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Human Olfactory Perception: A Literature Review

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by

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Each person whose signature appears below certifies that this doctoral project in his/her opinion is adequate, in scope and quality, as a doctoral project for the degree Doctor of Psychology.

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TABLE OF CONTENTS

LIST OF FIGURES

Figures

ABBREVIATIONS

AIO	Affective Impact of Odor Scale
AKA	Also known as
AND	16-androstadiene-3-one
AS	Androstadienone
BT	Body temperature
CF	Cardiac frequency
CNS	Central nervous system
CSA	Childhood sexual abuse
OERP	Event-related potentials
OFC	Orbitofrontal cortex
PEA	Phenyl ethyl alcohol
PSP	Putative sex pheromone
EDA	Electrodermal activity
EEG	Electroencephalograms
EOG	Olfactory epithelium
EST	oestra-1, 3, 5 (10), 16-tetraen-3-ol
HLA	Human leukocyte antigen
fMRI	Functional magnetic resonance imaging
FSH	Follicle-stimulating hormone
LH	Luteinizing hormone
LHRH	Luteinizing hormone-releasing hormone
MHC	Major histocompatibility complex
PDD	Pregna-4,20-diene-3,6-dione

PET Positron emission tomography

PRL Prolactin

PNS Peripheral nervous system

RF Respiratory frequency

TUA Trimethylundecylenic aldehyde

VND Vomeronasal duct

VNO Vomeronasal organ

VNS Vomeronasal system

ABSTRACT

Human Olfactory Perception: A Literature Review

by

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There has been wide debate about the degree to which humans are impacted by olfaction. Despite former assumptions that we are dominantly visual/auditory creatures, recent studies suggest that humans are more highly macrosmatic than originally thought. Humans have demonstrated behavioral, physiological, cognitive and affective responses to olfactory stimuli even when the stimuli were perceived unconsciously. The mechanism by which humans perceive these signals is unclear; there is much debate as to whether the vomeronasal organ is functional in humans. Regardless of the mechanism of perception, it is clear olfaction is psychologically impactful for humans. The following literature review summarizes research in the field related to olfactory functioning and perception.

The review discusses animals and their interactions with and use of olfactory cues, the human olfactory system, parallels among animals and humans in reactions to odorants, human sensitivity to odorants, and the vomeronasal organ debate. Human research areas included in the review: human-odorant interaction, odor as an identification marker for individual humans, human psychological response to odors, the impact of odor on human affect and sexual behavior, odor production and preference linked to human characteristics, and the effect of odor on human learning.

CHAPTER 1

INTRODUCTION

Recent studies suggest that humans react to olfaction in a variety of ways (Earls & Castonguay, 1989; Grammer, Fink, & Neave, 2004; Grosser B. I., Monti-Bloch, Jennings-White, & Berliner, 2000; Kirk-Smith, Van Toller, & Dodd, 1983; Zucco, Paolini, & Schaal, 2009). It has long been understood that animals use olfaction and pheromones in communication and sexual interactions (Bruce & Parrott, 1960; Kennedy & Brown, 1970; Whitten, 1956; Whitten, 1959) and there are many parallels between animal and human responses to olfaction (Cutler, et al., 1986; Ellis & Garber, 2000; McClintock, 1971; Preti, et al., 1986). There is much debate as to what mechanism might allow for humans to perceive pheromones (Boschat, et al., 2002; Hays, 2003; Knecht, et al., 2003; Tirindelli, Dibattista, Pifferi, & Menini, 2009). It is possible that because of this debate there has been less emphasis in research and understanding of olfaction as it relates to humans. Despite former assumptions that we are dominantly visual/auditory creatures, there is much evidence we are more highly macrosmatic than originally thought (Gleason & Reynierse, 1969; Havlicek & Roberts, 2009; Jacob, McClintock, Zelano, & Ober, 2002; Wysocki, Dorries, & Beauchamp, 1989). Humans have demonstrated behavioral (Pierce, Cohen, & Ulrich, 2004; Spencer N. A., et al., 2004), physiological (Grosser B. I., Monti-Bloch, Jennings-White, & Berliner, 2000; Moller & Dijksterhuis, 2003; Soussignan R. , Schaal, Marlier, & Jiang, 1997; Wang, Chen, & Jacob, 2003), cognitive (Gottfried & Dolan, 2003; Hummer & McClintock, 2009), and affective (Jacob & McClintock, 2000; Spencer N. A., et al., 2004; Villemurea, Slotnick, & Bushnell, 2003; Wrzeniewski, McCauley, & Rozin, 1999) responses to olfactory

stimuli even when the stimuli were perceived unconsciously (Zucco, Paolini, & Schaal, 2009). Whether or not the vomeronasal organ is the mechanism by which these reactions occur, it is clear olfaction is psychologically impactful for humans; and, therefore, a review of the existing literature on olfaction is necessary.

CHAPTER 2

ANIMALS AND OLFACTION

It has long been understood that animals use olfaction in a variety of ways, particularly via pheromone production and reception. The term pheromone was proposed by Karlson and Luscher and is derived from the Greek *pherin* meaning to transfer and *hormōn* meaning to excite (Karlson & Luscher, 1959). Pheromones are chemicals emitted from an organism's body into their environment; into the air, water, or marking their land surroundings. Pheromones function in two major ways: they aid in physiological regulation and act as a communication device within a species. There are subcategories of pheromones including those that are olfactory-based or ingested orally. In animals, pheromone functions include sex attractants, alarm substances, trail substances, territoriality markers, and individual recognition signals (Gleason & Reynierse, 1969). One organism, via pheromone release, can impact the neuroendocrine system and delay or speed physiological processes (Tirindelli, Dibattista, Pifferi, & Menini, 2009).

When examining mammals for pheromone activity much research has focused on rats. One well-documented response seen among rats is the Lee-Boot effect. When a group of female rats is housed together in the absence of males, it alters their estrus cycles. When housed in groups of 4 it was noted that their estrous cycles became synchronized and extended so that they were fertile less frequently (Whitten, 1959). Whitten replicated the Lee-Boot effect, causing female rats' estrus cycles to synchronize, and subsequently separated the females and exposed them to male stimuli (Whitten, 1956). After experiencing the Lee-Boot effect female mice exposed to male mice will return to a period of fertility. In Whitten's experiment the females were exposed to

different forms of male stimuli over several days. In the first group the female rats were paired directly with a male on the first day. In the second group they were each placed in an individual cage with a male rat but were separated from the male via a wire grid for two days. In the third group the females were exposed to male excreta for two days and then placed in contact with a male on the third day. On the third day of the experiment the majority of the pairs of mice in all of the experimental conditions mated. What was interesting was that the mice that were placed together on days 1 and 2 waited until day 3 to mate and mice that were not in direct contact on days 1 and 2 mated on day 3. Mating percentages among the groups dropped again on the fourth day. The results indicated that exposure to a male stimuli had the same effect as direct exposure to male mice. The female mice's ovulation synchronized in response to the exposure to both stimuli and direct contact with male mice, leading to breeding synchrony.

Another interesting effect among female mice is known as the Bruce Effect. (Bruce & Parrott, 1960). Recently impregnated mice are separated from the stud mouse and placed with a strange male mouse. Within 48 hours of their placement with a strange male an unusually high rate of the female mice experience failed pregnancies. Among female mice that have had their olfactory bulbs removed this effect is nearly eliminated, leading Bruce and Parrott to conclude that the smell of the strange male is the primary stimuli which leads to subsequent loss of pregnancy.

The Vandenburgh effect is seen when sexually immature female mice are exposed to the scent of unrelated male mice. If the exposure occurs within a critical period in their development the female mice become sexually mature significantly earlier than their non-exposed controls as measured by earlier estrus (Kennedy & Brown, 1970). It is noted that

this effect has been demonstrated in the direct presence of male mice or when the females are exposed to male scent alone.

The final animal study introduces an interesting concept into olfactory-based conditioning. Honey bees can be trained to respond to pheromones with "inappropriate" actions (Smith, 1993). Smith found that via association, honey bees can be trained to extend their proboscis, which is a feeding response, in the presence of their pheromone used for guiding other honeybees to nests and several components from their alarm pheromone, which they would otherwise respond to with avoidance. The authors noted that this training was very similar to training to more 'general' odors, the only noticeable difference being that the bees had difficulty learning to recognize the pheromones at first.

These results indicate that honeybees were able to learn to suppress their innate, instinctive response to pheromones and instead chose to respond differently (Smith, 1993). In a sense, they de-conditioned their instinct. The bees had difficulty discriminating the scent of the pheromones initially, but they were able to learn how to recognize the odor via training.

CHAPTER 3

HUMAN OLFACTORY SYSTEM

An examination of the olfactory system is a necessary precursor to understanding the implications of the research studies on olfaction. Within most mammals there are two olfactory tracks: the main olfactory track and the accessory olfactory track, which is associated with the transduction of pheromones rather than odors. Our first examination will be of the main olfactory track in humans.

The Main Olfactory System

A sensory system's first phase involves the encounter of an external stimulus with the peripheral nervous system (PNS). The receptive system transduces the stimuli into electrical information to be processed by the brain. In olfaction the perceived stimuli are odorants, highly volatile airborne chemical compounds, and transduction occurs within the olfactory epithelium. The olfactory epithelium is an epithelial sheet within the nasal mucosa that lines about half of the nasal cavity and consists of several types of cells: olfactory receptor neurons, basal cells, Bowman's glands, and supporting cells.

The olfactory receptor neurons are bipolar neurons with dendrites extending into the nasal cavity and axons which project into the brain. Each neuron has a single dendritic process on the apical end (away from the body) from which several finger-like olfactory cilia branch out into the mucus lining of the nasal cavity to receive odorant stimuli. At the opposite end of the neurons the axons project through openings in a porous bone at the top of the nasal cavity, the cribriform plate, into the olfactory bulb located below the frontal lobes forming the first cranial nerve.

The basal cells in the olfactory epithelium are a type of stem cell capable of dividing and specializing into other cells. Their presence in the olfactory system allows for the cells within the epithelial sheet to be replaced every two to four weeks. The supporting cells within the epithelium support and nurture the olfactory cells. Finally, the Bowman's glands produce the thick mucus that coats the inside of the nasal cavity. This mucus protects the exposed cells of the epithelial sheet and provides a chemical environment that traps and dissolves odorants, transmitting them to the olfactory cilia.

The membrane of the olfactory receptor neuron is embedded with receptor proteins that span the cell membrane. Outside of the cell these proteins have a receptor site capable of binding with a range of odor molecules. Within the cell the protein is linked to a G-protein that, in its inactive state, is bound to guanosine diphosphate (GDP). An odorant binding to the receptor protein on the outside of the membrane activates the G-protein on the inside of the cell that exchanges its GDP for guanosine-5'-triphosphate (GTP). This G-protein and GTP activate Adenylyl cyclase III, an enzyme that converts a large number of Andenosine triphosphate (ATP) molecules into cyclic adenosine monophosphate (cAMP). The cAMP function as second messengers binding to cyclic nucleotide-gated cation-selective channels also embedded in the membrane. The channels open, admitting positively charged ions sodium (NA^{+}) and calcium (CA^{2+}) into the cell, and depolarizes the cell. The increase in CA^{2+} opens CA^{2+}-gated chloride (Cl^{-}) ion channels, allowing the efflux of Cl^{-} from the cell, further contributing to cell depolarization. This process moves from the cilia of the dendrite to the axon hillock of the cell where an action potential is generated and transmitted to the olfactory bulb via the axon.

The return of the cell to its polarized state begins when CA^{2+}-activated enzymes, phosphodiesterases (PDE) break down cAMP. Simultaneously CA^{2+} links to calmodulin to form a protein complex that binds to the cyclic nucleotide-gated cation-selective channel, reducing its affinity for cAMP. The remaining high concentration of CA^{2+} is expelled through the CA^{2+} /NA^{+} exchange pathways embedded in the cell membrane, returning the cell to its resting potential.

The olfactory system's second phase involves the central nervous system (CNS). Once the odorant signals are converted to electrochemical signals within the olfactory receptor neuron the action potential is transmitted to the axons. These unmyelinated axons bundle together into groups of nerve tissue, to form the olfactory nerve, which projects through perforations in the cribriform plate to the olfactory bulb. The axons converge at the outer layer of the olfactory bulb into small astrocytic encircled structures called glomeruli. Within a glomerulus the axons form synapses with the dendrites of other cells of the olfactory bulb including mitral cells, which form the olfactory tract that projects into the CNS. The olfactory tract synapses in 5 major regions of the cerebrum: the anterior olfactory nucleus, piriform cortex, olfactory tubercle, portions of the amygdala, and the entorhinal cortex. These direct projections from input to cortex are unique to the olfactory system. All other sensory systems initially project to the thalamus which acts as a relay system, projecting to a neocortical region which processes the sensory information (The Chemical Senses, 2008).

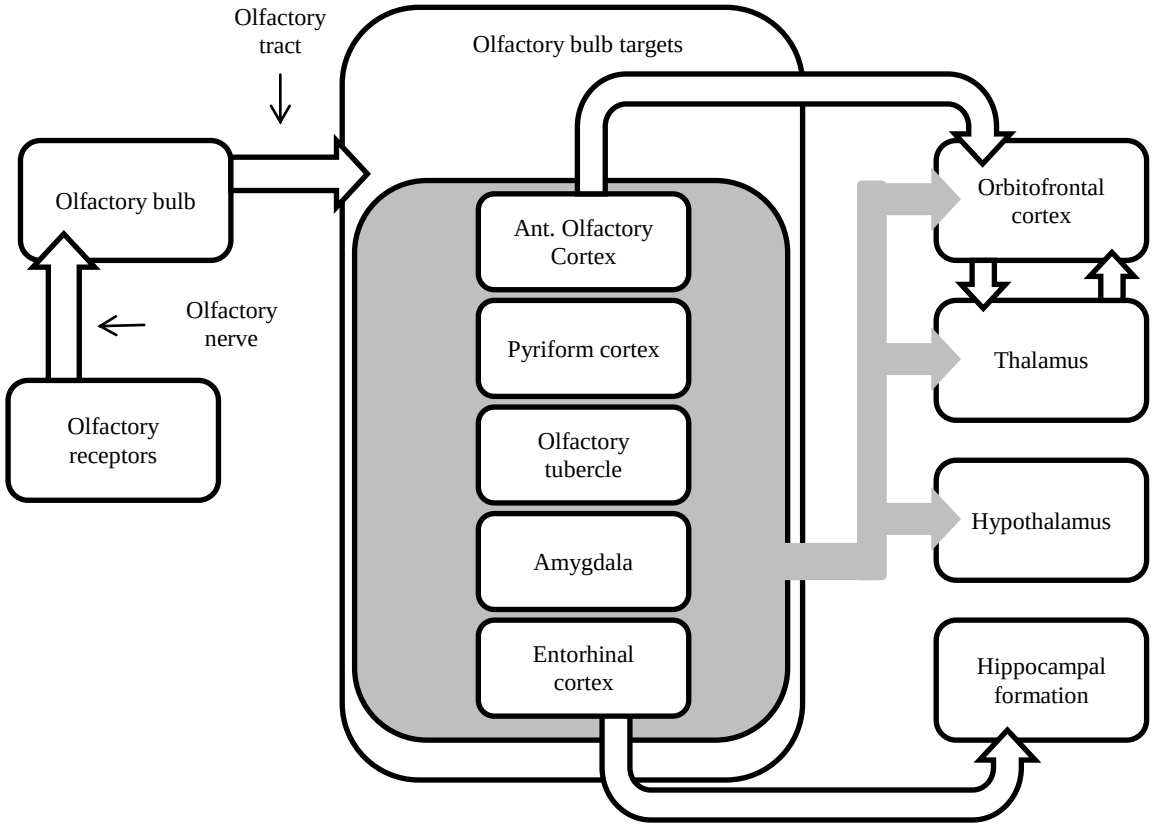

Figure 1. Main olfactory system

Royet and Plailly (2004) compiled a review of articles to describe what is understood about the neuroanatomy of the olfactory system, the methodology by which it is studied (e.g. PET scans vs. fMRI), the differences among structures involved in passively smelling odorants versus actively smelling odorants, attempting to identify odorants, or processing odorants related to affect, emotion, and or memory. In this article they describe a proposed "dissociation" of the olfaction processes to the left and right hemispheres of the brain that can be organized based on a hierarchy of increasingly complex processing demands. The model describes lower levels of analysis occurring in the right hemisphere; it participates in detecting the presence of an odor and processing

more ‘holistic’ qualities, such as familiarity. These processes demonstrate mild and moderate activation of the right orbitofrontal cortex (OFC), respectively. Familiarity analysis is made based on associative memory; there is not a detailed or conscious memory attached to this judgment. Put simply, the brain implicitly recognizes if it has encountered a scent before or not.

The left OFC becomes engaged when determining if an odor is pleasant or unpleasant (Royet & Plailly, 2004). Exposure to highly aversive olfactory stimuli (pungent, unpleasant scents) activates an emotional network in the left hemisphere which is associated with processing emotional visual and emotional auditory stimuli. In addition olfactory stimuli directly activate the left amygdala. Olfactory stimuli are the only sensory modality which directly activates the left amygdala in addition to the sensory emotional network. The regions activated by emotional olfactory stimuli (e.g. aversive scents) correspond to the neural regions activated with other salient emotional processes, such as dysphoria, anger, and obsessive-compulsive disorder. It also seemed apparent that the amygdala was processing on an unconscious level during the experimental olfactory activation.

The left hemisphere is involved in more complex tasks, such as identifying odors or determining their edibility (Royet & Plailly, 2004). These activate a region linked with semantic associations known as BA 47, the left inferior frontal gyrus. The authors propose this area assists by activating the semantic label, or name, for an odor to determine if it is edible.

Each of the processes described up to this point occur unconsciously in response to participants passively smelling odorants. Actively sniffing odorants has been shown to

activate differing brain tracks including the piriform cortex and parts of the orbital cortex involved in higher analytical processes (Kareken, et al., 2004). Actively sniffing is thought to prime the brain in such a manner that it increases a person's chance of detecting subtle odorants.

Royet and Plailly (2004) suggest lateral odorant processing is advantageous from an evolutionary standpoint as each hemisphere has a differing basic, rapid evaluation of odors. The olfactory bulb bypasses the thalamus. It feeds directly to the cortices in the right hemisphere that determine if an odor is familiar, and those in the left hemisphere that determine if the odor is emotionally salient and/or aversive. Thus unfamiliar or aversive odors may induce arousal rapidly, before the higher-level processes involving the details or properties of the stimulus can be inferred. An odor can induce an emotional and possibly corresponding behavioral response without taking the time required for analytical, higher-level, conscious processing. This pathway creates a more rapid fight or flight response, potentially increasing chances for survival. The authors note that the hemispheres likely work together for optimal processing, but that evidence suggests each hemisphere could work independently.

Anderson et al. (2003) proposed a similar model of dissociation in olfactory processing. Participants (N=16) underwent fMRI while presented with 4 odor conditions: intense-pleasant, intense unpleasant, unintense-pleasant, and unintense-unpleasant. Participants were directed to sniff every 20 seconds and indicate if an odor was present or not. Their results indicated amygdala activation corresponding to intensity (not valence) of odors, while valence of odors was associated with activation in the OFC.

Expanding on the dissociation processing hypothesis, lateralization would also be adaptive in relation to traumatic brain injury. Lesions or localized axonal shearing would not fully impair the basic processes required for a rapid, unconscious fight/flight response evoked by an odorant. In addition it has been shown that odor identification of unpleasant odors is invariant to the age-related decline in sensitivity seen in pleasant or neutral odors (Konstantinidis, Hummela, & Larsson, 2006). Lateral distribution might counteract age-based degradation in identifying unpleasant odors, which are more likely to be linked to threats to survival than neutral or pleasant stimuli.

Given this model, it is probable that most human reception and analysis of odors occurs unconsciously, lacking higher-level processing such as semantic associations. Indeed, even though the olfactory system is constantly processing stimuli, experience demonstrates that humans rarely consciously engage in these analyses, and even more rarely find it necessary to identify or name odors.

It follows that odor-based learning and behavioral conditioning predominantly occurs unconsciously, which has been frequently demonstrated (Kaitz & Eidleman, 1992; Kirk-Smith, Van Toller, & Dodd, 1983; Zucco, Paolini, & Schaal, 2009). It is also significant that the olfactory system has a direct, unconscious link to the amygdala and that emotionally valenced scents activate the same regions as dysphoria, anger, and obsessive-compulsive disorder. Practically, this indicates people can encounter odors that directly elicit salient emotions without conscious awareness of what has transpired.

Parallels Among Animals and Humans

Many have speculated that humans are affected by pheromones in ways similar to other animals. Grammer, Fink, and Neave (2004) note the parallels between animal responses to pheromones and studies on human responses to odorants. One of the earliest studies proposing human pheromone interaction demonstrated female synchrony in menstrual cycles, which the author argued paralleled the Lee-Boot effect in rats (McClintock, 1971). McClintock included 135 female college students, aged 17-22 years old in a study documenting menstrual cycles. Participants were asked the onset of their last and second to last menstrual cycles three times during the academic year. McClintock noted women who experienced loss of menstruation, or dysmenorrhea, the length of their cycles, and the average number of times in a week each participant was in the company of a male. McClintock then calculated the difference between menstrual cycle start dates for the women. This was calculated by arbitrarily selecting one participant and comparing her start date to the closest start date of the second participant. At the end of the experiment the calculation was slightly different. Participants noted the start date of a particular cycle number relative to the beginning of the experiment (e.g. the sixth onset occurred March 5) and the onset of the same cycle number for each woman was compared. Thus if a second participant noted onset dates of March 1 and March 29 for her fifth and sixth cycles, the March 5 onset date would be compared to March 29. McClintock utilized this strategy in order to minimize the possibility cycles appeared to gain synchrony via simple coincidence.

McClintock (1971) found a significant increase in synchronization among women who spent the most time together including groups such as close friends ($p \leq .003$),

roommates ($p \leq .0007$), and close friends and roommates combined ($p \leq .0003$). Subjects were then randomly paired and tested for synchrony. This was to test if confounding variables such as similar life pattern, similar diet (e.g. cafeteria food), and similar stress periods (e.g. timing of final exams) might have an effect on the results. This test showed no significant trends ($P \leq .08$). McClintock then chose to break students into larger groups to examine for group synchrony. These groups were created based on the participants' lists of people with whom they spent the most time. Mean onset dates were determined for each of the 15 resulting groups for the months of October, late November, January, late February, and April. The mean individual difference from the group onset mean was calculated for each group across time. The results indicated a significant decrease in individual differences from group onset and further demonstrated that most of the decrease occurred within the first four months with little subsequent variation. This supported McClintock's hypothesis that the decrease in differences from onset dates was in fact an increase in synchrony among friends.

In addition to synchrony among women who spent the most time together, McClintock (1971) found that women who were grouped together and also experienced little interaction with males (0 to 2 times per week) experienced significantly longer cycles ($P \leq .03$) than the women who interacted with males 3 or more times per week. There was no significant difference in the duration of menstruation itself ($P \geq .02$). The latter groups' cycle length was comparable to the national average of 28 days. Though this could be simply correlational evidence, McClintock noted that participants spontaneously made comments that their cycles shortened when they began dating more frequently. Taken together this data parallels the Lee-Boot effect seen in rats.

McClintock's work was later expanded upon in order to further eliminate the possibility of social interactions influencing menstrual cycle synchronization. In this double-blind study experimenters applied the sweat from donor females to the upper lips of participant females three times per week over the span of four months (Preti, et al., 1986). The results of Preti et al.'s study indicated a similar significant trend toward synchronizing the start date of menstrual cycles as McClintock's study, and this effect was based solely on the presence of female axillary sweat (McClintock, 1971).

A similar study was published that same year examining the effects of extract from the male axillary region on the female menstrual cycle (Cutler, et al., 1986). The male secretions were collected three times per week for four months. Fifteen women with an aberrant length menstrual cycle (<26 or >32 days) were selected to participate in this double blind study. The male sweat was applied to the upper lips of the female participants three times per week for four months. Cutler et al. found that presentation of the male stimulus reduced the incidents of variability in cycle lengths and reduced the proportion of aberrant length cycles among the participants. The regulation in menstrual cycle upon presentation of a male stimulus parallels the Whitten effect seen in rats.

Similarly there are human parallels to the Vandenburg effect. Ellis and Garber (2000) examined the rates of sexual maturation among young women as measured by the onset of their first menstrual cycle. They found that girls in homes with a stepfather present matured more quickly than girls in single-parent homes. In addition they found that the younger the girl was when the stepfather arrived, the earlier her maturation occurred. The fact that these parallels exist, that humans demonstrate similar responses

when exposed to human odors as animals do in response to pheromones, highlights the physiological impact odors have in human functioning.

Odorant Sensitivity

Sense of smell is generally not considered to be the strongest sensory modality among humans. High sensitivity and reliance on olfactory cues is customarily associated with animals. For example, historically people have relied on dogs to use olfactory perception in tracking. Yet human beings are highly macrosmatic, able to identify individuals based only on their body odor alone (Kaitz & Eidleman, 1992; Kaitz, Good, Rokem, & Eidelman, 1987; Russell, 1976). The major histocompatibility complex (MHC) is a gene believed to code for individual body odor and immunological function in humans. Research shows humans are able to discriminate, by scent alone, between people whose MHC genes differ by as little as one allele (Jacob, McClintock, Zelano, & Ober, 2002). This specificity and precision is remarkable.

In addition, research demonstrates that olfactory sensitivity is malleable: it can become more sensitive. Wang, Chen, and Jacob demonstrated plasticity in the peripheral olfactory system (Wang, Chen, & Jacob, 2003). Participants with an extremely high threshold for androstenone were selected to participate in an olfaction study. Nine of the participants were considered anosmic, meaning they could not smell androstenone at its highest concentration 0.1%. Participants in the experimental group were instructed to sniff androstenone for 3 minutes three times each day for three weeks. Participants in the control group followed the same procedure using amyl acetate. Experimenters measured the evoked potentials of the olfactory epithelium (EOGs) utilizing intra-nasal electrodes.

These measurements represent PNS stimulation, that is, activity within the nasal epithelium and not in the cortex. Event-related potentials (OERPs) recorded on the scalp via EEG measured activity in both the peripheral and central regions of the olfactory system. They also measured participant's thresholds for perceiving androstenone.

After one week the experimental group members' ability to detect androstenone had risen significantly, with no change in the control group (Wang, Chen, & Jacob, 2003). They became sensitized to the androstenone. Both the EOG and OERP recordings rose significantly. Participants began to perceive androstenone consciously, describing it as "sweaty" smelling. Analyses indicated that the lower an individual's threshold for perceiving androstenone, the higher the peripheral EOG response. As EOG increased, OERP was shown to increase in response, until it reached a plateau. In other words the higher the peripheral receptor response, the higher the corresponding central activation became. Participants with the highest initial thresholds had the lowest EOG and OERP responses, but all participants demonstrated an EOG response by the end of the exposures. One "anosmic" participant demonstrated EOG response in the absence of an OERP response. The authors suggest this is a neural demonstration of a case in which receptor activation does not lead to perception.

Interestingly the authors repeated the experimental protocol utilizing amyl acetate (Wang, Chen, & Jacob, 2003). There were no significant changes in sensitivity to the odorant. Exposure did not impact the EOG response or the OERP response in participants, suggesting that the plasticity of the olfactory system is dependent on the stimuli with which it interacts. It is possible that plasticity is more likely in the presence of pheromone-like odorants such as androstenone, and less likely in the presence of other

odorants (such as amyl acetate). Wysocki, Dorries, Beauchamp (1989) demonstrated similar results and hypothesized that the olfactory response may parallel the immune system response; peripherally exposure to an odorant might trigger some response which increases the signal transmitted to the central olfactory system. Alternatively the authors proposed a dominantly centrally controlled process. Lack of exposure to a stimulus over time could lead to deterioration of neural pathways, and subsequent exposure reverses this deterioration, strengthening the central responsivity to the peripheral nervous system. Whatever the mechanism, it is apparent that the olfactory system is malleable enough that it can adapt the ability to process novel olfactory stimuli.

Similar results have been shown in response to odorant mixtures and their components (Laska & Hudson, 1991). Thresholds for perception of the stimuli diminished over their first, second, and third presentation. Interestingly, inter- and intra-individual variability in thresholds for detecting stimuli was inversely correlated to stimulus complexity. As stimuli became more complex people could perceive it at lower thresholds. This wasn't, however, due to increasing concentrations of odor within the dilution. Participants could perceive mixed odors in which the amount of each of the individual components was lower than the threshold for their individual perception. Nor was the effect simply additive. The researchers hypothesized sub-threshold interaction occurred which led to enhancement.

Evidence suggests that the neural processing of olfactory cues beneficially interacts with visual processing, increasing perception abilities (Gottfried & Dolan, 2003). Gottfried and Dolan utilized event-related fMRI to examine the neural basis for cross-modal olfactory and visual integration in the brain. The experiment was organized

in a modified 2 x 2 x 2 factorial design utilizing the presence or absence of an odorant, the odor's valence (pleasant or unpleasant), and the presence or absence of a picture presented simultaneously with the odorant. They gave participants an auditory cue to sniff the air and requested participants indicate if there was an odor present "yes" or absent "no". There were 5 conditions: 1) odor-only, 2) picture only, 3) bimodal (odor and visual) in which the visual stimuli semantically corresponded to the odor (e.g. picture of a bus presented with a diesel odorant), 4) bimodal with a non-congruent picture (e.g. a fish-like odorant and a picture of cheese), 5) and a low-level baseline that had neither an odor nor a picture.

Results indicated that subjects' olfactory detection was faster and more accurate when odorants were presented with congruent visual stimuli (Gottfried & Dolan, 2003). The study identified bimodal congruent-specific increased neural activity in the anterior hippocampus and rostromedial orbitofrontal cortex. The authors also noted that effects did not require intentional engagement of association memory; Participants were asked only to identify if there was an odor present. They concluded that the hippocampus mediates reactivation of crossmodal semantic association even in the absence of explicit memory processing.

Overall, the human olfactory system is highly sensitive to odorants, able to distinguish between individuals whose MHC composition differs by as little as one allele. It is capable of sensitizing to olfactory stimuli, diminishing perception thresholds. Purported anosmic individuals develop peripheral and central activation, often to the point of conscious awareness of an odor, via repeated exposure. In addition the olfactory

system has been shown to engage in cross modal processing, increasing accuracy and response time.

Vomeronasal Organ Debate

Pheromones are chemicals emitted from an organism's body into their environment which aid physiological regulation and communication within a species. As pheromone research progressed, the evidence demonstrated that the most extensive use of pheromones occurs in the most social of animals (Gleason & Reynierse, 1969). This information led to an examination of human beings. Early pheromone researchers assumed humans were not a macrosmatic species; but in the late 1960's, Wiener established that man is influenced by external chemical messengers more than first believed (Gleason & Reynierse, 1969). Research on human olfaction and pheromone detection has slowly progressed, but debate continues as to whether humans utilize chemosignals, isolated, airborne steroids that impact human psychological state or mood, in communication with one another.

Research on olfaction and pheromones attempts to demonstrate a physiological, neurological, or behavioral change in a recipient when exposed to an odorant. These odorants are defined by their ability to regulate the physiology of others or communicate some information within a species. As Sorensen (1996, p. 245) describes, "it implies that particular odors have specific instinctual effects on the behavior and/or physiology of particular organisms. This, of course, implies the existence of at least somewhat specialized neural pathways mediating responsiveness to these cues". Sensory transduction requires receptor cells that are altered in some way by the presence of

sensory stimuli and can transform those stimuli into interpretable information. In many vertebrates pheromone receptor cells are a part of a specialized chemoreceptor epithelium located in the vomeronasal organ (VNO) that is located in the nasal cavity (Knecht, et al., 2003). Studies have demonstrated that 90% of adult humans have visible VNOs on their nasal septa; these are believed to be the epithelia that transduce pheromones (Hays, 2003). Some researchers argue that the VNO receptor genetic loci appear to be pseudogenes; and, therefore, are nonfunctional.

The vomeronasal system, like the olfactory system, includes the peripheral nervous system receptors which transduce stimuli into electrochemical signals, the bundled axons that form the vomeronalsa-terminalis nerve and transmit these signals to the CNS, and the cortical regions involved in processing the information. Monti-Bloch, Jennings-White, and Berliner (2006) published a review of the development and peripheral anatomical structure of the human vomeronasal system (VNS). They discuss central nervous system regions that are linked to VNO stimulation and give evidence that the human VNO is functional. Briefly, the human VNO is located beneath the nasal respiratory mucosa. It is between 2-10 mm long and lies parallel to the base of the nasal septum, opening to the nasal vestibule through VNO pit which is approximately 2 cm from the nostril.

The authors describe a set of chemicals, 'vomeropherins,' that cause activation in the VNO, pheromones being a potential subclass of this group (Monti-Bloch, Jennings-White, & Berliner, 2006). The term is created from 'vomero' from the vomeronasal organ, and 'pherin', meaning to carry. These chemicals have been shown to stimulate the VNO, and subsequently various regions of the brain, mediating autonomic,

psychological, and endocrine responses, but have no impact on the olfactory or respiratory epithelium. From their findings it is possible that substances from human origin (such as skin secretions) that qualify as vomeropherins may be odorless. The authors note that this characteristic may explain the lack of clear neural connections between the VNO and the primary olfactory cortex.

In one example of research into vomeropherins, Berliner, Monti-Bloch, Jennings-White, and Diaz-Sanches (1996) examined the impact of the pregna-4,20-diene-3,6-dione (PDD) on the human VNO, olfactory, and respiratory epithelium. They found that PDD depolarizes the VNO and creates electrophysiological changes in the CNS, but elicits no response when applied to the olfactory or respiratory epitheliums. In a later study they demonstrate that the response is dose dependent such that increasing concentrations of PDD correspond to larger electrical amplitudes in the VNO (Monti-Bloch, Diaz-Sanches, Jennings-White, & Berliner, 1998). In their first study PDD was delivered to the lumen of the VNO, the olfactory epithelium, or the respiratory epithelium. They measured changes in cardiac frequency (CF), respiratory frequency (RF), body temperature (BT), electrodermal activity (EDA), and electroencephalograms (EEG). PDD produces significant increase in heart rate for approximately 2 minutes after a single stimulation, a significant decrease in respiratory rate (though small) lasting approximately 5 minutes after stimulation, a significant increase in skin conductance, and significantly changed alpha/beta brain ratio from .11 prior to PDD stimulation to 1.58 after stimulation. There was no significant impact on BT. Again, there was no effect of PDD on the olfactory or respiratory epitheliums. In their second study they conducted a blood analysis of plasma levels of pituitary hormones prolactin (PRL), luteinizing hormone (LH), and follicle-

stimulating hormone (FSH) before and after PDD exposure. They found that in male participants the release of the gonadotrophins LH and FSH was significantly diminished during exposure to PDD. LH and FSH are necessary for the production of testosterone and sperm in men. The study found PDD had no significant effect on women. The pituitary hormone PRL did not show significant changes in either males or females. This study demonstrates the impact of the VNO on the hypothalamus, which synthesizes and releases luteinizing hormone-releasing hormone (LHRH), and via LHRH its impact on the pituitary, which produces and releases FSH and LH. This indicates that the VNO is functionally linked to and impacting parts of the brain that control reproduction.

There have also been contradictory results demonstrated (Knecht, et al., 2003). The study examined participants' with and without a vomeronasal duct (VND) on their sensitivity to and thresholds for odorants including androstenone, a proposed human pheromone. Participants with functional VNDs had two conditions: in one they freely scented the odors, and in the second researchers covered the participants' VND with latex, preventing particles from being transported into the VND. Results indicated that participants with and without a VND did not differ on odor sensitivity or androstenone odor thresholds. There was a significant correlation between general olfactory function and detection thresholds for androstenone, suggesting participants who were more sensitive to odors in general were also more sensitive to detecting androstenone. Finally, covering the VND had no effect on olfactory sensitivity or androstenone detection. The authors state that this evidence supports the notion that the human VNO is vestigial. In other words the VNO may have processed pheromone signals in human ancestors, but through the process of evolution it is no longer functioning in humans today.

Savic, Heden-Blomqvist, and Berglund (2009) utilized PET scans to compare the cerebral activation of men with nasal polyps to healthy controls when smelling pheromone-like substances 4, 16-androstadiene-3-one (AND) and oestra-1, 3, 5 (10), 16-tetraen-3-ol (EST) along with vanillin, acetone, and neutral air, which functioned as the baseline for the PET scans. The anosmia was based on nasal polyps which only effects olfactory mucosa, not the VND or VNO. Results of their study indicated activation in the olfactory areas in controls in the presence of AND, vanillin, and acetone, and anterior hypothalamus activation in the presence of EST, but not in the anosmic participants. The authors suggest that signals from the pheromone component of EST are not mediated by the VNO, but rather the main olfactory bulb via olfactory epithelium.

In his review of the functioning of the VNO, Meredith (2001) explains that the microvillar vomeronasal sensory organs of the human VNO are dissimilar from any other species and they have no obvious way of communicating with the brain. At the same time, evidence demonstrates EVG responses of the VNO area to human-derived chemicals and this evidence cannot be ignored.

It is not the purpose of this paper to make an argument for or against the existence and use of the human VNO. Nor is it intended to make an argument that humans are capable or incapable of utilizing pheromones. It seems evident, however, that whatever the mechanism of delivery, olfactory cues impact human functioning—possibly to a great extent. The question of whether humans utilize olfaction in affectively or behaviorally responding to their environment has immense clinical relevance. If parallel processes occur in humans then human behavior, emotion, and physiology may all be affected by the chemical signals of others. Olfaction could play a role in human communication and

interactions, learning, and the development of interpersonal patterns. In addition if scent has been playing a part in human communication over the course of history, their presence has gone relatively unnoticed. Thus olfactory cues are potentially functioning outside of conscious awareness creating an undetermined impact on human psychological development and health.

CHAPTER 4

HUMAN-ODORANT INTERACTION

Odor as Individual Identification

Every person produces a unique odor and research indicates that humans are able to distinguish among people and identify individuals based on their unique scent (Kaitz & Eidleman, 1992; Russell, 1976). Russell (1976) examined infants' ability to identify their own mothers' scent as noted by behavioral response to the stimuli such as sucking. The participants included 14 healthy full term breastfeeding infants and their mothers recruited from a delivery ward. Each mother was asked to place a breastpad (white cotton sponge) in her bra for three hours before testing. At each test the experimenter held the pad under the infant's nose for 30 seconds. Infants were exposed to a clean moist pad, their own mother's pad, a strange mother's pad, and on the final testing date raw cow's milk. The presentations occurred while the infants were sleeping. The infants' behavioral responses to the presentation of the pads were recorded. The presentations occurred at two days, two weeks, and six weeks after the infants' births. Results indicated that at two days old the infants generally did not respond to the stimuli. At two weeks old infants showed minimal discrimination between their own mother's milk and the milk of a strange mother. This was defined as infants responding to their own mother's scent by making a sucking motion with their mouths while they were still asleep, but not making a sucking motion when presented with the breastpad of a strange mother. At the 6 week point nearly all of the infants showed differential responding, making a response to their own mothers scent while disregarding the strange mother's scent and the scent of cow's milk. The infants ignored the moist/clean pad throughout the experiment. Overall this

research demonstrated that infants are increasingly able to utilize scent as a means of individual identification and further that they did this on an unconscious level as they were sleeping during the experiment.

Research indicates that mothers are able to identify their newborns based on scent alone (Kaitz, Good, Rokem, & Eidelman, 1987). Researchers went to a hospital in Jerusalem and inquired if new mothers would participate in a study. Participants were not in the same room with their infant when they were asked to participate. Those who agreed were screened for olfactory dysfunction and then researchers went to the nursery and obtained the undershirt of the mother's infant and two other infants. All of the undershirts looked the same and did not have stains on them. These were each placed in a plastic bag and brought back to the participant. The mother was then asked to identify which bag contained the clothing of her own infant. Kaitz et al. found that the percentage of correct answers varied based on the mother's amount of time spent with her infant. In the first group mothers reported having spent less than 10 minutes with their infants. In this group 20% correctly identified their infant, which was comparable to chance. In the group that had spent between 10 minutes and 1 hour with their infants 90% correctly identified their own infants' scent, and of the group that had spent more than 1 hour with their infant 100% correctly identified their own infants scent. Researchers hypothesized that many mothers could not identify their infants scent in the first group (less than 10 minutes spent together) due to the amount of other birthing scents that would have interfered with the infants scent (e.g. feces, blood, etc.)

Human Physiological Response to Odors

As previously mentioned, studies have demonstrated electroph,.ysiological changes in the CNS including altered heart rate, respiration rate, and skin conductance in addition to altered levels of pituitary hormones in response to odors (Berliner, Monti-Bloch, Jennings-White, & Diaz-Sanches, 1996; Monti-Bloch, Jennings-White, & Berliner, 2006) The preceding discussion focused on results that were sexually dimorphic; while the males demonstrated significant changes after exposure to PDD, there were no significant changes demonstrated in women.

Both men and women have been shown to respond physiologically to odorants (Moller & Dijksterhuis, 2003; Soussignan R. , Schaal, Marlier, & Jiang, 1997). Moller and Dijksterhuis (2003) measured 14 subjects' skin conductance response to the presentation of four separate odors, two pleasant odors (peach and citral) and two unpleasant odors (skatole and butyric acid). The odors were presented twice, inter-dispersed with blank stimuli while subjects were instructed to relax and breathe normally through their noses. Subjects were wearing black goggles and ear plugs to reduce the possibility that other stimuli confounded the results. The results indicated a significant effect of odor on mean skin conductance amplitudes in participants, demonstrating different skin conductance means for different odors. The authors cited data that suggests the right hemisphere is more involved in processing olfactory cues than the left hemisphere. Due to this hemispheric difference, they also hypothesized that there would be a greater skin conductance response to olfactory cues in the left, or contralateral, hand than that seen in the right hand. Their second hypothesis was not supported, leading them

to conclude that olfactory processing is neurologically ipsilateral, occurring within both hemispheres of the brain.

In a study on human neonates authors demonstrated infants responded behaviorally and autonomically to presentation of odor stimuli (Soussignan R. , Schaal, Marlier, & Jiang, 1997). Researchers strapped pneumobelts around infants' abdomens to record respiratory changes and video recorded facial responses of 46 full-term healthy neonates to the presentation of vanillin, butyric acid, synthetic milk formula, synthetic hypoallergenic milk formula, amniotic fluid, and breast milk. In addition they taped two miniature thermistors to the left and right wrists of the infants to record skin temperature changes during the presentation of the odor stimuli. The stimuli were presented on cotton pads held by a stick in front of the infant. The researcher stood behind the infant during presentation and held the pad there for at least 10 seconds and waited an interval of 45 seconds before presenting the next stimulus. The two autonomic dependent measures were calculated by subtracting for each trial the mean of physiological data at baseline (the 10 seconds prior to stimulus presentation) from the mean physiological data during stimulation (the 10 seconds during which the stimuli was presented). Results indicated a main odor effect on respiratory rate; there were significant breathing changes to odorants as compared to the control stimulus. Infants' body temperatures indicated only that babies generally had a greater body temperature when awake. Finally, babies responded to scent stimuli behaviorally with characteristic facial and oral movements. These results indicate that infants only a few days old respond behaviorally and autonomically to odors.

Impact of Odor on Affect

Odors have been shown to impact people's emotional state and sensory experiences (Filsinger E. E., Braun, Monte, & Linder, 1984; Grosser B. I., Monti-Bloch, Jennings-White, & Berliner, 2000; Suma, Garcia, Hayreh, & McClintock, 2002; Villemurea, Slotnick, & Bushnell, 2003). Some of the significant research into this relationship has focused on putative human pheromones, particularly Androstadienone (AS), which is found in human plasma, axillary hair, male semen, and sweat, and is found in greater amounts in men than in women (Hummer & McClintock, 2009). In one of the earlier experiments utilizing a closely related compound androstenone, men and women were given a packet with photographs and a description of a hypothetical male college student, instructions, and rating scales to evaluate the hypothetical student on various bi-polar dimensions (e.g. ugly—handsome, weak—strong, sexually unattractive—sexually attractive) (Filsinger E. E., Braun, Monte, & Linder, 1984). The packet also included a self-rating mood scale participants were instructed to complete based on the way, "you feel about yourself right now." The packets were impregnated with alpha androstenone, methyl anthranilate (a fruity odor), 3-methylindole (a fecal odor), or were left unscented. Results indicated that in the androstenone condition men rated the male stimulus as more passive and women rated themselves as less sexy.

PET scans have demonstrated AS presentation is associated with significant changes in glucose metabolism within the prefrontal cortex, cingulate cortex, amygdala, and hypothalamus, which are all associated with emotional processing, olfactory areas, and areas associated with visuomotor processing and sensory integration areas (Suma, Kinnunen, Metz, Cooper, & McClintock, 2001). In this study 10 female participants

underwent PET scans in the presence of clove oil as a control and AS mixed into clove oil in the experimental condition. They presented the stimuli at indiscernible (and thus unconscious) levels. They found that AS presented at undetectable, unconscious levels, widely modulates brain functioning in areas beyond those associated with olfaction. They concluded that the presentation of AS was causal in activating neural areas including the prefrontal cortex, cingulate cortex, amygdala, and hypothalamus, all neural systems that are associated with the regulation of emotional states.

Hummer and McClintock later completed a very thorough series of studies examining AS to determine the specific psychological processes it altered in humans (Hummer & McClintock, 2009). In study 1, participants engaged in a dot probe task. Individuals were instructed to focus on a cross in the center of the screen and to identify which side of the screen an asterisk (the dot probe) appeared. Prior to the appearance of the dot probe the screen presented a face briefly (27ms), just below the ability to perceive the face consciously. The faces were neutral, happy, or angry. On emotional trials the probe was presented on either the same (match) or opposite (nonmatch) side of the emotional face. Participants then identified the probe location. In the control condition, participants were exposed to a clove odor carrier. In the experimental condition participants were exposed to minute amounts of AS masked in the clove odor carrier. Results of the study demonstrated that AS biased attention toward both the positive and negative emotional faces while not altering reaction times to neutral (non-emotional) faces.

Their second experiment utilized the Stroop effect, which occurs when a separate psychological process interferes with the goal of the task and utilizes attentional

resources (Hummer & McClintock, 2009). An example of such a task is requiring participants to identify the ink color of presented words. Participants are slower to identify ink color if the word spells out a different color. Thus, attention is measured in the delay caused by the experimental words as compared to control words. In this study, attention was quantified and then compared between experimental (AS) and control conditions. The results indicate AS enhanced attention to emotional words, diminishing their ability to quickly respond, but did not show the same interference to nonwords (e.g. "wwww"). This indicates that AS enhanced attention to emotional information even in nonsocial contexts.

The third study examined if AS is only modulating the processing of emotional stimuli or if it was also enhancing social cognition (Hummer & McClintock, 2009). Participants were asked to monitor a set of visually presented stimuli and respond to whether the stimulus presented was identical to the stimulus presented 2 objects prior. The social condition presented emotionally neutral faces while the nonsocial condition presented seven-sided shape images as stimuli. The authors contrasted performance on the social and nonsocial versions of the task in the control and experimental conditions. Results indicated AS did not increase attention to the neutral faces and did not significantly alter performance in any way.

The fourth study required participants to fill out mood scales prior to and after engaging in the computer tasks (Hummer & McClintock, 2009). Participants were then measured on their arousal and attention in response to AS, their ability to detect AS at two concentration levels, and how pleasant and familiar they ranked the odors of these solutions. The results demonstrated that participants exposed to AS experienced feeling a

diminished drop in attention as compared to the control groups. AS was not found to alter the participants' mood. The authors predicted this result and theorized that AS only influences mood indirectly in conjunction with emotional cues, such as other people present in the social setting. Finally, in the absence of clove-odor mask most participants could still not detect AS at the concentration used in the study. Even at a much higher concentration than the one used in the experiment only 20% of the participants could detect AS. Participants better able to smell the AS rated the solution as less pleasant. Overall, these experiments indicate that the passive, subliminal presentation of AS drew attention to emotional facial expression and emotional words. AS modulates emotional processing by accentuating the impact of emotional information, altering how people respond to their surroundings. This occurs without modulating attention specifically to social information and does not affect other psychological processes.

AS has also been shown to reduce nervousness, tension, and other negative feeling states in women exposed to the steroid (Grosser B. I., Monti-Bloch, Jennings-White, & Berliner, 2000). Grosser et al. administered either AS or a control substance directly on the VNO via mini-probe in a double-blind study. After completing a psychometric inventory and taking 10 minutes of baseline electrophysiological measurements, a 1-second vapor pulse containing AS or the control was delivered to the subjects' VNO. After 25 minutes participants completed the same inventory and subjects' electrophysiology was again measured. Results indicated administration of the AS reduced overall negativity, negative character, and negative affect according to participants self-reports. In addition administration of AS led to significant decreases in respiration, cardiac frequency, a lowering of galvanic skin response, and an increase in

alpha cortical activity and body temperature, all physiological indicators of reduced tension.

These findings demonstrate how odorants have an impact on people's impressions of themselves, impressions of others, psychological state, and mood. Frequently the odors are presented at indiscernible levels and the various cortical areas, including emotionally-relevant regions, process them at unconscious levels. These results are consistent with a theory by Zajonc (1980) in which he states that very low-level stimuli can impact humans' affect for both positive and negative outcomes, without cognitive or analytical input/processing. These stimuli frequently pass by without evoking conscious awareness. In other words humans become happy or fearful, have no understanding why, and are unable to detect the stimulus responsible.

Impact of Odor on Human Sexual Behavior

Chemicals hypothesized to be pheromones have been shown to modulate motivation and behavior. Spencer et al. (2004) examined the effects of breastfeeding compounds on the sexual motivation of other women. The authors hypothesized that these compounds would increase sexual desire in other women. In terms of evolutionary adaptation, synchronization of pregnancy has been shown to increase survival rates in offspring. The authors speculated that the presence of breastfeeding women may serve as an indication that the environment contains the resources necessary for successful pregnancy and birth, such as plentiful food. In this experiment axillary and breast secretions were collected on pads from lactating women who were breastfeeding their infants. Control pads were doused in a carrier solution (potassium phosphate) which was

similar in pH and concentration to female breast milk and sweat. The recipient women were studied for baseline sexual motivation and activity while being exposed to control pads. After the initial baseline measures were collected half of the women placed control pads under their noses while half placed the two breastfeeding pads under their noses: one with axillary scent and one with breastfeeding secretions. The participants did this every day for three months and were then assessed on sexual motivation and sexual activity again. Women exposed to the experimental pads reported a significant increase in sexual desire as compared to the control group. In addition, this effect increased with time in contrast with the control group which had a non-significant decrease in sexual desire. The experimental group also had a significantly higher level of sexual fantasies in contrast to the control group. These data support the hypothesis that human olfactory secretions alter human motivation and behavior.

AS has been found to allocate attention toward emotional information, impact interpersonal relationships, and convey socioemotional meanings, including sexual meaning to participants exposed to it (Hummer & McClintock, 2009; Pierce, Cohen, & Ulrich, 2004; Zhou & Chen, 2008). Zhou and Chen (2008) recently examined how heterosexual female participants' brains functionally process the human sexual sweat of male donors. Sweat was collected from 20 heterosexual men who refrained from using scented products throughout the experiment. They kept a rayon/polyester pad in each armpit while watching 20 minute long videos of sexual intercourse between heterosexual couples (experimental) and educational documentaries (neutral). New pads were used for each segment. The female participants underwent fMRI scans for while being presented with 4 scent conditions for 12 seconds each: the pooled sweat of three donors during the

experimental (sexual) condition, pooled sweat from the same males during the neutral condition, the putative sex pheromone (PSP), and phenyl ethyl alcohol (PEA), which was used as a nonsocial control smell. Each scent was presented to the female participants for 12 seconds while undergoing fMRI scans. After each scan the women rated the pleasantness of the odor. Results demonstrated that the right orbitofrontal cortex, the right fusiform gyrus (Talairach 35, -51, -7), and the right hypothalamus significantly responded to the sexual sweat as compared with all other conditions. These areas were not differentiated among the control, neutral sweat, and the PSP. The lack of effect in PSP and neutral sweat indicate that the results are not caused by autonomic arousal. The areas implicated, with the exception of the hypothalamus, have not been implicated in sexual motivation and behavior. This lead the authors to surmise that the information from natural human sexual sweat was encoded more holistically in the brain as opposed to encoded specifically for its sexual quality.

Pierce, Cohen, and Ulrich (2004) examined the relationship between individual differences in olfactory sensitivity and participants' self-report of the emotional impact of odors. The study utilized AS and amyl acetate, a synthetic odor generally rated as pleasant. Typically when people are exposed to AS approximately 15% report it as a pleasant scent (musky/sandalwood), 23% report it as intensely foul (urinous/sweaty), and some people report they cannot smell it. Participants completed the Affective Impact of Odor Scale (AIO) and were assessed for responsiveness to the two odors. Results indicated that people who were more highly sensitive to AS associated it with more negative smell and were more likely to describe odors as having a negative effect on interpersonal relationships. "Participants sensitive to AS had significantly higher scores

on the Negative Smells Scale than did nonsmellers, indicating that those participants who were sensitive to AS more frequently used smells as a means of rejecting people in interpersonal contexts" (Pierce, Cohen, & Ulrich, 2004, p. 16).

An individual's scent is based in part on their genetic code, and recent research indicates that women are able to detect minute genetic differences in males based on their scent and make preferential selection based on this information (Jacob, McClintock, Zelano, & Ober, 2002). Research has indicated specific portions of the vertebrate genetic code as contributing to individual odor production. One genomic region responsible is known as the major histocompatibility complex or MHC. MHC is a large gene family found in most vertebrates and it codes for a set of molecules and proteins that affect the immune system and autoimmunity. In humans MHC is known as the human leukocyte antigen (HLA). In the literature HLA is often used to refer to the protein molecules which are produced and MCH for the region of the genome that encodes for the molecules, which is how they will be referred to in this paper. HLA proteins are found within cell bodies in humans and alert the immune system if foreign material is present inside of a cell. HLA does this by producing a peptide which binds with specific forms of T cells or natural killer cells which in turn activate an immune response. Due to the wide range of pathogens they must identify, HLA molecules must be able to produce a wide array of peptides. Thus there are several MHC genes, these genes are polymorphic with numerous allels, and they are codominantly expressed. This means that it is possible to produce millions of unique combinations of genotypes. Despite this huge range of differences research indicates that women can detect differences in MHC genes via scent up to a shift in one HLA allele (Jacob, McClintock, Zelano, & Ober, 2002).

In their study Jacob et al. selected females from a relatively isolated community and recorded each woman's MHC sequence as inherited from both her father and her mother (2002). The participants were 49 women who had never been pregnant or married. The authors then selected 6 donor males of a diverse ethnicity who carried alleles that were both foreign to the women and some that were shared with the women. The researchers focused on five MHC loci and at each locus there was a possibility of up to 2 allele matches between the donors and smellers for a maximum of 10 matches. The sample had a median of 2 allele matches (with a range of 0-7 matches) between the men and women. The men were asked to wear the same t-shirt for two consecutive nights. The women, who were not aware of the source of the odors, were asked to rate the t-shirts on four characteristics: familiarity, intensity, pleasantness, and spiciness. The women were then asked if they had to smell an odor all the time which they would choose and which they would not choose.

Results indicated that no one man was preferred most or least by the women, but that the preferences were specifically correlated to each woman's genetic makeup in relation to each donor's genetic makeup (Jacob, McClintock, Zelano, & Ober, 2002). Women showed preference for odor that came from a donor who had significantly more MHC matches with herself than the odor of donors who were least preferred. Woman's most preferred males were within 2.3 .2 allele matches of her own MHC makeup while her least preferred males were within 1.5 .2 allele matches of her own MHC makeup. This indicates that women were able to preferentially discriminate among donors who were, on average, within 1 allele of each other. Further the matches were found to correlate to the women's paternally inherited allels and were not correlated to the

women's maternally inherited allels. The authors found a linear relationship between the number of allels a donor shared with the woman's father and his ranking on the preference scale.

The authors then attempted to clarify the nature of the relationship between a woman's genetic makeup and her preference. It was suggested that perhaps a woman's exposure to her father (postnatal) might influence her preference of scents rather than her own genetic makeup. To test this idea authors examined allels present in the participant's fathers but that were not genetically inherited by the women and compared these allels to the donors. There was no significant relationship, indicating that only a woman's inherited allels contributed to her preference.

Thus, the study demonstrates women's ability to detect minimal genetic differences within millions of potential variations of genes based on body odor alone. This detection occurs despite the vast array of variability on other environmental odors which might alter or mask the scents correlated to the MHC allels. In addition, the authors note that they did not screen for menstruation cycles during participant selection, which is known to alter olfactory perception.

Several studies have demonstrated women's ability to perceive MHC type based on scent alone, but there have been discordant findings regarding if women seek men more similar to themselves or more different from themselves (Havlicek & Roberts, 2009). Havlicek and Roberts published a review on MHC-correlated mate choice in humans and suggested the possibility that these results demonstrate elimination of the extremes; that they point toward women achieving intermediate genetic variability for their potential offspring, which would be highly desirable. Many studies emphasize the

need for humans to avoid incestuous reproduction because inbreeding can lead to non-adaptive recessive traits. At the same time it might be beneficial to seek a partner with a somewhat similar genetic makeup to maintain those adaptations that are advantageous for the local environment. Together these findings demonstrate how olfactory cues impact sexual behavior, motivation, and preferences in partners.

Odor Production and Preference Linked to Human Characteristics

The composition of human sweat includes steroids, acids, and secretions from the eccrine, sebaceous, and apocrine glands which function in response to emotion (Zhou & Chen, 2008). Individual body odor is derived from the body's secretions and excretion (Liddell, 1976). Thus how a human smells is a function of their sweat composition, which is composed of various chemical compounds which are in turn subject to human genetics, steroid levels, emotion, and their personality characteristics. Liddell reviews a list of human disorders, including certain metabolic issues and enzyme deficiencies, which produce a distinctive body odor. He includes a description of these odors in his article suggesting that medical professionals should become familiar with the scents associated with these disorders and use body odor as a method of determining diagnoses in patients. As an example, trimethylaminuria is a genetic disorder in which people lack the appropriate enzymes to break down trimethylamine into odorless byproducts (Al-Waiz, Ayesh, Mitchell, Idle, & Smith, 1987). People with this disorder produce an odor resembling the smell of rotting fish (Al-Waiz, Ayesh, Mitchell, Idle, & Smith, 1987; Leopold, Preti, Mozell, Youngentob, & Wright, 1990). The sweat produced by people with schizophrenia can be distinguished from the sweat of controls by scent (Liddell,

1976). It was discovered that people diagnosed with schizophrenia excrete trans-3-methyl-2 hexonic acid in their sweat, producing a pungent body odor. Thus genetic and psychological disorders are associated with altered human body odor.

Evidence demonstrates that sweat also is related to and conveys the affect of the sweat donor (Archer, 2006). Archer's meta analysis of testosterone research indicates that higher levels of testosterone in humans are associated with winning competitions, being a tough leader, and situations involving sexual stimuli. Levels of steroids in the body, particularly testosterone, are correlated to situational variables, such as competition, and also personality variables, such as aggression among male humans. Interestingly, testosterone concentrations were slightly negatively correlated with fighting among boys. Dihydroepiandrosterone sulfate, a steroid related to testosterone, was found to be much higher among conduct disordered boys and associated with high levels of aggression and delinquency. Similarly, high rates of physical aggression were correlated to lower rates of testosterone among teenage boys (Schaal, Tremblay, Soussignan, & Susman, 1996). Testosterone in these teenage males was linked perceived social dominance as rated by peers unfamiliar with the target. A lower level of testosterone was correlated to boys who were rated as more unpopular by their peers and were failing in school. Levels of cortisol in the body have also been shown to correlate to early childhood environmental conditions (Gunnar, Morrison, Chisholm, & Schuder, 2001).

Havlicek, Roberts, and Flegr (2005) found that women in the fertile phase of their menstrual cycle prefer the odor of socially dominant males over the odor of men who were rated as less dominant. The women rated dominant males' odor as more sexy, but there was no correlation between dominance and perceived odor masculinity.

Interestingly, the link between males' body odor sexiness and psychological dominance was found among women who identified themselves as in a relationship and not among the single women. This study demonstrates that this personality characteristic, dominance, is linked to human male's individual body odor. It demonstrates that women show discrimination for various levels of social dominance via smelling male body odor, and also demonstrate preference for the odor of males who were rated as more socially dominant.

Jarboe (2004) proposed the possibility that the body odor of abusive males is distinguishable from non-abusive males, and that this might contribute to how abused women end up in abusive situations. Research indicates that women who have experienced childhood sexual abuse (CSA) are at a high risk for revictimization later in life (Carrey, Butter, Persinger, & Bialik, 1995; Gidycz, Orchowski, & Turchik, 2007). The association between CSA and revictimization has spurred many theories as to why CSA individuals are susceptible to further revictimization. Gobin and Freyd (2009) suggested that revictimization is linked to an inability of CSA individuals to protect themselves or inability to identify specific intimate partner betrayals. Jarboe (2004) had women who were classified as CSA and controls with no history of abuse smell four pairs of t-shirts. The women responded to the question "rate which scent is more attractive" by choosing one t-shirt from each pair. The pairs contained one control t-shirt from a non-abusive male and one from an abusive male (sexually or physically). Results indicated a significant majority of all women preferred the t-shirts belonging to the non-abusive males. More specifically, although they did overall prefer the non-abusive man's t-shirt, CSA women picked the sexually abusive male's t-shirts significantly more

frequently than the control women. Jarboe hypothesized that CSA women were less adept at avoiding sexually abusive male based on body odor than women without a history of abuse.

These findings indicate medical and psychological disorders, personality characterisitcs, and situational or behavioral experiences alter human body odor. And, these variations are detectible by other human beings and alter their perceptions of and attraction to the stimulus participant.

Effect of Odor on Learning

Memory for initial odor association is very primitive and research suggests it is resistant to decay and later interference (Lawless & Cain, 1975; Lawless & Engen, 1977) especially if the association is made during and emotionally arousing circumstance (Engen & Ross, 1973). Thus it is important to understand how odorants function in learning, especially given the evidence that much of olfactory processing occurs unconsciously.

Kirk-Smith, Van Toller, and Dodd (1983) did a study on potential unconscious odor conditioning. Subjects were asked to attend two separate training sessions several days apart. During session one, subjects were given a stressful task to complete within a restricted amount of time. To increase levels of stress subjects were told that their times were below average and if they completed that task incorrectly they were asked to correct it. The time it took to complete the exercise and whether or not it was correct was recorded. For the experimental group the instruction sheets were infused with the odor trimethylundecylenic aldehyde (TUA) and therefore present during the stressor. The

instruction sheets were unscented in the control group. Pilot studies indicated that subjects were unaware of TUA in the room unless their attention was specifically drawn to it.

In the second session participants completed a mood rating scale then they entered a second room where the TUA was present (Kirk-Smith, Van Toller, & Dodd, 1983). Here they were asked to judge the photographs of 4 females and 4 males on a 9-point bipolar scale indicating where each photographed person lay on a set of characteristics. These characteristics included dimensions such as aggressive/unaggressive and disagreeable/agreeable. Subjects were then asked to complete a second mood survey. At the completion of the survey all subjects were asked several questions. They were asked if they observed anything unusual about the conditions of the experiment, if they had any ideas what the experiment was actually about, and if they noticed any similarities between the first and second session. Finally participants were presented with a strip impregnated with TUA and asked where they had smelled the odor before. No subjects indicated they had made an association between the two sessions. Two of the male subjects indicated that they had smelled the TUA before in the photograph judging room, and two women (one from each condition) indicated they had smelled it before, but they did not know where.

Initial analyses indicated that women made more mistakes and were slower at completing the task during session 1 (Kirk-Smith, Van Toller, & Dodd, 1983). The authors inferred from this that women had increased stress during the task and therefore should have a more strongly conditioned response to the odor than men. An analysis of the results demonstrated that women in the odor-present group showed increased anxiety

on the mood survey in the presence of TUA. They also rated the photographs of people with higher anxiety scores. Women in the odor-present group and men in the odor-free group both rated photos as more hostile, though the reason for this was unclear. The authors concluded from this study that an unfamiliar odor paired with stress can later elicit a mood change and alter people's perceptions or attitudes to others. In addition, this process can occur without conscious awareness.

The results of this study were later criticized for their methodology and statistical analyses (Black & Smith, 1994). Black and Smith noted that Kirk-Smith et al. did not adequately demonstrate that the task in phase one of the experiment induced anxiety in the participants. There were no control groups that did not participate in an anxiety-free initial session, for example. Thus it is not possible to establish that conditioning is occurring. Second, results section indicates that the odor-present female group showed increased anxiety but the article does not clarify with whom this group is being compared. Finally, Black and Smith note that the ANOVA performed is a one-way ANOVA, which is inappropriate due to the fact that the experiment included two variables (gender and odor).

Zucco et al. (2009) responded to Black and Smith's (1994) criticisms of Kirk-Smith, Van Toller, and Dodd (1983) via an expanded, more methodologically sound study which demonstrated classical conditioning occurs in humans when pairing olfactory cues with stressful events. During the first session, as in Kirk-Smith et al.'s experiment, participants performed an executive task with a time-constraint that was intended to induce stress (Zucco, Paolini, & Schaal, 2009). While they were working, they were exposed to a faint odor. Session two was run 4 days later and consisted of re-

exposing the participants to the previous odor while they rated their mood and judged the emotional value of eight photographs of people. There were four experimental groups. In the first group the participants were exposed to stress and the odor in both session 1 and 2. In the second group the participants were exposed to the stress condition in the absence of odor at both sessions. The third group received stress-induction in the presence of the odor at session 1, but did not receive the odor in session 2. The fourth group underwent stress-induction but did not experience the odor in session 1 or in session 2. The results indicated that group one, which was exposed to stress combined with odor during session 1 and re-exposed to the odor during session 2, assessed their mood as significantly more negative and less positive in session 2 than the three control groups, who gave similar assessment scores. The post-experimental interview revealed the conditioning effect occurred outside of awareness. Thus the study reaffirmed evidence that people can form conditioned emotional reactions to olfactory stimuli, even when it is presented below the level of awareness. This study, however, failed to demonstrate a significant difference among groups in their judgment of the pictures of people.

Wrzeniewski, McCauley and Rozin (1999) examined people's sensitivity to odors and how that correlated to the affective importance of odors. Participants completed the Affective Impact of Odor (AIO) scale which asks about the impact of good or bad smells in determining if a subject likes novel places, foods, health products, or cosmetics. People who produced high scores on the AIO demonstrated higher associations between scent and memory, scent and emotional evaluations, and judgments of the valence of scent. It was also noted that they judged the valence of scents based on their respective association with liked or disliked persons.

In an interesting aversion conditioning case study, a pedophile was shown pictures of male and female children and audio tapes depicting violent interactions between an adult and a child (Earls & Castonguay, 1989). The participant was given a jar of ammonia crystals and was instructed to inhale deeply when he began feeling aroused until his arousal decreased. His penile responses (erection as measured by penile strain-gauge) to the stimuli gradually decreased over 4 weeks to below 20%. These remained at low levels at the one-year follow up. This final study introduces an interesting concept into olfactory-based conditioning. The researchers in this case intentionally paired an aversive odorant with the subject's autonomic response to the unconditioned stimulus and were thereby able to alter his autonomic response. These results remained effective even at the one-year follow up, indicating a long-term repression of unconscious, automatic responding via olfactory conditioning.

CHAPTER 5

CONCLUSIONS

In summary it is apparent olfaction impacts a wide array of human functioning. There are parallels between humans' and animals' responses to pheromones. Humans respond physiologically to odors. Olfaction is tied to learning, and memory for odor association is highly resistant to decay or modification, particularly if the association is made during an emotionally arousing circumstance. Odors can impact sexual motivation, sexual behavior, interpersonal relationships, judgments of others, and mate selection. Odor is indicated as a marker of individual identity among humans and can be used to distinguish gender in the absence of other sensory cues. Odor production is linked to an individual's genes and metabolic and enzymatic characteristics. It is linked to human personality, emotional, and environmental characteristics. Scent impacts affect, mood, autonomic response, and can attune people's focus toward emotional information. Odors can be utilized as a conditioned stimulus resulting in emotional, affective, and attitude changes in human subjects. In addition to all of this, most human reception and analysis of odors occurs unconsciously.

Implications

There are some interesting clinical implications to these studies. The first is that humans are engaging in olfactory processes constantly, evoking emotional reactions, and creating new, highly resistant, associations with odorants. These associations are more resistant to decay if they are created during emotionally arousing circumstances. It follows that incidents of trauma, which evoke strong, negative emotions, might be

associated with whatever olfactory cues are present in the environment. The decay of this association is slow, thus it is possible that years after a trauma a person will suddenly experience salient, negative emotions in relation to an imperceptible odorant they processed on an unconscious level. From a clinical perspective many people with trauma-based anxiety disorders experience sudden symptoms of anxiety and panic without discerning clear antecedents. This can potentially be interpreted by the individual as uncontrollable emotional lability, leaving a sense of powerlessness detrimental to therapeutic outcomes.

Humans have extreme olfactory sensitivity that is capable of detecting minute genetic differences in other people. In addition, it has been shown that people are able to diminish their thresholds for perceiving certain scents to the point where they become consciously aware of those scents when they are presented. It is possible that, like honey bees, humans can alter their behavioral, even autonomic or instinctive responses to olfactory stimuli. For clients triggered by olfactory cues they could perceive the antecedent to the onset of their negative emotions consciously. If they become triggered, they could actively sniff, increasing the chance that they will perceive and identify an odorant in the environment. They could then engage in biofeedback training and relaxation techniques to diminish their cognitive and physiological responses. Furthermore, this discrimination and sensitization training has been shown to occur rapidly, making it time effective and clinically practical.

If research is able to more precisely replicate the link between human behaviors, such as aggression/abuse, and body odor production, there are interesting theoretical possibilities. Could it be possible to train people to identify body odor that is associated

with aggression or abusive traits? Would this be a possible therapeutic route for people who have experienced childhood abuse and revictimization? Could they be trained to consciously identify this smell and condition a behavioral response of avoidance?

It might be possible to utilize a novel scent in therapy during meditation and/or relaxation exercises to condition autonomic responses of diminished heart rate, muscle tension, and blood pressure in the presence of the stimuli. This would allow for clients to carry scented items or lotion to diminish their anxiety outside of sessions. If a person begins experiencing anxiety or panic they could open their scented bottle, sniff the odor that was paired with a state of relaxation, and trigger a physiological reduction in anxiety.

The extreme precision of human olfactory perception is a fascinating area to explore, particularly when considering how human socialization places very little emphasis on awareness or utilization of olfactory senses. We have the capacity to distinguish minor genetic differences based on scent alone, yet we rarely acknowledge what scents we are processing at any given moment. Hypothetically humans could utilize scent as a means of studying genetic structure, diagnosing disease, and analyzing the personality characteristics of other people. Olfaction could be incorporated into forensic profiling and interviewing as eye movement, facial expression, and body movements are used to give an interviewer additional, unspoken information. It is possible that humans already make these types of olfactory analyses, but at an unconscious level. Simply fostering awareness into these processes could alter the method by which we interact with others, learn, and treat patients in a psychological setting.

These studies also raise some concerns about the use of scent. Recent technological innovation has produced televisions that have an olfaction port which will

produce different scents to be paired with television and commercials. This type of device could be utilized positively, such as within an educational context to offer multi-sensory transmission of information, or in a therapeutic process such as the ones mentioned above. It might prove wise to be cautious about utilizing this technology in some situations. For example, pairing horror movies with scent may create higher fear responses, but will it also contribute to a maladaptive rise in anxiety? Will people pair odors with negative emotional states which later might be triggered unconsciously? In addition, considering the strong link between olfaction and posttraumatic stress disorder, piping scent into homes could become a problematic trigger for some individuals. Individual genetic composition influences how people experience smells, thus the responses are as potentially diverse as the human genetic code.

These studies provide a basic foundation of information on olfaction in humans. They indicate that humans are much more highly macrosmatic than previously believed. Humans have demonstrated behavioral, physiological, cognitive, and affective responses to olfactory stimuli even when the stimuli were perceived unconsciously. Olfaction impacts human learning, interpersonal impressions, and sexual attraction and motivation. It is clear that olfaction is a powerful sense in humans and its impact on human functioning should be pursued further.

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