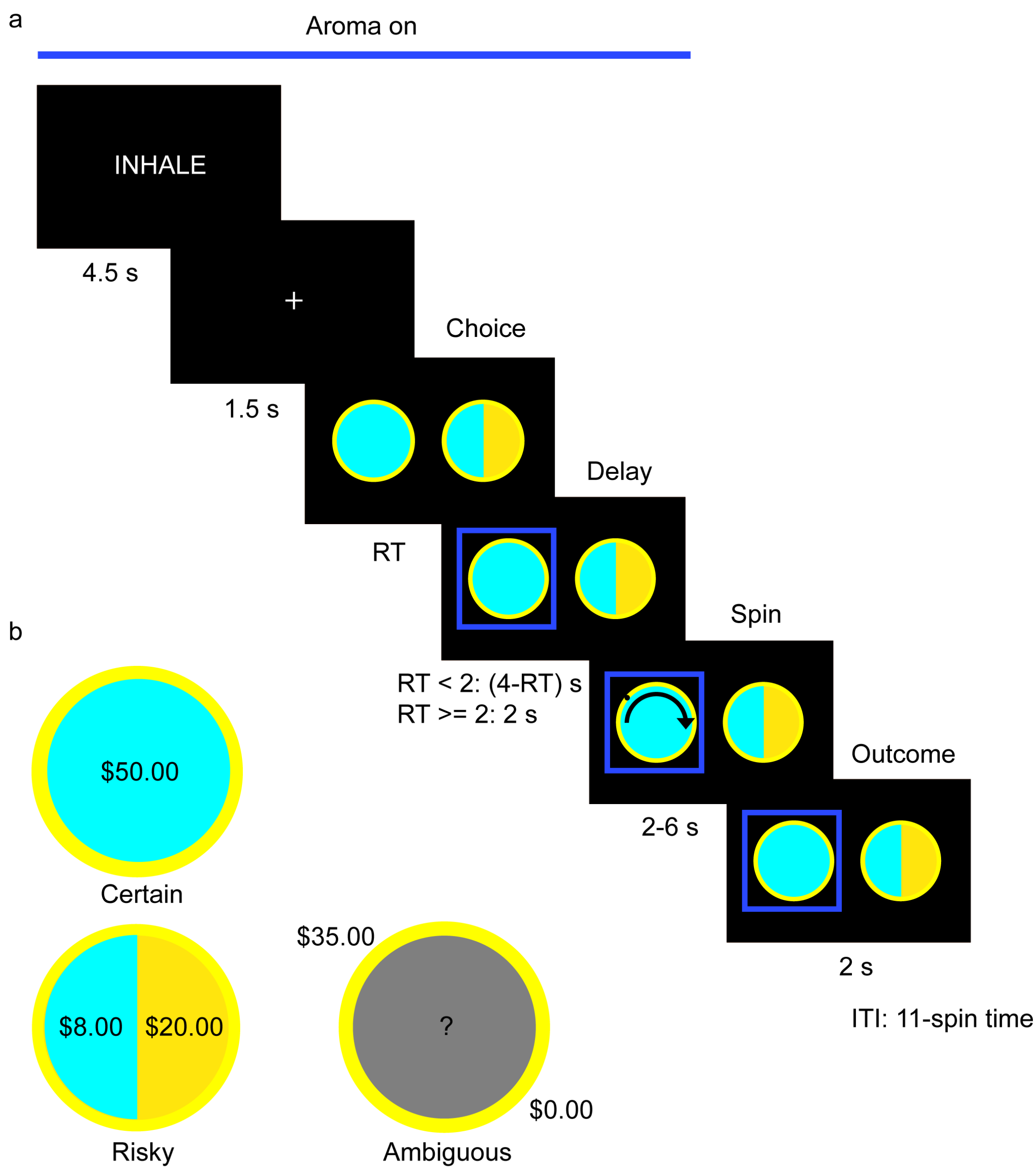

Figure 4-1. Trial structure and option types. (a) Onset of aroma delivery occurred 6 s before options were displayed. For the first 4.5 s, the word "INHALE" was displayed on screen to alert participants to aroma onset, and to prompt them to inhale. A fixation cross was then displayed 1.5 s before choice onset, to inform participants that the choice period was about to begin. When participants made their choice, a blue square was displayed around their chosen option. After a delay, a roulette style ball spun around the outer circle

of the chosen option for 2, 4, or 6 s. The outcome of the chosen option was then displayed for 2 s, followed by an inter-trial interval. (b) The task included three types of option with varying amounts of uncertainty. Certain options involved no probability, and participants were guaranteed the displayed sum of money if that option was chosen. Risky options involved two monetary sums with fixed and known probabilities, represented by the size of the corresponding pie slice. Ambiguous options involved two sums of money with fixed but unknown probabilities.

Subjects indicated their choice on each trial by pressing one of two buttons. When a choice was selected, a blue square appeared around their selected option for 2 s. Aromas were turned off at the end of this delay period. To discourage fast responses with the goal of minimizing aroma exposure, this delay period was extended if a subject's response time was shorter than 2 s, such that the minimum exposure time to the aroma was at least 4 s from time of cue onset. Subjects were informed that their response times would not affect length of aroma exposure. Following the delay, a black "roulette ball" would spin outside the pie chart for 2, 4, or 6 s at a random speed. The outcome was then revealed, and stayed on screen for two seconds. A fixation cross was then displayed during the inter-trial interval, which lasted 11 s minus the time the ball was spinning, so that time between aroma offset and onset was at least 11 s. A relatively short ITI was necessary to keep the total time in scanner manageable. Intervals of the length we employed have been used in other studies involving aromas (Savic & Berglund, 2000, 2004; Veldhuizen et al., 2010; Veldhuizen & Small, 2011).

fMRI data acquisition and preprocessing

Magnetic resonance imaging was performed with a 3.0 T General Electric scanner with a Nova 32 channel whole-brain coil. Head movement was minimized using foam padding. High-resolution T1-weighted fast spin-echo structural images (BRAVO) were acquired for anatomical reference (TR = 8.2 ms, TE = 3.2 ms, flip angle = 12°, slice thickness = 1.0 mm, FOV = 24 cm, 256×256). Whole-brain functional scans were acquired with a T2*-weighted gradient echo pulse sequence (TR = 2 s, TE = 30 ms, flip angle = 77°, in-plane resolution 3.4 mm isotropic, FOV 21.8 cm, 64x64, no gap, descending interleaved acquisition).

Data were analyzed using Analysis of Functional Neural Images (AFNI) software (Cox, 1996). For preprocessing, retrospective correction for physiological motion effects was first performed on images with Retroicor, using respiration data recorded with respiratory bellows during the task (Glover et al., 2000). Images were then slice-time corrected, deobliqued, realigned to the last image for motion-correction, co-registered to each subject's anatomical image, z-scored, and high-pass filtered. For group analyses, images were spatially normalized to a Montreal Neurological Institute (MNI) template image. A General Linear Model (GLM) analysis was carried out with separate regressors for each of the four gamble types, and for each possible decision, resulting in 11 separate regressors. Gamble types will be abbreviated AC (Ambiguous/Certain), AR (Ambiguous/Risky), RC (Risky/Certain), RR (Risky/Risky). Decisions within each gamble type were abbreviated with lower case letters, a (ambiguous), r (risky), and c (certain), such that AC-a stands for trials in the ambiguous-certain (AC) condition in which the ambiguous (a) option was chosen. Regressors of interest were convolved with a canonical hemodynamic response function. Regressors of non-interest included 6 regressors for residual head motion.

AlphaSim was used to calculate the appropriate cluster size for a corrected significance threshold of $p < 0.05$ (1000 Monte Carlo simulations). A minimum cluster size of 63 was required with a voxel-wise threshold of $p < 0.005$ given the smoothness of our preprocessed data.

Ratings procedure

Following the gambling task, participants were asked to rate the aromas along several dimensions. Ratings were collected after the gambling task to avoid drawing attention to aroma affect, and to avoid neural activity due to judgment and semantic processing (Royet et al., 1999). For the fMRI sessions, though no scanner data was collected during ratings, participants were asked to remain in scanner so that ratings would be obtained in the same environment as the scanning portion of the study. Participants initiated the delivery of each aroma with a button press. Nine-point Likert scales were used to obtain ratings for pleasantness (Extremes were labeled “Very pleasant” and “Very unpleasant”, midpoint labeled “Neutral”) and intensity (“Very intense” to “Undetectable”, midpoint labeled “Moderate intensity”). Additionally, as a measure of familiarity of the aroma, participants were asked to guess the identity of the aroma, and rate their confidence in their guess (Jehl et al., 1995) (“Extremely confident” to “Purely guessing”, midpoint labeled “Moderately confident”). The starting value of the cursor for pleasantness was the center of the scale, while the default value for all other scales was the right extreme. All ratings were reverse-scored such that increasing value corresponded to increasing levels of the dimension the scale was named after, e.g. pleasantness scale reflected increasing pleasantness. Pleasantness scores were shifted to a -4 to 4 scale, such that -4 reflected maximum unpleasantness. Other ratings were adjusted to a 0 to 8 scale, with 0 reflecting the lowest value. Intensity and pleasantness were found to correlate strongly with arousal and valence in an earlier study (Chapter 2). The effects of aroma intensity, pleasantness, and familiarity on choice were investigated using mixed-effects linear regression with subjects as random effects.

To ensure that breath volume was independent of valence and arousal, correlation analyses were conducted between chest volume data collected with respiratory bellows and intensity and pleasantness ratings. No significant relationships were found ($p > 0.1$).

4.3 Results

Data from the behavior-only and neuroimaging sessions were combined in the subsequent analyses. One subject from the behavior-only session and 5 from the neuroimaging session were excluded from analyses because they exclusively chose the certain option during AC trials. In the behavioral study, due to technical error, values in AC trials were not properly counterbalanced, and only data from the scanner study was analyzed.

Participants displayed a slight bias towards the certain option (with a non-probabilistic outcome) when one was available. In AC trials, the average proportion of times a subject chose the certain option was 0.593 (SD = 0.178, range = 0.300 to 0.933), and in RC trials, 0.539 (SD = 0.166, range = 0.263 to 0.867). In AR trials, choices were fairly evenly split between the ambiguous and risky outcomes, with a mean percentage of choices for the ambiguous outcomes of 0.511 across subjects (SD = 0.179, range = 0.143 to 0.867).

Effects of aromas on risk and ambiguity preferences

We hypothesized that aroma-induced affect would cause changes in risk preferences. To test this, we ran mixed effects logistic regression models to test the effects of aroma pleasantness and intensity on choice. In the RC condition, the intensity of affect elicited by preceding aromas was associated with increased preferences for the certain options (p = 0.0434, Figure 4-2a), while pleasantness predicted increased preference for the risky options (p = 0.0232, Figure 4-2b).

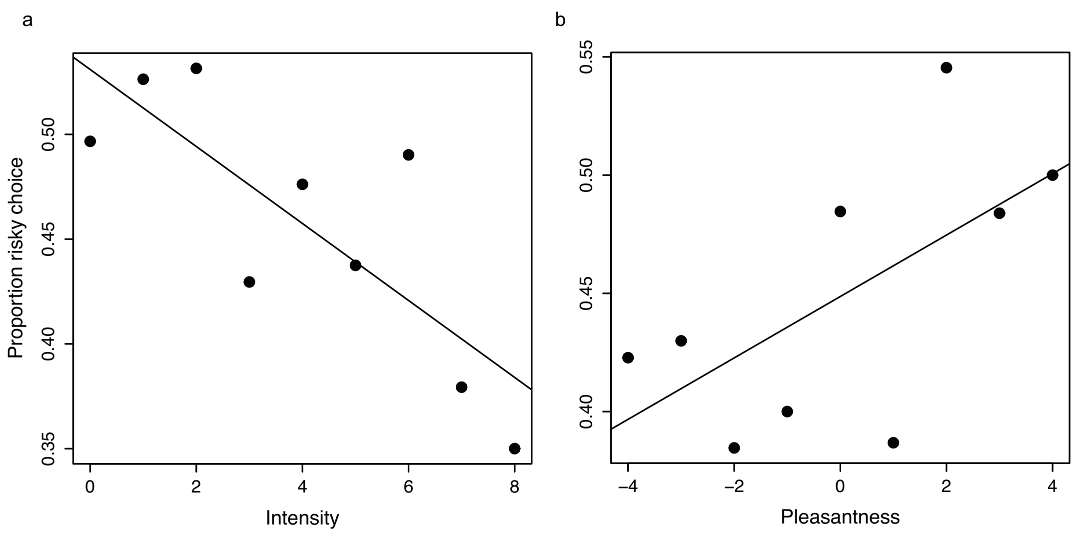

Figure 4-2. Aroma effects on risk preference. In the RC condition, (a) increasing aroma intensity increased risk-aversion, while (b) aroma pleasantness increased risk preference. For illustrative purposes, RC trials were divided into 8 bins based on subjective intensity and pleasantness ratings of the aroma used in each trial. The proportion of risky choices was then computed for each bin.

Neuroimaging results

Neural basis of aroma-induced affect. Regions that correlated with aroma intensity included the bilateral ventral and dorsal posterior regions of the insula, bilateral amygdala extending into the piriform cortex, and the left inferior frontal gyrus (IFG) (Figure 4-3). These regions have been found in previous studies of aroma-induced affect and flavor perception (Anderson et al., 2003; Sobel et al., 1999; Winston et al., 2005).

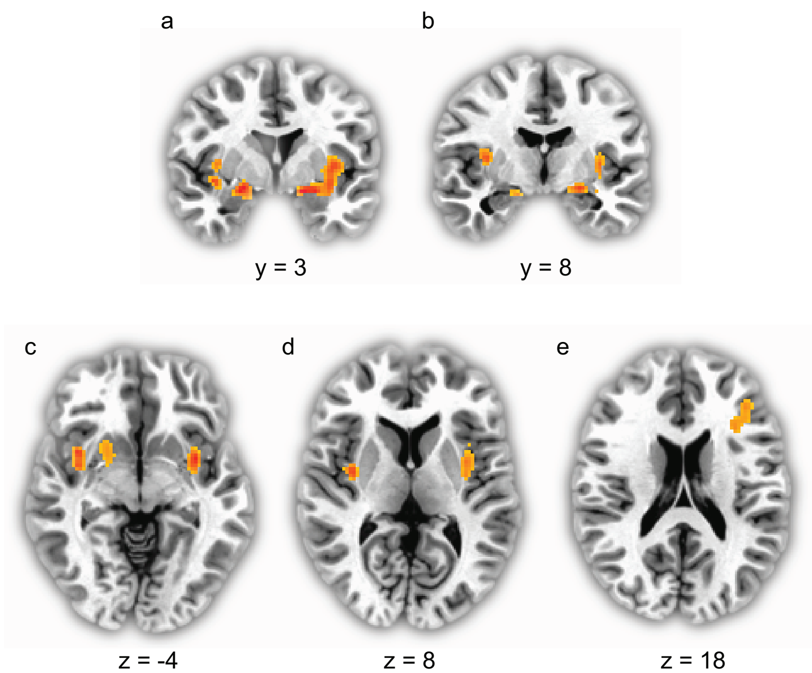

Figure 4-3. Neural response to aroma intensity. Brain regions (shown in radiological convention, left on right) activated by aroma intensity included the bilateral insula extending from the ventral regions (c) to the dorsal posterior regions (d). Other regions responding to aroma intensity included the left inferior frontal gyrus, (e) and the amygdala (a), extending into the piriform cortex (b).

Neural correlates of effects of aromas on risk and ambiguity preferences. To investigate the neural mechanisms through which aromas influence preference for varying degrees of uncertainty, we next examined how neural responses to aromas differed with respect to eventual choice outcome. We focused on differences in neural responses between trials where the choice was between a certain option and an option involving uncertainty (AC and RC conditions). For both AC and RC conditions, the response of the anterior insula towards aroma intensity was higher when certain options were chosen, compared to when the less certain option was chosen (RC-c > RC-r, Figure 4-4a, and AC-c > AC-a, Figure 4-4b). The activation spanned both ventral and dorsal regions of the anterior insula, in a region that was more anterior compared to the activation related to aroma intensity overall (Figure 4-3). Activation was also limited to the right hemisphere, consistent with the observation that the right insula is more frequently observed to be linked to emotion and interoception than is the left insula (Chang et al., 2013), and that right anterior insula activation during anticipation predicts risk aversion (Kuhnen & Knutson, 2005).

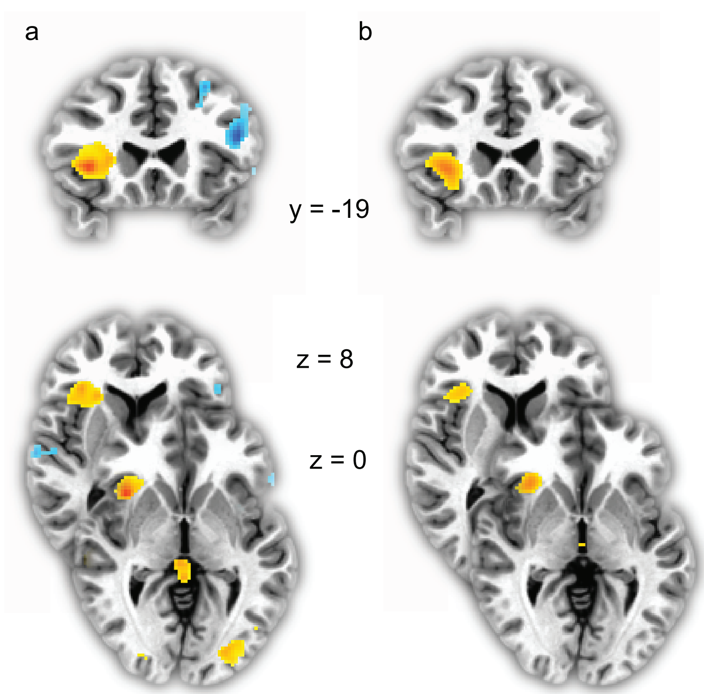

Figure 4-4. Responses to intensity in the anterior insula correlate with preference for certainty. Neural response to intensity in trials in the (a) RC condition, and (b) AC condition where the certain option was chosen, contrasted against trials where the alternative option was chosen (RC-c > RC-r or AC-c > AC-a). In both conditions,

activation was observed in the right anterior insula, and extended from the ventral to the dorsal regions.

4.4 Discussion

We investigated the effects of aroma-induced affect on choices involving risk and ambiguity. Supporting our hypotheses, several analyses in this study indicate that higher aroma intensity leads to increased preferences for certainty, and this effect is mediated by the anterior insula. Firstly, in the RC condition, higher intensity significantly increases preference for the certain option over the risky option. Secondly, in both the AC and RC conditions, higher insula activation towards intensity was observed in trials where the certain option was chosen.

The insula has been found to be involved in a multitude of processes, which take place in at least three functionally distinct regions of the insula (Chang et al., 2013). In our study, the region of the anterior insula we found spanned the ventral region, which is associated with processing of chemosensory stimuli (Small et al., 2004), emotions (Stein, Simmons, Feinstein, & Paulus, 2007), and moral judgment (Sanfey, Rilling, Aronson, Nystrom, & Cohen, 2003), to the dorsal region, which has been shown to be associated with response switching and inhibition, conflict and error processing, decisions involving risk and harm avoidance (Paulus et al., 2003), financial decision-making (e.g. Knutson, Rick, Wimmer, Prelec, & Loewenstein, 2007) as well as risky decisions involving social interactions (Tang, van den Bos, Andrade, & McClure, 2012). A region of the dorsal insula has also been shown to mediate uncertainty aversion (Simmons, Matthews, Paulus, & Stein, 2008). Given the wide range of functions associated with the ventral and dorsal insula, recent theories suggest that the anterior insula might serve as the site where integration of emotions, internal physiological arousal, external sensory signals, and information about risk and uncertainty occurs (Singer et al., 2009). This signal is further integrated with personal preferences for risk and ambiguity to produce a global feeling state, which then guides decisions. In the current study, the integration of affective arousal from aromas and information about risk and ambiguity might take place in the insula, allowing simultaneously presented aromas to exert a bias on risky decision-making. Furthermore, these regions of the insula are functionally connected with a variety of regions involved in decision-making and emotion (Chang et al., 2013), suggesting that the insula integrates incoming signals from distinct networks of the brain which process cognitive and emotional parts of the decision task.

Overall, aroma-induced emotional arousal appears to be able to affect preferences between certainty, risk, and ambiguity. Aroma intensity is correlated with preferences towards the safer, certain option when the alternative is risky or ambiguous, and this affect-induced preference for certainty appears to be mediated by the anterior insula. In sum, the current study is the first to link neural processes related to decision-making and olfaction, providing potential neural mechanisms by which aromas influence decision-making involving uncertainty.

Chapter 5

Conclusions

A central goal of this dissertation was to demonstrate the usefulness of aromas as a tool to study decision-making processes. The olfactory system is very different from other sensory modalities in a number of ways, making it important to document aroma characteristics before using them in research. In Chapter 2, I compared aromas to stimuli in other domains that are commonly used to induce emotional states. It was found that the way aromas are distributed in the affective circumplex is very similar to stimuli in other modalities used in affective research used to elicit emotion. Variances in ratings are also comparable, and test-retest and inter-rater reliabilities are high. Collecting ratings on a large number of stimuli also allowed us to identify aromas that fit desired affective profiles for use in subsequent studies. We used selected aromas in Chapter 4 to study the effect of aroma pleasantness and intensity (and induced emotional valence and arousal) on risk aversion, and found that aroma intensity exerts an effect on certainty-preferences via activity in the anterior insula.

An influential theory states that pleasantness is the sole dimension of aromas, which is perhaps surprising given the diversity of odor qualities (Yeshurun & Sobel, 2010). After showing that intensity (in addition to pleasantness) is an important dimension in Chapter 2, we addressed the apparent lack of dimensionality of olfactory space in another way in Chapter 3 – by determining if independent factors were driving perceived aroma pleasantness. In agreement with studies that link familiarity and nostalgia with pleasantness (Bornstein & D'Agostino, 1994; Delplanque et al., 2008;

Orth & Bourrain, 2008), we found a factor related to familiarity that contributed significantly to perceived pleasantness. While we found an effect of pleasantness and intensity on risk-aversion in Chapter 4, we did not find an effect of familiarity, but future studies might consider investigating the effect of this aroma quality when studying other decision processes.

Limitations and future directions

Despite the distinct advantages associated with using aromas as affective stimuli, they also come with their fair share of drawbacks. From a practical standpoint, since aromas cannot yet be digitized, olfactory stimuli are harder to distribute and more costly to produce than digital media such as words, pictures, videos, and sounds. Specialized equipment is required for stimulus delivery, and as there is currently no agreed upon standard method of delivery, methods and stimuli differ across sites, making results harder to compare. In our study in Chapter 2, we had a limited number of stimuli available to us (47 aromas, compared to hundreds of stimuli assessed in other modalities). Because of this, our study contained less power than studies of other types of affective stimuli. Future studies may wish to expand the range of aromas tested.

Olfactory percepts are hard to verbalize and describe (Yeshurun & Sobel, 2010), making it hard to obtain detailed assessments of responses to olfactory stimuli with subjective description alone. Furthermore, despite high inter-rater reliability across a number of dimensions, we cannot discount the fact that aromas might be eliciting a very specific reaction in each individual, given that aromas are strongly tied to emotional memories, especially those autobiographical in nature. This is reflected in the relatively low inter-rater reliability of aroma familiarity ratings. To take individual differences into account, analyses in all studies in this dissertation were performed using subjective ratings from each individual participant towards each aroma (instead of group differences between effects of individual aromas).

In Chapter 2, we characterized aromas using a dimensional viewpoint. Future work might consider using a categorical approach, characterizing aromas based on discrete emotions. Though there has been some difficulty classifying aromas in terms of classical emotional terms, such as anger and sadness, progress has been made in identifying suitable emotional descriptors for olfaction (Ferdenzi et al., 2011). Given the hypothesized role of nostalgic memories in mediating some of the effects of aromas (Orth & Bourrain, 2008), it might be worthwhile to probe the emotions generated by these memories in more detail as well.

In Chapter 3, we employed a form of PLS, Partial Least Squares Correlation (PLSC), that is commonly used to analyze neuroimaging data. There exists another type of PLS analysis technique known as Partial Least Squares Regression (PLSR) (Krishnan, Williams, McIntosh, & Abdi, 2011). While PLSC is not directional and therefore cannot be used to make predictions off brain activity, PLSR is a predictive method. Since the goal of the analysis in Chapter 3 was to find relationships between brain activation patterns and subjective pleasantness, and not prediction, we adhered to the more common method for analyzing neuroimaging data, PLSC. Future studies might look into using PLSR to predict pleasantness scores from brain activity.

Conscious awareness of the presence of aromas might create demand characteristics, or cause people to attribute (correctly or not) their behavioral tendencies to the aromas, which might trigger measures to counter these effects, decreasing, eliminating, or even reversing them (Kelley, 1973; Schwarz & Clore, 1983). In these studies, aromas were delivered via olfactometer, such that the subject was aware of aroma delivery. Ideally, aromas could be delivered in a manner that does not alert the subject to their presence. However, the use of an olfactometer was necessary to ensure precise control on the concentration of aromas and timing of delivery. Subliminal delivery of aromas would also be useful to study the subconscious effects of scents. Unfortunately, it is also hard to titrate aroma strength such that aromas are not consciously detected and yet still have an effect on mood and behavior.

Final remarks

The studies conducted in this dissertation provide an example that show how aromas can be used to study cognitive and neural mechanisms of decision-making. It is hoped that aromas, with all their associated advantages as experimental stimuli, will be more widely used in research to elucidate behavioral and neural mechanisms of affect and decision-making.

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