UPPSALA
UNIVERSITET

Digital Comprehensive Summaries of Uppsala Dissertations from the Faculty of Social Sciences 121

The alluring nature of episodic odor memory

Sensory and cognitive correlates across age and sex

CHRISTINA BLÅVARG

ACTA
UNIVERSITATIS
UPSALIENSIS
UPPSALA
2016

ISSN 1652-9030
ISBN 978-91-554-9415-5
urn:nbn:se:uu:diva-265010

Dissertation presented at Uppsala University to be publicly examined in Universitetshuset, sal IV, Biskopsgatan 3, Uppsala, Friday, 22 January 2016 at 13:15 for the degree of Doctor of Philosophy. The examination will be conducted in English. Faculty examiner: Professor Steven Nordin (Department of Psychology, Umeå University).

Abstract

Blåvarg, C. 2016. The alluring nature of episodic odor memory. – sensory and cognitive correlates across age and sex. *Digital Comprehensive Summaries of Uppsala Dissertations from the Faculty of Social Sciences* 121. 79 pp. Uppsala: Acta Universitatis Upsaliensis. ISBN 978-91-554-9415-5.

Episodic memory for olfactory information is still relatively uncharted. The overall purpose of this thesis is to investigate the sensory and cognitive causes of the well-established age-related decline in olfactory episodic odor memory and of the age-independent sex difference in olfactory episodic memory. The purpose of **Study I** was to investigate the causes of the sex difference in olfactory episodic memory. The results show that the female advantage in episodic recognition memory seems to be explained by women´s higher aptitude in odor identification for familiar odors. With this background, the purpose of **Study II** was to investigate the age-related decline in olfactory episodic memory, with a particular eye to the role of odor identification. When controlling for the sensory variables olfactory threshold and odor quality discrimination, and the cognitive factor mental speed, the age-related deterioration in odor identification was eliminated. This suggests that changes in basic sensory and cognitive abilities underlie the age-related impairment in odor identification. The purpose of **Study III** was to investigate the role of recollective experience and intention to memorize for age-related and sex-related differences in episodic odor memory. Younger adults reported more experiences of remembering, and the elderly adults more experiences of feeling of knowing. The participants benefited from intentionality at encoding when the odors were unfamiliar, but intentionality did not affect memory for the familiar odors. The purpose of **Study IV** was to investigate the role of subjectively perceived qualities of the encoded odors for episodic memory across age and sex. Odors perceived as unpleasant, intense, and irritable were more easily remembered throughout the adult life span. The oldest adults selectively recognized the odors they rated as highly irritable indicating compensatory use of trigeminal activation. Overall, the result suggests that episodic odor memory rely heavily on both sensory and cognitive abilities, but in a different manner depending on demographic factors. The age-related decline appears to be driven by a sensory flattening disabling adequate cognitive processing. The age-independent sex difference on the other hand, is mainly cognitively mediated and driven by cognitive factors such as the ability to verbalize olfactory information.

Keywords: Olfaction, Age, Sex, Episodic odor memory, Odor identification, Recollective experience, Hedonic, Healthy, Adults

Christina Blåvarg, Department of Psychology, Box 1225, Uppsala University, SE-75142 Uppsala, Sweden.

ISSN 1652-9030
ISBN 978-91-554-9415-5
urn:nbn:se:uu:diva-265010 (http://urn.kb.se/resolve?urn=urn:nbn:se:uu:diva-265010)

To Ingrid Karlsson

List of Papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals.

I Öberg, C., Larsson, M., & Bäckman, L. (2002). Differential sex effects in olfactory functioning: The role of verbal processing. *Journal of the International Neuropsychological Society*, 8, 691-698.

II Larsson, M., Öberg, C., & Bäckman, L. (2005). Odor identification in old age: Demographic, sensory and cognitive correlates. *Aging, Neuropsychology, and Cognition,* 12, 231-244.

III Larsson, M., Öberg, C., & Bäckman, L. (2006). Recollective experience in odor recognition: Influences of adult age and familiarity. *Psychological research,* 70, 68-75.

IV Larsson, M., Öberg-Blåvarg, C., & Jönsson, F. (2009). Bad odors stick better than good ones. Olfactory qualities and odor recognition. *Experimental Psychology,* 56(6), 375-380.

Contents

Abbreviations

ANOVA	Analysis of Variance
d’	Statistic sensitivity index (e.g., Elliot, 1964; Hochhaus, 1972)
G	Guess
K	Know
MANOVA	Multivariate analysis of Variance
MMSE	Mini Mental State Examination (Folstein, Folstein, & McHugh, 1975)
R	Remember
TMT-A	Trail Making Test: Part A (Reitan & Davidson, 1974)
TMT-B	Trail Making Test: Part B (Reitan & Davidson, 1974)
VAS	Visual Analog Scale

Introduction

We go about our daily lives understanding almost nothing about the neurobiological processing required for our sense of smell to function. That is, if we are not expert scientists on the matter. We give little thought to the machinery that makes this chemosensory experience possible, to the complex and intricate nervous system that interacts with and decodes these perceptual happenings that would otherwise leave us clueless of many marvelous things, as well as the sensory warning system on whose alertness we fundamentally depend.[1]

One of the things that help us navigate through life is our ability to recognize odors from previous encounters and grasp their nature and meaning. Although research on odor memory and olfactory functioning has increased considerably in the last decades, our knowledge is still scarce and incomplete. The main objective of this thesis is to investigate the sensory and cognitive causes of the well-established age-related decline in episodic odor memory and of the age-independent sex difference in olfactory memory. Through four studies, olfactory memory in the healthy adult human is investigated and the relations between olfactory functions with different sensory and cognitive load are examined. Moreover, the various roles of the ability to identify odors, of the recollective experience and of instructions to memorize in the encoding situation will be investigated. Finally, the effects of the individual perceptual experience of odors on episodic odor memory are explored in relation to the observed age-related and the sex-related differences.

[1] Homage to Steven Hawking - A Brief History of Time.

The Human Olfactory System

Of the human sensory systems the sense of smell is probably the least explored. Generally, the available knowledge about this system, its structure and functions is limited compared to other sensory systems such as hearing and vision (e.g., see Serby & Chobor, 1992, for a review). However, in the past decades, the interest in olfactory functioning and aspects of olfactory cognitive processing has increased (e.g., Richardson & Zucco, 1989; Schab, 1991; Zucco, Schaal, Olsson, & Croy, 2014). But olfaction is more than a scientifically described chemosensory system; it is also a vital part of our every day life. The ability to recognize odors and understand their significance is of great importance. In this section an overview of how olfaction and olfactory abilities influence our daily life will be given, followed by accounts of psychological aspects of olfaction and the neural basis of olfaction, of potential damages to the olfactory system, an finally, of assessments in olfaction.

Olfaction in everyday life

The olfactory sensory system follows us through every day life like a secret companion. Always there, but seldom articulated, it influences our perceptions of the surrounding world. For instance, our sense of smell is strongly correlated with feelings of love and care in the sense that smelling our newborn child will affect us strongly and also trigger our protective feelings towards the little softly scented and dependent person we are holding (Porter, Cernoch, & Balogh, 1985). There is also evidence that we are predisposed to recognize signals hidden within ”the body odor cocktail”, informing about kinship or suitable mates (Lundström, Boyle, Zatorre, & Jones-Gotman, 2009). The ability of odors to evoke immediate and strong emotions (see more below) is systematically used by the commercial industry to trigger memory and jump start positive emotions and temptation to buy (e.g., Dooley, 2011; Morrison, Gan, Dubelaar, & Oppewal, 2011). Today many big brands actively market their trademarks through aroma marketing (e.g., Abercrombie & Fitch, Disney, Hollister; Prolitec, 2015). Scenting oneself to make a better impression or just the right impression taps the same systematic function. However, the right scent for the occasion is highly context dependent (Fiore & Kim, 1997).

Olfaction between humans is not only used to recognize potential mates, trigger acts of caring or give professional impressions. It also functions as a signal of health, or the opposite of health. In the early days of medicine smell was an important variable in the diagnostic process (Olsson, Lundström, Kimbal, Gordon, et al., 2014), and also today some diseases are described as resulting in a characteristic body odor with time (Penn & Potts, 1998). Olsson et al., (2014) tested the human ability to detect firsthand activation of the innate immune system and found that we might detect decease early on by smell. However, as a standard today, olfaction in a clinical setting is not chiefly a matter of the smell of the patient, rather it is the patients olfactory functioning that is the focal point.

The psychology of olfaction

Detection

Being able to sense the presence of an odor is the most fundamental part of olfactory functioning. The ability to detect an odor is traditionally measured in terms of an olfactory threshold, the lowest concentration of an odor that is perceived by a person. The administration of an olfactory threshold task usually serves as the standard approach when clinically assessing olfactory functioning, often in connection with an identification task (Frank, Dulay, & Gesteland, 2003). Lötsch et al., (2008) concluded that combining testing of odor threshold with testing of other olfactory measures, such as odor identification, provides the most accurate answers when diagnosing loss of smell, but also that the threshold is the most valid measure of smell loss. A fast and commonly used method is the staircase or up-down procedure that concentrates the stimulus presentation near the threshold level and therefore limits the number of trials and also the possible risk for above threshold stimuli adaptation. This method of assessing olfactory threshold has proven to be both time efficient and reliable (Doty, 1992).

Olfactory thresholds have been measured and studied since the middle of the nineteenth century, (e.g., Cain, 1978; Cain & Gent, 1991). There is an abundance of published threshold data concerning thousands of different odorants and many different methods of assessment (e.g., Cain, Cometto-Muñiz, & de Wijk, 1992; Doty, 1992; Lötsch, Reichmann, & Hummel, 2008). For a thorough historical overview on early olfactory research, see Cain (1978). The motivations for these data collections vary (e.g., psychophysical curiosity, examining the presence of fragrance and flavoring effects, or possible presence of pollution). This diversity has led to a corpus of data that has yet little thematic uniformity. To further complicate the interpretations of these data, an individual's olfactory sensitivity varies from moment to moment depending on the chemical structure of the compound, which places specific demands on the method of assessment (Amoore, 1971; Doty, Gregor & Settle, 1986; Stevens & Cain, 1987; Stevens, Cain, & Burke, 1988). Sensitivity to water-soluble compounds has been found to be higher than to non-water soluble odorants, and also the length and size of the molecules is a factor behind differences in olfactory sensitivity (e.g., Cain, 1969; Cain & Gent, 1991). Sensitivity when smelling via the right or left nostril is found to vary from hour to hour, due to swelling in the nose, and on the airflow, determined by sniffing (e.g., Sobel, Khan, Saltman, Sullivan, & Gabrieli, 1999).

Discrimination

In order to understand the meaning of the variety of odors in everyday life, an ability to discriminate between them is of essence, both to discriminate odors in terms of their strength and their complexity or quality (i.e., odor intensity discrimination, odor quality discrimination). Odor intensity discrimination is typically assessed in the same manner as olfactory threshold, with comparison stimuli not being a blank but a supra-threshold stimulus. The aim of the test is to measure discrimination between different concentrations of the same stimuli and to find the smallest difference between concentrations that the participant can discriminate. The compound used needs to be easy to distribute in set concentrations and among the most commonly used are ethyl-phenyl-alcohol and n-butanol (e.g., Doty 1992). The basic structure of an odor quality assessment is to provide different odorants and ask the participant to decide whether they are the same or different. The number of stimuli and the number of trials may vary.

Due to a very influential study in 1927 by Crocker and Henderson, the number of discriminable odors have earlier been estimated to be around 10 000 (Bushdid, Magnasco, Vosshal, & Keller, 2014). However, a recent study claims that humans can discriminate between several more than a trillion different odors. This is based on the notion that most smells are mixtures of compounds; much like combinations of specific sounds can form chords, different odorous components form coherent odors. For instance, the smell of rose is a mixture of no less than 275 components. Odor discrimination ability is improved if the odors are familiar, and when the task is to distinguish an odor in a mixture of odors (Rabin, 1988). There are several studies showing that knowledge of a particular group of odors through label and profile training enhances the ability to discriminate between them (e.g., Rabin 1988; Stevenson, Mahmut, & Sundquist, 2007).

Cain, de Wijk, Nordin, and Nordin (2008) found that the odor discrimination ability varies independently of the olfactory sensitivity. Odor quality discrimination performance has a progressive decline with increasing age that lacks association with the absolute sensitivity, suggesting mainly independent processing of odor quality discrimination and intensity discrimination (Cain et al., 2008). An aspect that appears to be specific for olfactory quality discrimination is the right-nostril advantage. This asymmetry is interpreted to relate to increased activation in specialized areas for olfactory discrimination in the right hemisphere (Zatorre & Jones-Gotman, 1990).

Identification

The identification of an odor is a substantially more complex task than olfactory detection and odor discrimination tasks. In real life the identification of an odor is usually aided by contextual cues. In odor identity assessments these cues are removed through occlusion and removal of real-life contextual information. In the typical assessment the participant is asked to provide a name for each presented odor in a set (e.g., Doty, 1992; Doty, Shaman, & Dann, 1984b). Apart from sensing and discrimination of the odor, identification requires both generating and finding a verbal label in semantic memory, and a search for the best match (e.g., Cain, 1982; Corwin, 1992). If asked to assess one's own ability to verbally identify some common every-day odors, the expectations of the ability are generally high (Cain, 1982). However, without any contextual markers or visual stimuli an odor is surprisingly difficult to identify. It is common to express a rough estimate of what category the smell belongs to (e.g., fruit, edible; de Wijk, Schab, & Cain, 1995). In a free identification task with a set of familiar everyday odors, it is normal for an able layman to identify about 50 % of the odors accurately at best. About 10 % are incorrectly identified as being a related stimulus, and the other 40 % are completely misidentified (e.g., de Wijk, Schab, & Cain, 1995; Richardson & Zucco, 1989). But with semantic support, such as multiple choices there is a higher success rate. For instance, Kjelvik, Evensmoen, Brezova, and Håberg (2012) obtained a success rate of 85 % using multiple-choice assessment.

Not to be able to identify a scent perceived as well known is a recurring event and usually described as the "tip-of-the-nose" phenomenon (e.g., Jönsson & Olsson, 2003; Lawless & Engen 1977). This lack of ability to verbalize sensory experiences is unique to the olfactory system. It is suggestibly due to an inherited weakness of the link between our language and olfactory sensations (Guyton, 1991). It is also suggested that the reason behind the weak identification performance is predominantly due to a failure to know the odor (e.g., Jönsson, Tchekhova, Lönner, & Olsson, 2005; Larsson, Finkel, & Pedersen. 2000; Schab, 1991). The more expert someone is on an area of odors, the more precise the person is in identification of those odors and also, it seems, the more aware of odors altogether (Adams, Douc, Janssens, Vanrie, & Petermans, 2014; Arshamian, Willander, & Larsson, 2011). This is in line with research stating that olfactory exposure and training will enhance the overall olfactory ability (e.g., Cain & Stevens, 1989; Doty, 1989; Royet, Delon-Martin, & Plailly, 2013; Schriever, Lehman, Prange, & Hummel, 2014). Research also suggests that faster perceptual speed (also referred to as mental or cognitive speed) is related to higher odor identification performance (Finkel, Pedersen, & Larsson, 2001).

There is a possible impact of sensory abilities in odor identification. For example, older adults exhibit a lower sensitivity for odors (e.g., Cain & Gent, 1991; Dulay & Murphy, 2002), which may affect the identification of olfactory information (Murphy, Cain, Gilmore, & Skinner, 1991). The ability to discriminative odors is another essential sensory variable, implicating that misperception of the olfactory stimuli lies behind misidentification of the odor (Cain & Potts, 1996; de Wijk & Cain, 1994; Eskenazi, Cain, & Friend, 1986).

Demographic variables also interact with odor identification. There are well-established findings that odor identification ability decreases with increasing age, and that women perform better than men in odor identification tasks. Less is known regarding the relationship between level of education and identification proficiency. However, research on semantic memory functioning in general (e.g., knowledge) has indicated that higher educational level is associated with higher performance (e.g., Bäckman & Nilsson, 1996; Nyberg, Bäckman, Erngrund, Olofsson, & Nilsson, 1996a). The ability to identify odors also fluctuates within an individual, such that an individual can fail to identify an odor one day and yet succeed at it another. Once success occurred, it tends to reoccur for that specific odor (Cain et al., 1998).

The task of identifying an odor thus requires a high degree of awareness of the individual and includes, among other things, episodic, semantic, and working memory functions, in concordance with sensory components like olfactory sensitivity and discrimination ability (Larsson et al., 2000). Of great interest in relation to this thesis is the fact that odor identification has been found to play a fundamental role with regard to deficits in episodic odor recognition (Larsson & Bäckman, 1993; 1997).

Subjective experience

Generally, everyday contact with odors involves making some form of hedonic evaluation (Herz & Engen, 1996). In scientific research, assessing the subjective experience of odors typically includes rating by the participant of the presented odors based on different parameters (e.g., familiarity, intensity, pleasantness) on some sort of scale (e.g., ranging from 0-10 or 0-100; e.g., Alaoui-Ismaïli, Robin, Rada, Dittmar, & Vernet-Maury, 1997a; Alaoui-Ismaïli, Vernet-Maury, Dittmar, Delhomme, & Chanel, 1997b).

The hedonic tone is an important aspect of the olfactory experience and judgments of odor similarities have reported a strong pleasantness-unpleasantness dimension in olfactory perception (e.g., Berglund, Berglund, Engen, & Ekman, 1973). It appears that these hedonic responses, in general, are processed with a low level of cognitive involvement. The perceived hedonic tone varies from person to person depending on a multitude of reasons. It seems that the label given to an odor affects the perceived experience of that same odor. For instance, Herz and von Clef (2001) found that an odor (isobutyric acid), when labeled ”vomit” was scored as having a lower hedonic tone than when labeled ”parmesan cheese”. Also, beliefs (e.g., hazardous vs. healthy) about an odor will interact with the hedonic perception (Dalton 1996; Nordin, Claeson, Andersson, Sommar et al., 2013). Perceived odor quality is considered to be a highly individual experience (Lundström, Seven, Olsson, Schaal, & Hummel, 2006; Stevens & O'Conell, 1991). Some studies indicate that perceived hedonic tone is also culture-specific, and geographic variations in hedonic ratings have been found (Ferdenzi, Roberts, Schirmer, Delplanque, et al. 2012: Wysocki & Gilbert, 1989). But there is also a certain consensus found between cultures. Chrea, Valentin, Sulmont-Rossé, Mai and colleagues (2004) found that pleasantness and edibility was rated similarly among French, Vietnamese and American participants. Other research indicates similarities in negative evaluations of odors of decay, feces, and various body odors (e.g., Schleidt, Hold, & Attili, 1981). It has been shown repeatedly that judgments of subjective odor experiences interrelate. For instance, familiarity ratings and pleasantness ratings relate positively (e.g., Engen, 1988; Rabin & Cain, 1986; Distel, Ayabe-Kanamura, Martinez-Gómez, Schicker et al., 1999; Sulmont, Issanchou, & Köster, 2002), and positive relationship is also found between identification and pleasantness (Ayabe-Kanamura, Schicker, Laska, Hudson et al., 1998; Distel & Hudson, 2001; Djordevic, Jones-Gotman, De Sousa, & Chertkow, 2008; Rouby, Pouliot, & Bensafi 2009). In Study IV, the focus is on the correlation between subjective experience and subsequent episodic odor memory.

The neural basis of olfaction

This section provides a brief overview of the olfactory system and the event of smelling an odor, and of typical potential damages and malfunctions of the olfactory system.

The olfactory system, the physical event of smelling and olfactory brain activation

Perception of an odor typically begins with an inhalation or a sniff. Volatile molecules from different chemical compounds in the environment accompany the breathing air in through the nose and the nasal cavity. The upper back of the nasal cavity is lined with a soft and moist mucosa and a specialized olfactory neuroephitelium that interacts with the molecules and triggers a cascade of nerve impulses. The impulses travel along the olfactory nerves on their way through the holes in the cribriform plate on to the olfactory bulb of the brain. The processing of olfactory information is a speedy and unique process in the human and mammalian brain. Information about the olfactory stimuli is forwarded immediately after detection to the olfactory bulb and thereafter straight to the amygdala, without thalamic gating. The perceived quality of the signal forwarded seems to depend on both a large family of olfactory receptors, their combinatory activation, and spatial arrangement (Buck, 2000; Buck & Axel, 1991; Stucker, de Souza, Kenyon, Lian et al., 2009).

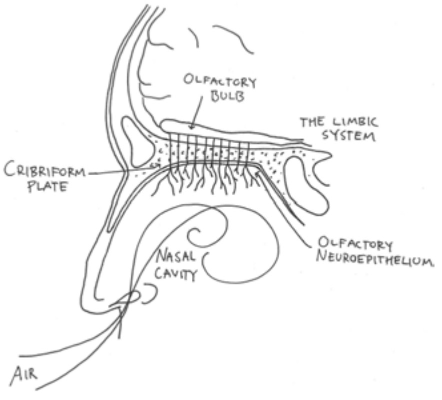

Figure 1. Overview of the Olfactory System[2]

The amygdala is involved in the processing and modulating of emotional arousal in relation to memory processing (Cahill & McGaugh, 1998). Consequently, that is why odors can be such fast gateways to emotions (Buck, 2000). The amygdala in turn, is directly connected to the hippocampus, being a part of the processing and redirecting of olfactory input. The hippocampus is also crucial in learning and memory processes, especially episodic memory, and the activation of memory functions is therefore almost instantaneous (e.g., Moscovitch, Nadel, Winocur, Gilboa, & Rosenbaum, 2006; Nadel, Samsonovich, Ryan, & Moscovitch, 2000).

Knowledge of the neuroanatomical correlates in relation to different olfactory functions is still incomplete. However, there are a number of studies trying to pinpoint activated areas. Savic, Gulyas, Larsson, and Roland (2000) showed, using Positron Emission Tomography (PET), that olfactory functions are hierarchically arranged depending on the complexity of the task and processed by both task-specific and more general networks. Olfactory tasks with higher cognitive complexity (i.e., odor quality discrimination, episodic odor memory) tax on larger areas and more innervate structures.

An additional aspect of sensing an odor is activation of the trigeminal nervous system (cranial nerve V; Bryant & Silver, 2000). The trigeminal

[2] Illustration: E. Blåvarg

part of an odor can be referred to as the sticky aspect of an odor experience, which is the nervous signal of pain. The olfactory and the trigeminal systems are closely related and volatile compounds can elicit both olfactory and trigeminal activity. Stuck, Frey, Freiburg, Hormann and colleagues (2006) state that the trigeminal system is more age-independent than the olfactory system. However, adults with anosmia (se below) tend to exhibit a decreased trigeminal activity (Frasnelli, Schuster, & Hummel, 2007).

Malfunctions of and damages to the olfactory system

There are numerous ways in which the olfactory system might malfunction. Anosmia is the inability to perceive odors and that is the most common olfactory pathology (Young, 2014). Anosmia can be categorized into two major kinds, absolute anosmia and specific anosmia (e.g., Amoore, 1977; Bremner, Mainland, Khan, and Sobel, 2003). The importance of olfactory functioning has been increasingly recognized as a significant symptom in neurodegenerative disorders like Alzheimer and Parkinson's disease (e.g., Hawkes, 2006; Lötsch et al., 2008; Postuma & Gagnon, 2010), and also as a marker of early cognitive decline (e.g., Olofsson, Rönnlund, Nordin, Nyberg et al., 2009). Olfactory ability (i.e., lowered olfactory discrimination ability, reduced brain activation) is also a marker for psychiatric disease (e.g., depression; Croy, Symmank, Schellong, Hummel et al., 2014). Traumatic incidents and surgical interventions can affect olfactory functioning, both temporarily and also permanently (e.g., Pade & Hummel, 2008; Shemshadi, Azimian, Onsosri, & Farahani, 2008; van Damme and Freihofer 1992). Unhealthy working environments might affect the ability to smell. For instance, exposure to a dusty environment (Ahman, Holmström, Cynkier, & Söderman, 1996), or to corrosive compounds is known to impair olfactory functioning (e.g., acetone, ammonia, chlorine, formaldehyde; for more see: Amoore, 1986; Doty, 1992). Finally, it is common knowledge that temporary loss of olfactory sensitivity due to common cold is to be expected. It is also scientifically validated (e.g., Deems, Doty, Settle, Moore-Gillon et al., 1991; Åkerlund, Bende, & Murphy, 1995). Almost all persons regain their olfactory functioning within a few weeks after a viral infection due to the regeneration of the olfactory epithelium (Seiden, 2004). This regeneration occurs at a rate of about 30 days (Køling, 1986), and also relates to recovery of the trigeminal sensitivity (Frasnelli et al., 2007).

Assessments in olfaction

When scientifically studying olfaction there are methodological, physiological, and technical considerations to take, irrespectively of which aspect of olfactory functioning that is being measured and studied. These considerations concern for instance the administration of the odors, the time and tempo of administration, and choice of odorous compounds.

One main aspect of assessing olfactory functioning is to find reliable means for distribution of the different olfactory stimuli to the test participant. A variety of different methods has been proposed. For instance, sniff bottles (Doty et al., 1986), squeeze bottles (Amoore & Ollman, 1983), microencapsules (e.g., Doty, Shaman, Applebaum, Giberson et al., 1984a), Sniffin' Sticks (e.g., Hummel, Sekinger, Wolf, Pauli, & Kobal, 1997), various glass rods, wooden sticks, or strips of paper dipped in the odorant (e.g., Semb, 1968; see also Doty, 1992) or different forms of so called olfactometers (e.g., Johnson & Sobel, 2007; Punter, 1983). Olfactometers deliver gas pulses to the nose with the temporal control necessary for different types of physiological registration techniques that measure the stimulus-induced activity of the autonomic and central nervous systems. The physical act of sniffing also plays an important role in administering the olfactory stimuli and in olfactory perception (e.g., LeMagnen, 1944; Sobel, Prabhakaran, Desmond, Glover et al., 1998). Laing (1986) found that the first sniff, or the participants natural multiple-sniffing technique is sufficient for both threshold and intensity measures, and also that a short sniff (0.42 sec) is sufficient for olfactory identification. Furthermore, it needs to be considered if the odorant is administered birhinally or monorhinally since it might affect the outcome (e.g., Zatorre & Jones-Gotman, 1990; Sobel et al., 1999). In addition, time and tempo are of importance when assessing olfactory functioning since adaptation is a potential consequence if the tempo is to high. To prevent potential effects of adaptation, an inter-stimulus interval between odorant stimuli is essential. A 30 s interval is the typically stipulated interval (e.g., Cain, 1969; Cain & Gent, 1991). Finally, the compounds used when assessing olfactory functioning are dependent on the aim of the investigation and what olfactory functioning that is targeted. Sometimes real life odorous items are used but very often various essences, natural and synthetic, are the preferred choice. These are easier to control and they have a longer shelf life, and stay the same for each test participant (e.g., Doty, 1992).

Summary of olfactory system

Olfactory functions play a vital, but often unarticulated, role in our daily life. Olfactory functioning includes the ability to sense the presence of an odor and to discriminate between odors, both in terms of varying intensity and different qualities. It can include verbalization of odors. Odors are perceived differently in terms of hedonic tone, which influences subsequent olfactory processing. Odors are frequently recognized via the episodic odor memory, something that will be elaborated on in a later section. The experience of an odor is a direct chemosensory interaction with molecules from the environment that immediately engages areas in the brain related to memory and emotion. Consequently, odors are very potent in evoking memories and emotional experiences. However, due to its unprotected morphology, the olfactory system is vulnerable to damage, for instance through various disease, head trauma and corrosive chemicals. Assessing olfactory functioning puts special demands on equipment and administration and the method varies depending on which olfactory functioning that is targeted.

Human Memory

In everyday life, human memory is all about what was decided on the last staff meeting, remembering to pack the children's sports wear, and what summers used to be like when you were younger. In science the concept of memory is considerably more elaborate and systematic. In this thesis statements are made concerning specific aspects of episodic memory. In order to put that in a scientific perspective a brief general presentation of memory systems and approaches will be provided, with specific focus on the subareas of episodic memory that are of relevance in this thesis.

Memory systems

The most common approach on human memory is to see it as composed of a number of distinct and dissociable systems and processes (Schacter & Tulving, 1994). These systems operate both interactively and as separate functional entities, each system serving somewhat different purposes and operating according to different principles (Tulving, 1984).

A basic and accepted model of memory is the distinction between short-term memory and long-term memory (see Figure 2). Short-term memory concerns temporary storage and manipulation of information. It is limited in time and space, and often referred to as being the same as, or partially the same as, working memory (e.g., Baddeley, 2003). Different parts of the memory system are viewed as declarative or non-declarative, where the declarative is being based on awareness and directed effort (Squire, 1992). Working memory is one of the declarative subsystems, since it concerns the active processing of information.

Long-term memory, on the other hand, involves various experiences and knowledge that are acquired over time and might be retained over time. It is considered to involve several different subsystems. These are thought of as being acquired phylogenetically and ontogenetically in order. The first two to evolve are considered to be the non-declarative systems, the perceptual representation system (PRS), and the procedural memory (Schacter, 1990). PRS is an implicit memory system that does not require explicit recollection but is important for recognizing and identifying perceptual experiences. This system is vigorously targeted by commercial brands, for instance by aroma marketing (see more under Olfaction in everyday life). The procedural memory (Gupta & Cohen, 2002) concerns a variety of motor skills, for example: plain walking, chewing gum, or the formal swirling procedure to catch the bouquet of a good wine at a wine sampling. These two parts of long term memory are followed by, firstly what sometimes is referred to as the library of the mind, the semantic memory. The semantic memory is a declarative memory primarily concerned with factual knowledge about the world like Stockholm is the capital of Sweden, winter is coming and this is a freshly printed thesis. Secondly, the episodic memory, also declarative, is considered to be the last part to evolve among the long-term memory subsystems, possibly the most complex and therefore also the most vulnerable in case of trauma or disease (Squire, 1992). Episodic memory enables us to remember personal experiences such as your experience of this morning's breakfast, your very first proper kiss, and your thoughts about *Das Parfüm*[3]. More is to be said about episodic memory in the next section.

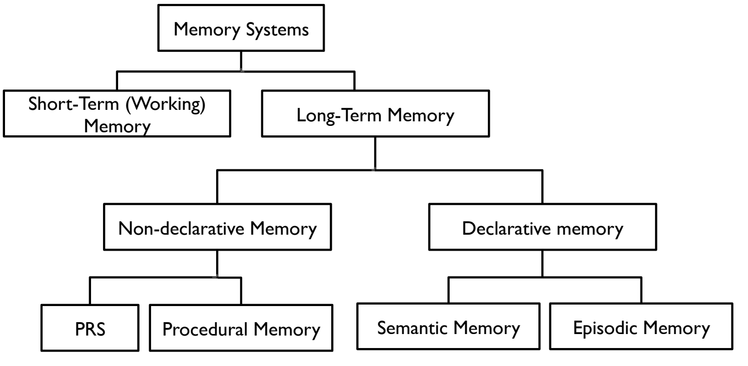

Figure 2. Taxonomy of the human memory

Episodic memory

Episodic memory, uniquely different and dissociated from other memory systems, is a neurocognitive system that makes remembering personal past experiences possible. Humans have the ability, when feeling like it or when triggered by sensory experience, to indulge in time travel. In our mind we can visit past experiences from our childhood or from last week. This cognitive trick puts time on its head and gives us the ability not only to ponder the past, but also to draw conclusions from it to estimate the possible future (Tulving, 2002; Wheeler, 2000).

[3] Süskind, Patrick (1985). *Das Parfüm*. Diogenes.

The concept of episodic memory

Episodic memory has been occurring in psychological writing since late 19th century, possibly starting with William James in 1890. James made the distinction that episodic memories should not only be concerned with past experience, they should be specifically personal experiences of the past. This statement yielded no significant attention. However, in the 1970ies Endel Tulving proposed a division of long-term memory into semantic and episodic memory, a suggestion that now is a generally accepted division (e.g., Wheeler, 2000). Episodic memory is different from other varieties of memory and can therefore be dissociated from them. For instance, the autonoetic aspect of episodic memory enables the ability of reliving a previous episode. Semantic memory in comparison is characterized by noetic (knowing) awareness and contains no feeling of reliving a previous episode. Episodic memory is easy to distinguish from motor learning and priming, but it is close to semantic memory that handles knowledge about the world (Wheeler, 2000), both being conscious and declarative varieties of memory guiding our behavior. They are, however, found to be experimentally dissociated in many ways (see, e.g., review by Buchner & Tulving, 1995).

Brain imaging has shown that different areas of the brain are involved when healthy humans retrieve information from semantic or episodic memory (e.g., Nyberg, Cabeza, & Tulving, 1996b). Episodic memory is also closely related to other higher order mental activities. Moscovitch (1995) emphasized that episodic memory also includes the conscious experience accompanying the specific episode, which means that episodic memory refers to memories of the experience of an event, and the conscious awareness is part of that experience.

Episodic memory in general is clearly the form of memory that is affected the most by aging processes. This was scientifically valid when the studies were executed (e.g., Hultch & Dixon, 1990; Larsson & Bäckman, 1997; Salthouse, 1991) and is still valid today (e.g., Lundervold, Wollschläger, & Wehling, 2014). There are findings of sex differences in episodic memory, especially if the item to remember is possible to verbalize (Herlitz, Nilsson, & Bäckman, 1997; Herlitz, Airaksinen, & Nordström, 1999; Lehrner, 1993) but evidence is inconclusive and other studies have not established sex differences in episodic memory (e.g., Persson, 2015).

Recollective experience

One aspect of episodic memory that was overlooked for a long time is the ”recollective experience” (Tulving, 2002). There are two major theoretical frameworks for explaining recollective experience. One theoretical framework relates to the theory of signal detection in that different recollective experiences are assumed to be the product of unidimensional memory processing of different strength (Tulving, 2002). In other words, the idea is that different recollective experiences are qualitatively the same in nature, but differ in strength. In assessments of recollective experience, correctly recognizing a target odor is scored as a hit, incorrectly recognizing a distractor odor as being a target is scored as a false alarm. To determine the overall outcome, a transformation of hits and false alarm rates into d'-scores as a measure of sensitivity, is often applied (e.g., Elliot, 1964; Hochhaus, 1972). The other theoretical framework is that recollective experiences are the result of two qualitatively different memory processes, two different states of conscious awareness of the past. In scientific work, these two states are referred to as ”remember” (R) and ”know” (K) experiences.

There are three major explanations concerning the remember-know approach. Tulving's (1983; 1985) memory system theories claims that R and K responses correlate to two different conscious states. One autonoetic state that involves self-recollection and corresponds to R responses, and noetic that involves semantic memory and corresponds to K responses. Rajaram (1993; Rajaram & Roedinger, 1996) has presented a fluency framework, where R depends on distinctiveness whereas K is affected by processing fluency. A third approach presented by Jacoby (1991) states that recognition memory has two components: one conceptual component based on meaningful elaborations (R responses) and one familiarity component, based on perceptual processing (K responses). To summarize, these three major explanations of remember-know disagree on both conceptual and theoretical levels, but they all support the idea that remembering and knowing reflect qualitatively different memory traces (Gardiner, Ramponi, & Richardson-Klavehn, 2002).

When the task is to also assess recollective experience, participants are typically asked to make R responses for odors that evoked some specific contextual recollection from the learning phase (e.g., an association, image, or some other more personal feature) and to make K responses when the target is associated with feelings of knowing, but with the absence of any specific contextual recollection of that item's previous presentation (Tulving, 1986). To prevent from bias forcing participants to indicate ‘‘know’’ when they are unsure as to their response and to reduce the effects of guessing on R and K responses, a ”guess” (G) response can be included as a response alternative. These procedures have been applied in earlier research (e.g., Mäntylä, 1997). It seems that it is the K responses that are purified if G is included as an alternative (Gardiner & Conway, 1999).

In a review by Gardiner and colleagues (2002) no support for the signal detection assumption was obtained. Lately, Wixted and Mickes (2010) have presented support for a new signal detection model in the form of a continuous dual-process model of remember/know judgments. The idea of a qualitatively difference in R and K responses has, however, very strong support (Gardiner at el., 2002). Evidence of different activation patterns as measured by event-related potentials supports this conclusion (Duzel, Yonelinas, Magun, Heinze, & Tulving, 1997), as do findings using functional magnetic resonance imaging (Eldrige, Knowlton, Furmanski, Bookheimer, & Engel, 2000). Likewise, various independent variables affect the amount of R and K responses differently. For example, R responses are negatively affected by longer retention intervals, divided attention, incidental learning and are sensitive to levels of processing, whereas K responses remains unaffected by these variables (e.g., Gardiner, 1988; Gardiner & Java, 1991; Gardiner & Parkin 1990; Mäntylä, 1993). Consequently, the idea that two states of awareness, remember and know, in recollective experience are qualitatively different has a strong support.

Summary of memory

In conclusion, episodic memory is an autonoetic memory function that enables us to store our experiences and to draw conclusions from them about the past, the present, and also the future. Episodic memory is different from other kinds of memory, a statement that today is validated through psychological and neuroimaging studies. It is a memory system clearly affected by age and also by sex, favoring women in episodic memory tasks tapping verbal abilities. Two different states of awareness have been recognized in recollective experiences. These states are referred to as remember and know. Their origins are debated but there is general consensus that they represent qualitatively different memory traces.

The Olfactory System and Memory

The area of research concerning olfaction and memory was for a long time neglected. In 1995 Psychlitt gave a mere 25 hits on the keywords: ODOR, RECOGNITION, MEMORY (Crowder & Schab, 1995). Today, twenty years later, this field of research has expanded, although remaining fairly exclusive since the same search in PsychInfo culminates in a mere 311 hits (on the 18th of October 2015). In this section an overview of memory research concerning olfactory information will be given. Especially episodic odor memory and assessment of episodic odor memory, and the methods included in this thesis will be addressed.

Olfaction and memory in general

In line with the fivefold classification system of human memory (e.g., Schacter & Tulving, 1994; also Figure 2) an effort to conceptualize the various expressions of olfactory memory in relation to the current memory systems framework has been made. Of particular interest in relation to the presented studies are olfactory functions that correlate to memory systems that depend on higher cognitive processing. Based on the past decades of research in olfaction, brain imaging, and interrelated areas, the following model was put forward by Larsson (2002; see Table 1).

Table 1. *Classification Scheme of Olfactory Functions and Corresponding Memory Systems (adapted after Larsson, 2002).*

Memory system	**Olfactory function**
Procedural memory	Conditioning; Aversions
Perceptual representations system	Perceptual priming
Semantic memory	Hedonics; Familiarity; Identification; Metamemory
Working memory	Discrimination
Episodic memory	Recognition memory

As previously stated, it is a well-established finding that odors have a strong and direct connection to emotional memories (e.g., Arshamian, Iannilli, Gerber, Willander, et al., 2013; Chu & Downes, 2002; Gheusi & Lledo, 2014; Herz, Eliassen, Beland, & Souza, 2004; Willander, 2007). Odors are powerful cues in trigging episodic memories (Savie, Royet, & Plailly, 2014). That smells have the ability to awaken long lost memories, sometimes referred to as *”The Proust phenomenon”*, can be regarded as common knowledge about olfaction. Chu and Downes (2002) took it to the test in their study on both emotional quality and quantity of information for memories awoken by verbal labels or odors. Participants related more vivid and detailed recollections by odor stimulation than by verbal labels. They also found that odor-cued autobiographical memories are in general older, that is from earlier in life, than those retrieved by verbal cues (see also Chu & Downes, 2002; Toffolo, Smeets, & van den Hout, 2012). Willander and Larsson (2006) found that these odor-evoked memories in addition carry a stronger feeling of being brought back in time as compared to verbal or visual cues. Odors can also be effective as retrieval cues for some more stressful memories (Wiemers, Sauvage, & Wolf, 2014). For instance, if a strong negative emotional experience has become associated with a particular odor, then that association can persist even over a longer period of time (Robin, Alaoui-Ismaïli, Dittmar, & Vernet-Maury, 1999). This is also sometimes generalized to an aversion to all forms of that odor (Engen, 1987).

Episodic odor memory

Earlier research on episodic odor memory suggested that it is different from episodic memory for verbal or visual information, but later research has proposed that episodic odor memory is governed by the same principles as episodic memory for other modalities (for a review see Larsson, 1997; 2002). The scientific assessment of the ability to recall odors can obviously not be made in the same fashion as the recall of other sensory modalities, for instance words or tunes. Participants can be asked to recall the names of odors they have encountered, but then focus is turned to verbalizations skills in relation to odors to be remembered, not to recall the actual odors themselves (Lyman & McDaniel, 1990). Therefore, most research on memory for odors has gravitated towards recognition memory. A typical odor recognition assessment is that the participant encodes a number of target odors, and after a decided retention interval they are presented with a set of odors comprising ”new” and ”old” odors. The task is to decide which of the odors are new and which were included in the previously encoded set of odors, the ”old” odors (e.g., Larsson & Bäckman, 1993).

When considering the fast and strong anatomical connection between brain structures processing olfactory stimuli, memory, and emotions, it is not surprising that odors appear to have a unique part to play in memory processes, particularly emotional memory processes. Memories for odors are found to be very long lasting in terms of emotional reactions (Engen, 1987). Olofsson, Bowman, Khatibi, and Gottfried (2012) investigated whether odor perception is guided by activations of recognition of unique odor qualities (i.e., memory) or valence evaluation (i.e., emotion). They found that memory-dependent object evaluation preceded valence evaluation. However, according to Yeshurun and Sobel (2010) the emotional reaction comes first due to poor language access in relation to odors. Odor pleasantness is put forward as the principal axis of odors perception, which is in line with basic ideas about olfaction and its importance for survival. Mankind, through reasoning and experience, has obviously experienced it like this already a long time ago: *"the varieties of smell have no name, ... but they are distinguished only as painful and pleasant"* (Plato, trans 2009, p.147; quote humbly stolen from Olofsson, Bowman, Khatibi, & Gottfried, 2012)[4].

Encoding of odors

The encoding of odors can entail many different systems and consequently be qualitatively different. The possible encoding could be a memory of the odor itself as an olfactory imagery, much like a visual image can be encoded by visual imagery. It could be that the participant smells an odor, identifies it as for example lemon, and generates a visual image of a lemon, which then is retained. The same odor is perceived again for recognition; it is identified again and generates an image matching the remembered image. In this case the smell itself is not recognized, but the encoded event is through the medium of visual imagery. A third option is that the odor presented is identified and encoded verbally and then at testing verbalized in the same way and a correct match is then achieved through verbalization (Crowder & Schab, 1995). Supporting the expanded encoding by using several modalities, Olsson, Lundgren, Soares, and Johansson (2009) found that identified odors exhibit more similarities with memory for words than did odors that were unidentified.

Episodic odor memory has proven to vary in relation to degree and type of elaboration during encoding (Larsson & Bäckman, 1993; Lyman & McDaniel, 1990; Nguyen, Ober, & Shenaut, 2012). Research suggests that episodic memory for verbal and visual information may be enhanced following intentional encoding, as compared with incidental encoding conditions (e.g., Kausler, 1994; Larsson, Nyberg, Bäckman, & Nilsson, 2003b). Lyman and McDaniel (1986) measured the effect of encoding procedure for odors and found that more elaborate encoding, such as providing short definitions or life episodes to remember the odors by, are more effective as encoding strategies than providing short labels or to give no instruction to elaborate on the odors. In contrast to these findings, intention to learn showed no reliable impact on subsequent recognition performance or on recollective experience

[4] In line with academic tradition, I am happy to get the opportunity to mention an "old greek" like Plato 428-348 B.C. at least once in my thesis.

of odors (see also: Larsson, Lövdén, & Nilsson, 2003a). Earlier research also suggests that semantic processing of information in a design with incidental encoding may in fact be as effective as intentional encoding (Craik & Lockhart, 1972).

Retrieval of odors

Memory for unfamiliar olfactory information is weaker than that for familiar odors. This is suggested to be related to contextual information at encoding as well as the modalities activated (Stevenson & Mahmut, 2013). But it is also suggested that unfamiliar odors are more difficult to remember due to their less stable representations than familiar odors. According to the Pattern-matching theory, this occurs because unfamiliar odors induce weak activations of many nodes in memory and thus is less stable as a memory code (Stevenson & Mahmut, 2013). Verbalization and other elaborations during encoding, see above, will also have an impact on the subsequent retrieval process (e.g., Crowder & Schab, 1995).

The subjective experience of an odor is of importance in relation to subsequent olfactory processing (Berglund et al., 1973). Research focusing on memory for verbal and visual information indicates better retention for arousing or emotional information than for neutral information, and that memory for negative information is more robust than for positive information. Evidently, enhanced memory for significant events has survival value in that negatively laden representations may drive better predictions regarding biologically important occurrences when re-encountering similar future events (e.g., Kensinger, 2007).

Recollective experience in episodic odor memory

As previously stated, recollective experience can be divided into two functionally independent states of awareness (e.g., Gardiner et al., 2002; Tulving, 1985; Yonelinas, 2002). This is typically captured in assessment of recollective experience by asking participants to rate their memory experience in terms of "remember" or "know" (i.e., R, K).

Previous research on recollective experience for olfactory information is scarce. Broman, Olsson, and Nordin (2001) measured remember and know experiences in a study concerning effects of left or right rhinal stimulation in young adults. No difference was obtained related to side of stimulation. Larsson and colleagues (2003a) investigated sex differences in recollective experience for olfactory and verbal information and they found that women produced more R responses than men but that both sexes produced equal levels of K responses. This was true for both modalities. When verbal ability was controlled for, the difference in produced R responses disappeared. More recently the importance of identification for an R experience has also been confirmed in a study on young adults (Olsson, Lundgren, Soares, & Johansson, 2009). They found that encoding activity (i.e., similarity judgments, edibility ratings) and retention interval (i.e., 15 min, one week) respectively relates to subsequent recollective experience.

Summary of olfaction and memory

Research on olfactory memory functions has expanded dramatically during the last decades. This has led to new insights. Episodic odor memory is now generally believed to follow the same principles as episodic memory for other modalities. However, some aspects seem to be unique for olfactory memory, for instance the ability to evoke strong emotions, detailed memories from long time ago, and that these emotional memories are long lasting. The encoding of odors is dependent on the context and the odors. The encoding also seems to depend heavily on whether the odors are identified and named or not. Odors are proposed to be more difficult to remember than information tapping other modalities. The more familiar and identified an odor is, the more likely it is to be recollected as a clear and contextually specified memory, a remember experience. If the odors are evoking a stronger subjective experience (e.g., pleasantness-unpleasantness) they also seem to be easier to recognize at a later stage. The subject of episodic odor memory in relation to age and sex will be analyzed in the following section.

General Cognitive Abilities, Aging, Sex, and Olfaction

When studying olfactory ability a variety of factors influence the outcome. Two major demographic factors behind interindividual variability are generally put forward: age and sex, and they are also the focal points in this thesis. Accounts of them will begin this section, followed by a section on cognitive abilities that have been established to be of specific relevance to understanding aging effects in olfactory functioning. Finally, I will discuss hormonal influences on olfactory functioning, and smoking and olfaction.

Olfactory functions in normal aging

The bulk of research concludes that olfactory sensitivity decreases with increased age (e.g., Doty & Kamath, 2014; Doty et al., 1984a; Wysocki & Gilbert, 1989; Larsson, Nilsson, Olofsson, & Nordin, 2004). In general the olfactory threshold seems stable from at least 10 years of age, staying at the same level through adulthood, with a decline starting around the age of 70 or a few years earlier.

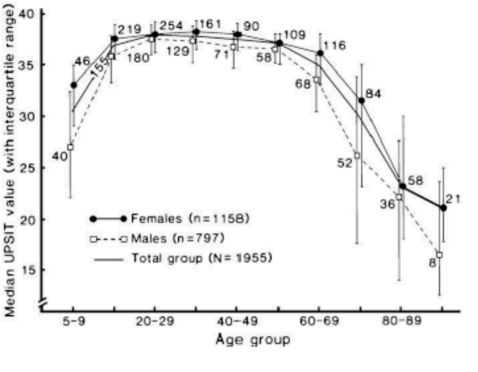

Figure 1. University of Pennsylvania Smell Identification Test (UPSIT) scores as a function of age and sex. Numbers by data point indicate sample sizes. From [Doty, R.L., Shaman, P., Applebaum, S.L., Giberson, R., Sikorski, L., & Rosenberg, L. (1984a). Smell identification ability: changes with age. *Science, 226,* 1441–1443.]. Reprinted with permission from AAAS.

That elderly adults yield thresholds two to tenfold above young adults is the typical finding in olfactory research (e.g., Cain & Stevens, 1989; Stevens, Cain, & Weinstein, 1987). However, Nordin, Almkvist, and Berglund (2012) investigated olfactory sensitivity in a group of specifically "successfully aged", 77 to 87 years of age, in order to establish if decline in old age is inevitable or if it might be due to factors secondary to aging. Their result suggests no significant decline when participants are classified as very healthy in relation to their age. Cain, de Wijk, Nordin, and Nordin (2008) found that odor quality discrimination varies independently of olfactory sensitivity. Odor quality discrimination also had a progressive decline with increasing age, that lacked association with the absolute sensitivity in the same participants, suggesting mainly independent processing of odor quality discrimination and intensity discrimination. It is a robust finding that odor identification ability decreases with increasing age (e.g., Doty & Kamath, 2014; Larsson et al., 2004; Wehling, Nordin, Espeseth, Reinvang, & Lundervold, 2010). For instance, a high level of performance is established before 20 years of age and it remains stable until a sharp deterioration from about age 60-70 years (e.g., Doty et al., 1984a; Wysocki & Gilbert, 1989). The observed decrease in naming ability with increased age is not found to be an accidental cohort effect, but a reflection of a real phenomenon in normal aging (Au, Joung, Nicholas, Obler et al., 1995; Wehling, Wollschlaeger, Nordin, & Lundervold, 2015). Few studies have targeted the subjective qualitative experience of odors in relation to young and old age. However, Stevens and Cain (1986) found that older people generally estimate odors as less intensive, which could be related to a sensory decline in olfactory sensitivity. Identification of unpleasant odors has shown more age invariance than identification of pleasant odors (Konstantinidis, Hummel, & Larsson, 2006).

Age-related deficiency in episodic odor recognition memory is well documented and it is suggested that this is due to cognitive rather than to sensory limitations (e.g., Larsson et al., 2000; Murphy et al., 1991). For instance, older people have more difficulty to verbally identify odors, particularly in free identification assessments. Training in identifying odors gives a better result in young people, but gives no improvement in the elderly. According to Schemper, Voss, and Cain (1981) this further suggests that the age-related decrease in episodic odor memory is cognitively mediated. Research also indicates that episodic memory for familiar olfactory information is largely mediated by semantic factors (e.g., Hedner, Larsson, Arnold, Zucco et al., 2010; Jehl, Royet, & Holley, 1997; Larsson, 1997; Lyman & McDaniel, 1990). Age-related impairments in odor recognition might consequently reflect age-related difficulties in identifying odors (Larsson & Bäckman, 1998). Lehrner, Laska, and Decke (1999) investigated odor naming and retention of olfactory information across the life span. Interestingly, they found that odors that were incorrectly named were recognized equally well across age groups. Correctly named odors showed a decrease in recognition memory across the age range examined.

Olfactory ability in women and in men

An overview of sex differences in olfactory functioning reveals an ambiguous picture. Present research suggests that women perform better than men in olfactory tasks (e.g., Cain, 1982; Fornazieri, dos Santos, Pinto Bezzera, Rezende Pinna et al., 2015; Lehrner, 1993). Over the years a number of studies indicating that women have a more sensitive sense of smell than men, as reflected in absolute threshold has been put forward (e.g., Deems & Doty, 1987; Doty, 1976; Koelega, 1994; LeMagnen 1952). However, there are also studies that report no sex differences in odor sensitivity (e.g., Amoore & Venstrom, 1966; Cain & Gent, 1991; Venstrom & Amoore, 1968) and recently one that established a higher sensitivity in men than in women (Olsson & Laska, 2010). One reason for the mixed evidence may be that the presence of sex differences in sensitivity varies according to the specific odor stimuli used in the assessment of the olfactory threshold (e.g., Koelega, 1994; Olsson & Laska, 2010). Little empirical work has examined the relationship between sex and odor discrimination abilities. This holds for both intensity and quality discrimination. However, research in which women and men have sought to recognize the odors of human hands or of t-shirts worn by themselves or others suggests a female advantage in quality discrimination (Schleidt et al., 1981; Wallace, 1977). A well-established finding in the olfactory literature is the female advantage in odor identification (e.g., Cain, Gent, Goodspeed, & Leonard, 1988; Doty et al., 1984a; Fornazieri, dos Santos, Bezerra, Pinna et al., 2015). This is true for both free identification measures (Cain, 1982), and for tasks where multiple-choice alternatives are available (Doty et al., 1984a; Wysocki & Gilbert, 1989). Longitudinal data on olfactory functions showed that women retain an intact olfactory identification ability up to the age of 75, while men in the same study showed significantly impaired ability at the age of 55 (Ship, Pearson, Cruise, Brant, & Metter, 1996). Women's higher capability to verbalize olfactory information has also been proven to be age invariant (Corwin, Loury, & Gilbert, 1995; Doty et al., 1984a; Maccoby & Jacklin, 1974; Richman, Wallace, & Sheehe, 1995). Moreover, research indicates that the female advantage in odor identification may generalize across different cultural settings, including African, Asian, North and South American populations (e.g., Barber, 1997; Doty, Applebaum, Zusho, & Settle, 1985; Ferdenzi et al., 2012; Fornazieri et al., 2015). When rating their experience of odors, women and men do not differ in familiarity and pleasantness ratings, but women rate odors as more intense than men (Ferdenzi et al., 2012). Physiologically, women exhibit a greater affective reactivity to odors by greater electrophysiological response than men do (Olofsson & Nordin, 2004; Pause, Lübke, Laudien, & Ferstl, 2010) and have larger olfactory evoked potentials (Evans, Cui, & Starr, 1995).

Evidence is limited with regard to sex differences in episodic odor memory. However, Lehrner (1993) reported that women outperformed men in episodic odor memory, and that this advantage in performance was maintained over a retention interval of three weeks. One factor that may underlie sex differences in episodic memory overall is the female advantage in verbal abilities (see also Hyde & Linn, 1988; Larsson et al., 2003a). This is supported by findings that the influence of sex is pronounced in memory tasks where verbalization of the material is explicitly required or possible (Herlitz, et al., 1999; Lewin, Wolgers, & Herlitz, 2001).

Neurological differences between women and men in relation to olfactory processing have been established. Women appear to have more cells in the olfactory bulbs than men (Oliveira Pinto, Santos, Couhino, Oliviera et al. 2014). Also, the activation patterns seem to differ. Women are more likely to have a cluster-like activation and activate more voxels in the amygdala than men following olfactory stimulation (e.g., Garzia-Falgueras, Junque, Giménez, Caldú et al., 2006; Seubert, Freiherr, Djordjevic, & Lundström, 2013; Yousem, Maldjian, Siddiqi, Hummel et al., 1999).

Cognitive measures and olfaction

Depending on the complexity of the olfactory task, olfactory functioning depends on cognitive abilities as well as sensory abilities. For instance, the more complex task of odor identification has been strongly associated with cognitive performance (e.g., Hedner et al., 2010; Larsson, 1997; Lehrner, Glück, & Laska, 1999). Cognitive abilities typically required in performance in olfactory tasks are cognitive speed, intact working memory, executive functioning, verbal comprehension, and labeling ability (Larsson, 2002). Cognitive speed, sometimes referred to as perceptual speed or mental speed, is often specified as being related to age-related variance (e.g., Salthouse, 1995; 2000; Wehling et al., 2015). Wehling and colleagues (2015) established in a longitudinal study that cognitive speed is strongly correlated to performance in odor identification. Previously, variance in both olfactory threshold and odor identification has been associated with performance in cognitive speed (e.g., Dulay, Gesteland, Shear, Ritchey, & Frank, 2008; Larsson et al., 2004; Wilson, Arnold, Tang, & Bennett, 2005). Dulay and colleagues (2008) also established that a significant variance (10.5 % - 2.1 %) in olfactory functioning (i.e., University of Pennsylvania Smell Identification Test, Phenyl Ethyl Alcohol Threshold test) was accounted for by working memory. Olfactory tasks like odor discrimination and odor identification are tasks that, due to the operations performed, including the formation of functional constructs, draw on executive functioning (Hedner et al., 2010). Vocabulary proficiency is also a known mediator in olfactory functioning (i.e., odor identification; Larsson, Hedner, & Olofsson, 2009), as is verbal fluency, sometimes referred to as phonemic fluency (e.g., Finkel et al., 2001; Nordin et al., 2013; Wehling et al. 2015).

Hormonal influence on olfaction

When studying hormonal influence on olfactory ability, hormonal variations in women with regard to their menstrual cycle is traditionally what is studied. Historically, research has shown that women's odor sensitivity vary over the menstrual cycle, with a higher sensitivity during ovulation and prior to menstruation and a reduced sensitivity during menstruation (e.g., Dorries, 1992; Doty, Hall, Flickinger, & Sondheimer, 1982). The influence of reproductive hormones on olfactory functioning is complex and simple associations are rarely present (see Doty & Cameron, 2009 for a review). Mair, Bouffard, Engen, and Morton (1978) found that sensitivity for highly volatile compounds is invariant over the menstruation cycle, whereas sensitivity for less volatile compounds is higher during ovulation and reduced during menstruation. A proposed explanation to this difference is that a hormonally induced swelling in the nasal cavity and mucus area prevents the molecules from accessing the olfactory receptors (Schneider, Costiloe, Howard, & Wolf, 1958). Women following a natural menstrual cycle exhibited a higher sense of smell for social substances like androstenone, androsterone, and musk than women regulating the cycle by taking monophasic oral contraceptives, supporting the notion that hormone levels affect olfactory functioning in women (Lundström, McClintock, & Olsson, 2005; Renfro & Hoffman, 2013).

Smoking and olfaction

There is a common idea that smoking impairs olfactory abilities, but scientifically the results regarding smoking and olfaction are inconclusive. Amoore (1991) for instance, claims that smoking is unrelated to olfactory sensitivity, given that the smokers have refrained from smoking for at least fifteen minutes prior to testing. Other studies (e.g., Doty, 1991; Frye, Schwartz, & Doty, 1990; Green & Lawless, 1991) provide results that indicate effects of smoking on olfactory ability. A neuroanatomical difference has recently been established, showing that smokers have a smaller olfactory bulb volume than non-smokers (Schriever, Reiter, Gerber, Iannilli, & Hummel, 2012).

Summary of cognitive abilities, aging, sex, and olfaction

Age matters in olfaction. In congruence with other sensory modalities the olfactory ability decreases with increasing age. Also, sex matters in olfaction. Primarily in the more cognitively complex olfactory tasks such as episodic odor memory and especially in odor identification the results are favoring women. Cognitive measures, such as mental speed, working memory, executive functioning and verbal fluency are known to have a positive correlation with olfactory functioning. Hormonal status in relation to menstrual cycle in women as well as smoking habits have a possible, but not definitive, effect on olfactory ability and need to be taken into account when evaluating research outcomes.

Research Objectives

Based on the review above, the general aim of this thesis is to investigate sensory and cognitive factors that influence episodic odor memory. Through four studies on olfactory memory in the adult human, both young and aging, both in women and in men will be addressed. The main issues to be addressed in this thesis concern the causes behind the well-established age-related effects in episodic odor memory (Study II, III, & IV), and the causes behind the age-independent sex differences in episodic odor memory (Study I, II, III, & IV).

I The purpose in the first study was to investigate the causes of the age-independent sex difference in olfactory episodic memory by examining the relations between olfactory tasks varying in sensory or cognitive load in the same participants.

II The purpose in the second study was to investigate the age-related decline in olfactory episodic memory, with a particular eye to the role of odor identification by investigating sensory and cognitive factors that determine odor identification and thereby have an important part in determining the ability to recognize odors.

III The purpose in the third study was to investigate the role of recollective experience and intention to memorize for age-related and sex-related differences in episodic odor memory.

IV The purpose in the fourth study was to investigate the role of subjectively perceived qualities of the encoded odors for age-related and sex-related differences in episodic odor memory.

Methods

The Smell Research Project

The data included in this thesis derives from a larger project on olfactory functioning and age conducted at the Stockholm Gerontology Research Center and led by Professor Maria Larsson. The project was funded by grants from the Humanities and Social Science Research Council (HSFR). The overall aim of the project was to study olfactory features of age-related factors, with great emphasis on episodic odor memory functions. Some of the data collected are the basis for this thesis.

Participants

All participants were community-dwelling adults residing in the Stockholm area. They responded to advertisement for participation and reported being in good health. Background data concerning demographic (i.e., age, educational level) and general health status (perceived state of health) were collected. Means (M) and standard deviations (SD) are presented in Table 2. Participants received no monetary reward for their participation, but were offered information about their own results after the data collection was completed.

Table 2. *Participant Characteristics Study I-IV.*

Study	**Age M (SD)**	**N Sex W/M M (SD)**	**Years of Education M (SD)**	**Health Status[a]**	**Olfactory Threshold[b]**
I	27.11 (4.65)	--/36	14.10 (2.62)	3.25 (.65)	9.42 (1.02)
	28.46 (4.46)	35/--	14.74 (2.27)	3.11 (.80)	9.51 (.61)
II	75.0 (8.0)	68/64	12.3 (3.6)	--	8.5 (1.3)
III	27.55 (4.72)	33/36	14.42 (2.49)	3.17 (.73)	9.45 (.85)*
	68.52 (4.72)	30/27	13.00 (3.76)	3.61 (.86)	8.83 (1.29)
IV	27.23 (4.61)	35/36	14.44 (2.45)	3.18 (.72)	9.46 (.84)
	68.41 (4.72)	32/36	13.29 (3.67)	3.60 (.87)	8.73 (1.35)*
	84.32 (4.90)	37/26	11.25 (3.2)*	3.57 (.84)	8.09 (1.33)*

* $p < .05$, ** $p < .01$, [a]1 = very poor to 5 = very good, [b] Min = 0, Max = 10, 10 being the lowest threshold.

The focused age groups were young adults (18+) and older adults (60+). The choice of age segments was made to increase the possibility to depict the well-documented age-related olfactory decline and sex-related olfactory differences, and was based on previous research (e.g., Doty et al. 1984a; see Figure 1). To control for possible dementia, participants were also screened with Mini Mental State Examination (MMSE; Devanand, Michaels-Marston, Liu, Pelton et al., 2000; Folstein, Folstein, & McHugh, 1975). A cut-off of +25 was applied to prevent from possible early dementia. Concerning olfactory threshold, a cut-off of 5 was applied to exclude participants suffering from anosmia or hyposmia.

Included assessments of olfactory function

Included method for assessing olfactory sensitivity

The method used in this thesis is the well-established forced-choice staircase test with sniff bottles containing N-butyl alcohol (1-butanol) that has been recommended for use as a standard in research on olfactory sensitivity (Moskowitz, Dravniek, Cain, & Turk, 1976). This test contains a series of concentrations, from 8 ml (strongest) to 0.1 µl (weakest) of n-butanol/200 ml of distilled water (Larsson & Bäckman, 1993; Murphy et al., 1991). The sensitivity was assessed birhinally with a free sniffing procedure. Eleven dilutions were prepared, where each successive dilution decreased the concentration of the odorant by a factor of three. The experimenter presented a pair of bottles: one containing a butanol solution and one blank containing distilled water only. The instruction was to smell each bottle and decide which contained an odor. The presentation of the odorant and the blank was randomized. The assessment started with the weakest concentration. If the participant was able to pick out the odorant from the blank, the experimenter presented a new stimulus-pair containing the same concentration again until the criterion of five correct responses in a row was met. If the participant failed, the experimenter presented a stronger concentration until the criterion was met. Approximately 30 seconds passed between each presentation to prevent from adaptation. If a participant could detect the weakest concentration the highest score, 10, was given; if the second-weakest concentration was detected, the score of 9 was given, and so forth.

Included methods for assessing odor discrimination

Intensity discrimination. A staircase procedure was used in the assessment of intensity discrimination. The test included six concentrations of n-butyl alcohol ranging in concentration from 0.03 ml (strongest: 5) to 0.1 µl (weakest: 10) of n-butanol/200 ml of distilled water. Each successive dilution decreased the concentration of the odorant by a factor of three. The intensity discrimination was assessed birhinally with a free sniffing procedure. The participant was presented with two different concentrations in sniff bottles, and was instructed to determine which contained the strongest smell. Five different pairs were prepared and the weakest concentration (10) was used as standard (i.e., 10-9, 10-8, 10-7, 10-6, 10-5). The assessment started with the intermediate 10-7 pair, and if the participant could discriminate the stronger from the weaker four times in a row, a new pair with a smaller concentration difference (i.e., 10-8) was presented. If the participant failed to discriminate at the 10-7 level, a new pair with a larger concentration difference was presented (i.e., 10-6). If the person could discriminate the pair with least concentration difference (i.e., 10-9), a score of 9 was given; if the person discriminated at the 10-8 level, a score of 8 was given, and so forth.

Quality discrimination. In the assessment of quality discrimination, four similar fruit-like odors were used (i.e., orange oil, bitter orange oil, lemon oil winter, cardamom oil). The quality discrimination was assessed birhinally with a free sniffing procedure. Participants were presented with one target odor and then instructed to select a match for this odor from two odor alternatives (i.e., one target odor, one distractor). Twelve different combinations were presented and participants scored one point for each of the correct discriminations.

Included method for assessing odor identification

In this thesis, free identification assessments are included. In conjunction with the recollection phase of the episodic odor memory test the participants were asked to name the odors and to write down the answers in the response sheet. Participants received one point for each correctly identified odor and a maximum of 24 points was awarded on each task. A strict criterion was used when scoring the odors and only responses identical to the corresponding target words were scored as correct. For example: for the smell of petrol, the answer "petrol" would be considered correct, but not answers like "garage", "gas station" or "car-like smell"; for the smell of cloves, "cloves" would score as correct but not answers like "dentist, "spicy" or "ginger breads"; for the smell of apple, the answer "apple" was considered correct whereas answers like "fruit", "sweet" or "some kind of candy" were not, and so forth. That also means that both incorrect but reasonable (e.g., nutmeg for cloves) and more unreasonable guesses (e.g., mosquito repellent for apple) were scored as misidentification (see also Cain & Krause, 1979).

Included method for assessing perceived hedonic tone

In the included material, the subjective experience of the odors was assessed as follows: As a part of the encoding procedure of the odors in the episodic odor memory test, participants were asked to rate the perceived quality of each presented target odor (n = 12) on 100 mm Visual Analog Scales (VAS) across different dimensions: Pleasantness (0 mm = very unpleasant and 100 mm = very pleasant), intensity (0 mm = very low intensity and 100 mm = very high intensity), and irritability (0 mm = very low irritability and 100 mm = very high irritability).

Included method for assessing episodic odor memory and recollective experience

Two sets of odor recognition stimuli are represented: One set of familiar odors (n = 24) and one set of unfamiliar odors (n = 24; see Study I & III). The familiar test set was based on real-world substances and has partly been used in earlier studies (Larsson & Bäckman, 1993; Larsson 1997). Odor substances were placed in 60-ml opaque bottles with narrow mouths and screw-on-lids that occluded any visual cues. Twelve odors served as targets and 12 served as distractors in each set. Odors serving as targets on one test occasion were used as distractors on the next, and vice versa. The order of test sets was counterbalanced so that half of the participants within each age and encoding instruction group received the familiar odors before the unfamiliar ones, and vice versa for the other half. Two different orders of the specific odor items were prepared at encoding and testing respectively. The episodic odor memory was assessed birhinally and with free sniffing. All participants smelled each odor for approximately 10 seconds at encoding. In the recognition tests, participants were allowed to smell each odor for 10 seconds, but no time restrictions were put on the recognition and identification responses. The procedure was as follows: After completion of the initial olfactory threshold test, participants were presented with one of the odor test sets. Participants assigned to incidental encoding condition were told that the aim of the experiment was to collect information on subjective experiences of various odors. They were instructed to rate the presented odors according to a number of different dimensions (e.g., pleasantness). Participants in intentional encoding condition were presented with the same rating protocol, but they were also asked to try to memorize the odorants for purposes of a later memory test. Then, the participants were presented with cognitive distractor tasks, which took about 25 min to complete. This was followed by a presentation of the odor recognition test set. In this part of the assessment, participants were presented with 24 odors, the 12 target odors along with 12 distractor odors that were randomly intermixed. For each of the odors, participants were asked to indicate whether they recognized (yes-response) or did not recognize (no-response) the presented odor from the earlier presentation. To also assess recollective experience participants were asked, for each odor, to classify their response into one of three categories: ''remember'' (R), ''know'' (K), or ''guess'' (G). The purpose of including a guess option was to reduce the effects of guessing on R and K responses (i.e., that participants would be biased to indicate ‘‘know’’ when they were unsure as to their response).

Included assessments of cognitive functioning

A number of cognitive measures were included in the search of determinants of episodic odor memory. In the studies that constitute this thesis these were: two measures of cognitive speed, The Trail-Making Test, part A (TMT-A) from the Halstead Reitan Battery (Reitan & Davidson, 1974), and the pattern comparisons test devised by Salthouse and Babcock (1991). One measure of executive functioning: The Trail-Making Test, Part B (TMT-B) (Reitan & Davidson, 1974). The Controlled Word Association Test was used as a test of verbal fluency (Benton & Hamsher, 1976).

In TMT-A (Reitan & Davidson, 1974), participants were presented with a white sheet of paper on which circles were distributed. The circles were numbered from 1 to 25 and participants were asked to draw lines to connect the 25 circles in the correct order (i.e., 1-2-3…-25). Participants were told to work as fast as they could and completion time was recorded.

In the pattern comparisons task (Salthouse & Babcock, 1991), participants were presented with 60 pairs of geometric figures that consisted of six or nine line segments. Their task was to compare the geometric figures and rapidly decide whether these were the same or different, by writing S or D. Thirty seconds were allowed for task completion at each level (six or nine line segments). The dependent measure was the total number of correct decisions made in the two trials, and data was summarized across the two measures.

In the TMT-B (Reitan & Davidson, 1974) assessment participants were presented with circles that contained numbers from 1 to 13 and letters from A to L. They were instructed to connect, as fast as possible, the consecutively numbered and alphabetically lettered circles by alternating between the two sequences (i.e., 1-A-2-B-…12-L). TMT-B poses demands on mental flexibility in managing more than one stimulus category at a time and in shifting the course of an ongoing activity. The number of seconds needed to finish the task was registered.

The Controlled Word Association Test (Benton & Hamsher, 1976). This test consisted of three word-finding trials, using the letters F, A, and S. The participants were instructed to produce as many words as possible in one minute, beginning with each of the target letters, excluding names on persons or places. The number of words correctly generated in the three trials was summarized to provide a total letter fluency score.

Empirical Studies

Included measures across studies

Table 3. *Included Measures Study I-IV*

Study	Demographic	Olfactory measures	Other measures
I	Sex	Threshold Intensity discrimination Quality discrimination Episodic odor memory - unfamiliar odors - familiar odors Odor identification	Smoking habits Menstrual cycle
II	Age Sex	Threshold Intensity discrimination Quality discrimination Odor identification	MMSE The Patterns Comparison Test TMT-A TMT-B Letter Fluency Test Visual Identification
III	Age Sex	Threshold Episodic odor memory - unfamiliar odors - familiar odors Odor identification	--
IV	Age Sex	Threshold Episodic odor memory - unfamiliar odors Subjective olfactory experience	Smoking habits

Study I (Öberg, Larsson, & Bäckman, 2002)

The purpose of Study I was to investigate the causes of the sex difference in olfactory episodic memory by examining relations between olfactory tasks varying in sensory or cognitive load in the same participants. Previous research on sex differences in olfactory ability is not conclusive and the available evidence suggests a mixed pattern of results (e.g., Deems & Doty, 1987; Cain & Gent, 1991). In episodic odor memory, women seem to perform at a higher level (Lehrner, 1993), but evidence is sparse. For other modalities, the ability to verbalize the information to remember appears to be of significant importance for subsequent memory performance (Herlitz et al., 1999; Lewin et al. 2001). It is established that in odor identification the outcome favors women (e.g., Cain et al., 1988; Doty et al., 1984a). When the odors selected are controlled for gender bias, women still seem to have a better access to verbal information, which is an advantage in identification tasks. In the light of previous research there is a need to determine whether the sex differences in olfactory functioning is mainly sensory mediated, as proposed by Lehrner (1993), or cognitively mediated by differences in verbalizations skills in line with research on other modalities (Herlitz et al, 1999). Consequently, this study aspires to refine the knowledge of the impact of sensory and cognitive load in olfactory task across sexes and to specify the possible impact of odor identification in relation to episodic odor memory. To more conclusively determine if episodic odor memory performance correlates with the ability to identify odors, a set of odors that were more unfamiliar and difficult to verbalize was included as well as a set of odors that were highly familiar and more likely to be identified.

The study involves three tasks tapping primarily sensory demands: olfactory detection threshold for n-butanol, odor intensity discrimination and odor quality discrimination. Three tasks posing more cognitive demands were also included. Of these, one was tapping semantic memory: odor identification, and two were tapping episodic memory: recognition of unfamiliar and familiar olfactory information. To make sure that the odors chosen were balanced equally in terms of feminine and masculine bias, perceived familiarity of the test odors, as indexed by rating of familiarity on a 100 mm VAS, was collected. The result yielded no difference in perceived familiarity between women and men on any of the test sets. A total of 71 women and men participated, 19-36 years of age. All participants were tested individually and all tasks were well interspersed to prevent carry-over effects.

The main results from Study I is summarized in Figure 3. In general the result was found be in congruence with most previous research. No reliable effects of sex were found in detection threshold for n-butanol, intensity discrimination, quality discrimination or episodic memory for unfamiliar odors. However, women were more adept at the more cognitively and verbally loaded olfactory tasks. In episodic memory for familiar odors and in odor identification there was a more prominent difference, favoring women. Possibly the most important finding was the strong impact of the ability to identify the odors on subsequent odor memory performance. When controlling for odor identification, the significant sex difference disappears. This result concerned episodic odor memory for the familiar odors. No such effect was obtained concerning the unfamiliar olfactory information. Using the same procedure the potential impact of threshold, intensity discrimination, and quality discrimination was also examined. These analyses revealed an augmentation of the sex effect in episodic odor memory when controlling for quality discrimination. Controlling for threshold and intensity discrimination did not change the statistical outcome, where women performed at a higher level in the more cognitively loaded olfactory tasks, indicating that olfactory memory performance is not chiefly determined by olfactory sensitivity.

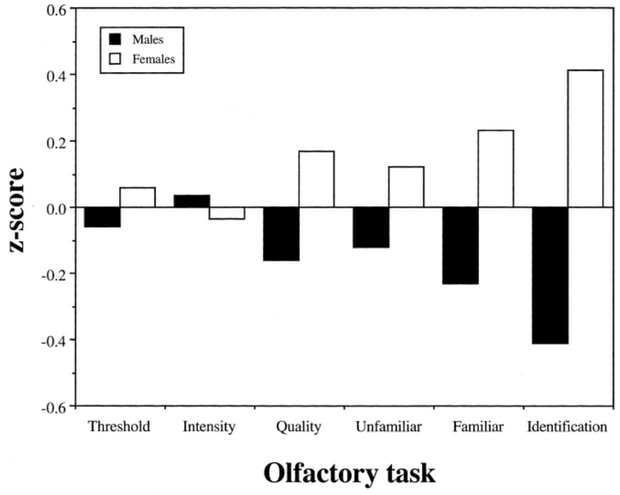

Figure 3. Z-score distribution of performance in various tasks (i.e., olfactory threshold, odor intensity discrimination, odor quality discrimination, episodic odor memory for unfamiliar odors, episodic odor memory for familiar odors, and odor identification) as a function of sex in Study I.

Conclusion

No sex differences were obtained in the task assessing mainly sensory olfactory functioning or the memory assessment including unfamiliar odors. The outcome clearly suggests, however, sex differences in olfactory functioning in the more complex tasks tapping cognitive ability. Interestingly, women's higher proficiency in odor identification was mediating their greater performance in episodic odor memory for familiar odors. This indicates that semantic knowledge in the form of ability to verbalize the odors is sex-related, even though the odors were rated as equally familiar by both sexes.

Study II (Larsson, Öberg, & Bäckman, 2005)

The purpose of Study II was to investigate sensory and cognitive factors that relate to the age-related decline in episodic odor memory. Study I clearly pointed towards a strong relation between the ability to identify odors and subsequent episodic odor memory. It is therefore of interest to further explore what determines odor identification and thereby determines also the ability to recognize odors. As demonstrated in other studies, age-related differences in episodic odor memory appear to be strongly related to olfactory identification performance (e.g., Larsson & Bäckman, 1993, 1997). There is ample evidence that aging is associated with impairment in olfactory identification (e.g., Corwin et al., 1995; Larsson et al., 2000), although the basis for this impairment is not yet determined. There are also indications that sensory loss, in the form of higher threshold (e.g., Cain & Gent, 1991; Murphy et al., 1991), and in terms of discrimination ability (e.g., Cain & Potts, 1996; de Wijk & Cain, 1994), is the source of the age-related impairment to identify odors. Cognitive functioning is also critical in olfactory identification (Larsson, 1997; Lehrner et al., 1999) based on the notion that odor identification can be conceptualized as a semantic memory task, where an individual's knowledge of specific odors is of importance (e.g., Larsson, 2002; Schab, 1991; Tulving, 1986). Cognitive abilities, like cognitive speed, are age-related (e.g., Salthouse, 1995; 2000) and the age-related impairment in odor identification is well documented, but the underlying mechanisms are not yet well understood. This study was designed to investigate the causes of the age-related decline in odor identification by examining the relative contributions by demographic, sensory, and cognitive factors.

The studied sample consisted of 132 adults ranging in age from 60 to 91 years. All participants were living in the Stockholm area, and reported being in good health. Demographic background data (age, sex, years of education), sensory data (i.e., threshold, intensity discrimination, quality discrimination, odor identification) and cognitive data (i.e., TMT-A, TMT-B, Pattern comparison, Word Association Test) were collected. To control for possible lack of knowledge of the included familiar odors, all participants were also assessed in a visual identification test with pictures corresponding to the 24 familiar odors (e.g., a picture of an apple being considered to correspond to the smell of apple). As expected this proved to be an undemanding task with results close to ceiling ($M = 22.5$, $SD = 1.6$). As an illuminating comparison the identification rate on the odors were substantially lower ($M = 3.6$, $SD = 3.0$).

Initially product-moment correlations were calculated to determine how the demographic, sensory, and cognitive variables were related to performance in odor identification. This served as a base for arranging the hierarchical regression analyses. Two sets of hierarchical regression analyses were chosen. In the first, regression analysis age was entered first, followed by other demographic variables (i.e., sex, education), the sensory variables (i.e., threshold, intensity discrimination, quality discrimination), and finally the cognitive variables in three blocks (i.e., perceptual speed, executive functioning, verbal fluency), as displayed in Table 4. The result confirms that age is a strong predictor of odor identification, but it also shows that sex, as well as sensory and cognitive measures, are significant predictors of odor identification also after controlling for age. In the second regression analysis, demographic variables (i.e., sex, education) were entered first, followed by the sensory variables, the sets of cognitive measures, and finally age, as displayed in Table 5. As anticipated, when the sensory, cognitive, and demographic variables were entered prior to age in the regression, they were sufficient to explain the age-related effect in odor identification.

Table 4. *Hierarchical Regression Analysis for Predicting Odor identification in Study II.*

Predictor	**Incr R^2**	**Cum R^2**	**β**	***p***
1. **Age.**	.19	.19	-.44	**.00**
2. Demographic variables	.04	.23		
Sex			.19	**.01**
Education			.04	n.s.
3. Sensory Acuity	.09	.32		
Threshold			.25	**.00**
Intensity discrimination			.03	n.s
Quality discrimination			.16	**.05**
4. Cognitive speed	.09	.41		
Pattern comparison			.31	**.00**
Trail Making Test-A			-.11	n.s
5. Executive functioning	.00	.41		
Trail Making Test-B			.05	n.s
6. Verbal fluency	.02	.43		
Word Association Test			.16	**.05**

Table 5. *Hierarchical Regression Analysis for Identifying Mediators of the Age-related Variance in Odor Identification in Study II.*

Predictor	**Incr R^2**	**Cum R^2**	**β**	***p***
1. Demographic variables	.05	.05		
Sex			.18	**.05**
Education			.16	n.s.
2. Sensory Acuity	.18	.23		
Threshold			.29	**.00**
Intensity discrimination			.02	n.s
Quality discrimination			.27	**.00**
3. Cognitive speed	.17	.40		
Pattern comparison			.36	**.00**
Trail Making Test-A			-.12	n.s
4. Executive functioning	.00	.40		
Trail Making Test-B			.04	n.s
5. Verbal fluency	.02	.42		
Word Association Test			.13	n.s
6. Age	.01	.43	-.15	n.s

The most important finding in relation to the aim of this thesis, was that the results provide an explanation for the age-related effect on odor identification in terms of sensory and cognitive variables. Particularly olfactory threshold, quality discrimination, and cognitive speed (i.e., Pattern comparison, TMT-A) accounted for the age-related deficits in the odor identification task, whereas executive functioning made no difference.

Conclusion

The results of Study II replicates the sex difference observed in Study I, and further suggests that the observed age-related decline in odor identification is explained by decline in sensory and cognitive variables. Moreover, the findings highlight that the demographic variable age surpasses other variables when predicting performance in odor identification. However, controlling for sensory variables like olfactory threshold and quality discrimination, and the cognitive variable mental speed eliminates the age-related deterioration in identification of olfactory information. As noted, age-related differences in episodic odor memory appear to be strongly related to olfactory identification performance (e.g., Larsson & Bäckman, 1993; 1997). This strengthens the notion that sensory factors primarily underlie the age-impairment in odor identification, which in turn determines the identification-dependent and age-related impairment in episodic odor memory.

Study III (Larsson, Öberg, & Bäckman, 2006)

The purpose of Study III was to investigate the role of recollective experience and intention to memorize for the age-related differences in episodic odor memory. Recollective experience in episodic odor memory is an uncharted area of research. No previously published study targets age-related differences in recollective experience of odors. However, research on recollective experience for other modalities has established age-related differences. Typically, younger adults report more R experiences associated with a clearer contextual recollection. Older adults, in contrast, report less R experiences and equal or more K experiences associated with feelings of familiarity (e.g., Mäntylä. 1993; Nyberg et al., 1996a; Parkin & Walter, 1992; Salthouse, Toth, Hancock, & Woodard, 1997). In a study targeting sex differences in recollective experience for olfactory information in young adults, the overall finding was that the reported R experiences in general were significantly more frequent than K experiences and G experiences and that women exhibited more R experiences than men did. No sex difference was obtained in reported K or G experiences or for intention to memorize (Larsson et al., 2003a).

One group of younger adults (18-35 years of age) and one group of older adults (60-75 years of age) were included in this study. Participants in each age group were randomly assigned to each of the two encoding conditions. In the subsequent recognition test the participants also stated the nature of their recollective experience, and classified it as an R, K or G experience.

The data analysis in this study consists of three main parts, odor recognition memory, odor naming ability, and recollective experience.

The overall findings concerning recognition memory are that younger adults show more hits, fewer false alarms, and thus a higher overall odor memory performance (i.e., d') than old adults. No sex-effect in episodic odor memory (i.e., d') was obtained. The outcome concerning odor naming was in line with previous findings. The young adults identified more of the familiar odors than the older adults. Women identified more of the odors than the men.

A main effect of response type was observed. R responses, mainly tapping episodic memory, were more frequent than K responses, mainly tapping semantic memory. These were in turn more common than G responses

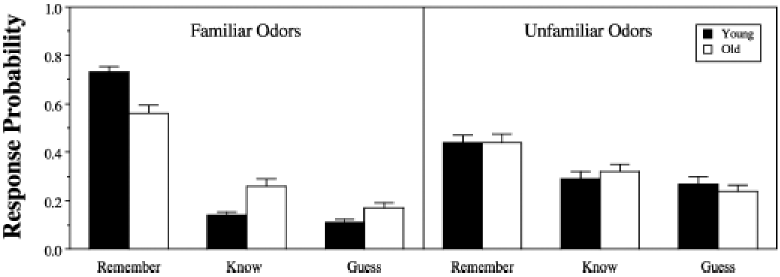

Figure 4. Recollective experience as a function of age, responsive type, and olfactory familiarity in Study III.

A three-way interaction regarding age, odor familiarity and response type was obtained, as displayed in Figure 4. Age interacted reliably with response type and odor type, such that younger adults generated more R responses and fewer K responses than older adults for familiar odors. Young and old generated equal response patterns for unfamiliar odors. The old adults generated the same response pattern regardless of odor type. Encoding condition did not interact with response type. The false alarm data were also broken down by response type. Older adults reported more R responses than young adults in relation to false alarms, whereas no age differences were obtained for K or G responses. Odor type also interacted with response type for false alarms such that familiar odors were more related with R responses and more K and G responses were generated for unfamiliar odors. The observed age-related difference in R responses for the false alarms was also eliminated when odor naming was controlled for. This suggests that age-related deficits in odor naming play an important role for the age differences in the rate of R responses, indicating episodic memory. Importantly, when controlling for odor naming the age-related differences in R responses for the hits disappeared, indicating that odor naming has a profound influence on the rate of R responses, in turn signifying episodic memory for olfactory information.

An intriguing finding regarding recognition memory in this study, is that the participants benefited from intentional encoding of the unfamiliar olfactory information but no difference between intentional and incidental encoding was obtained for the familiar olfactory information.

Conclusion

Taken together, these findings support the view that odor recognition memory involves two measurable states of awareness that are differently affected by age and odor familiarity. Both age groups produced more R responses than K responses. Older adults exhibited less explicit recollection, R, and equal or greater amounts of familiarity based odor-recognition, K, as compared to younger adults. A three-way interaction was obtained showing that when the olfactory information to remember was unfamiliar, young and old adults reported the same type of recollective experience. But when the olfactory information was familiar young reported more R responses and fewer K responses than the older adults. In line with previous findings (Study I & II), the differences in recollective experience between familiar and unfamiliar odors disappeared when controlling for odor identification. Intention to memorize affected the memory performance for the unfamiliar odors but had no effect on memory performance for familiar odors.

Study IV (Larsson, Öberg-Blåvarg, & Jönsson, 2009)

The purpose of Study IV was to examine the role of the subjective experience (i.e., perceived intensity, pleasantness, and irritability) of the encoded odors in relation to the age-related and the sex-related differences on olfactory recognition memory. To the author's knowledge, no previous research has been published on the influence of the subjective experience of odors on episodic odor memory. Age-related deficits in episodic odor recognition memory are well established (see Study III) and sex-related differences in episodic odor memory are influenced by semantic knowledge in the form of identification and verbalization (see Study I), which in turn depend heavily on sensory variables and cognitive speed (see Study II). Previous studies suggest that odors are processed differently depending on hedonic tone and also that they produce different autonomic reactions as measured by skin conductance and heart rate (Alaoui-Ismaïli et al., 1997a; 1997b). It is suggested that the central-nervous system processes pleasant odors differently than unpleasant ones (Bensafi, Rouby, Farget, Bertrand et al., 2002; Zald & Pardo 1997). Konstantinidis and colleagues (2006) found that identification of unpleasant odors was more age invariant than the identification of odors perceived as pleasant.

This study includes data from 202 participants (i.e., 104 females, 98 males), ranging in age from 19 to 91 years, see Table 2. Given that the ability to name an odor is a powerful determinant in episodic odor recognition for olfactory information (e.g., Larsson, 1997; Larsson & Bäckman, 1993, 1997; and also Study I & III) only the test set with odors considered to have a low familiarity was included. As an encoding procedure the participants rated the target odors across different dimensions (i.e., pleasantness, intensity, irritability). These dimensional ratings were later combined with the memory data.

The overall finding on memory for olfactory information in this study was that the young (19-36 years) remembered more of the odors than the older (60-74 years), who in turn remembered more than the oldest (75-91 years). Women had more hits than men, but no sex effects on d'-scores were obtained. Overall, participants rated odors as more pleasant, less intense and less irritable with increasing age, which was statistically unrelated to their olfactory threshold performance. Odors perceived as unpleasant, intense and irritable olfactory information were more easily recognized through the adult life span as compared to pleasant, less intense and less irritable olfactory information. Regarding level of rating in relation to subsequent recognition (i.e., hit-score), one sex effect and one age effect was obtained. The sex effect was that women recognized relatively more odors centered on the pleasantness-unpleasantness scale, in specific odors they perceived as more neutral compared to the men. No sex difference in hit-score was obtained for odors perceived as either unpleasant or pleasant. The age-related effect obtained was that the oldest adults (75-91 years) showed selective beneficial memory effects for the odors they rated as highly irritable as compared to the participants in the younger age groups, suggesting a compensatory use of trigeminal activation, as illustrated in Figure 5. Controlling for threshold did not change the outcome of the analyses.

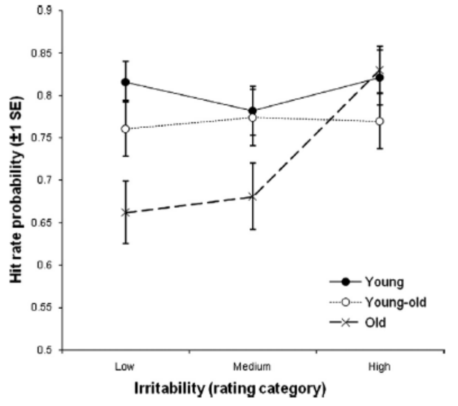

Figure 5. Hit rate probability at low, medium, and high irritability rating across age groups in Study IV.

Conclusion

The examined odors in this study were unfamiliar and therefore to a great extent deprived of semantic load. The finding was that age related to recognition memory such that younger recognized more odors than successively older adults. No sex difference in episodic odor memory was obtained. Participants rated odors as more pleasant, less intense and less irritable with increasing age, unrelated to their olfactory threshold. Women rated the odors in general as more unpleasant. No differences in relation to sex were obtained in intensity or irritability ratings. Unpleasant, intense and irritable olfactory information was more easily recognized through the adult life span as compared to pleasant, less intense and less irritable olfactory information. Women also recognized odors centered on the pleasantness-unpleasantness scale better, in particular odors they perceived as more neutral, as compared to the men. No sex difference in hit-rate probability was obtained for odors perceived as either unpleasant or pleasant. The most unexpected findings in relation to age were that the oldest adults showed selective beneficial memory effects for the odors they rated as highly irritable as compared to the participants in the younger age groups. Taken together, this indicates that olfactory information holding more pronounced hedonic tone, as determined on a personal experiential level, is more easily recognized than olfactory information with a lower hedonic tone. It also indicates that the older participants might compensate their loss of olfactory sensitivity with experienced trigeminal activation.

General Discussion

Summary of main results

The ambition with this thesis is to examine the sensory and cognitive causes of the well-established age-related decline in olfactory episodic odor memory and of the age-independent sex difference in olfactory episodic memory. In Study I, no sex differences were obtained in the tasks tapping mainly sensory abilities, but in the more cognitively laden tasks women had an advantage that seems to be explained by their superior ability to verbalize the olfactory information. In likeness with these findings, Study II established that verbal ability (i.e., verbal fluency) was a significant contributor to the ability to identify olfactory information. However, it did not explain the age-related impairment in odor identification. Instead, sensory variables like olfactory threshold and quality discrimination, and also mental speed eliminated the age-related deterioration in identification of olfactory information. The results suggest that these factors underlie the age-related impairment in odor identification and also determine the age-related impairment in episodic odor memory. In Study III, young adults exhibited more remember responses and fewer know responses for familiar odors than the old adults. Both the young and the old adults exhibited the same patterns of recollective experience for unfamiliar odors. The old adults exhibited the same response patterns for unfamiliar and familiar odors. The differences in recollective experience between familiar and unfamiliar odors disappeared when controlling for odor identification. These findings emphasize the importance of familiarity (i.e., well-known odor objects) and odor identification for episodic odor memory performance. Finally, Study IV showed that negatively laden odors are more easily recognized, and that the older adults rated the odors overall as less negative. When the odors were perceived as very irritable, the oldest age group benefited from that in their episodic odor memory performance.

When summarizing the outcome of the studies, some interesting patterns emerge. One very distinct theme is the importance of verbalization and of familiarity for successful episodic odor memory functioning. Another is something that could be interpreted as a flattening of the olfactory experience in older adults. Subjective experience of the encoded odors and the interesting aspect of trigeminal activation aiding memory in old age open up for new thoughts. The results also illuminate the reasons for the established sex difference in episodic odor memory. In the following discussion, these results in particular will be addressed.

Identification and familiarity – a role for verbal coding?

Maybe the most prominent finding in this thesis is the importance of the ability to verbalize the olfactory information for subsequent memory performance. The ability to verbalize olfactory information proved to be as crucial for excellence in episodic odor memory in younger adults (Study I) and younger adults relative to older adults (Study III), as for women relative to men (Study I & III).

Before venturing further into the discussion on episodic odor memory, identification, and familiarity, it might be wise to straighten out any uncertainties concerning the odors and their claimed familiarity. To make sure that the odors were in fact equally well-known to all groups of participants, all participants made a visual identification of pictures of items corresponding to the test-set of familiar odors included. Identification performance was close to ceiling for both young and old adults. The young adults also rated each odor in terms of perceived familiarity and no difference between women and men was obtained. Both of these measurements indicate that the included set of familiar odors was well known to the participants and that failure to know the odors, as previously observed by Jönsson, Theckhova, Lönner, and Olsson (2005), was not behind the failure to identify the odors.

Looking closer at the memory performance, women and men recognized overall more of the familiar odors than unfamiliar odors. Young women performed at a higher level than young men in all olfactory tasks that were tapping verbal processing. When data included older adults the pattern was similar. However, young adults identified more odors than did old adults, and subsequently they also recognized more odors than did the old adults. Statistically controlling for odor identification eliminated the female advantage in odor recognition, emphasizing the important role of verbal factors in episodic odor memory for the familiar odors. This is a typical finding in episodic odor memory research when the material to be remembered is possible to verbalize (Cain, 1982; Doty et al., 1984a; Olsson et al., 2009), and in accordance with other memory research using other modalities of sensory information (e.g., Herlitz et al., 1997; 1999).

When studying predictors of odor identification to further pinpoint what influences episodic odor memory, verbal fluency arises as one of the variables making a difference (Study II). Even though it was not as powerful as for instance age or cognitive speed, it is one of the factors underlying the ability to identify odors and therefore also one of the variables behind performance in episodic odor memory. This correlation is also in agreement with previous findings (e.g., Larsson et al., 2000; Finkel et al., 2001; Frank, Rybalsky, Brearton, & Mannea, 2011). Interestingly, previous research has shown that necessary abilities for proficiency in verbal fluency are cognitive speed (Lezak, 1995), executive functioning (Perlmuter, Tun, Sizer, McGlinchey, & Nathan, 1987), and vocabulary (Bolla et al., 1990). In Study II, verbal fluency, riding on the level of significance, added to odor identification ability, also when cognitive speed and executive functioning were controlled for. This suggests that word fluency is of additional importance for successful identification of olfactory information.

A demographic factor potentially related to verbal proficiency is educational level. Level of education has been shown to have a positive influence on both episodic and semantic memory performance (e.g., Nyberg et al., 1996a). Contrary to these findings, the results presented here suggest that education may be of some, but minor, importance for odor identification performance (see also Larsson & Bäckman, 1998). However, education is a measure that needs to be treated with caution when the included participants' educational background is spanned over several different educational systems (for more history on Sweden's educational system see Larsson & Westberg, 2015). Controlling for education within the age groups in relation to the various included olfactory measurements did not change the outcome.

The pattern emerging in these studies is that when given the possibility to identify and name the odors, that appears to fortify the episodic odor memory performance.

Age dependent flattening of olfactory experiences

A recurrent finding (Study II, III, & IV) is what could be referred to as an age-dependent overall flattening of the olfactory experiences. A basic finding is that increasing age involves decreasing olfactory threshold. This is in line with the bulk of the previous research (e.g., Doty et al., 1984a; 1984b; 1989). A strong and consistent finding throughout the results in this thesis is also the correlation between age and olfactory tasks that are more cognitively demanding (i.e., odor identification, episodic odor memory). This is consistent with previous research as well (e.g., Au et al., 1995; Doty et al., 1984a; 1984b; Hedner et al., 2010; Wysocki & Gilbert, 1989).

When exploring whether individual variation in perceived olfactory qualities influence retention of olfactory information across the adult lifespan, the proposal of an age-related flattening becomes marked (Study IV), in terms of rated quality (i.e., intensity, pleasantness, irritability) and subsequent memory performance. The oldest age group rated the odors as more pleasant, less intense, and less irritable. The younger old age group (60-75 years) rated the odor as equally pleasant as the young group, and in between the two other groups when rating intensity and irritability. Research in this area is scarce, but Stevens and Cain (1986) found that older adults tend to rate odors as less intense which could indicate sensory loss. This conclusion is partially contradicted by the present data, as controlling for sensitivity threshold did not change the distributions of the ratings. Doty (1989) has proposed that age-related differences in perceived pleasantness of odors may be related to a decreased olfactory sensitivity among the elderly. In general, odors that were perceived as less pleasant and more intense were easier remembered. The age difference in hedonic perception is in congruence with recent observations by Markovic, Reulbach, Vassiliadu, Lunkenheimer and colleagues (2007), who reported a rise in olfactory pleasure with increasing age. For irritability, there was an age effect such that the old adults showed selectively better recognition for odors perceived as highly irritable. This outcome may reflect that irritability activates the trigeminal system, and compensate for the otherwise flattened olfactory experience in old age.

In Study II, cognitive (i.e., cognitive speed) and sensory (i.e., olfactory threshold and odor quality discrimination) impairment accounts for the decrease in odor identification ability with increasing age. However, in episodic odor memory (Study III), the old adults perform on equal levels for familiar and unfamiliar odors regardless of loss in olfactory sensitivity, whereas the young adults perform at a higher level for familiar olfactory information. It seems that the older adults are unable to benefit from the semantic knowledge of the odors in their memory processing. This is also evident in relation to the recollective experience. Older adults exhibited the same pattern in hits and d' for familiar and unfamiliar odors as compared to young adults whose response pattern varied depending on odor type. Older adults also showed the same patterns of response type (i.e., R, K, & G) for familiar and unfamiliar odors (Study III). The young adults exhibited a difference in response pattern depending on odor type. An age-related decrease in R responses for familiar odors was eliminated when controlling for odor identification, which could be an indication of the importance of odor identification for episodic odor memory. The old adults reported remember responses for the false alarms (Study III). These findings indicate that the familiarity of the odors affects the recollective experience and episodic odor memory in the young adults, but among the older adults level of familiarity, in terms of well-known odor objects, made no difference. The olfactory experience appears to be somehow flattened or blurred. This is also in line with the idea that the odors induce weak neural activations and are therefore less stable and coherent as perceptual happenings (Stevenson & Mahmut, 2013). A possible explanation is consequently that the age-related decreased olfactory sensitivity prevents adequate cognitive elaborations (e.g., verbalization, identification) of the odors, thus rendering familiar and unfamiliar olfactory information equal.

One additional explanation for this olfactory flattening is neuroanatomical changes with old age. For instance, there could be a reduction in the number of receptors, changes in morphology, cellular patterns of receptor neurons or second-order neurons, as well as broader tuning of receptor cells for discrimination and a thinning of the epithelium in general (e.g., Doty &

Kamath, 2014; Loo, Youngentob, Kent, & Schwob, 1996; Rawson, Gomez, Cowart, & Restrepo, 1998). Abnormal numbers of neurofibrillary tangles have also been documented in elderly in areas of major importance for higher-order olfactory processing (Price, Davis, Morris, & White, 1991).

With old age the episodic odor memory works differently than it does in the younger adults. Old adults depend more heavily on semantic memory experiences. However, the overall olfactory experience seems to flatten. With a fading olfactory sensitivity, in concurrence with a decrease in the ability to verbalize the olfactory information, the ability to memorize odors becomes markedly reduced.

Subjective experience and episodic odor memory

In Study IV, the odors examined were unfamiliar and stripped of the semantic load that accompanies familiar odors. Study focus was thereby shifted towards personal interpretation (i.e., subjective experience) of the odors. It could be argued that heightened memory for events with a negative and unpleasant nature have a higher survival value when predicting outcomes of future events by serving as a protective mechanism from potential dangers (e.g., Kensinger, 2007). This thesis supports that notion in that more negatively laden odors (i.e., unpleasant, intense, irritable) were related to a higher memory performance. Berglund and colleagues (1973) suggested that the hedonic tone (i.e., pleasantness) is a fundamental aspect of an olfactory experience and is processed with a low level of cognitive involvement. The present observations suggest that the perceived odor quality also has a significant impact on higher-order olfactory processes (i.e., episodic odor memory). In these results the memory advantage for unpleasant over pleasant information was constant across the studied age groups. This is in line with research focusing on memory for verbal and visual information, where retention for arousing or emotional information is better than for neutral information, and memory for negative information is more robust than for positive information (e.g., Kensinger, 2007). In addition, identification of unpleasant olfactory information was found to be less affected by aging than identification of pleasant odors (Konstantinidis, Hummel, & Larsson, 2006).

Recognition performance (i.e, hit-rate probability) for odors that were experienced as high in intensity and irritability was better than for odors rated with low or medium scores (Study IV). The analysis also showed that the old adults (76-91 years) showed selective beneficial memory effects for odors perceived as highly irritable, whereas retention was of similar magnitude across rating categories in the young (19-36 years) and young old adults (60-75 years). Perceptions of high irritability reflect an activation of the trigeminal sensory system. The present findings suggest that older adults may use trigeminal components in odor information to compensate for age-related impairments in olfactory memory. Indeed, available evidence suggests that the olfactory sensory system is more vulnerable to the ageing process than the trigeminal system (Stuck et al., 2006).

The results also showed that the subjective ratings were affected by age. Interestingly, statistical control for odor sensitivity did not moderate the age difference in hedonic perception even though the results clearly show that olfactory threshold was negatively affected by age. Although women perceived the odors as more unpleasant than the men, there was no difference between women and men in olfactory threshold. However, the threshold performance suffered from possible ceiling effects especially in the youngest group, suggesting that any conclusions concerning the threshold data should be interpreted with some caution. Research shows that olfactory perception is highly idiosyncratic and varies across age cohorts and cultural contexts (e.g., Ayabe-Kanamura et al., 1998), and the plasticity of hedonic evaluations is consistent with odor preference primarily being learned rather than biologically determined (Gottfried, 2007; Herz, 2001).

Taken together, the subjective experience of odors relates to odor recognition performance. The results can be interpreted such that the quality of the olfactory experience, like with identification of an odor, adds to the cognitive processing of the odor and subsequently enhances episodic odor memory performance. More research is needed to further establish the impact of subjective experience of odors and olfactory functioning.

Sex differences in episodic odor memory

Sex differences in episodic odor memory were obtained for all age groups (Study I, III, & IV). The difference was generally present when the olfactory stimuli to be remembered were well-known odor objects and loaded with semantic features, thus inviting verbalization. This is in complete accordance with memory research using other types of sensory information, where women excel in episodic memory tasks that allowed verbal processing (Herlitz et al., 1997; 1999; Hyde & Linn, 1988; Lewin et al., 2001). In addition, statistically controlling for odor naming eliminated the female advantage in recognition, highlighting the important role of verbal factors for sex differences in episodic odor memory specifically of familiar odors. This outcome suggests that women's performance in episodic odor memory is largely mediated by their proficiency in odor identification (Cain, 1982; Doty et al., 1984a). Of the unfamiliar olfactory information that is considerably more difficult to verbalize, women and men recognized similar amounts, with the exception that young women also managed to identify more of the unfamiliar odors included than did the young men. Old women and men identified an equal amount of the unfamiliar odors, which was close to null. However, the actual number of identified unfamiliar odors, behind the difference favoring the young women significantly, was very low (Study III). There are several explanations for this female advantage in odor identification. For example, there is a typical sex difference in verbal skills (Hyde & Linn, 1988), in the psychosocial environment that tend to differ for women and men (Cain, 1982), in the modulating role of sex hormones on olfactory and cognitive abilities (Collaer & Hines, 1995; Doty et al., 1985), and possibly also olfactory sensitivity (Deems & Doty, 1987). Studies have established a sex difference in identification ability already from four years of age (Richman et al., 1995), which may be a reflection of an inborn neuroanatomical dimorphic trait that differs between women and men.

The female advantage was also significantly attenuated in episodic odor memory when odor quality discrimination was controlled for, even though there was no reliable difference in odor quality discrimination task between women and men (Study I). Although a smaller obtained effect than for odor identification, the finding suggests that discrimination skills may contribute to women's advantage in odor episodic memory. A possible reason behind this might be that odor quality discrimination activates the same neural areas as working memory functions do (Larsson, 2002; Savic et al., 2000). Jönsson, Møller and Olsson (2011) found that olfactory working memory seems to depend on the ability to discriminate odors. It is possible that this advantage in working memory influences odor quality discrimination in such way that it enables more elaborate processing of the odor to remember. When controlling for reported phase in the menstrual cycle our results suggested that phase in the menstrual cycle is unrelated to olfactory performance. However, women in the ovulatory phase tended to perform better in odor quality discrimination than women in follicular or menstrual phase. But, it is reasonable to treat these data with caution since the sample size is relatively small and the assessment was given at one trial only. The classification of menstrual stages was unrefined, at best, since it is based on number of days from menses in conjunction with cycle length, rendering the determination of stage somewhat imprecise. To be more precise, longitudinal hormonal blood sampling and plasma estimates would have been the preferred method (Browerman, Vogel, Klaiber, Majcher et al., 1981; Dorries, 1992). To conclude, the correlation between quality discrimination and episodic odor memory might partly reflect differences in working memory and in young women also a hormonal influence.

There is an obtained sex difference in rated quality of the odors (Study IV). Women rated the odors as more unpleasant than the men, although their threshold levels did not differentiate. This could be due to different use of the scale, but this explanation appears inconsistent with the fact that the ratings on intensity and irritability are similar. In relation to episodic odor memory performance, the women recognized more odors that were both very unpleasant and neutral in terms of pleasantness than the men who mainly recognized the odors they had rated as very unpleasant. This is of interest considering the notion that not only did the women perceive the odors as potentially more unpleasant. They were also more adept at recognizing odors that they rated as in between pleasant and unpleasant on the rating scale. In other words, they showed a better memory for odors they rated as even slightly unpleasant. In relation to the discussion above, this could be interpreted as a form of additional information regarding the odor that makes it easier to elaborate on. But, this does not explain why there was no difference between women and men for odors perceived as irritable.

The obtained sex differences seem to be primarily cognitively mediated. It is clear that the ability to verbalize is the dominant factor for the female advantage in episodic odor memory. Together with discrimination ability this is what seems to power the female advantage in episodic odor memory.

Additional limitations

Is strict identification rating being too strict?

Strong statements are made concerning the ability to identify odors throughout this thesis. A reservation that could be made in this context concerns the measurement of odor identification. In the method, a strict criterion on what is the correct identification is used (see Assessment of odor identification and forward). But, has an odor really only one correct name? An objection that can be raised is that a particular odor, or object, does not have a single name, meaning or description (e.g., Craik & Lockhart, 1972). How an item is described depends also on how it is discriminated from other items, and how this discrimination takes place is dependent on personal experience and contextual factors, as well as on the sensory, cognitive and demographic factors that are in focus in this thesis. Relatedly, Lehrner and colleagues (1999) investigated odor naming and retention of olfactory information across the life span. They found that odors that were incorrectly named were recognized equally well across age groups, although there was a decrease in recognition across the age range examined for odors that were correctly named. A more nuanced perspective (e.g., veridical, near miss, far miss, omission; Wehling et al., 2010), on odor identification in these studies might have added to the understanding of identification and naming in relation to episodic odor memory.

The representativeness of participants

Noteworthy when interpreting the results put forward in this thesis is that among the included group of adults, the oldest (i.e., around and above average life span) to a great extent belong to the successfully aged (Nordin et al, 2012), and as such the collected material and subsequent results may portray a somewhat higher performance than what would be expected in a randomly selected section of that age group. A reasonable interpretation is that an average age group would perform similarly but at a slightly lower level, but that is merely a hypothesis. To be sure, a randomized sample of the average population would be needed. On the other hand, although efforts were made to make sure that participants were healthy (i.e., rated health, community dwelling, MMSE, sense of smell), all the groups of participants might well include persons suffering from illnesses lacking overt symptoms, somatic (e.g., hypertension, endocrine malfunctions) and psychiatric (e.g., delusions, depression) that can influence the results in unexpected ways. However, when examining the data, no unexpected outliers were found that could have indicated covert illnesses.

Additional thoughts on reported sex differences being based on a sexual dichotomy

The more research on sex and gender (i.e., biological sex, social sex) that is performed, the more it is becoming clear that sex is more multifaceted than previously believed. There is more to it, than only women and men. In terms of genetic and hormonal issues there is a large part of the population that has a ”non-traditional” dichotomy male-female set (e.g., Ainsworth, 2015). This was not controlled for in these studies. Neither was social gender. If these studies were made today, this would have been controlled for. It could be done via blood samples and plasma estimates (e.g., Browerman et al., 1981; Dorries, 1992) to account for hormones, and ideally genetics as well, together with more and other questions in the initial questionnaire (e.g., self-perceived gender). However, the outcome might very well have been exactly the same.

Concluding remarks

The most pervasive finding in this thesis is that episodic odor memory is heavily dependent on odor identification ability. Additional prominent findings are firstly, that the age-related decline in episodic memory and also in odor identification is mainly due to a flattening of the olfactory experience rendering cognitive elaborations and use of semantic memory inaccessible. Secondly, that sex differences in episodic odor memory is mainly present when the olfactory information to be remembered is possible to verbalize (i.e., identify), indicating that women’s advantage in episodic odor memory is chiefly cognitively mediated. Thirdly, those odors subjectively perceived as strong or with a negative hedonic tone are more likely to be remembered. In addition, two findings of unexpected scientific value were obtained. One was that when statistically controlling for olfactory threshold, odor quality discrimination, and cognitive speed, the well-established age-related decline in odor identification disappeared. The other was the oldest participants' apparent compensatory use of trigeminal activation in recognition memory.

Acknowledgments

It is not always clear when something really starts. In this case it probably started long before I was aware of it. As a young psychology student I was obliged to give a short presentation about something related to cognition. By accident I stumbled upon an old slightly funky-looking book in an antiquarian bookshop. It contained a number of cognitive practices and I performed some of them on myself to see if they were a good fit for the presentation. One of them was to make a mental journey and experience the smell of a since long lost place, item or person. I travelled in time and actually sensed a childhood smell merely from my memory. That definitely awoke my interest in memory and olfaction. And this is probably when it started.

Initially, my doctoral work was supported and supervised by Professor Lars Bäckman and Professor Maria Larsson. I am grateful that you invited me to your world of science. The memories of your generosity are firmly embedded in my episodic memory system.

Later during my studies I had the good fortune to be assigned to my supervisor Professor Peter Juslin, possessing both scientific skill and amazing coolness. I am also grateful to my co-supervisor Professor Mats Olsson, whose olfactory expertise has guided me during the last few years. My gratitude also extends to Åke Wahlin for great support in the pursuit of predictors, to Fredrik Jönsson for the hedonic tone, and to Hedvig Söderlund and Anders Winman for many helpful comments.

This work was achieved during a timespan of several years, so the sheer number of people that have encouraged me, and my work, is large. Colleagues at Stockholm Gerontology Research Center and at the Department of Psychology have contributed in many ways, both as scientific sparring partners and as lunch companions.

All my family, in particular my four children, and my close friends have been very supportive. I want to express special gratitude to my late grandmother Ingrid, to whom this book is dedicated. Her devoted love and encouraging curiosity has impregnated me for life and I am deeply grateful for that.

Finally, a very special thanks to my incredibly patient husband and life companion Bo.

Christina Blåvarg

References

Adams, C., Douc, L., Janssens, W., Vanrie, J., & Petermans, A. (2014). Tasting the smell: Effects of ambient scent on scent experts' evaluations of (in)congruent food products. *Food Quality and Preference, 38,* 92–97.

Ahman, M., Holmström, M., Cynkier, I., & Söderman, E. (1996). Work related impairment of nasal function in Swedish woodwork teachers. *Occupational Environmental Medicine, 53*(3), 112–117.

Ainsworth, C.C. (2015). Sex redefined. *Nature, 518*(7539), 288–291.

Åkerlund, A., Bende. M., & Murphy, C. (1995). Olfactory threshold and nasal mucosal changes in experimentally induced common cold. *Acta Otolaryngology, 115*(1), 88–92.

Alaoui-Ismaïli, O., Robin, O., Rada, H., Dittmar, A., & Vernet-Maury, E. (1997a). Basic emotions evoked by odorants: Comparison between autonomic responses and self-evaluation. *Physiology & Behavior, 62*, 713–720.

Alaoui-Ismaïli, O. Vernet-Maury, E., Dittmar, A., Delhomme, G., & Chanel, J. (1997b). Odor hedonics: Connection with emotional response estimated by autonomic parameters. *Chemical Senses, 22*, 237–248.

Amoore, J.E. (1971). Stereochemical and vibrational theories of odour. *Nature, 233*, 279–271.

Amoore, J.E. (1977). Specific anosmia and the concept of primary odors. *Chemical senses and Flavor, 2*, 267–282.

Amoore, J.E. (1986). Effects of chemical exposure on olfcations in humans. In C. S. Barrows (Ed.), *Toxicology of the nasal passage* (pp. 155–190). Washington: Hemisphere Publishing Corporation.

Amoore, J.E. (1991). Specific anosmias. In T. V. Getchell (Ed.), *Smell and taste in health and disease*. New York: Raven Press.

Amoore, J.E. & Ollman, B.G. (1983). Practical test kits for quantitatively evaluating the sense of smell. *Rhinology, 21*(1), 49–54.

Amoore, J.E. & Venstrom, D. (1966). Sensory analysis of odor qualities in terms of stereochemical theory. *Journal of Food Science, 31*, 118–128.

Arshamian, A., Willander, J., & Larsson, M. (2011). Olfactory awareness is positively associated to odour memory, *Journal of Cognitive Psychology, 23*(2), 220–226,

Arshamian, A., Iannilli, E., Gerberc, J.C., Willander, J., Persson, J., Seoa, H.S., Hummel, T., & Larsson, M. (2013). The functional neuroanatomy of odor evoked autobiographical memories cued by odors and words. *Neuropsychologica, 51*(1), 123–131.

Au, R., Joung, P., Nicholas, M., Obler, L.K., Kass, R., & Albert, M.L. (1995). Naming ability across the adult life span. *Aging and Cognition, 2*(4), 300–311.

Ayabe-Kanamura, S., Schicker, I., Laska, M., Hudson, R., Distel, H., Kobayakawa, T., & Saito, S. (1998). Differences in perception of everyday odors: A Japanese-German cross cultural study. *Chemical Senses, 23*, 31–38.

Bäckman, L. & Nilsson, L.G. (1996). Semantic memory functioning across the adult life span. *European Psychologist, 1*, 27–33.

Baddelely, A. (2003). Working memory: looking back and looking forward. *Nature Reviews Neuroscience, 4*, 829–839.

Barber, C.E. (1997). Olfactory acuity as a function of age and gender: A comparison of African and American samples. *Aging and Human Development, 44*, 317–334.

Bensafi, M., Rouby, C., Farget, V., Bertrand, B., Vigouroux, M., & Holley, A. (2002). Autonomic nervous system responses to odours: The role of pleasantness and arousal. *Chemical Senses, 27*, 703–709.

Benton, A.L. & Hamsher, K. (1976). *Multilingual aphasia examination.* Iowa City: University of Iowa Press.

Berglund, B., Berglund, U., Engen, T., & Ekman, G. (1973). Multidimensional analysis of twenty-one odors. *Scandinavian Journal of Psychology, 14*, 131–137.

Bolla, K.I., Lindgren, K.N., Bonaccorsy, C., & Bleecker, M. L. (1990). Predictors of verbal fluency (FAS) in the healthy elderly. *Journal of Clinical Psychology, 26*, 623–628.

Bremner, E.A., Mainland, J.D., Khan, R.M., & Sobel, N. (2003). The prevalence of androstenone anosmia. *Chemical Senses, 28*, 423–432.

Broman, D.A., Olsson, M.J., & Nordin, S. (2001). Lateralization of olfactory cognitive functions. Effects of rhinal side of stimulation. *Chemical Senses, 26*(9), 1187–1192.

Browerman, D.M., Vogel, W., Klaiber, E.L., Majcher, D., Shea, D., & Paul, V. (1981). Changes in cognitive task performance across the menstrual cycle. *Journal of Comparative Physiological Psychology, 95*, 646–654.

Bryant, B. & Silver, W.L. (2000). Chemestesis: the common chemical sense. In F. E. Finger, W. L. Silver, & D. Restrepo (Eds.), *The neurobiology of taste and smell, 2nd ed.* (pp. 73–100). New York: Wiley-Liss.

Buchner, R. L. & Tulving E. (1995). Neuroimaging studies of memory: Theory and recent PET results. In F. Boller & J. Grafman (Eds.), *Handbook of Neuropsychology, 10* (pp. 439–446). Elsevier Science B. V.

Buck, L. (2000). Smell and taste: The chemical senses. In E. R. Kandel, J. H. Schwartz, & T. M. Jessel (Eds.), *Principles of neural science, 4th ed*. (pp. 625–647). New York, NY: Mc Graw Hill.

Buck. L. & Axel, R. (1991). A novel multigene family may encode odorants receptors: A molecular basis for odor recognition. *Cell, 65*, 175–187.

Bushdid, C., Magnasco, M.O., Vosshall, L.B., & Keller, A. (2014). Humans Can Discriminate More than 1 Trillion Olfactory Stimuli. *Science, 343*, 1370.

Cahill, L. & McGaugh, J.L. (1998). Mechanisms of emotional arousal and lasting declarative memory. *Trends in neuroscience, 21*(7), 294–299.

Cain, W.S. (1969). Odor intensity: Differences in the exponent of the psychophysical function. *Perception & psychophysics, 6*(6), 349–354.

Cain, W.S. (1978). History of research on smell. In E. C. Carterette & M. P. Friedman (Eds.), *Handbook of Perception, Vol. 6A, Tasting and Smelling* (pp. 197–222). New York: Academic.

Cain, W.S. (1982). Odor identification by males and females: prediction vs performance. *Chemical Senses, 7*(2), 129–142.

Cain, W.S., Cometto-Muñiz, J.E., & de Wijk, R.A. (1992). Techniques in the quantitative study of human olfaction. In M. J. Serby & K. L. Chobor (Eds.), *Science of Olfaction* (pp. 279–308). New York Berlin: Springer-Verlag.

Cain, W.S., de Wijk, R., Lulejian, C., Schiet, F., & See, L.C. (1998). Odor identification: Perceptual and semantic dimensions. *Chemical Senses, 23*, 309–26.
Cain, W.S. & Gent, J.F. (1991). Olfactory sensitivity: Reliability, generality, and association with aging. *Journal of Experimental Psychology: Human Perception and Performance, 17*, 382–391.
Cain, W.S., Gent, J.F., Goodspeed, R.B., & Leonard, G. (1988). Evaluation of olfactory dysfunction in the Connecticut chemosensory clinical research center. *The Laryngoscope*, *98*(1), 83–88.
Cain, W.S. & Krause, R.J. (1979). Olfactory testing: Rules for odor identification. *Neurological Research, 1*(1), 1–9.
Cain, W.S. & Potts, B.C. (1996). Switch and bait: Probing the discriminative basis of odor identification via recognition memory. *Chemical Senses, 21*, 35–44.
Cain, W.S & Stevens, J.C. (1989). Uniformity of olfactory loss in aging. *Annals of New York Academi of Science, 561*, 29–38
Cain, W.S., de Wijk, R.A., Nordin, S., & Nordin, M. (2008). Independence of odor quality and absolute sensitivity in a study of aging. *Chemical Perception, 1*, 24–33.
Chrea, C., Valentin, D., Sulmont-Rossé, C., Ly Mai, H., Hoang Nguyen, D., & Abdi, H. (2004). Culture and odor categorization: agreement between cultures depends upon the odors. *Food quality and preference, 15*(7), 669–679.
Chu, S. & Downes, J.J. (2002). Proust nose best: Odors are better cues of autobiographical memory. *Memory & Cognition, 30*(4), 511–518.
Collaer, M.L. & Hines, M. (1995). Workplace, age, and sex as mediators of olfactory functioning: Data from the National Geographic Smell Survey. *Journal of Gerontology, 50*, 179–186.
Corwin, J. (1992). Assessing olfaction: Cognitive and measurement issues. In M. J. Serby & K. L. Chobor (Eds.), *Science of olfaction* (pp. 335–354). New York Berlin: Springer-Verlag.
Corwin, J., Loury, M., & Gilbert, A.N. (1995). Workplace, age, and sex as mediators of olfactory function: data from the National Geographic Smell Survey. *Journal of Gerontology, 50*, 179–186.
Craik, F.I.M. & Lockhart, R.S. (1972). Levels of processing: A framework for memory research. *Journal of Verbal Learning and Verbal Behavior, 11*, 671–684.
Croy, I., Symmank, A., Schellong, J., Hummel, C., Gerber, J., Joraschky, P., & Hummel, T. (2014). Olfaction as a marker for depression in humans. *Journal of Affective Disorders, 160*, 80–86.
Crowder, R.G. & Schab, F.R. (1995). *Memory for odors.* Mahwah, N.J.: Erlbaum,
Dalton, P. (1996). Odor Perception and Beliefs about Risk. *Chemical Senses, 21*(4), 447–458.
Deems, D.S. & Doty, R.L. (1987). Age-related changes in the phenyl ethyl alcohol odors detection threshold. *Transaction Pennsylvania Academy Opthalmol Otalryngology, 39*(1), 646–650.
Deems, D.A., Doty, R.L., Settle, R.G., Moore-Gillon, V., Shaman, P., Mester, A.F., Kimmelman, C.P., Brightman, V.J., & Snow Jr, J.B. (1991). Smell and taste disorders, A study of 750 patients from the University of Pennsylvania Smell and Taste Center. *Archives of otolaryngology - head & neck surgery, 117*(5), 519–528.
Devanand, D.P., Michaels-Marston, K.S., Liu, X., Pelton, G.H., Padilla, M., Marder, K., Bell, K., Stern, Y., & Mayeux, R. (2000). Olfactory deficit in patients with mild cognitive impairment predict Alzheimer’s disease at follow-up. American *Journal of Psychiatry, 157*, 1399–1405.

de Wijk, R.A. & Cain, W.S. (1994). Odor quality: discrimination vs. free and cued identification. *Perception and Psychophysics, 56*, 12–18.
de Wijk, R.A., Schab, F.R., & Cain, W.S. (1995) Odor identification. In R. G. Crowder & F. R. Schab (Eds.), *Memory for Odors* (pp. 21–37). Hillsdale, NJ: Lawrence Erlbaum Associates.
Distel, H., Ayabe-Kanamura, S., Martinez-Gómez, M., Schicker, I., Kobayakawa, T., Saito, S., & Hudson, R. (1999). Perception of everyday odors - Correlation between intensity, familiarity and strength of hedonic judgement. *Chemical Senses, 24*(2), 191–199.
Distel, H. & Hudson, R. (2001). Judgement of odor intensity is influenced by subjects' knowledge of the odor source. *Chemical Senses, 26*(3), 247–251.
Djordevic, J., Jones-Gotman, M., De Sousa, K., & Chertkow, H. (2008). Olfaction in patients with mild cognitive impairment and Alzheimer's disease. *Neurobiology of Aging, 29*(5), 693–706
Dooley, R. (2011). *Brainfluence: 100 ways to persuade and convince consumers with neuromarketing.* John Wiley & Sons Inc.
Dorries, K.M. (1992). Sex differences in olfaction in mammals. In M. J. Serby & K. L. Chobor (Eds.), *Science of olfaction.* New York Berlin: Springer-Verlag.
Doty, R.L. (1976). *Mammalian olfaction, reproductive processes, and behavior.* New York: Academic Press.
Doty, R.L. (1989). Age-related alterations in taste and smell function. In J. C. Goldstein, H. K., Kashima, & C. F. Koopman Jr. (Eds.), *Geriatric otorhinolaryngology* (pp. 97–104). Burlingston: B. C. Decker.
Doty, R.L. (1991). Olfactory system. In T. V. Getchell (Ed.), *Smell and taste in health and disease.* New York: Raven Press.
Doty, R.L. (1992). Psychophysical measurement of odor perception in humans. In D. G. Laing, R. L. Doty, & W. Breipohl (Eds.), *The human sense of smell* (pp. 95–134). Berlin: Springer-Verlag.
Doty, R.L. & Cameron, E.L. (2009). Sex differences and reproductive hormones influences on human odor perception. *Physiology & Behavior, 97*, 213–228.
Doty, R.L., Hall, J.W., Flickinger, G.L., & Sondheimer, S.J. (1982). Cyclial changes in olfactory and auditory sensitivity during menstrual cycle: no attenuation by oral contraceptive medication. In W. Breipohl (Ed.), *Olfaction and endocrine regulation* (pp. 35–34). London: IRL Press.
Doty, R.L., Gregor, T.P., & Settle, R.G. (1986). Influence of intertrial interval and sniff-bottle volume on phenyl ethyl alcohol odor detection thresholds. *Chemical Senses, 11*, 259–264.
Doty, R.L. & Kamath, V. (2014). The influences of age on olfaction: a review. *Frontiers in Psychology, 5*(20).
Doty, R.L., Shaman, P., Applebaum, S.L., Giberson, R., Sikorski, L., & Rosenberg, L. (1984a). Smell identification ability: changes with age. *Science, 226*, 1441–1443.
Doty, R.L., Shaman, P., & Dann, M. (1984b). Development of the University of Pennsylvania Smell Identification Test: A standardized microencapsulated test of olfactory function. *Physiology & Behavior, 32*, 3.
Doty, R.L., Applebaum, S.L., Zusho, H., & Settle, R.G. (1985). Sex differences in odor identification ability: a cross-cultural analysis. *Neuropsychologia, 23*(5), 667–672.
Dulay, M.F., Gesteland, R.C., Shear, P.K., Ritchey, P.N., & Frank, R.A. (2008). Assessment of the influence of cognition and cognitive processing speed on three tests of olfaction. *Journal of Clinical and Experimental Neuropsychology, 30*(3), 327–337.

Dulay, M.F. & Murphy, C. (2002). Olfactory acuity and cognitive function converge in older adulthood: Support for the common cause hypothesis. *Psychology and Aging, 17*, 392–404.
Duzel, E., Yonelinas, A.P., Mangun, G.R., Heinze, H.J., & Tulving, E. (1997). Event-related brain potential correlates of two states of conscious awareness in memory*, Proceedings of the National Academy of Science of the United States of America, 94*(11), 5973–5978.
Eldrige, L.L., Knowlton, B.J., Furmanski, C.S., Bookheimer, S.Y., & Engel, S.A. (2000). Remembering episodes: a selective role for the hippocampus during retrieval. *Nature Neuroscience, 3*, 1149–1152.
Elliot, P.B. (1964). Appendix 1: Tables of d'. In J. A. Swets (Ed.), *Signal detection and recognition by human observers* (pp. 659–678). New York: Wiley.
Engen, T. (1987). Remembering odors and their names. *American Scientist, 75*, 497–503.
Engen T. 1988. The acquisition of odour hedonics. In S. Van Toller & G. H. Dodd (Eds.), *Perfumery: the psychology and biology of fragrance* (pp.79–90). London: Chapman and Hall.
Eskenazi, B., Cain, W.S., & Friend, K. (1983). Exploration of olfactory aptitude. *Bulletin of the Psychonomic Society, 24*, 203–206.
Evans, W.J., Cui, L., & Starr, A. (1995). Olfactory event-related potentials in normal human subjects: effects of age and gender. *Electroencephalography and clinical Neurophysiology, 95*, 293–301
Ferdenzi, C., Roberts, C.S., Schirmer, A., Delplanque, S., Cekic, S., Porcherot, C., Cayeux, I., Sander, D., & Grandjean, D. (2012). Variability of affective responses to odors: Culture, gender, and olfactory knowledge. *Chemical Senses, 38*, 175–186.
Finkel, D., Pedersen, N.L, & Larsson, M. (2001). Olfactory functioning and cognitive abilities: A twin study. *Journal of Gerontology: Psychological Sciences, 56B*, 226–233.
Fiore A.M. & Kim, S. (1997). Olfactory cues of appearance affecting impressions of professional image of women. *Journal of Career Development, 23*(4), 247–263.
Folstein, M.G., Folstein, S.E., & McHugh, P.R. (1975). "Mini-mental state". A practical method for grading the cognitive state of patients for the clinician. *Journal of Psychiatiric Research, 12*, 189–198.
Fornazieri, M.A., dos Santos, C.A., Bezerra, T.F., Pinna, F.D.R., Voegels, R.L., & Doty, R.L. (2015). Development of normative data for the Brazilian adaptation of the University of Pennsylvania Smell Identification Test. *Chemical Senses, 40*(2), 141–149.
Frank, R.A., Dulay, M.F., & Gesteland, R.C. (2003). Assessment of the Sniff Magnitude Test as a clinical test of olfactory function. *Physiology & Behavior, 78*(2), 195–204.
Frank, R.A., Rybalsky, K., Brearton, M., & Mannea, E. (2011). Odor recognition memory as a function of odor naming performance. *Chemical Senses, 36*, 29–41.
Frasnelli, J., Schuster, B., & Hummel, T. (2007). Inteactions between olfaction and the trigeminal system: What can be learned from olfactory loss. *Cerebral Cortex, 17*, 2268–2275.
Frye, R.E., Schwartz, B.S., & Doty, R.L. (1990). Dose-related effects of cigarette smoking on olfactory function. *The Journal of the American Medical Association, 263*(9), 1233–1236.
Gardiner, J.M. (1988). Functional aspects of recollective experience. *Memory and Cognition, 16*, 309–313.

Gardiner, J.M. & Conway, M.A. (1999). Levels of awareness and varieties of experience. In B. H. Challis & B. M. Velichkovsky (Eds.), *Stratification in cognition and consciousness. Advances in consciousness research* (pp. 237–254). Amsterdam, Netherlands: John Benjamins Publishing Company.

Gardiner, J.M. & Java, R.I. (1991). Forgetting in recognition memory with and without recollective experience. *Memory and Cognition, 19*, 617–623.

Gardiner, J.M. & Parkin A.J. (1990). Attention and recollective experience in recognition memory. *Memory & Cognition, 18*(6), 579–583.

Gardiner, J.M., Ramponi C., & Richardson-Klavehn, A. (2002). Recognition memory and decision processes: A meta-analysis of remember, know and guess responses. *Memory, 10*(2), 83–98.

Garzia-Falgueras, A., Junque, C., Giménez, M. Caldú, X., Segovia, S., & Guillamon, A. (2006). Sex differences the human olfactory system. *Brain Research, 1116,* 103–111.

Gheusi, G. & Lledo, P.M. (2014). Adult neurogenesis in the olfactory system shapes odor memory and perception. *Progress in Brain Research, 208*, 157–175.

Green, B.G. & Lawless, H.T. (1991). The psychophysics of somatosensory chemoreceptor in the nose and mouth. In T. V. Getchell (Ed.), *Smell and taste in health and disease.* New York: Raven Press.

Gottfried, J.A. (2007). What can an orbitofrontal cortexendowed animal do with smells? *Annals of the New York Academy of Sciences, 1121*, 102–120.

Gupta, P. & Cohen, N.J. (2002). Theoretical and computational analysis of skill learning, repetition priming, and procedural memory. *Psychological Review, 109*(2), 401–448.

Guyton A.C. (1991). *Textbook of medical physiology. 8th Edition.* Philadelphia, PA: Saunders.

Hawkes, C. (2003). Olfaction in neurodegenerative disorder. *Movement Disorders, 18*(4), 364–372.

Hawking, S. (1988). *A brief history of time. From the big bang to black holes.* Bantam Books.

Hedner, M., Larsson, M., Arnold, N., Zucco, G.M., & Hummel, T. (2010). Cognitive factors in odor detection, odor discrimination, and odor identification tasks. *Journal of Clinical and Experimental Neuropsychology, 32*(10), 1062–1067.

Herlitz, A., Nilsson, L.G., & Bäckman, L. (1997). Gender differences in episodic memory. *Memory & Cognition, 25*, 801–811.

Herlitz, A., Airaksinen, E., & Nordström, E. (1999). Sex differences in episodic memory: The impact of verbal and visuospatial ability. *Neuropsychology, 13*(4), 590–597.

Herz, R.S. (2001). Ah, sweet skunk: Why we like or dislike what we smell. *Cerebrum, 3*, 31–47.

Herz, R.S. & Engen, T. (1996) Odor memory: review and analysis. *Psychonomic Bulletin & Review, 3*, 300–313

Herz, R.S. & von Clef, J. (2001). The influence of verbal labeling on the perception of odors: Evidence for olfactory illusions? *Perception, 30*, 381–391.

Herz, R.S., Eliassen, J., Beland, S., & Souza, T. (2004). Neuroimaging evidence for the emotional potency of odor-evoked memory. *Neuropsychologia, 42*, 371–378

Hochhaus, L. (1972). A table for the calculation of d' and BETA. *Psychological Bulletin, 77*, 375–376.

Hultsch, D.F. & Dixon, R.A. (1990). Learning and memory in aging. In J. E. Birren & K. W. Schaie (Eds.), *Handbook of the psychology of aging, 3rd ed.* (pp. 258–274). San Diego, CA, US: Academic Press.

Hummel, T., Sekinger, B., Wolf, S.R., Pauli, E., & Kobal, G. (1997). Sniffin' Sticks': Olfactory performance assessed by the combined testing of odor identification, odor discrimination and olfactory threshold. *Chemical Senses, 22*(1), 39–52.

Hyde, J.S. & Linn, M.C. (1988). Gender differences in verbal ability: A meta-analysis. *Psychological Bulletin, 104*, 53–69.

Jacoby, L.L. (1991). A process dissociation framework: Separating automatic from intentional uses of memory. *Journal of Memory and Language, 30*, 513–541.

James, W. (1890). *Principles of Psychology.* Internet resource: http://psychclassics.yorku.ca/James/Principles/ 2015-09-24.

Jehl, C., Royet, J.P., & Holley, A. (1997). Role of verbal encoding in short- and long-term odor recognition. *Perception and Psychophysics, 59*, 100–110.

Johnson, B.N. & Sobel, N. (2007). Methods for building an olfactometer with known concentration outcomes. *Journal of Neuroscience Methods, 160*, 231–245.

Jönsson, F., Møller, P., & Olsson, M.J. (2011). Olfactory working memory: effects of verbalization on the 2-back task. *Memory & Cognition, 39*, 1023–1032.

Jönsson, F. & Olsson, M.J. (2003). Olfactory metacognition. *Chemical Senses, 28*, 651–658.

Jönsson, F., Tchekhova, A., Lönner, P., & Olsson, M.J. (2005). A metamemory perspective on odor naming and identification. *Chemical Senses, 30*, 353–365.

Kausler, D.H. (1994). *Learning and memory in normal aging.* San Diego: Academic.

Kensinger, E.A. (2007). Negative emotion enhances memory accuracy: Behavioral and neuroimaging evidence. *Current Directions in Psychological Science, 16*(4), 213–218.

Kjelvik G., Evensmoen H., Brezova V., & Håberg, A.K. (2012). The human brain representation of odor identification. *Journal of Neurophysiology, 108*, 645–657

Koelega, H.S. (1994). Sex differences in olfactory sensitivity and the problem of the generality of smell acuity. *Perceptual and Motor Skills, 78*, 203–213.

Køling, A. (1986). Luktsinne och lukt hos människan. *Draco pro Medico, 5–6*.

Konstantinidis, I., Hummel, T., & Larsson, M. (2006). Identification of unpleasant odors is independent of age. *Archives of Clinical Neuropsychology, 21*, 615–621.

Laing, D.G. (1986). Identification of single dissimilar odors is achieved with a single sniff. *Physiology & Behavior, 37*, 163–179.

Larsson. E. & Westberg, J. (2015). *Utbildningshistoria – en introduktion.* Lund: Studentlitteratur.

Larsson, M. (1997). The influence of semantic factors in episodic recognition of common odors: A review. *Chemical Senses, 22*, 623–633.

Larsson, M. (2002). Odor memory: A memory systems approach. In C. Rouby, B. Schaal, D. Dubois, R. Gervais, & A. Holley (Eds.), *Olfaction, Taste, and Cognition* (pp. 231–245). New York: Cambridge University Press.

Larsson, M. & Bäckman, L. (1993). Semantic activation and episodic odor recognition in young and older adults. *Psychology and Aging, 8*, 582–588.

Larsson, M. & Bäckman, L. (1997). Age-related differences in episodic odour recognition: The role of access to specific odour names. *Memory, 5*, 361–378.

Larsson, M. & Bäckman, L. (1998). Semantic mediation of age-related deficits in recognition of common odors. *Annals of the New York Academy of Sciences, 855*, 675–680.

Larsson, M., Finkel, D., & Pedersen, N. L. (2000). Odor identification: Influences of age, gender, cognition, and personality. *Journal of Gerontology: Psychological Sciences, 55B*, 304–310.

Larsson, M., Hedner, M., & Olofsson, J. (2009). Differential age and sex effects in semantic recognition of odors and words. *Acta Psychologica Sinica, 41*(11), 1049–1053.

Larsson, M., Nilsson, L.G., Olofsson, J., & Nordin, S. (2004). Demographic and cognitive predictors of cued odor identification: Evidence from a population-based study *Chemical Senses, 29*, 547–554.

Larsson, M., Lövdén, M., & Nilsson, L.G. (2003a). Sex differences in recollective experience for olfactory and verbal information. *Acta Psychologica, 112*, 89–103.

Larsson, M., Nyberg, L., Bäckman, L., & Nilsson, L.G. (2003b). Effects on episodic memory of stimulus richness, intention to learn, and extra-study repetition: Similar profiles across the adult life span. *Journal of Adult Development, 10*, 67–73.

Lawless, H. & Engen, T. (1977). Associations to odors: Interference, mnemonics, and verbal labeling. *Journal of Experimental Psychology: Human Learning and Memory, 3*(1), 52–59.

Lehrner, J.P. (1993). Gender differences in long-term odor recognition memory: verbal versus sensory influences and the consistency of label use. *Chemical Senses, 18*, 17–26.

Lehrner, J.P., Glück, J., & Laska, M. (1999). Odor identification, consistency of label use, olfactory threshold, and their relationships to odor memory over the human life span. *Chemical Senses, 24*, 337–346.

LeMagnen, J. (1944). Étude des facteurs dynamique de l'excitation olfactive. *L'année psychologique, 45–46*, 77–89.

LeMagnen, J. (1952). Les phénomène olfacto-sexuels chez l'homme. *Archives de Science Physiologiques, 6*, 125–160.

Lewin, C., Wolgers, G., & Herlitz, A. (2001). Sex differences favoring women in verbal but not in visuospatial episodic memory. *Neuropsychology, 15*, 165–173

Lezak, M. (1995). *Neuropsychological assessment, 3rd ed.* New York: Oxford University Press.

Loo, A.T., Youngentob, S.L., Kent, P.F., & Schwob, J.E. (1996). The aging olfactory epithelium: Neurogenesis, response to damage, and odorant-induced activity. *International Journal of Developmental Neuroscience, 14*, 881–900.

Lötsch, J., Reichman, H., & Hummel, T. (2008). Different odor test contribute differently to the evaluation of olfactory loss. *Chemical Senses, 33*, 17–21.

Lundervold, A.J., Wollschläger, D., & Wehling, E. (2014). Age and sex related changes in episodic memory function in middle aged and older adults. *Scandinavian Journal of Psychology, 55*(3), 225–232.

Lundström, J.N., Boyle, J.A., Zatorre, R.J., & Jones-Gotman, M. (2009). The neuronal substrates of human olfactory based kin recognition. *Human Brain Mapping, 30*, 2571–2580.

Lundström, J.N., McClintock, M.K., & Olsson, M.J. (2006). Effects of reproductive state on olfactory sensitivity suggest odor specificity. *Biological Psychology, 71*(3), 244–247.

Lundström, J.N., Seven, S., Olsson, M.J., Schaal, B., & Hummel, T. (2006). Olfactory event-related potentials reflect individual differences in odor valence perception. *Chemical Senses, 31*, 705–711.

Lyman, B.J. & McDaniel. M.A. (1986) Effects of encoding strategy on long-term memory for odours. Human memory. *Quarterly Journal of Experimental Psychology: Human Experimental Psychology, 38*(4A), 753–765.

Lyman, B.J. & McDaniel, M.A. (1990). Memory for odors and odor names: Modalities of elaboration and imagery. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 16*, 656–664.

Maccoby, E. & Jacklin, C. (1974). *The psychology of sex differences.* Stanford, CA: Stanford University Press.

Mäntylä, T. (1993). Knowing but not remembering: Adult age differences in recollective experience. *Memory and Cognition, 21*, 379–388.

Mäntylä, T. (1997). Recollection of faces: Remembering differences and knowing similarities. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 23*, 1203–1216.

Markovic, K., Reulbach, U., Vassiliadu, A., Lunkenheimer, J., Lunkenheimer, B., Spannenberger, R., & Tuernauf, N. (2007). Good news for elderly persons: Olfactory pleasure increases at later stages of the life span. *The Journals of Gerontology. Series A, Biological Sciences and Medical Sciences, 62*, 1287–1293.

Mair, R.G., Bouffard, J. A., Engen, T., & Morton, T.H. (1978). Olfactory sensitivity during the menstrual cycle. *Sensory Processes, 2*, 90–98.

Morrison, M., Gan, S., Dubelaar, C., & Oppewal, H. (2011). In-store music and aroma influences on shopper behavior and satisfaction. *Journal of Business Research*, *64*(6), 558–564.

Moscovitch, M. (1995). Recovered consciousness: A hypothesis concerning modularity and episodic memory. *Journal of Clinical and Experimental Neuropsychology, 17*(2), 276–290.

Moscovitch, M., Nadel L., Wincour, G., Gilboa, A., & Rosenbaum, R.S. (2006). The cognitive neuroscience of remote episodic, semantic and spatial memory. *Current Opinion in Neurobiology, 16*, 179–190.

Moskowitz, H.R., Dravniek, A., Cain, W. S., & Turk, A. (1976). Standardized procedure for expressing odor intensity. *Chemical Senses and Flavor, 1*, 235–237.

Murphy, C., Cain, W.S., Gilmore, M.M., & Skinner, R.B. (1991). Sensory and semantic factors in recognition memory for odors and graphic stimuli: Elderly vs. young persons. *American Journal of Psychology, 104*, 161–192.

Nadel, L., Samsonovich, A., Ryan, L., & Moscovitch, M. (2000). Multiple trace theory of human memory: Computational, neuroimaging, and neuropsychological results. *Hippocampus, 10*(4), 352–368.

Nguyen, L.A., Ober, B.A., & Shenaut. G.K. (2012). Odor Recognition Memory: Two Encoding Trials are Better Than One. *Chemical Senses, 37*, 745–754.

Nordin, S., Almkvist, O., & Berglund, B. (2012). Is loss in odor sensitivity inevitable to the aging individual? A study of "Successfully Aged" elderly. *Chemical Perception, 5*, 188–196.

Nordin, S., Claeson, A.S., Andersson, M., Sommar, L., Andrée, J., Lundqvist, K., & Andersson, L. (2013). Impact of health-risk perception on odor perception and cognitive performance. *Chemical Perception, 6*, 190–197.

Nyberg, L., Bäckman, L., Erngrund, K., Olofsson, U., & Nilsson, L.G. (1996a). Age differences in episodic memory, semantic memory, and priming: relationships to demographic, intellectual, and biological factors. *Journal of Gerontology: Psychological Sciences, 51B*, 234–240.

Nyberg, L., Cabeeza, R., & Tulving, E. (1996b). PET studies of encoding and retrieval: The HERA model. *Psychonomic Bulletin & Review, 3*(2), 135–148.

Oliveira Pinto, A.V., Santos, R.M., Couthino, R.A., Oliviera, L.M., Santos, G.B., Alho, A.T.L., Leite, R.E.P., Farfel, J.M., Suemoto, C.K., Grinberg, L.T., Pasqualucci, C.A., Jacobi-Filho, W., & Lent, R. (2014). Sexual dimorphism in the human olfactory bulbs: Females have more neurons and glial cells than males. *PLoS ONE, 9*(11).

Olofsson J.K. & Nordin, S. (2004). Gender differences in chemosensory perception of event-related potentials. *Chemical Senses, 29*, 629–637.

Olofsson, J.K., Bowman, N.E., Khatibi, K., & Gottfried, J.A. (2012). A time-based account of the perception of odor objects and valences. *Psychological Science, 23*(10), 1224–1232.

Olofsson, J.K., Rönnlund, M., Nordin, S., Nyberg, L., Nilsson, L.G., & Larsson, M. (2009). Odor identification deficit as a predictor in five-year global cognitive change: Interactive effects with age and ApoE-e4. *Behavioral Genetics, 39*, 496–503.

Olsson, M.J., Lundström, J.N., Kimball, B.A., Gordon, A.R., Karshikoff, B., Hosseini, N., Sorjonen, K., Höglund, C.O., Solares, C., Soop, A., Axelsson, J., & Lekander, M. (2014). The scent of disease: Human body odor contains an early chemosensory cue of sickness. *Psychological Science, 25*(3), 817–823.

Olsson, M.J., Lundgren, J.N., Soares, S.C., & Johansson, M. (2009). Odor memory performance and memory awareness: A comparison to word memory across orienting tasks and retention intervals. *Chemical Perception, 2*, 161–171.

Olsson, P. & Laska, M. (2010). Human male superiority in olfactory sensitivity to the sperm attractant odorant bourgeonal. *Chemical Senses, 35*, 427–432.

Pade, J. & Hummel, T. (2008). Olfactory functioning following nasal surgery. *Laryngoscope, 118*(7), 1260–1264.

Parkin, A.J. & Walter, B.M. (1992). Recollective experience, normal aging, and frontal dysfunciton. *Psychology & Aging, 7*(2), 290–298.

Pause, B.M., Lübke, K., Laudien, J.H., & Ferstl, R. (2010). Intensified neuronal investment in the processing of chemosensory anxiety signals in non-socially anxious and socially anxious individuals. *PLoS ONE 5*(4).

Penn, D. & Potts, W.K. (1998). Chemical signals and parasite mediated sexual selection. *Trends in Ecology & Evolution, 13*, 391–396.

Perlmuter, L.C., Tun, P., Sizer, N., McGlinchey, R.E., & Nathan, D.M. (1987). Age and diabetes related changes in verbal fluency. *Experimental Aging Research, 13*, 9–14.

Persson, J. (2015). Making head or tail of the hippocampus. A long-axis account of episodic and spatial memory. *Digital Comprehensive Summaries of Uppsala Dissertations from the Faculty of Social Sciences 114*. Uppsala University.

Plato, *Timeus.* On: Stanford Encyclopedia of Philosophy. http://plato.stanford.edu/entries/plato-timaeus/ 2015-09-24.

Porter, R.H., Cernoch, J.M., & Balogh, R.D. (1985). Odor signatures and kin recognition. *Physiology & Behavior, 34*(3), 445–448.

Postuma, R. & Gagnon, J.F. (2010). Cognition and olfaction in Parkinson's disease. *Brain, 133*, 1–2.

Price, J.L., Davis, P. B., Morris, J.C., & White, D.L. (1991). The distribution of tangles, plaques, and related immunohistochemical markers in healthy aging and Alzheimer's disease. *Neurobiology of Aging, 12*, 295–312.

Prolitec (2015). Advanced air treatment systems. www.prolitec.com 2015-09-15.

Punter, P.H. (1983). Measurement of human olfactory thresholds for several groups of structurally related compounds. *Chemical Senses, 7*, 215–235.

Rabin, M.D. (1988). Experience facilitates olfactory quality discrimination. *Perception & Psychophysics, 44*, 532–540.

Rabin, M.D. & Cain, W.S. (1986). Determinants of measured olfactory sensitivity. *Perception & Psychophysics, 39*, 281–286

Rajaram, S. (1993). Remembering and knowing: Two means of access to the personal past. *Memory and Cognition, 21*, 89–102.

Rajaram, S. & Roediger, H.L.III. (1996). Remembering and knowing as states of consciousness during retrieval. In J. D. Cohen & J. W. Schooler (Eds.), *Scientific approaches to the question of consciousness*. Hillsdale, NJ: Erlbaum.

Rawson, N.E., Gomez, G., Cowart, B., & Restrepo, D. (1998). The use of olfactory receptor neurons (ORNs) from biopsies to study changes in aging and neurodegenerative disease. *Annals of the New York Academy of Sciences, 855*, 701–707.

Reitan, R.M. & Davidson, L.A. (1974). *Clinical neuropsychology: Current Status and Applications*. New York: John Wiley.

Renfro, K.J. & Hoffmann, H. (2013). The relationship between oral contraceptive use and sensitivity to olfactory stimuli. *Hormones and Behavior, 63*(3), 491–496.

Richardson, J.T.E. & Zucco, G.M. (1989). Cognition and olfaction: A review. *Psychological Bulletin, 105*(3), 352–360.

Richman, R.A., Wallace, K., & Sheehe, P. R. (1995). Assessment of an abbreviated odorant identification task for children: A rapid screening device for schools and clinics. *Acta Paediatrica, 84*, 434–37.

Robin, O., Alaoui-Ismaili, O., Dittmar, A., & Vernet-Maury, E. (1999). Basic emotions evoked by eugenol odor differ according to the dental experience. A neurovegetative analysis. *Chemical Senses, 24*, 327–335.

Rouby, C., Pouliot, S., & Bensafi, M. (2009). Odor hedonics and their modulators. *Food Quality and Preference, 20*, 545–549.

Royet, J.P., Delon-Martin, C., & Plailly, J. (2013). Odor mental imagery in non-experts in odors: a paradox? *Frontiers in Human Neuroscience, 7*(87), 1–6

Salthouse T.A. (1991). Mediation of adult age differences in cognition by reductions in working memory and speed of processing. *Psychological Science, 2*, 179–183.

Salthouse, T.A. (1995). Aging, inhibition, working memory, and speed. *Journal of Gerontology: Psychological Sciences, 50B*, 297–306.

Salthouse, T.A. (2000). Aging and measures of processing speed. *Biological Psychology, 54*, 35–54.

Salthouse, T.A. & Babcock, R.L. (1991). Decomposing adult age differences in working memory. *Developmental Psychology, 27*, 763–776.

Salthouse, TA., Toth, J.P., Hancock, H.E, & Woodard, J.L. (1997). Controlled and automatic forms of memory and attention: Process purity and the uniqueness of age-related influences. *Journal of Gerontology: Psychological Sciences, 52B*(5), 216–228.

Savic, I., Gulyas, B., Larsson, M., & Roland, P. (2000). Olfactory functions are mediated by parallel and hierarchical processing. *Neuron, 26*, 735–745.

Saive, A.L., Royet, J.P., & Plailly, J. (2014). A review on the neural bases of episodic odor memory: from laboratory-based to autobiographical approaches. *Frontiers of Behavioral Neuroscience, 8*, 240.

Schab, F.R. (1991). Odor memory: Taking stock. *Psychological Bulletin, 2*, 242–251.

Schacter, D.L. (1990). Perceptual representations systems and implicit memory. *Annals of the New York Academy of Sciences, 608*, 543–571.

Schacter, D.L. & Tulving E. (1994). *Memory Systems.* Cambridge: Bradford book.

Schemper, T., Voss, S., & Cain, W.S. (1981). Odor identification in young and elderly persons: Sensory and cognitive limitations. *Journal of Gerontology, 36*, 446–452.

Schleidt, M., Hold, B., & Attili, G. (1981). A cross-cultural study in the attitude towards personal odor. *Journal of Clinical Ecology, 7*, 19–31.

Schneider, R.A., Costiloe, J.P., Howard, R.P., & Wolf, S. (1958). Olfactory perception thresholds in hypogonadal women: changes accompanying administration of androgen and estrogen. *Journal of Clinical Endocrinology, 18*, 379–390.

Schriever, V.A., Lehmann, S., Prange, J., & Hummel, T. (2014). Preventing olfactory deterioration: Olfactory training may be of help in older people. *Journal of the American Geriatrics Society, 62*(2), 384–386.

Schriever, V.A., Reiter, N., Gerber, J., Iannilli, E., & Hummel, T. (2012). Olfactory bulb volume in smokers. *Experimental Brain Research, 225*(2), 153–157.

Seiden, A.M. (2004). Postviral olfactory loss. *Otolaryngologic Clinics of North America, 37*(6), 1159–1166.

Semb, G. (1968). The detectability of the odor of butanol. *Perception & Psychophysics, 4*(6), 335–340.

Serby, M.J. & Chobor, K.L. (1992). *Science of Olfaction.* New York Berlin: Springer-Verlag.

Seubert, J., Freiherr, J., Djordjevic, J., & Lundström, J.N. (2013). Statistical localization of human olfactory cortex. *NeuroImage, 66*, 333–342.

Shemshadi, H., Azimian, M., Onsosri, M. A., & Farahani, M. (2008). Olfactory function following open rhinoplasty: A 6-month follow up-study. *BMC Ear Nose Troat Discorders, 8*(6).

Ship, J.A., Pearson, J.D., Cruise, L.J., Brant, L.J., & Metter, E.J. (1996). Longitudinal changes in smell identification. *Journal of Gerontology: Medical Sciences, 51A*, 86–91.

Sobel, N., Khan, R.M., Saltman, A., Sullivan, E.V., & Gabrieli, J.D.E. (1999). The world smells different to each nostril. *Nature, 402*, 35.

Sobel, N., Prabhakaran, V., Desmond, J.E., Glover, G.H., Goode, R.L., Sullivan, E.V., & Gabrielli, J.D.E. (1998). Sniffing and smelling: separate subsystems in the human olfactory cortex. *Nature, 392*, 282–286.

Stevens, D.A. & O'Conell, R.J. (1991). Individual differences in threshold and quality reports of human subjects to various odors. *Chemical Senses, 16*, 57–67.

Stevens, J.C. & Cain, W.S. (1986). Smelling via the mouth: Effect of aging. *Perception & Psychophysics, 40*, 142–146.

Stevens, J.C. & Cain, W.S. (1987). Old age deficits in the sense of smell gauged by thresholds, magnitude matching, and odor identification. *Psychology and Aging, 2*, 36–42.

Stevens, J.C., Cain, W.S., & Burke, R.J. (1988). Variability of olfactory thresholds. *Chemical Senses, 13*(4), 643–653.

Stevens, J.C., Cain, W.S., & Weinstein C. (1987). Aging impairs the ability to detect gas odor. *Fire Technology, 23*(3), 198–204

Stevenson, R.J. & Mahmut, M.K. (2013). Familiarity influences odor memory stability. *Psychological Bulletin Review, 20*, 754–759.

Stevenson, R.J., Mahmut, M., & Sundqvist, N. (2007). Age-related changes in odor discrimination. *Developmental Psychology, 43*, 253–260.

Squire, L.R. (1992). Declarative and nondeclarative memory: Multiple brain systems supporting learning and memory. *Journal of cognitive neuroscience, 4*(3), 232–243.

Stuck, B.A., Frey, S., Freiburg, C., Hormann, K., Zahnert, T., & Hummel, T. (2006). Chemosensory event-related potentials in relation to side of stimulation, age, sex, and stimulus concentration. *Clinical Neurophysiology, 117*, 1367–1375.

Stucker, F.J., de Souza, C., Kenyon, G.S., Lian, T.S., Draf, W., & Schick, B. (Eds.). (2009). *Rhinology and plastic surgery.* Berlin: Springer Verlag.

Sulmont, C., Issanchou, S., & Köster, E. P. (2002). Selection of odorants for memory test on the basis of familiarity, perceived complexity, pleasantness, similarity and identification. *Chemical Senses, 27*, 307–317.

Süskind, P. (1985). *Das Parfüm. Die Geschichte eines Mörders.* Diogenes Verlag.

Toffolo, M.B.J., Smeets, M.A.M., & van den Hout, M.A. (2012). Proust revisited: Odours as triggers of aversive memories. *Cognition and Emotion, 26*(1), 83–92.

Tulving, E. (1972; 1983). Episodic and semantic memory. In E. Tulving & W. Donaldson (Eds.), *Organization of memory* (xiii, p. 423). Oxford, England: Academic Press.

Tulving, E. (1984). How many memory systems are there? *American Psychologist, 40*(4), 385–398.

Tulving, E. (1985). Memory and consciousness. *Canadian Journal of Psychology, 26*, 1–12.

Tulving, E. (1986). Episodic and semantic memory: Where should we go from here? *Behavioral & Brain Sciences, 9*, 573–577.

Tulving, E. (2002). Episodic memory: From mind to brain. *Annual Review of Psychology, 52*, 1–25.

van Damme, P.A. & Freihofer, H.P. (1992). Disturbances of smell and taste after high centralmid face fractures. *Journal of Cranio-Maxillofacial Surgery, 20*(6), 248–250.

Wallace, P. (1977). Individual Discriminations of Humans by Odor. *Physiology & Behavior, 19*, 577–579.

Wehling, E.I., Nordin, S., Espeseth, T., Reinvang, I., & Lundervold, A.J. (2010). Familiarity, free and cued odor identification and their association with cognitive functioning in middle aged and older adults. *Aging, Neuropsychology, and Cognition: A Journal on Normal and Dysfunctional Development, 17*(2), 205–219.

Wehling, E.I., Wollschlaeger, D., Nordin, S., & Lundervold, A.J. (2015). Longitudinal changes in odor identification performance and neuropsychological measures in aging individuals. *Neuropsychology*. Advance online publication.

Venstrom, D. & Amoore, J.E. (1968). Olfactory threshold in relation to age, sex, or smoking. *Journal of Food Science, 33*, 264–265.

Wheeler, M.A. (2000). Episodic memory and autonoetic awareness. In E. Tulving & F. I. M. Craik (Eds.), *The Oxford handbook of memory* (pp. 597–608). New York: Oxford University Press.

Wiemers, U.S., Sauvage, M.M., & Wolf, O.S. (2014). Odors as effective retrieval cues for stressful episodes. *Neurobiology of Learning and Memory, 11*, 230–235.

Willander, J. (2007). *Autobiographical odor memory.* Doctoral Thesis in Psychology at Stockholm University, Sweden.

Willander, J. & Larsson, M. (2006). Smell your way back to childhood: Autobiographical odor memory. *Psychonomic Bulletin & Review, 13*(2), 240–244.

Wilson, R.S., Arnold, S.E., Tang, Y., & Bennett, D.A. (2006). Odor identification and decline in different cognitive domains in old age. *Neuroepidemiology, 26*, 61–67.

Wixted, J.T. & Mickes, L. (2010). A continuous dual-process model of member/know judgments. *Psychological Review, 117*(4), 1025–1054.

Wysocki, C.J. & Gilbert, A.N. (1989). National Geographic smell survey. Effects of age are heterogeneous. *Annals of the New York Academy of Sciences, 561*, 12–28.

Yeshurun, Y. & Sobel, N. (2010). An odor is not worth a thousand words: From multidimensional odors to unidimensional odor objects. *Annual Review of Psychology, 61*, 219–241.
Yonelinas, A.P. (2002). The nature of recollection and familiarity: A review of 30 years of research. *Journal of Memory and Language, 34*, 622–643.
Young, B.D. (2014). Smelling phenomenal. *Frontiers in Psychology, 5*(713), 1–9.
Yousem, D.M., Maldjian, J.A., Siddiqi, F., Hummel, T., Alsop, D.C., Geckle, R.J., Bilker, W.B., & Doty, R.L. (1999). Gender effects on odor-stimulated functional magnetic resonance imaging. *Brain Research, 818*, 480–487.
Zald, D.H. & Pardo, J.V. (1997). Emotion, olfaction and the amygdala: Amygdala activation during aversive olfaction in humans. *Proceedings of the National Academy of Sciences, 94*, 4119–4124.
Zatorre, R.J. & Jones-Gotman, M. (1990). Right nostril advantage for discrimination of odors. *Perception & Psychophysics, 47*(6), 526–531.
Zucco, G.M., Schaal, B., Olsson, M.J., & Croy, I. (2014). Applied olfactory cognition. *Frontiers in Psychology, 5*, 823.

Errata

Study I

p. 693 µm should be µl

Study II.

p. 238 Table 3: Perceptual speed should be Cognitive speed, like in Table 4.

Study III

p. 70 …which took about 25 min to complete.
p. 71 Table 2: In the first columns under Unfamiliar odors, Intentional and Incidental has swished place. They should be ordered like in the following columns under Familiar odors, first Incidental then Intentional

Acta Universitatis Upsaliensis

Digital Comprehensive Summaries of Uppsala Dissertations from the Faculty of Social Sciences 121

Editor: The Dean of the Faculty of Social Sciences

A doctoral dissertation from the Faculty of Social Sciences, Uppsala University, is usually a summary of a number of papers. A few copies of the complete dissertation are kept at major Swedish research libraries, while the summary alone is distributed internationally through the series Digital Comprehensive Summaries of Uppsala Dissertations from the Faculty of Social Sciences. (Prior to January, 2005, the series was published under the title "Comprehensive Summaries of Uppsala Dissertations from the Faculty of Social Sciences".)

Distribution: publications.uu.se
urn:nbn:se:uu:diva-265010

ACTA
UNIVERSITATIS
UPSALIENSIS
UPPSALA
2016