

The Interconnection of the Olfactory System and Autobiographical Memory and its Significance

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Abstract

When inhaling odor molecules, they bind to receptors in the olfactory tract, at the back of the nasal cavity, which subsequently send signals to various parts of the brain. These areas notably include the amygdala, which generates emotion, and the hippocampus, which stores and organizes short-term memories into long-term memories. These functions are intimately linked through a series of regional connectivities. On account of this, if a certain scent stimulus is related to an emotional event, the brain will connect that particular smell to its corresponding emotions and memories. Thus the question emerges: to what extent can odor cues elicit emotional memories or feelings of nostalgia? This paper will examine several aspects of odor memories including age distribution of memories, emotional experience, and physiological correlations between the olfactory system and the limbic system of the brain. The conclusion has been drawn that, especially compared to auditory and visual stimuli, the psychological effects are more sentimental and tend to originate from moments in early childhood rather than later in life. There is also a direct interaction between olfaction and the amygdala and hippocampus that is unique from other sensory systems, which may be due in part to evolutionary occurrences in the mammalian brain. Regarding the implications of these findings, a better comprehension of how the olfactory system functions is gained. In addition, the potential to utilize its distinctive characteristics to understand the role that loss of smell plays in memory loss disorders, notably dementia, and how these memories may be evoked with odor-related cues is a possible field of exploration. The unique attributes of olfaction offers insight into how the human body works together in a way to permanently link external experiences with internal processing centers.

Key words: Olfactory system, amygdala, hippocampus, autobiographical memories, limbic system, Proust effect, nostalgia

1. INTRODUCTION

Fundamentally, it has been understood that the olfactory system, which is related to scent, differs from other sensory systems, such as visual and auditory complexes, particularly regarding anatomical proximity in the brain. This proximity, which will be explored later in the paper, helps to convey the singularity of odor and memory relations, emphasizing the importance of understanding them. While people tend to focus on senses related to the visual or auditory systems, olfaction has distinctive characteristics in terms of its ability to elicit poignant memories from childhood. This phenomenon has been dubbed as the “Proust effect”⁵ in courtesy of early 20th century French author Marcel Proust who describes a unique experience



in his seven-volume work, *Remembrance of Things Past*.⁸ He recollects smelling a madeleine cake dipped in tea, which transported him to his childhood and various vivid memories of his aunt, her house, and her village.

The sentimentality related to odor cued memories may relate to the olfactory system's circuit level connections to the emotional processing centers of the brain, notably the amygdala and the hippocampus. Furthermore, a structure named the lateral entorhinal cortex has been found to be in a position to transmit signals directly from the olfactory tract to both the amygdala and hippocampus, potentially explaining the interconnectedness of the structures and its effect on humans.⁶

Studying the relationship between scent and memory is critical in animals as well to form a better understanding of its significance in all of nature. Olfactory learning is an essential part of an animal's life and can impact their reproductive success along with survival, as it can affect how the mother and offspring interact and accept each other.⁶ This conveys the idea that this interconnection is an essential component in nature and equally applies to both animals and humans.

Overall, a variety of previous studies and review articles will be examined to better ascertain the effect scent has on emotional memory and how this connection implies that olfaction plays a more significant role in the psychology of humans and even non-human animals than previously assumed. The following paper will summarize these findings and attempt to determine their broader implications, and finally, convey the prevalence of this relationship.

2. REGIONAL CONNECTIVITY

Inherently, the way scents are processed and stored in association with memories is distinctive and important to note when examining their relationship. It has been established that fragrance-associated memories are inclined to induce more emotionality compared to other sensory recollections.⁹ This is in major part due to the circuitry of the brain and the connections between the olfactory system and memory and emotion processing centers of the brain.

Furthermore, we can explore the way adolescents process scents in their childhood. Odors that are repetitive, strong, and new are notably susceptible to producing emotional odor-associations.⁹ This particularly occurs during childhood, because there is a higher proportion of olfactory experiences during childhood that are both meaningful and novel. Whether it is smelling something for the first time or learning to associate a scent with a positive moment, such as baking cookies with a parental figure, scents are inclined to create emotional memories during childhood. As such, the distinct characteristics of an odor including its familiarity or lack thereof, potency, and frequency can all contribute to how it is perceived and categorized by an individual.

Likewise, regarding the processing of information, semantic processing is how the brain assigns meaning to various triggers, particularly words, phrases, and sensory cues. Different memory retrieval strategies may impact the autobiographical event selected and its age distribution. Primarily, there are two types of memory retrieval: recognition and recall. Recognition refers to when a given stimulus causes an intricate search until the information is pulled from long term memory and a memory can be reconstructed. This tends to occur with verbal cues. Recall is automatic and immediately pulls an event from memory, and is associated with odor cues. Odors that were given with their labels were considered verbal cues, as participants used recognition to strategically retrieve the relevant information. Odors administered directly without labels might have caused more automatic activation of memories specific to sensory experiences. The feelings that tend to be associated with odor cues, such as a higher level of sentimentality and happiness, were lower when the labels were given, indicating the difference between verbal and odor cues regarding their psychological effects.⁵

Moreover, there has been a recent interest in the regional connectivity between the olfactory system and brain structures integral to emotional and memory processing, such as the amygdala and hippocampus. Specifically, the projections from the olfactory bulb to these regions are explored in particular studies and investigations. In “The Neurobiology of Olfaction”, Anne-Marie Mouly and Regina Sullivan concisely describe the regional connectivities of olfaction and the limbic system. Olfactory sensory neurons can be found in the olfactory epithelium, covering the back of the nasal cavity.⁶ The axons of the neurons, the part of the nerve cell where its impulses can be projected to other body cells, travel through the cribriform plate to the olfactory bulb in the first relay of olfactory input. The olfactory bulb output neurons transmit projections to the olfactory cortex, which includes the anterior olfactory nucleus, the olfactory tubercle, and the piriform. In mammals, the thalamus acts as a relay station for sensory information. However, olfactory pathways do not need to pass through the thalamus to reach cortical areas, including the orbitofrontal cortex.⁶ Between the first relay of sensory information, into the olfactory bulb, and the primary olfactory cortex, there is no thalamic relay. This differentiates olfactory pathways from other sensory systems. While the piriform cortex does send few projections to the mediodorsal thalamus, which eventually reaches the orbitofrontal cortex, it usually forms direct monosynaptic connections to the orbitofrontal cortex. This indicates that one variance in olfactory pathways from other sensory pathways is the lack of connection to the thalamus. As a result of it bypassing the thalamus, which processes sensory input from all senses except for smell, any olfactory information goes directly to the cortex. The raw, unprocessed information being what we receive in our cerebral cortex is an explanation for why scent has such a powerful influence on our emotions and memories.

Additionally, the output neurons have quick connections to brain structures involved in emotion and memory formation, namely the amygdala and hippocampus. The main olfactory bulb makes

monosynaptic connections with the nuclei of the corticomedial amygdaloid, which include the nucleus of the lateral olfactory tract, the cortical nucleus of the amygdala, and the periamygdaloid cortex. The strong projection to the cortical medial amygdaloid implies that the amygdaloid is an integral part of the olfactory system. In addition, the superficial nuclei, meaning they are closer to the surface of the brain, are important sources of the projections from the amygdala to the hypothalamus. Amygdaloid nuclei that are deeper, including the basolateral nuclear group, do not receive projections from the olfactory bulb, which is the first recipient of olfactory input. However, they do receive weak projections from the olfactory piriform cortex, which processes the olfactory information. The deeper nuclei additionally receive dense projections from the corticomedial nuclei within the amygdala. As such, any olfactory information received from the bulb has a direct access to the amygdala, a characteristic that distinguishes it from other sensory input.

Regarding the hippocampus, anatomical and electrophysiological studies demonstrate the connections between the olfactory bulb and piriform cortex to the lateral entorhinal cortex by direct projections through the lateral olfactory tract. The lateral entorhinal cortex can project to the hippocampus through the lateral perforant path, providing a pathway to it. It also sends monosynaptic projections to the amygdala. From the entorhinal cortex, it transmits information to the basolateral amygdala and the cortical nuclear complex. As such, the lateral entorhinal cortex can project input from the olfactory cortical areas to both the amygdala and hippocampus, and additionally send information back.⁶

Overall, from the information collected from previous review studies and articles, it can be ascertained that there does exist direct functional connectivities between the systems of olfactions to the limbic system structures involved in emotional behavior. These interconnections are distinct from other sensory processing, such as the pathways of verbal stimuli, indicating the unique position olfaction has in emotional memory formation in humans.

3. EVOLUTION OF THE OLFACTORY SYSTEM AND ITS SIGNIFICANCE IN ANIMALS

Furthermore, in terms of functional connectivity, the olfactory system is indicated to have a stronger link with the hippocampus compared to other sensory complexes and can explain its unique relationship with emotional memory. This connection may be explained by certain evolutionary phenomena. During the evolution of mammals, the primate neocortex expanded, which shifted the hippocampal networks away from primary sensory cortices and towards association cortices.¹⁰ This rerouting has since been reflected in research of the visual, auditory, and somatosensory systems in humans. The olfactory system, in contrast, has retained its structural positioning throughout evolution. Scientists used functional neuroimaging and intracranial electrophysiology to determine whether the olfactory cortex in humans was also rerouted and found that the primary olfactory cortex projected more strongly to the hippocampus

than other sensory systems.¹⁰ These results suggest that the location and connectivity of the olfactory cortex have been conserved throughout mammalian evolution.

These results are crucial for supporting the ongoing hypothesis that interactions between olfactory and hippocampal functional networks form odor memories. Odor memories tend to be more vivid and involve more experiences in childhood compared to other stimuli such as visual and auditory. They are also less inclined to be forgotten over an extended period of time. Olfactory inputs are potentially less processed than input from other senses, reaching the hippocampus in direct projections rather than indirect, an idea that has been previously examined in the prior sections.

Furthermore, scent memory is equally as integral in animal lives as it is in humans. In animals, memory for environmental odors is critical in regulating behaviors that are necessary for survival. Highly emotional olfactory learning typically occurs during the major life events of an animal.⁷ For instance, during the early postnatal period, when altricial pups are dependent on their mothers for maternal care and feeding, they learn the odor of their mother. This learning is especially rapid and potent. The pups then tend to prefer this learned odor, which brings them in contact with their mother. Additionally, in adulthood of animals, there are two types of particularly powerful ethological olfactory learning that have been distinguished. Similar to the pups learning the mother scents, the mother learns the odor of the newborn in the postpartum period. This allows her to accept her young and nurse them⁷ which is crucial in the development of the offspring and their ability to survive. The phenomenon of odor learning by the mothers has been observed in postpartum sheep and rats.

Various animals have a keen sense of smell, such as dogs, and this sense is a remarkable aspect of their lives and how they interact with each other. Despite the shifting of the neocortex not applying to dogs, they have around 250 million olfactory receptors, unlike humans who have around 5 million.² Dogs trained to respond to particular odors are able to detect them at concentrations 1,000-1,000,000 times lower than humans, explaining their nasal sensitivity and its intensity compared to people.¹ This dissimilarity provides a plausible explanation for their enhanced sense of smell and strong ability to relate scent with familiar people or situations despite the assumed lack of rerouting of its hippocampal networks. Another instance of olfactory learning in animal adulthood is mate recognition. Scent allows animals to recognize potential mates based on reproductive and health status, regulating reproductive behavior. Rapid olfactory learning is essential as it influences an animal's ability to reproduce and therefore survive. Therefore, through examination of animal behavior, the critical nature of odor memory can be realized as it is a fundamental aspect of their learned and developed behaviors.

Through an evolutionary perspective, it is unclear as to why exactly the olfactory system stayed in close functional contact with the hippocampus, while other sensory systems were rerouted.

More so, why this seemed to mainly occur with primates. However, evidence of this evolution is apparent in the behaviors of animals, especially their reliance on scent to survive and connect with each other. Odor memory provides the basis upon which living beings rely on to navigate the natural world.

4. INFLUENCE OF DIFFERENT ASPECTS OF SCENT MEMORY

Moreover, odor memory itself has several varying aspects that all contribute to its unique role in how humans categorize emotions and situations. Predominantly, these traits include the age distribution of scent-evoked recollections and their tendency to be more emotional, based on self-reporting⁸ compared to memories stimulated by visual or auditory cues.

A notable experiment was conducted with the leading question of “Can scents evoke nostalgia?” Participants were given twelve samples of scents and rated the extent to which each scent was familiar and their level of nostalgia.⁸ Those who experience higher levels of nostalgia described more scent-induced nostalgia, meaning scent has the ability to extract more potent nostalgic feelings. Two major observations were made from what the participants reported after smelling the scents: the age distribution of odor-cued memories tends to be from the earlier years of life, and these memories are higher in emotional value.

Age distribution refers to the general time period in which the memories originate from, as they are autobiographically relevant to the individual. Memories elicited by fragrance are observed to be more distant in time, usually from the first decade of life and peaking at ages 6-10.⁸ Regarding verbally-induced memories, two decades of research indicate that age distribution can be separated into three categories: childhood amnesia, the bump, and recency⁶. Childhood amnesia refers to the loss of memories from early childhood, and recency refers to memories within the last ten years of a person’s life. However, a significant number of verbally-elicited memories has appeared to be retrieved from the ages of 10-30, a phenomenon known as the “bump”. It is known as the “bump” due to the peak in memories from this age period. This is where verbal cues differ from odors, as recent studies have shown that older age participants experienced a bump from an earlier age, the first decade of life, for olfactorily-cued memories. The prevalence of these remembrances in the early stages of life provides reasoning for why they are particularly nostalgic, as nostalgia tends to be defined by sentimental feelings towards a person’s earlier moments.

Emotional experience can refer to the level of sentimentality felt by the individual when memories are cued by odors. Particularly, scent-evoked memories tend to be more emotional and vivid compared to other sensory-cued evocations. As previously mentioned, this occurrence, the Proust effect, describes the unique impact of odor-evoked memories and how they tend to be especially potent. The emotions elicited by these memories are additionally

more positive than other methods of evocation. These sensations can include enhanced self esteem, feelings of social connectedness, and deeper meaning in life.⁸

To explore the psychological effects of nostalgic smells, older patients at a long-term care facility discussed these odors. Those who reminisced over their odor memories described lower levels of state anxiety and depression, typically recalling memories of their family. Though actual scents were not used, the emotional effect of simply talking about certain nostalgic fragrances is noteworthy enough to indicate more powerful results if actual stimuli were utilized.

Primarily, an explanation for why odor-cued memories tend to be more sentimental than memories that are verbally-cued may be due to the close synapsing between the olfactory bulb and the hippocampus and prefrontal cortex. The hippocampus is a brain region involved in temporal processing of information and important for memory retrieval. The prefrontal cortex shares a similar role of recollection of autobiographical information. When an individual experiences a certain food or scent, the hippocampus is activated, clarifying the close relationship between odor and memory. Fragrance cues may activate the hippocampus and prefrontal regions during memory retrieval, which produces a more potent temporal autonoetic awareness.⁸ This refers to the mental ability to place oneself in the future or past.

Furthermore, the amygdala is a region corresponding to emotional memory and has an involvement in the formation of taste and scent memory. When odor cues are administered, there is stronger activation in the amygdala compared to auditory or visual cues. Because the amygdala acts as an emotional processing center, this regional connectivity explains the emotionality of odor memories. The exact processing of odors through regions such as the amygdala will be explored in the later section.

5. SPECULATION IN COGNITION AND PREVENTION OF COGNITIVE DECLINE

The significance of the correlation between scent and memory is in its implications in preventing cognitive decline. Degradation of scent memory or olfactory functions is usually an early indicator of Alzheimer's disease. While it is unknown if scent memory can fully be restored and therefore prevent neurodegenerative diseases, there is potential for the effects of cognitive decline to be mitigated or even reversed with odor-related cues. For instance, recent studies have shown that odor might be able to restore autobiographical memories in Alzheimer's disease.³ Although additional research must be implemented to explore the possibilities of olfactory stimuli, understanding its relationship with autobiographical memory provides a reasonable basis for further investigation.

6. CONCLUSION

Overall, it can be surmised that there is a direct connection between scent and memory, much of which is due to the physiological proximity of the olfactory structure to emotion and memory processing centers of the brain. We can contribute much of this proximity to evolution, which rerouted hippocampal networks away from other sensory cortices but not from the olfactory system. Due to this connectivity, odor-cued memories have an inclination to be more emotional and nostalgic. These memories usually originate from early childhood, as new and vivid experiences, a regularity in childhood, tend to create more sentimental remembrances. Scent memory is additionally important in animals, as it is necessary for reproductive success, survival, and the nurturing of a child from the mother.

Regarding current research efforts, there exists a plethora of limitations and constraints. For instance, the main parameter is the autobiographical memory of individuals and it cannot be measured through standard means. The primary source of data collection is subjective and qualitative and is unable to be quantified into concrete variables. Furthermore, there is difficulty in tracking the more complex physiological pathways between the olfactory system and the brain that aren't direct, including the projections from the olfactory region. In particular, this issue can be further explored through means such as functional Magnetic Resonance Imaging (fMRI), which allows us to view the brain and which regions are active during certain activities or responses to stimuli.⁴ Once we collect an increasing amount of data that supports the connectivity between the olfactory and limbic system, we can delve deeper into the mechanics behind it and administer tests that correspond to potential neural networks.

In a broader sense, the implications of this research can be a stronger understanding of olfaction in our emotional health, as well as how the loss of scent can affect memory degeneration. As more is understood about how the two factors influence each other, the specific causes of memory disorders and potential ways to evoke lost memories can be explored. Supplementary research can be done on how exactly odors are processed through the brain, and how this is distinct from other senses. While the regional connectivity between the olfactory and limbic systems has been examined, the extensive implications of this relationship has yet to be fully assessed. An additional question pertains to the lateral entorhinal cortex, and how its position to project information from the olfactory bulb and piriform cortex to the amygdala and hippocampus can be extensively studied. Its implications regarding the correlation of scent and emotional memory are significant. While the majority of studies primarily speculate about the effects of odor with limited experiments, more experiments have been done for verbal cues, something that may need to be changed if a deeper understanding is to be formed.

Through comprehensive research and experimentation, we can better recognize how every part of the limbic system and olfactory complex work together to improve the quality of life and immortalize every emotion we feel in our lifetime.

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