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Multiple sources of variation in perception and working memory for facial emotional expressions

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Multiple sources of variation in perception and working memory for facial emotional expressions

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Department of Psychology, University of Tartu, Estonia

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

This dissertation is based on the following original studies, which are referred to in the text by their respective Roman numerals:

I. **Tamm, G**., Kreegipuu, K., Harro, J., & Cowan, N. (2017). Updating schematic emotional facial expressions in working memory: Response bias and sensitivity. *Acta Psychologica*, *172*, 10–18.

II. **Tamm, G**., Orunurm, T. (in manuscript). Positive motivational context helps to remember: happy facial expressions with and without experimentally reinforced positive value enhance implicit memory for neutral written words.

III. **Tamm, G**., Kreegipuu, K., & Harro, J. (2016). Perception of emotion in facial stimuli: The interaction of *ADRA2A* and *COMT* genotypes, and sex. *Progress in Neuro-Psychopharmacology and Biological Psychiatry*, *64*, 87–95.

IV. **Tamm, G**., Kreegipuu, K., & Harro, J. (2021). Platelet MAO activity and *COMT* Val158Met genotype interaction predicts visual working memory updating efficiency. *Behavioural Brain Research, 407,* 113255.

V. **Tamm, G**., Kreegipuu, K., & Harro, J. (2020). Updating facial emotional expressions in working memory: Differentiating trait anxiety and depressiveness. *Acta Psychologica*, *209*, 103117.

VI. **Tamm, G**., Kreegipuu, K. & Harro, J. (in manuscript). The past is in the past? Preliminary exploration of facial expression updating in past vs present social anxiety disorder.

The author of the dissertation contributed to these publications as follows:

- In studies I, and III–VI, the author formulated the research questions, and hypotheses, conducted the literature review, proposed the original experimental design, and modified it together with the advisors. The author selected and created the experimental stimuli, participated in programming the experiments in Java, and data collection, selected the methods for statistical analysis, carried out the analysis, wrote and edited the manuscripts as the first author. In Study I, the author formulated the signal detection approach together with Nelson Cowan.
- In Study II, the author formulated the main research questions, selected the experimental paradigms and designed the three experiments, coordinated the research project which included four bachelor's research studies and a master's thesis, and collected additional data. The manuscript is based on data from four undergraduate research projects by Deniss Kovaljov, Kristi Luha, Triin Alliksoo (Orunurm) and Kati Kivistik, and a master's project by Triin Orunurm, supervised by the author, and from an additional data collection which was carried out together with Triin Orunurm. The author merged, and analysed the data, made conclusions, and wrote the manuscript as the first author.

ABBREVIATIONS

5-HIAA	–	5-hydroxyindoleacetic acid (the main stable serotonin metabolite)
5-HT	–	5-hydroxytryptamine (serotonin)
ADHD	–	attention deficit hyperactivity disorder
ADRA2A	–	adrenoceptor Alpha 2A adrenoceptor gene
ADRA2A C-1291GC	–	adrenoceptor Alpha 2A adrenoceptor gene linked single nucleotide promoter polymorphism C to G at position –1291 (rs1800544)
ANOVA	–	analysis of variance
CNS	–	central nervous system
COMT	–	catechol-O-methyltransferase
COMT Val158Met	–	a functional single nucleotide polymorphism (SNP) in the catechol-O-methyltransferase (COMT) gene (rs4680), which results in valine (Val) to methionine (Met) substitution in the enzyme protein
CT	–	control group
DA	–	dopamine
DNA	–	deoxyribonucleic acid
ECPBHS	–	Estonian Children Personality Behaviour and Health Study
HA	–	high anxiety
HAHD	–	high anxiety and high depressiveness
HD	–	high depressiveness
MADRS	–	Montgomery-Åsberg Depression Rating Scale
MAO	–	monoamine oxidase
MLM	–	multilevel modelling (also known as mixed models, or hierarchical models)
NA	–	noradrenaline
PFC	–	prefrontal cortex
RT	–	response time
SAD	–	social anxiety disorder
SDA	–	signal detection analysis
5-HT	–	serotonin
SNP	–	single nucleotide polymorphism
STAI	–	Spielberger State-Trait Anxiety Inventory
WM	–	working memory

AIMS OF THE DISSERTATION

Cognitive abilities, including visual perception and working memory (WM), are relevant in everyday social situations (such as face to face communication), and are crucial in learning, reading, and writing. Decline in cognitive abilities is common in several psychiatric and neurological disorders (social anxiety disorder, autism, depression, Alzheimer's disease, etc.). From a broad and practical viewpoint, it is important to know the mechanisms behind perception and WM for facial emotional expressions to design better prevention, and treatment programs that relieve the burden of cognitive impairment to the society; to provide an input to artificial intelligence solutions, and educational programs that would enhance human-computer interaction, and learning. The studies that are presented in this dissertation contribute to understanding the mechanisms behind variation in perception and WM for facial expressions.

The main aim of this dissertation was to explore the multiple sources of variation in perception and WM for facial emotional expressions in a framework that included both emotion and cognition. Studies I–VI describe different factors, ranging from facial stimulus properties to neurobiological markers of serotonin, noradrenaline and dopamine, that contribute to variation in perception and WM for emotional facial expressions.

1) Study I aimed to describe the contribution of physical features vs emotional content of schematic facial stimuli on WM updating performance, and to separate response bias from sensitivity by applying the signal detection paradigm.
2) Study II aimed to explore the effect of facial emotional context and experimentally manipulated motivational value of facial expressions on implicit memory for neutral words.
3) Study III aimed to describe the interaction of noradrenaline and dopamine system biomarkers (*ADRA2A* C-1291G and *COMT* Val148Met accordingly), and sex on facial emotion perception.
4) Study IV aimed to describe the contribution of dopamine and serotonin system biomarkers (*COMT* Val158Met and platelet MAO activity) on WM updating.
5) Study V aimed to explore differences between high trait anxiety and high depressiveness in WM for emotional facial expressions.
6) Study VI aimed to differentiate between the effects of past social anxiety disorder from present social anxiety disorder in contrast to a matched control group in recognition and updating of facial emotional expressions.

INTRODUCTION

Towards a unified theory of emotion and cognition in perception and working memory for human facial expressions

The ongoing era of psychological science has shifted the focus of psychological studies towards the integration of theories of emotion and cognition. Understanding the interaction of emotional and cognitive processes in the brain, and in behaviour has become an important challenge. In the twentieth century, many psychological scientists were influenced by behaviourism, and simplistic separation of emotional and cognitive processes, including separation of *emotional* and *cognitive* brain regions (e.g., criticism has been summarized by LeDoux, 1993, and Pessoa, 2008). Today, emotional processes are no longer considered separate from cognitive processes, they are integrated (Carstensen, 2019): the findings from neuroscience, and cognitive psychology have started to converge. However, a unified theory for emotion and working memory is yet to be described. Many prominent models of WM do not include emotion[1] (e.g., Cowan, 1997, 2010; Baddeley, 1992, 2010). This does not mean that emotion is considered irrelevant, it just has not been in the focus of WM research. Some have tried to integrate it but have not yet succeeded. The work is still in progress (e.g., Baddeley's hedonic detector hypothesis, 2007, 2012, 2013). On the other hand, neuroscientific models of WM have moved closer to a unified theory. Some of them have proposed that emotions play a crucial role in perception and memory (e.g., LeDoux, 1989; Gray et al., 2002). LeDoux has suggested that all emotional experiences result when stimulus representations, affect representation, and self-representations coincide in WM (LeDoux, 1989). This suggests that WM is the core process in emotion-cognition interactions.

Human faces comprise one of the most important kinds of visual stimuli that people encounter every day since birth. It is also one of the main kinds of social stimuli that are constantly processed in WM as we communicate with other people. By a broad definition, working memory is a set of cognitive functions that helps to maintain, update and refresh relevant information, and use it in a purposeful manner (Miyake and Shah, 1999; Cowan, 2010; Schneider et al., 2016; Baddeley, 1992). Cowan (1997) has described working memory as *ideas that are thought*

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[1] Author's personal conversations at meetings and conferences with several leading experts in the field of working memory can be summarized as follows: emotion has long been neglected in working memory research due to complexity that involves definitions of emotion (since there is no consensus on the definition of emotion), this does not mean that cognition researchers do not consider them as relevant; it is just easier to simplify the models and leave emotions out of the context of cognitive theories, and it is easier to conduct laboratory experimental research, and easier to interpret the findings if emotions are not included. A very pragmatic view which has led to a dissonance between cognitive vs neuroscientific models of working memory.

of, or made available to the mind, just when they are needed in order to carry out a mental task or solve a problem. His experiments have shown that human subjects can hold, on average, four separate items in mind at the same time, within the focus of attention (Cowan, 2010). The embedded processes model of WM (Cowan, 1988) includes long-term memory, which is activated by attention that holds information in WM. So, WM is directly connected to prior knowledge, and, also to attention. Baddeley (1992) has described how the working memory concept has evolved from the term *short-term memory* and has suggested that working memory is *a brain system that provides temporary storage and manipulation of the information necessary for such complex cognitive tasks as language comprehension, learning, and reasoning.* Many alternative definitions for working memory have been suggested as summarized in Cowan et al. (2017). From a neuroscientist viewpoint, working memory emerges as a result of functional connectivity and synchronous oscillations between various brain regions, where the contents of working memory are possibly stored (including amygdala), orchestrated by the prefrontal cortex as the central executive (Goldman-Rakic, 1996; D'Esposito and Postle, 2015; Courtney et al., 1997). Working memory is crucial in discrimination and recognition of facial expressions.

Detecting changes in other's emotional facial expressions, recognizing their meaning, and memorizing it is evolutionarily relevant in understanding the intentions of foes and friends. Starting from the theory of universal emotions by Darwin (1872) and continuing with the theory of basic emotions by Ekman and Friesen (1971) up to a recent constructionist view of facial emotion processing by Barrett (2017), it remains unclear how the emotional content of facial expressions is perceived, encoded and further processed in WM. Some relevant factors that contribute to facial emotion processing in WM include featural configurations of the facial stimuli, operationalization of perception as part of the encoding process, individual differences in neurobiology, emotional dispositions, and sex. All these factors have been considered in this dissertation in order to move towards a comprehensive model for facial emotion processing in WM. The majority of WM research in individual differences has focused on differences in intelligence, attention, executive functions, cognitive capacity, age, and development as the main predictors of WM variability (see Conway et al., 2008 for an overview). The neuroscientific models of WM suggest that emotions play a crucial role (e.g., LeDoux, 1989; Gray et al., 2002). Conscious experiences, regardless of their content, arise from one system in the brain, so it is extremely difficult to separate cognitive and emotional components (LeDoux and Brown, 2017). The controversies in the facial emotion processing and WM literature, and the debate about the role of emotional content in WM led to a series of studies presented in this dissertation. Some of the general leading questions which inspired the series of studies (studies I–VI) were: Do emotions affect perception and memory? Can emotion vs cognition contribution to performance be separated in WM? Do emotions enhance or impair perception and memory for facial expressions? What is the underlying brain mechanism for this? What is the role of individual differences in explaining variation in perception and WM?

The perceptual process, and working memory

Perception is a complex cognitive process that results in mental representations of objects that surround us in the environment. The perceptual process (Figure 1) starts with a sensation of the external stimulus. The stimulus is encoded into the neural "language" by transduction on the receptors, followed by a neural transmission process in the CNS up to the more complex cognitive processing in the brain where a representation of the stimulus emerges. The representation is further processed in WM in relation to prior knowledge. Finally, a decision about the stimulus is made which leads to action. In this framework, perception and WM are interconnected. WM integrates existing knowledge with new perceptual input. Here (Figure 1), attention is assumed to be focused on the stimulus that is being processed. All visual WM tasks where subjects retain stimulus in memory for a short period of time, e.g., such as change detection, number-spans, letter-spans, and n-back tasks, require both the perceptual encoding of the stimulus, and the maintenance of its representation after the stimulus is no longer present in the visual field (Courtney et al., 1997). The relationship between perception and WM is reciprocal. The item that is held in mind affects what is perceived, even at the most fundamental stages of processing (Teng and Kravitz, 2019).

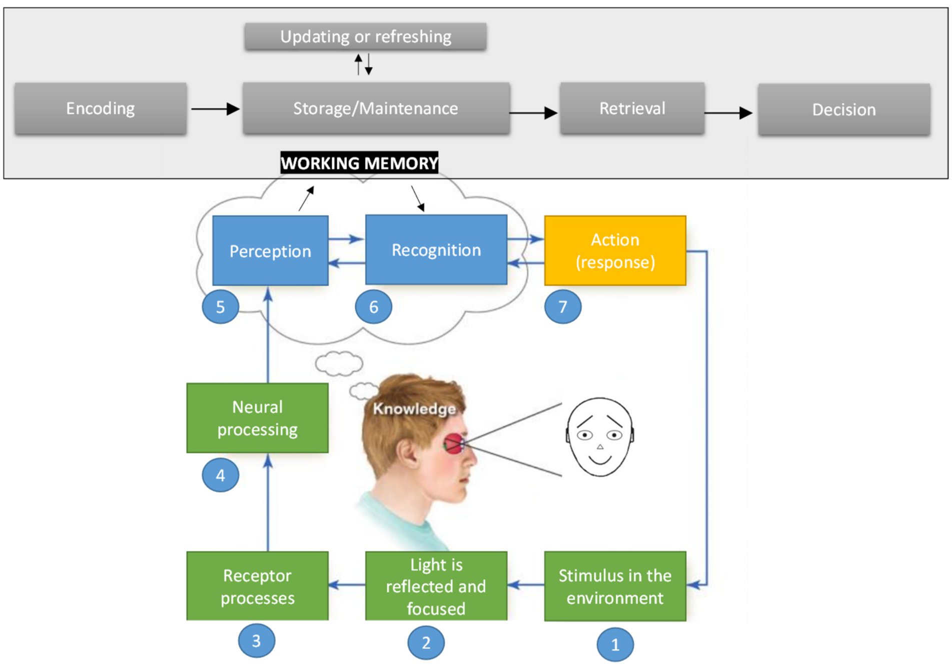


Figure 1. The perceptual process and working memory. The illustration of the perceptual process is based on Goldstein and Brockmole (2016, Figure 1.1.). In this model, attention is assumed to be focused on the stimulus in encoding, and retrieval. The working memory process was added and sketched by the author based on the experimental findings about the time-course of memory processes from Melton (1963) and Anderson et al. (2018). The happy facial stimulus was sketched by the author.

WM involves multiple stages and subprocesses. Experimental data from Melton (1963), and many others after him have suggested that the three principal stages of memory are encoding, storage/maintenance and retrieval. Recently, Anderson et al. (2018) have extended this by distinguishing between encoding, retrieval, decision, and response stages in WM. Moreover, WM can be separated into recognition, and discrimination processes based on brain imaging and behavioural outcomes. The first relates to refreshing, and the second to updating in WM. Refreshing is crucial for recognition. Refreshing is a covert WM subprocess in which information, that is stored in WM, is renewed with that same information during active maintenance (Vergauwe and Cowan, 2015). In contrast, updating is a WM subprocess in which old information is replaced by new information within hundreds of milliseconds (Schneider et al., 2016). The N-back task is a well-known WM task that has been widely used in behavioural and brain-imaging research primarily to study updating. In the two-back version of the n-back WM updating paradigm stimuli are presented one by one, and the subject has to respond each time if the new stimulus (n) is the same or different than the stimulus that was presented 2-stimuli back (n-2). In this paradigm, the three stages can be operationalized as follows: responses to the probe (n) stimulus (in comparison to the stimulus in memory) as the encoding process, the n-1 stimulus in memory as the storage/maintenance process, and responses to the n-2 stimulus (in comparison to the probe) as the retrieval process. In studies I, IV, V and VI, encoding and retrieval processes were separated based on the idea of separating WM updating into encoding, and retrieval phases. Study II explored implicit encoding, and maintenance in priming and letter-completion tasks, and Study III focused on updating efficiency.

Most perception and WM researchers agree that perception and WM resources are limited (Cowan, 2010; Oberauer et al., 2016; Holcombe, 2009; Allik et al., 2013 etc.). WM can be characterised by its capacity, speed, and precision, all of which have limits. WM limits vary between subjects (e.g., Jarrold and Towse, 2006). This can be well illustrated by experimental data from Study I (raw data): response times within one person in a WM task with 140 trials can vary from 411 to 2107 ms, or, for example, from 241 to 2500 ms. Average response times between 500 subjects can vary from 358 to 1981 ms (see Figure 2). For illustration, Participant A in Figure 2 represents a subject who had some missing or extremely slow responses (at 2500 ms), Participant B represents a subject whose responses were all within the expected range of responding. Participants A and B had different average response times (752 ms vs 1060 ms) and accuracies (71% vs 84%).

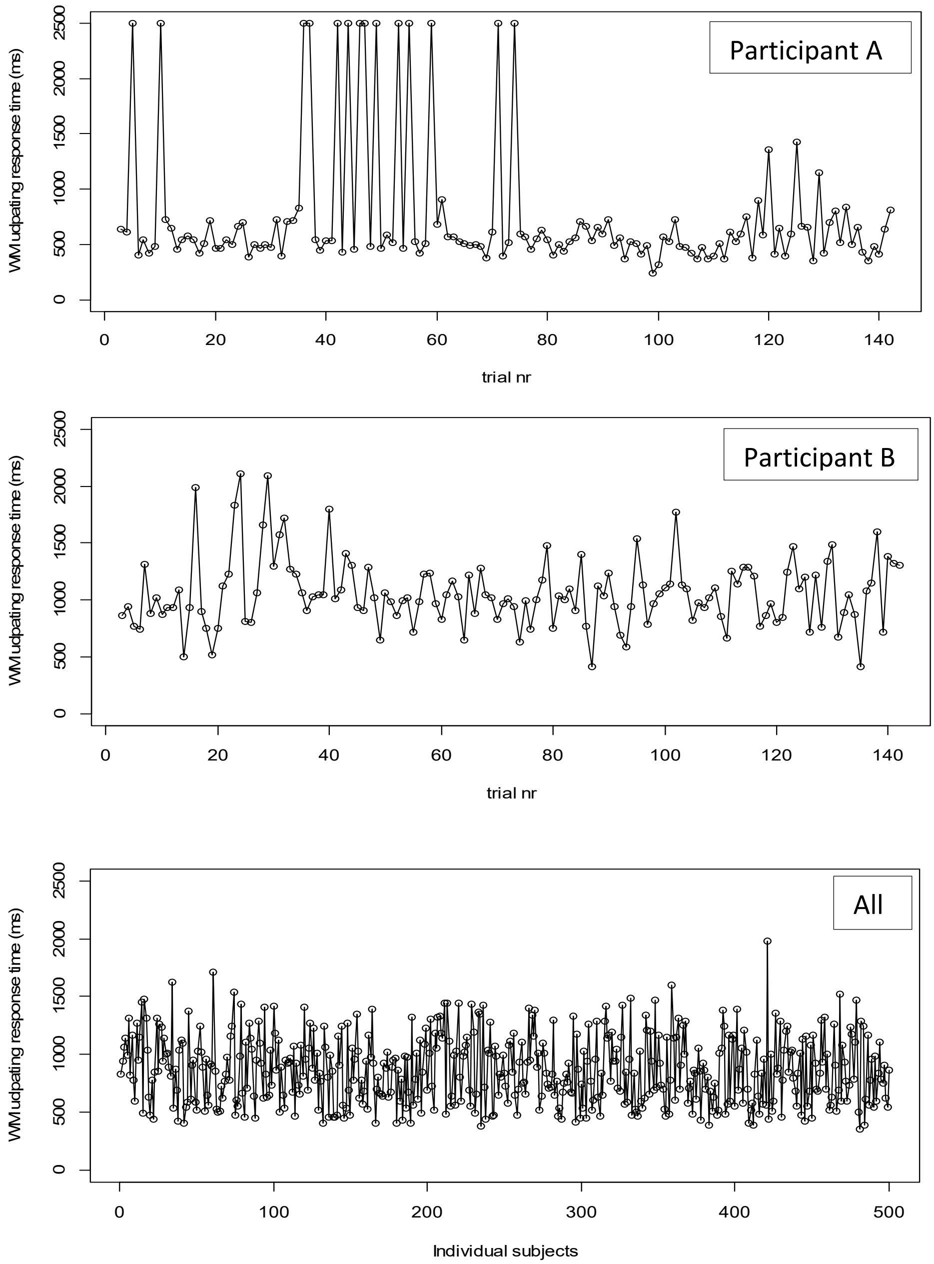


Figure 2. Illustration of the response time variation in the 2-back task (data from Study I). Panel Participant A: Data is from one random subject, all trials included. Range: 241 to 2500 ms. Panel Participant B: Data is from one random subject, all trials included. Range: 411 to 2107 ms. Data is from 507 subjects, all trials with < 2500 ms responses included. Range: from 358 to 1981 ms.

There are numerous factors that can contribute to this variability. In WM research, individual differences in age, neural capacity (incl. neurological disorders), WM capacity, and attention are the main topics that have been discussed in the literature (e.g., Conway et al., 2008; Logie et al., 2020). Individual differences that come from the interaction between stimulus characteristics, and individual dispositions (both neurobiological and emotional) have received less attention. However, in pursuit of a unified theory for facial emotion processing in WM, the contribution of these factors cannot be neglected. It has been suggested that the mechanisms that underlie the interaction of emotion and cognition are likely to be more complex than presented by a typical folk psychological view of emotion and cognition interactions. According to which, pleasant emotions are beneficial, and unpleasant detrimental to cognitive performance (Gray et al., 2002). This dissertation focuses on examining those factors which contribution to WM is less known. Studies I and II explored the effects of stimulus qualities (physical and emotional) of facial expressions. Studies III and IV focused on the role of genetic dispositions that lead to differences in neurobiology (as described by Vogler et al., 2014). Studies V and VI explored the role of emotional dispositions.

The role of emotions, and facial expressions in perception and memory

Emotions are neurobiological acute reactions that are conveyed by distinguishable facial emotional expressions in humans, and other primates. Emotional facial expressions have long been studied by many researchers. Ekman and Friesen proposed the six basic emotional expressions that are universally recognized across cultures (Ekman and Friesen, 1971): anger, disgust, fear, happiness, sadness and surprise. The majority of the studies about the effects of facial emotions on perception and memory have described the effects of threatening and angry faces. Some suggest that angry faces enhance perception (Fox et al., 2000), attention (Öhman et al., 2001; Xie et al., 2021), and WM (Jackson et al., 2014). In contrast, some studies have shown that happy faces enhance perception (Johnson et al., 2010; Becker and Srinivasan, 2014; Leppänen et al., 2003), and WM (Spotorno et al., 2018). Thus, the literature about the effects of different emotional faces on perception and WM is not straightforward.

The debate whether emotions affect perception, and memory processes per se, or if the effect of emotion on cognitive performance is modulated by some other cognitive processes, such as attention, appraisal, or prior knowledge, is ongoing. A recent meta-analysis included 65 studies that had used affective stimuli in a WM task, and showed that emotional content had a very mild effect on WM performance, however, the effect was stronger in people with an underlying mental illness (Schweizer et al., 2019). This supports the view that emotional dispositions, such as high anxiety and depressiveness, could play an important role in explaining WM variance for emotional facial expressions. This was explored in studies V and VI.

Another source of variation in perception and WM for emotional facial expressions can come from an acute emotional state during the task. Some studies have shown that sadness and state anxiety that are measured prior to cognitive tasks can impair task performance (e.g., Chepenik et al., 2007; Pacheco-Unguetti et al., 2010). However, if compared to other factors, such as task difficulty, the effect of emotional state could be relatively small. Preliminary results from a multicultural experimental study which was conducted in Estonia (n=158 adults) and in the USA (n=212 adults) by the author of this dissertation showed that the effect of a self-reported emotional state throughout a series of WM and other cognitive tasks that included common neutral stimuli (letters, shapes etc) was minor in comparison to the effect of task difficulty (Tamm and Cowan, 2015a, 2015b)[2]. In Figure 3, note that the change from a moderately difficult to an easy task (WM4 to GoNoGo) did not relate to any fluctuation in valence or arousal either before or after the tasks in neither of the two samples. The correlation coefficient between self-reported naturally occurring emotional arousal, and WM accuracy index (average % of correct responses in four WM tasks) was very low but statistically significant (Pearson's $r(358)=0.1$, $p<0.05$). The correlation between self-reported valence, and WM accuracy index was stronger, and statistically significant but still below moderate (Pearson's $r(358)=0.27$, $p<0.000001$) (Figure 4). The latter confirms the typical folk psychological view that pleasant self-reported emotions are associated with better cognitive performance, however, the association is not strong.

This suggests that naturally occurring emotional state has only a small effect on WM task performance. However, emotionally salient stimuli, such as facial expressions, could induce changes in emotional state which could have a stronger effect on WM. Indeed, some studies have shown that task difficulty interacts with the emotional content of the stimuli, so that the top-down effect of cognition can diminish the effect of emotion. WM load at emotion exposure can attenuate the effect of emotion on WM performance. However, the effect of emotional content of the stimuli seems to be present even if task difficulty is high (Miendlarzewska et al., 2013). The effect of facial emotional content in a relatively difficult WM task (2-back) was explored in Study I.

[2] The data has been presented at two conferences by Gerly Tamm and Nelson Cowan. A preliminary analysis has been carried out, and a manuscript is in preparation.

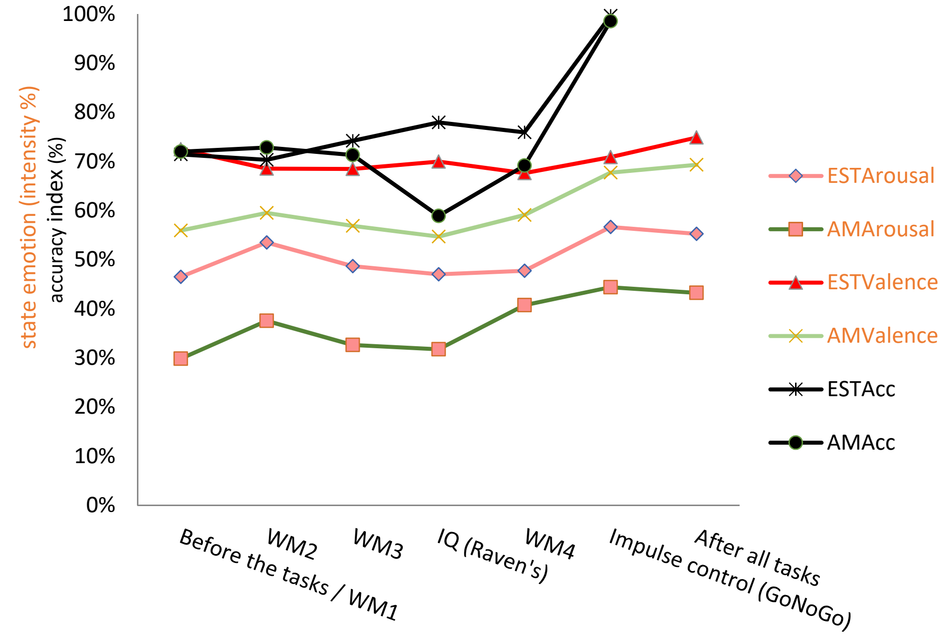


Figure 3. Emotional state in cognitive tasks: preliminary results from a study (Tamm and Cowan, 2015a, 2015b). *Notes. EST – Estonian sample, AM – American sample. Valence scale ranged from negative (0) to positive (100), arousal ranged from low (0) to high (100). Acc – accuracy. Y-axis refers separately to accuracy and emotion intensity.*

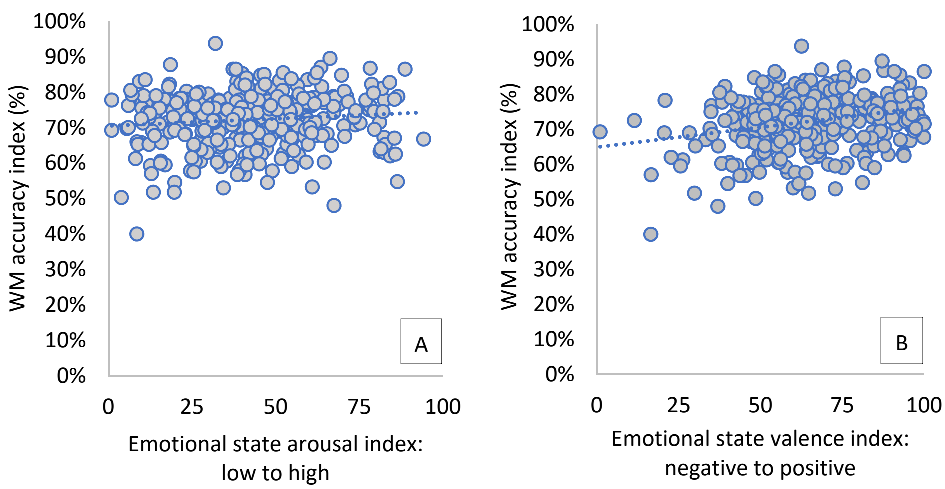


Figure 4. Scatter plots for WM accuracy and self-reported arousal (panel A), and valence (panel B). *Note. WM accuracy index refers to an overall average accuracy in four WM tasks. State valence and arousal refer to self-reported average valence, and average arousal throughout the experimental procedure.*

Some facial emotional expressions are perceived as more intense than others. According to the circumplex model of emotion (Russell, 1980), each facial expression is perceived as a unique combination of valence and arousal (Gerber et al., 2008; Vesker et al., 2018). For example, sad faces are generally perceived as negative but low arousing, angry faces are perceived as negative and high arousing (see Figure 5). Brain imaging experiments have shown that salient (fearful, threatening, or angry) facial expressions automatically activate amygdala (Morris et al., 1996) which activation is thought to reflect the emotional relevance (Sander et al., 2003). Amygdala activation modulates the consolidation of emotionally arousing experiences (McGaugh, 2004). Thus, a task that includes salient facial expressions could alter the emotional state during the task which in turn can modulate encoding of facial expressions into WM.

Encoding into WM involves attention (Cowan, 1988). There is an abundant amount of literature about the association between attention and emotion. Not all could be reviewed here. The results from attention research that are most relevant in WM are related to the attentional scope. Some studies have shown that positive emotions broaden the attentional scope, and negative emotions narrow it (Johnson et al., 2010; Fenske and Eastwood, 2003). This suggests that facial expressions that convey positive meaning could enhance WM by broadening the focus of attention during encoding which allows more information to enter WM. The role of attention in encoding was explored in Experiment III in Study II.

Moreover, intense stimuli can alter the emotional state by inducing mild acute stress (the arousal response; Puglisi-Allegra, 1991), which increases the release of neurotransmitters (Mora et al., 2012). Such stress-induced modulation by a mixture of facial expressions that can explain neurobiological individual differences in cognition was discussed in Study IV in relation to the effects of dopamine and serotonin system biomarkers on WM updating. Also, in Study III in relation to the effects of the noradrenaline system biomarker on face perception.

Serotonin, noradrenaline and dopamine in perception and working memory

Serotonin (5-HT) is a monoamine neurotransmitter that by conventional wisdom is usually associated with mood, but its role in perception and WM is as important, especially in modulating the prefrontal inhibitory processes (Puig and Gulledge, 2011). Central 5-HT-ergic neurotransmission can be examined by in vivo imaging techniques but their use is limited owing to cost and safety issues. However, for the individual capacity of the central 5-HT system a proxy measure is available in the form of monoamine oxidase activity as measured in platelets (Harro and Oreland, 2016). Platelet MAO activity strongly correlates with the level of serotonin metabolite 5-HIAA in the cerebrospinal fluid both in healthy humans and rhesus macaques (Oreland et al., 1981; Fahlke et al., 2002), indicative of 5-HT release capacity. Low central serotonin (and low platelet MAO) predicts impulsivity and other behavioural and cognitive problems (e.g., Paaver et al., 2007), however, it can also provide an advantage in some task conditions (e.g., Otsa et al., 2016). In Study IV, platelet MAO activity was used as a marker for the 5-HT capacity to study its contribution to the variance of facial emotion processing in WM with an emphasis on exploring its modulatory effect on the dopamine system.

Noradrenaline (NA, also known as norepinephrine) is a catecholamine neurotransmitter that plays an important role in vigilance, fight/flight response, perception, and attention processes (Gelbard-Sagiv et al., 2018). Its main function in the body is to prepare the body and mind for action. In the brain, NA level is low during sleep, and high during wakefulness (Mitchell and Weinshenker, 2010). In the Posner's attention network model that includes three main functions: orient, alert and executive attention, noradrenaline is mainly associated with alerting (Posner and Rothbart, 2007). Even though it might seem that the effect of noradrenaline is straightforward – more NA leads to better cognitive performance, the noradrenergic modulation of the PFC by the locus ceruleus is complex. The effects of noradrenaline in the PFC result from the interplay between different adrenergic receptor types. It has been suggested that in low to moderate extracellular NA concentrations the high affinity receptor type (α_{2A}) potentiates the activation of the PFC, however, in more stressful situations or in case the activation is already high (e.g., in ADHD), additional NA engages the lower affinity receptors (α_{1A}) which inhibit the PFC (Borodovitsyna et al., 2017). Furthermore, presynaptically located α_{2A}-adrenoceptors have the potential to inhibit further NA (and 5-HT) release. Because α_{2A}-adrenoceptors also serve as somatodendritic autoreceptors in the brainstem, they appear as a major source of control over NA-ergic neurotransmission with vast potential for individual differences at this level (e.g., Harro and Oreland., 2001). Thus, as one of the genetic markers of the NA system function, the *ADRA2A* gene promoter polymorphism in the form of a substitution of C to G at location –1291 holds promise, as the G-allele has been associated with impulsivity and inattention (Kiive et al., 2010). In Study III, *ADRA2A* C-1291G interaction with a genetic marker of the dopamine system in facial emotion perception was explored.

Dopamine (DA) is a catecholamine neurotransmitter that has mostly been associated with learning and motivation (Berke, 2018; Iversen and Iversen, 2007). In the Posner's attention network model, DA is mainly associated with executive attention (Posner and Rothbart, 2007). Dopamine plays an important role in the functions of the PFC, including WM (Goldman-Rakic, 1996, Meyer-Lindenberg et al., 2005). *COMT* Val158Met is a genetic marker for prefrontal dopamine. In the *COMT* gene, a single nucleotide substitution of adenine (A) for guanine (G) results in an amino acid change from valine to methionine at amino acid position 158 (108 in case of the soluble form of the enzyme), commonly referred to as Val158Met. The *COMT* Val158Met polymorphism predicts the levels of dopamine in the prefrontal cortex. *COMT* Val158Met Met/Met genotype has 3–4 times lower COMT activity than the Val/Val genotype. So, Met-allele indicates a higher level of dopamine available in the brain (Chen et al., 2004). There has been a long debate about the effects of *COMT* Val158Met on WM, and many explanations for the variety of results exist, such as ethnic differences between samples, differences in the experimental stimuli and tasks, differences in the context in which the tasks are carried out etc. However, more recent studies (Zareyan et al., 2021), including Study IV suggest that *COMT* Val158Met effect could be at least partly modulated by the emotional state which is elicited by the facial expressions during the WM task, which helps to explain the various results in the literature.

Sex differences

Differences between men and women are crucial to consider when studying perception and WM for facial expressions. It has been shown that, generally, men have faster response times (Der and Deary, 2006). This can contribute to differences in WM performance. Also, men and women use different attentional strategies when viewing emotional facial expressions. Women look at the eyes, and men pay more attention to the mouth (Hall et al., 2010), which can induce differences in how emotional facial expressions are processed in WM.

From the neurobiological perspective, the main difference between men and women is that from the 46 chromosomes, one – the Y-chromosome is present in men and not present in women. Y-chromosome includes numerous protein-coding genes, some of which can alter gene expression also in other chromosomes, including genes that are related to the monoamine neurotransmitter systems (e.g., Wu et al., 2009). *ADRA2A* C-1291G, *COMT* Val158Met, and platelet MAO have all been associated with sex differences. The genetic differences between men and women partly explain the variation in emotional dispositions (Seney et al., 2013), emotion perception (Filkowski et al., 2017), impulsivity and attention (Trent and Davies., 2012). Thus, sex differences were considered throughout studies II to VI.

METHODOLOGY

Samples

Studies I, III, IV, V, and VI included one cohort of the Estonian Children Personality Behaviour and Health Study (ECPBHS). Perception and WM tasks were completed by 507 subjects (228 men and 279 women) for studies I, III, IV, V and VI. Data collection was conducted when they were 25 years old (+/–1 year). With additional measures that were included into the analysis, the number of participants varied (Study I n=507 subjects, Study III n=507 subjects, Study IV n=455, Study V n=292, Study VI n=80). The data collection was carried out in Tartu and Tallinn. The original sample had been formed in 1998 (the beginning of the ECPBHS) at schools of Tartu city and county. The sample represents the corresponding Tartu county birth cohort (around 10% of the Tartu county same age subjects were recruited). According to the standardized framework for representation of ancestry data in genomic studies (Morales et al., 2018), the sample belonged to the European ancestry category.

Study II included three different samples from the local communities and universities of the cities Tartu and Tallinn (Experiment 1 n=117, Experiment 2 n= 69, Experiment 3 n=53, average age 33 years, range 18–50 years). Subjects could participate only in one of the three experiments.

All subjects confirmed their voluntary participation with a written consent. All research was approved by the local ethics committee at the University of Tartu.

Stimuli

In studies I, III, IV, V, and VI, the same schematic emotional expressions were used: sad, angry, scheming, happy, neutral, and two additional control-objects (scrambled faces). The stimuli were sketched by the author (see Figure 5) and were inspired by similar stimuli that had been used by Öhman et al. (2001). The rationale for using schematic facial expressions has been outlined in papers I, III and IV. In short, schematic emotional faces allow good experimental control over the stimulus features, they do not have birthmarks, sex differences, symmetry factors or other factors that could bias the effect. Similar stimuli have been used in other perception, and WM studies (e.g., Öhman et al., 2001; Sagiv and Bentin, 2001; Kreegipuu et al., 2013 etc.). Moreover, schematic facial expressions induce similar brain activation as real faces (e.g., Sagiv and Bentin, 2001). It is not to claim that schematic faces are better than real faces; schematic faces provide supporting and useful information in addition to studies that have used real faces.

In Study II, real photos of facial expressions were used from the Cohn-Kanade facial expression dataset (Lucey et al., 2010). Only full emotional expressions were chosen from the dataset: sad, angry, happy, neutral, fear, surprise, disgust. All stimuli were adjusted (size, brightness, contrast) by the author and Triin Orunurm.

Experimental research approaches, and data analysis

In Studies I, IV, V and VI, the 2-back WM updating task with emotional facial expressions was used. Each stimulus was presented one by one on a computer screen. There were 140 trials in total. The sequence of the facial stimuli was pseudorandomized. The subjects had to respond if the stimulus was the same (*match*) or different (*mismatch*) each time with their left or right index finger, accordingly. Speed and accuracy were recorded.

In Study III, a simple response time task with schematic emotional faces was used. All faces were presented on a computer screen one by one, and the subjects had to respond with their index finger on a keyboard as fast as they could as soon as they had detected the stimulus on the screen. The sequence of the facial stimuli was pseudorandomized. There were 140 trials in total. Speed and accuracy were recorded.

In Study II, an implicit memory task with neutral words was used. The implicit memory task consisted of two parts (see Figure 2 in Study II). First, all subjects completed the priming task in which words were presented on the screen together with emotional faces, and the subject had to respond to the location of the word in relation to the emotional face (up or down). The second part was a simple word-completion task in which the subjects had to fill in the gaps to complete a word. The neutral word dataset was constructed based on Triin Alliksoo's bachelor's research (2014), and Ene Vainik's word dataset (2010). The three experiments included the same implicit memory task. In Experiment II, prior to the priming task, the emotional meaning of the facial expressions was manipulated by a novel reinforcement conditioning procedure (see Figure 4 in Study II), and in Experiment III, the Navon's attention task was included to control for attentional processing style.

Additional measures of self-reported valence, arousal, verbal labelling of the emotional facial expressions, self-reported depressiveness (Montgomery and Åsberg Depression Rating Scale, MADRS, Montgomery and Åsberg 1977), and trait anxiety (Spielberger Trait Anxiety Inventory, STAI, Spielberger and Lushene, 1983), state fatigue (Borg Perceived Exertion Scale, Borg, 1998), IQ (Raven's Progressive Matrices, Raven and Court, 1938), education, and a clinical diagnosis of social anxiety disorder (clinical interview) were used throughout the studies.

In studies III and IV, biological markers, and their interactions were used to explore the effects of serotonin, dopamine and noradrenaline systems on perception and WM. These included *COMT* Val158Met as a marker for dopamine, *ADAR2A* C-1291G as a marker for noradrenaline, and platelet MAO activity as a marker for serotonin system. Biological data acquisition and genotyping procedures have been described in studies III, and IV.

Statistical analysis was carried out mainly in R, and partly in SPSS, Statistica, and Excel. Various statistical methods were used throughout the studies: descriptive statistics, correlations, ANOVA, linear and generalized mixed models. Mixed models were used in studies III, IV, and VI as an alternative to repeated measures ANOVA because it leads to more precise estimates than ANOVA, especially with unbalanced group sizes (Baayen et al., 2008), and includes all within-subjects variation into the analysis, not only averages from each person.

Signal detection analysis

Signal detection analysis (SDA) is a common approach in attention, and perception studies but not so much in memory research. In Study I, a novel approach was used to separate different types of responses in the 2-back task. SDA (Swets, 2014, Stanislaw and Todorov, 1999) was applied to calculate separate measures for recognition, sensitivity and response bias. Sensitivity (d-prime, d′) is a measure of discriminability. It reflects how well a subject discriminates between two stimuli by controlling for the noise in the responses. Response bias is a measure of decision criterion. It reflects the extent to which one response is more probable than another. In a simple task with two different choices (*same* or *different*) it shows if the subject preferred one, or the other.

Studies I, III, IV, V, and VI included the theoretical approach of separating different types of responses to study the subprocesses of WM updating. Hits and False alarms were operationalized based on the change detection paradigm (Rouder et al., 2011), and accordingly adapted to the n-back paradigm. Thus, Hits were defined as *correct* responses in *mismatch* trials, and Misses were defined as *incorrect* responses in *mismatch* trials. False alarms (FAs) were defined as *incorrect* responses in *match* trials. Correct rejections (CRs) were used as a measure for recognition, i.e., *correct* responses in *match* trials.

In the 2-back task, when calculating sensitivity (d′) and response bias (C-bias), it is important to separate the probe (n) from the stimulus in WM (n-2). The effects of emotional expressions can be present either during encoding (n) or in memory (n-2). Therefore, d′ and C-bias were calculated in two different ways in Study I:

(1) with a neutral face as a probe:

$$d' = Z(Hits(SOI\ in\ memory\ vs\ neutral\ probe)) + Z(FAs(SOI))$$

$$C = \frac{Z\big(Hits(SOI\ in\ memory\ vs\ neutral\ probe)\big) + Z\big(FAs(SOI)\big)}{2}$$

(2) with a neutral face as a reference in memory:

$$d' = Z(Hits(neutral\ in\ memory\ vs\ SOI\ as\ probe)) + Z(FAs(SOI))$$

$$C = \frac{Z\big(Hits(neutral\ in\ memory\ vs\ SOI\ as\ probe)\big) + Z\big(FAs(SOI)\big)}{2}$$

Z() refers to a standard deviation value from normal distribution according to the Hits or FAs probability, SOI – stimulus of interest.

RESULTS AND DISCUSSION OF STUDIES I–VI

The stimuli – facial emotional expressions: the effects of features vs emotional content (Studies I and II)

One of the most complex problems in studying the effect of emotional facial expressions on perception and memory is the interpretation of the effect of a certain facial expression. One particular question that has guided the debate in the literature is: whether it is the effect of emotional content or the physical configuration of that facial expression? One side of the literature has not directly controlled for the effect of perceptual features (e.g., Öhman et al. 2001). Some have concluded that all perceptual stimuli have some degree of *emotional content*, so that the effect of any stimulus is always confounded by emotion. For example, several studies with downward and upward pointing triangles demonstrated that humans might have an intrinsic tendency to interpret some geometrical configurations as threatening or unpleasant (downward pointing triangles) and others as friendly or pleasant (upward pointing triangles) (Larson et al. 2012; Watson et al., 2012). In contrast, some have suggested that the apparent effect of *emotional content* can mostly be explained by the physical features (Calvo and Nummenmaa, 2016) or prior knowledge (Gendron et al., 2012). The theory of basic emotion categories has been challenged by more recent theories (e.g., Barrett et al., 2019).

The effect of emotional content vs physical features was explored in Study I. Additionally, to control for the emotional experience that results from viewing emotional faces, self-reported valence and arousal of the schematic faces were analysed. Data from 507 subjects showed that emotional expressions can be categorized based on valence and arousal (Figure 5). In valence, all emotional face-pairs were significantly different except sad – angry. In arousal, all emotional face-pairs were significantly different, except neutral – happy. This ensures that emotional faces can be categorized, and their unique effects of *emotional content* on perception and WM can be studied (see Figure 5). That said, the main results in Study I showed that the WM updating performance depended more on the perceptual features of the emotional facial expressions than the emotional content (see Figure 5 in Study I). The analysis also showed that there was only a minor advantage for smiling faces (U-curved mouth in happy and scheming) in encoding response bias (see Figure 4 in Study I). It was concluded that the effect of displayed emotion comes from small shifts in the internal discrimination criterion, rather than in memory efficiency or sensitivity. No threat advantage or any other specific effects of emotion were found.

This inspired the series of experiments (three experiments in Study II) in which basic facial expressions (real faces, sad, angry, surprise, disgust, happy, fear, neutral) were used as context during encoding in a word priming task to explore their implicit contextual effect on the memory for neutral words. Experiment II in Study II showed that the effect comes from the emotional and motivational content which was experimentally controlled by applying a novel reinforcement procedure to attach meaning to facial expressions: happy faces were associated with a negative, neutral and positive outcome. Study II showed that the positive content, intrinsically conveyed by happy faces, or experimentally reinforced – enhanced implicit memory for neutral words (see Figures 3 and 5 in Study II). Possibly, WM is involved in priming (Hassin et al., 2009). Thus, even though studies I and II which had different methodological approaches, and different stimuli (schematic in Study I and real faces in Study II), they provided proof that perceptual features and emotional content both contribute to the variance in WM performance. In sum, in WM, the effect of emotion per se is minor, and only reliably present in the encoding phase in which smiling faces (happy and scheming) elicit a recognition bias towards *sameness*. Possibly, stronger effects could be seen with a different task design and different stimuli. Study II showed that the effect of emotional and motivational meaning of the facial expressions can be more explicitly seen in implicit memory.

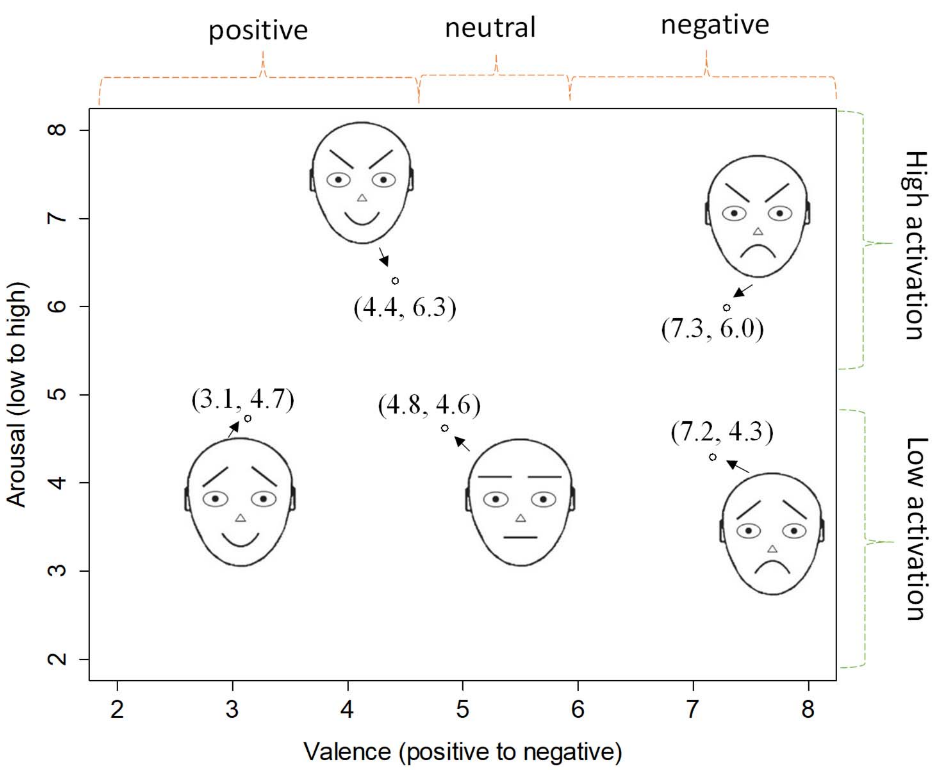


Figure 5. Two-dimensional (valence and arousal) representation of the schematic emotional faces that were used in studies I, III–VI. Each datapoint plotted in this figure is calculated from 507 subjects' self-reports for valence ("*how negative or positive is this stimulus?"*) and arousal ("*how does this stimulus make you feel?*") on a 1…9 scale.

Interestingly, studies I, and II did not clearly demonstrate a threat (angry) advantage effect. Perhaps due to only a mild stress-inducing effect of these schematic stimuli that were used in a relatively difficult 2-back task, and due to a mixed updating design in Study I. Angry or fearful faces seem to have stronger effects in implicit memory tasks. Indeed, Study II showed that angry and fearful faces significantly lowered the priming effect in contrast to happy faces. Others have shown that threatening stimuli automatically capture attention (e.g., Öhman et al., 2001; Xie et al., 2021), and activate amygdala (Morris et al., 1996; Sander et al., 2003), which plays an important role in linking external stimuli to defence responses (LeDoux, 2003). Even in small children, threatening faces elicit longer dwell times in contrast to happy or neutral faces (Leppänen et al., 2018) which suggests that processing of threatening faces is enhanced in simple tasks. However, when attentional resources are occupied by a difficult task then the automatic response can be inhibited by a top-down control mechanism (Pessoa et al., 2003). Thus, in a WM task, the effect of threat is not reliably present. The interaction of many different factors can explain why threat advantage could only be present in some task conditions, and in some subjects but not in others (see Study VI).

Neurobiological contribution to the variation in perception and working memory for facial expressions (Studies III and IV)

Studies I and II led to a new question. Assuming that the effect of emotion is mainly present in the encoding phase of WM then it should be detectable in a simple perception task with emotional facial expressions. It was concluded from Study I, and II that individual differences in emotional dispositions, and in genetic variants need to be explored to better understand the underlying mechanism for emotion perception and memory. Thus, in studies III and IV, the effects of individual neurobiological differences in noradrenaline, serotonin and dopamine systems, and sex on emotional face perception and WM were explored.

In Study III, *ADRA2A* C-1291G polymorphism was used as a biomarker for the noradrenaline system, and *COMT* Val158Met polymorphism as a biomarker for the dopamine system. Interactions between *ADRA2A, COMT,* sex and emotional expressions in a simple response time task were studied. It was found that variance in perception was predicted by a complex interaction between the aforementioned four factors.

ADRA2A gene encodes the α_{2A}-receptors that are distributed widely throughout the brain, especially in the areas that are related to emotion processing and memory, such as the cerebral cortex, locus ceruleus, hypotalamus, amygdala, and hippocampus (Arnsten, 1998; Scheinin et al., 1994). These receptors have a major role in presynaptic feedback inhibition: they control the amount of noradrenaline that is released into the synaptic cleft (Altman et al., 1999). The C-1291G polymorphism in the promoter region of the gene is thought to affect the noradrenergic function, however, its exact neurobiological mechanisms have not yet been described. Theoretically the G-allele could lead to an increase in the expression of α_{2A}-receptors which in turn could lead to better inhibition of the NA release that will result in low NA transmission (low NA related activation). This is compatible with the evidence that the sedative action of dexmedetomidine, the standard α_{2A}-receptor agonist, is more potent in *ADRA2A* C-1291G G-allele carriers (Yağar et al., 2011). However, the interpretation is not that straightforward because α_{2A}-receptors also occur postsynaptically.

Studies have demonstrated that C-1291G G-allele relates to inattention, ADHD, arousal, and impulsivity (Comings et al., 2000; Roman et al., 2006; Kiive et al., 2010 etc.). This suggests that G-allele does reflect a variation in noradrenaline release control. The results from Study III showed that *ADRA2A* C-1291G G-allele associated with slower responses, possibly due to poor attentional control during the task. But not in all participants. Some benefited from the G-allele: women, and those who had the *COMT* Val158Met Met/Met genotype (high DA availability) (see Figure 2 in Study III). Men only benefitted from G-allele if the stimulus was a scheming face. Thus, a complex interaction between individual differences in neurobiology (sex, *COMT* Val158Met, *ADRA2A* C-1291G) and stimulus properties (emotional facial expressions) contributes to the variance in perception of facial expressions.

Posner and Dehaene (1994), and Posner and Fan (2008) have proposed that alerting is a separate attentional system which functions as a detector. So, fast single response times were analysed separately based on the Posner's alerting hypothesis. *Fast*, responses were defined as responses that were above the awareness threshold (100 ms) and below the average response time (280). This separation showed that the interaction between *ADRA2A* × *COMT* × Sex and emotional expressions was different in *fast* vs *regular* detection times, adding complexity to the interpretations. In sum, Study III showed that *ADRA2A* C-1291G G-allele was the most important predictor of regular detection times. G-allele significantly influenced response times in interaction with sex, *COMT* Val158Met, and emotional facial conditions.

An important idea that emerged from this study was that some emotional facial expressions could act as mild stress-inducers during the experimental task which explains why more arousing stimuli (scheming faces) can have stimulant-like effects (i.e., better concentration, faster responses) in those who have higher risk for inattention (G-allele).

While NA affects the general alertness, and quality of perception, DA is more related to prefrontal executive control (Posner and Rothbart, 2007). The literature about the effects of a dopamine marker, *COMT* Val158Met, on WM is mixed (see Study IV for a review). It has been suggested that dopamine release could be regulated by the serotonin system in the PFC (Iyer and Bradberry, 1996; Briand et al., 2007). This idea was tested in Study IV in which the effects of a biomarker for the serotonin system (platelet MAO activity), and a marker to the dopamine system (*COMT* Val158Met) were explored. In study IV, emotional expressions were all merged together into one measure of WM updating due to a conclusion from Study I, and by Schweizer et al. (2019) which suggested that emotional facial expressions per se have very little effect on WM in a normal population but could have a stronger effect in subjects with underlying psychopathology. The latter was analysed in Studies V and VI.

The findings from Study IV suggested that in terms of WM performance serotonin modulates prefrontal dopamine only in subjects whose dopamine levels are average or high but not too high. The interaction of platelet MAO and *COMT* Val158Met showed that low MAO, which is usually related to impulsivity and several behavioural problems (Paaver et al., 2007; Kiive et al., 2005; Harro and Oreland et al., 2016 etc.), provided an advantage in a speeded WM updating task, but only in subjects with the Val/Met genotype, that is, with an average, according to some studies optimal, prefrontal dopamine function. The present study also suggests that the regulatory role of serotonin could become relevant only in stressful situations. Because emotional facial expressions in the 2-back task might have created a mild stress-inducing situation, all subjects likely had higher dopamine release than in a classical WM task (with letters, numbers, or colours). Thus, results from Study IV suggest that serotonin could modulate dopamine in WM updating only in stressful situations, when DA release is increased.

The contribution of sex to perception and WM performance was explored throughout the studies II–VI. The main effect of sex in the general speed of perception was present in Study III. However, even though the neurobiological mechanism in men and women may be different, sometimes, the behavioural outcomes are not. For example, in Study IV there were no significant differences between men and women in WM in general RTs for correct responses, only a tendency for the difference ($t(451)=-1.86$, $p=0.063$, M(men)=838 ms, M(women)=888 ms). This does not necessarily mean that there are no sex differences in WM. It has been demonstrated that sex differences emerge in stressful and difficult task conditions only (Schoofs et al., 2013; Reed et al., 2017). The absence of sex differences in the 2-back task with facial expressions suggests that the 2-back task with emotional facial expressions could induce only mild stress in subjects, which can explain why sex differences were not clearly present.

Emotional dispositions as a source of variation in perception and working memory for facial expressions (Studies V and VI)

As a follow up to Study I, the role of emotional dispositions in explaining the WM updating variance was described in Study V. As suggested by Study I and concluded by a recent meta-analysis (Schweizer et al., 2019), the effect of emotional content of facial expressions on WM could be seen in people with mental health problems. In Study V, subjects were divided into high-anxiety + low depressiveness (HA), high-depressiveness + low anxiety (HD), high-anxiety + high depressiveness (HAHD), and the control group. This separation into four different groups helped to separate the effect of trait anxiety from depressiveness. Only two studies were found in the literature that had described the effect of either depressiveness or trait anxiety on updating facial expressions in an n-back task (Ladouceur et al., 2009; Levens and Gotlib, 2010). In both studies, high depressiveness was not separated from high anxiety, thus the unique contribution of these emotional dispositions to WM updating had not been described. Study V filled this gap in the literature.

In general, Study V showed that happy faces were relevant in discriminating between the emotional disposition groups: HD was associated with the *happy disadvantage* in WM updating (from neutral to happy) which was not present in HA. Again (as noted in Study I), this effect was present only if the happy stimulus was being encoded into memory (neutral-to-happy updating). Confirming that emotional expressions affect WM mainly in the encoding phase. It was noteworthy that there were no significant differences between emotional disposition groups in any other emotional expression condition. One possible explanation comes from the reward devaluation theory (Winer and Salem, 2016) in which subjects with HD avoid positive emotions (happy faces). Happy faces are rewarding and promote prosocial behaviour (Johnson and Fredrickson, 2005), so that normal subjects could be tuned in to encoding happy faces which results in response bias towards *sameness*, and slightly higher sensitivity for happy faces as shown in Study I. In contrast, subjects with HD avoid happy faces as they do not coincide with the underlying negative schema (Beck et al., 1987). Study V showed that the individual differences in emotional dispositions can affect WM for happy faces.

In Study V, the HA group was constructed based on Spielberger's trait anxiety inventory cut-off scores, a clinical diagnosis of any anxiety disorder was not used in the analysis. As a follow up to Study V, Study VI explored the contribution of clinically diagnosed social anxiety in explaining the variance in WM for emotional facial expressions. Unlike trait anxiety, social anxiety disorder (SAD) is specific to social interactions. SAD is characterized by an irrational fear of negative evaluation by others. This is often conveyed by facial expressions. Moreover, because SAD has an extremely high relapse rate (up to 70%, Keller, 2003) its status (present or past diagnosis) was considered relevant in facial expression processing in WM in Study VI. Previous studies had not used a clinical SAD group, or compared subjects with present vs past diagnosis of SAD to a matched control group. Thus, it was unclear how SAD status associates with WM updating for emotional facial expressions. The main preliminary findings from Study VI were: 1) significant three-way interactions between social anxiety status (past vs control), trial type (matched vs nonmatched trials), and emotional facial expressions in updating accuracy, 2) present SAD enhanced recognition accuracy (*match* trials) for facial expressions, 3) past SAD impaired recognition accuracy (*match* trials), especially for angry faces in contrast to the present SAD.

The effects of SAD status on emotional face processing in WM indicate that subjects with past SAD are different from the control group and from the present SAD group. Active avoidance could not entirely explain the results. Subjects with present SAD rated the valence and arousal of facial expressions similar to the controls, and present SAD, which suggested that perhaps the automatic appraisal, or a coping mechanism (attention strategy) is reflected by the behavioural responses in the WM task. The heightened attentional vigilance (McTeague et al., 2018) in response to salient facial stimuli in the 2-back task could have enhanced recognition in subjects with a present SAD episode but not in those with past SAD. Moreover, stimulus physical qualities in combination with different avoidance strategies in past vs present SAD likely contributed to the difference between past vs present SAD in *match* and *mismatch* trials.

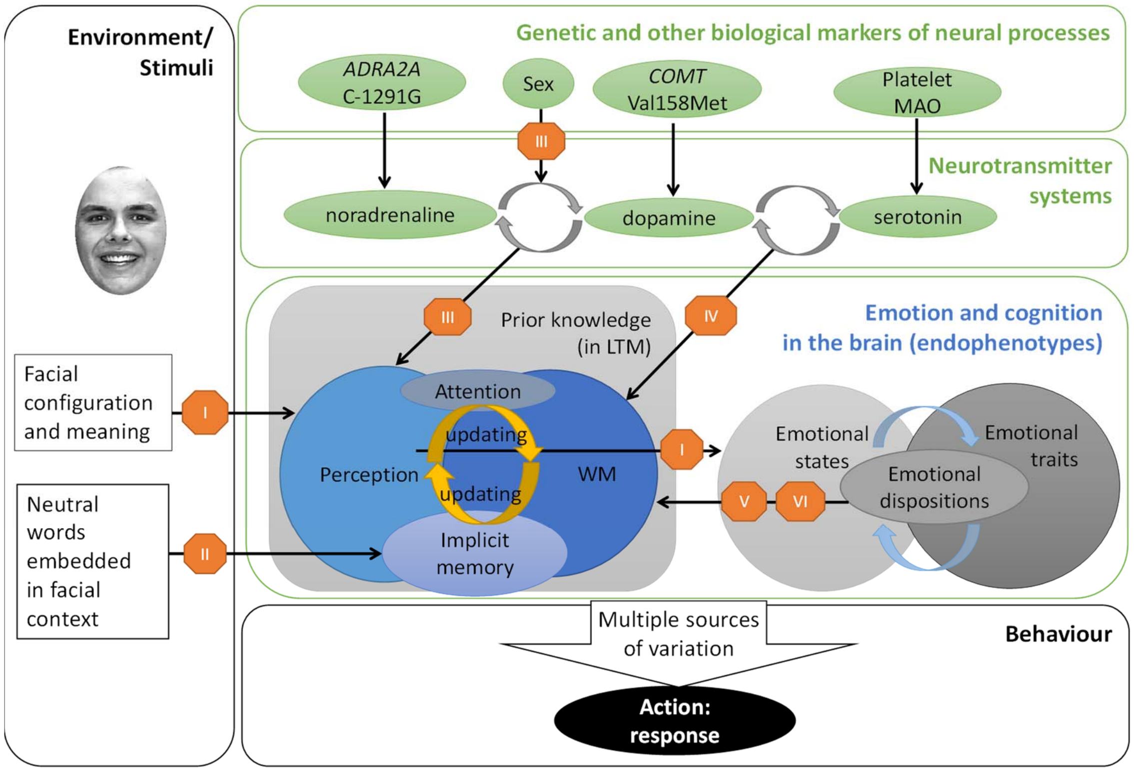
Some errors in *match* trials could have been induced by confusion between the perceived stimulus and WM content (same mouth in sad and angry, also see Study I) in subjects with past SAD. Subjects with present SAD automatically pay attention to the eyes first (Calvo et al., 2019). In contrast, perhaps a coping mechanism to avoid eyes resulted in confusion, and poorer recognition performance in past SAD who paid more attention to the mouth than the eyebrows.

In conclusion, Study VI showed that facial emotion processing in SAD is not straightforward. Predictions how subjects with either present or past SAD will react to a specific facial emotion can depend on stimulus qualities, as well as attentional strategies. In sum, Study VI showed that SAD status in combination with stimulus qualities significantly contributes to the variation in WM for emotional facial expressions.

Theoretical model for the multiple sources of variation in perception and working memory for facial expressions

The model (in Figure 6) describes the variation in perception and WM for facial expressions which comes from many sources. Studies I–VI demonstrated that perception and WM for facial expressions depends on stimulus qualities (physical and emotional), neurobiological differences in DA, NA and 5-HT systems, sex, and emotional dispositions (depressiveness, trait anxiety, SAD). Associations between these factors are visualized in Figure 6.

First, when a facial expression is captured by visual attention, its physical and emotional qualities continue to affect the encoding and further processing of that stimulus. The more different the perceived stimulus (the probe) is compared to what is being held in mind at that time (in WM) the easier it is to detect the difference, and to update the contents of WM (Study I). So, physical features and task difficulty significantly contribute to WM task performance. However, the emotional qualities are also relevant. If the face has a smiling upward U-curved mouth, its recognition is enhanced, mostly due to the positive emotional or rewarding meaning that is represented by smiles (Study I, and II). Smiling faces lead to *they all look the same to me* bias (Johnson and Fredrickson, 2005), which enhances accuracy in *match* trials.



Explanations:

I **Study I.** Facial configuration and meaning affects perception and WM encoding. Perception of emotion in facial stimuli induces arousal (mild acute stress).

II **Study II.** Facial context, and its motivational value modulates implicit memory for neutral words.

III **Study III.** DA modulates NA in perception, and sex modulates the interaction of NA and DA.

IV **Study IV.** 5-HT modulates DA in WM updating.

V **Study V.** Emotional dispositions (trait anxiety and depressiveness) modulate WM updating.

VI **Study VI.** Social anxiety disorder modulates WM updating.

Figure 6. Theoretical model for the underlying mechanism of variance in facial expression processing in perception and working memory. The model is based on studies I – VI. Roman numerals I–VI refer to the studies. The model intends to summarize the main findings, and the related literature, from the six studies, not to summarize all the literature. The model shows how responses for emotional facial stimuli depend on multiple cognitive, emotional, neural, and stimulus-driven factors as shown by experiments. This helps to explain the variation in responses to emotional facial expressions. Note. The happy facial stimulus is from the Cohn-Kanade Dataset (CK+). LTM – long-term memory.

However, not everyone benefits from smiling faces. This effect is modulated by emotional dispositions (Studies V and VI). High depressiveness is associated with the *happy disadvantage* in WM updating which is not present in high trait anxiety (Study V). The effects of anxiety on facial expression processing in WM are more complex. In contrast to the high trait anxiety, social anxiety disorder induces some specific effects depending on the SAD status, and trial type (Study VI). Past SAD in comparison to the controls and present SAD impairs WM recognition accuracy, especially for angry facial expressions. In contrast, present SAD enhances recognition accuracy for sad, angry, and happy facial expressions.

Scheming faces are a special case in comparison to basic emotional expressions due to their ambivalent meaning (angry eyebrows and smiling mouth). Paradoxically, even though these expressions are often labelled as *evil* (see verbal labels in Study V, Appendix B), they are rated as positive (similar to happy faces, Figure 5) but high arousing (similar to angry faces). These stimuli can induce some seemingly contradictory effects. Similar to happy faces, scheming faces enhance *sameness* recognition bias in WM (Study I). Scheming faces enhance perceptual speed in some subjects (men with a risk for inattention and high DA availability) but decrease it in others (women with a risk for inattention and high DA availability, Study III).

In conclusion, variation in perception and WM for emotional facial expressions comes from a complex interplay between various sources. The model does not intend to describe the variability behind perception and WM for all possible situations. It summarizes the main findings from studies I–VI, and the literature associated with these findings. The model intends to describe how different outcomes in perception and WM performance for facial expressions can be explained in the context of emotion-cognition interactions. Interactions between facial stimulus characteristics (emotional content and features), emotional dispositions (including SAD), individual differences in neurotransmitter systems, and sex lead to different perception, and WM performance outcomes. Simplified predictions about the main factors from studies I–VI that contribute to the WM outcome as shown in the theoretical model are visualized on Figure 7. Potential applications and future directions are discussed in the next section.

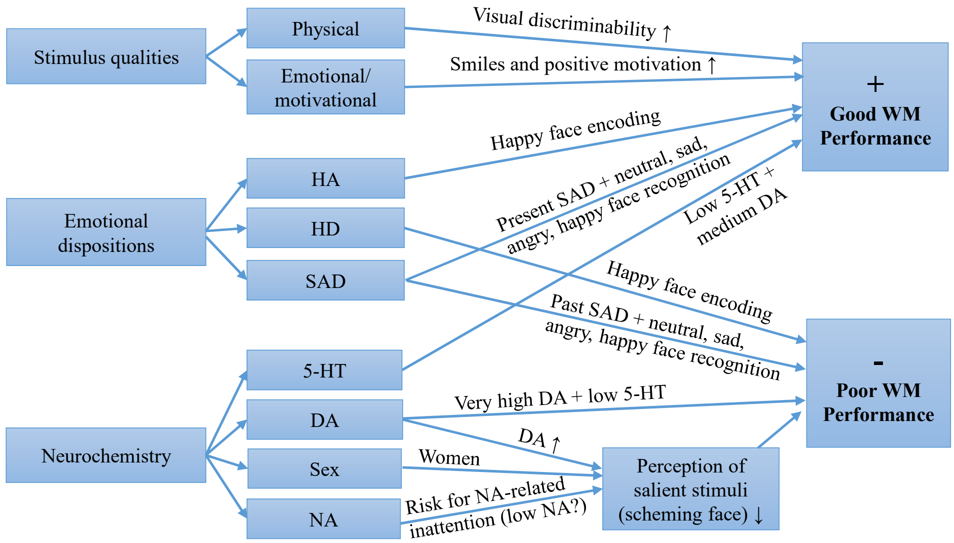


Figure 7. Illustration of the main predictions for WM performance from studies I–VI. *Note. HA – high trait anxiety, HD – high depressiveness, SAD – social anxiety disorder, 5-HT – serotonin, DA – dopamine, NA – noradrenaline.*

Applications and future directions

The analysis of the sources of variation in perception and WM for emotional facial expressions opens a broad range of opportunities for real-life applications that could be useful in clinical work with psychiatric patients, educational settings, human-computer interaction technologies, and discovery of drug targets. Some potential applications are:

- WM updating task as a screening tool for discriminating between high depressiveness and high anxiety in clinical work.
- Schematic emotional faces as a proxy for real faces in human/computer interaction technologies, including WM training programs with schematic facial expressions for autism spectrum disorders.
- α_{2A}-Adrenoceptors together with COMT activity modulators as a combination for potential targets for new ADHD drugs, or cognitive enhancers.
- WM facial emotion updating task as a relapse-preventative, and SAD progression monitoring tool for separating past SAD from present SAD.
- Positive emotional context (e.g., exposure to happy faces) as a memory enhancer in educational settings.

Future studies should examine the potential contribution of attention, task-type, emotional and motivational meaning and ambiguity of the facial stimuli, the role of serotonin and dopamine receptor subtypes in PFC regulation, and other relevant factors that can contribute to facial expression processing in perception and WM that exceeded the scope of the present dissertation. Studying the interactions between neurobiological markers and environmental factors (stimuli, and induced stress) during encoding into WM or during retrieval from WM can help to understand the mechanisms that underlie the variability between and within subjects in WM for facial expressions. WM is crucial in communication, reading, thinking, learning, and various other mental operations that we carry out every day. Understanding facial emotion processing in WM moves us closer to understanding the human mind and behaviour.

SUMMARY AND CONCLUSIONS

Working memory (also known as short-term memory) is a cognitive process that helps to bind perceived information with existing knowledge, hold it online for a short period of time, and use it in a purposeful manner to perform a task. Perception and WM are relevant in any purposeful activity. For example, when reading a book, WM helps to remember the words at the beginning of a sentence up to the end of a sentence. In mathematics, WM helps to carry out simple calculations. WM is relevant in face-to-face communication, it helps to understand other's facial expressions, and bind it with the verbal information to better understand the other person's intentions and message. WM is closely related to the perceptual process that results in representations of the external stimuli. One of the most important stimuli that we see on daily basis are facial expressions. Facial expressions can convey feelings, attitudes and opinions towards the observer. Thus, it is socially important to recognize and distinguish facial expressions well in WM. How well or poorly people distinguish between facial expressions in WM depends on many factors, some of which were discussed in this dissertation.

Study I focused on the effects of stimulus qualities. 507 adults from the Estonian Children Personality Behaviour and Health Survey (ECBPHS) participated in the experiment. We studied the effects of physical features (e.g., angry face with downward eyebrows and downward facing corners) and emotional content of the schematic facial stimuli on WM performance. The number of differences between facial expressions in WM (e.g., different mouth, different eyebrow, etc.) had greater effect on WM performance than the emotional content (sad, angry, scheming, happy, neutral). We also found some proof for a response bias, and a positive effect on WM accuracy in the experimental setting where happy facial expression was compared to the neutral face in memory.

Study II, throughout the three experiments, focused on the effect of the meaning of real emotional facial expressions on neutral word priming (n1=117, n2= 69, n3=53). While the first study showed that happy facial expressions promote an inclination towards *same* responses, and enhance accuracy, then the second study confirmed the positive effect of happy facial expressions on implicit memory. The novel part of this work was the operant conditioning procedure in which happy faces were associated with a negative, neutral, or positive meaning. This showed that the emotional content of facial expressions is important. Happy faces with a negative meaning did not enhance implicit memory, but the same happy faces that had been associated with positive meaning did. Thus, positive motivational context helps to remember neutral words.

Study III explored the effects of two genetic markers on perception of emotional expressions in the ECPBHS sample. For this, we used a simple reaction time task with schematic facial expressions. Based on Posner's attention theory, responses were divided into two groups: alert and regular detection. We used the *ADRA2A* C-1291G gene variant as a marker for the noradrenaline system and *COMT* Val158Met gene variant as a marker for the dopamine system. Study III showed that simple response times depended on the interaction of facial expressions, gene variants and sex. In women, risk-allele for inattention (G-allele) in combination with higher Met-dosage (high DA) was associated with slower regular response times. The opposite was present in men.

Study IV focused on the interaction of biomarkers for serotonin and dopamine systems on WM updating efficiency. Here, we explored the general WM efficiency for facial expressions (i.e., response times of correct responses) in the ECPBHS sample. The interaction of *COMT* Val158Met genotype and platelet monoamine oxidase activity (platelet MAO), as markers of the dopamine and serotonin system, predicted WM efficiency. Low platelet MAO activity, which is generally considered a risk factor, was beneficial in a speeded task, but only in the Val/Met genotype (average dopamine level in the prefrontal cortex). However, for the Met/Met genotype (high dopamine levels in the prefrontal cortex), high platelet MAO activity was beneficial. There were no clear sex differences.

Study V described the effects of depressiveness, trait anxiety, and their coexistence on the performance of emotional facial expressions compared to a matched control group (subsamples from the ECPBHS). Interestingly, high depression, but not high anxiety, was associated with poorer WM performance in an experimental condition where it was necessary to recall a neutral facial expression and compare it to a happy face. This happy face disadvantage in encoding may indicate that more depressed people avoid happy faces and, therefore, make mistakes in a task where they need to compare it to a neutral face.

Study VI continued the idea from Study V. We explored the effect of social anxiety disorder (SAD) on WM for emotional facial expressions (in a subsample from ECBHS). The sample included subjects who had been diagnosed with SAD in the past but had recovered, subjects who had been diagnosed with SAD at the time of the experiment, and a matched control group. The results showed that the past SAD can be differentiated from the control group and the acute SAD based on updating of facial expressions. In general, present SAD enhanced facial emotion recognition. The findings supported the heightened attentional vigilance hypothesis. The difference between acute and past SAD was most prevalent in angry face recognition: people with past SAD made significantly more errors in angry face recognition than those who were currently diagnosed with SAD or had never had SAD (control group).

In sum, perception and WM for facial emotional expressions depends on the interaction of many factors. It cannot be concluded from this dissertation that there is a simple “recipe” or one specific gene allele that determines how well a person perceives, recognises, or updates facial expressions. It can be concluded that the effect of emotion on WM is smaller than expected. Positive facial expressions tend to promote WM performance, but not in depressed subjects, nor in subjects with past social anxiety disorder. The interaction of the noradrenaline, dopamine, serotonin systems, and sex affects perception and WM for facial expressions. I proposed a theoretical model to summarize these results, and discussed some potential applications, and future directions of this research.

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SUMMARY IN ESTONIAN

Emotsionaalsete näoilmete taju ja töömälu variatiivsuse allikad

Töömälu ehk lühiajaline mälu on tunnetusprotsess, mis aitab tajutud informatsiooni siduda olemas olevate teadmistega ning kasutada lühiajaliselt salvestatud uut teadmist ülesande täitmiseks. Töömälu ja sellega tihedalt seotud taju protsess on igasuguse eesmärgipärase tegevuse aluseks. Näiteks raamatu lugemisel aitab töömälu hoida lause alguses olevaid sõnu meeles seni, kuni lause on lõpuni loetud. Matemaatikas aitab töömälu arve peast kokku liita. Suhtlemisel aitab töömälu kokku siduda näoilme ja jutus sisalduva sõnumi, et paremini mõista vestluskaaslase kavatsusi ja sõnumit. Töömälu on tihedalt seotud tajuprotsessiga, sellega, kuidas stiimul jõuab meelte kaudu ajju, kus moodustub representatsioon välismaailmast. Üks tähtsamatest stiimulitest, mida inimesed oma töömälus igapäevaselt hoiavad on näoilmed. Emotsionaalsete näoilmete tunnetamine ja lühiajaliselt mälus hoidmine on enamike inimeste jaoks igapäevane tegevus. Näoilmed annavad aimu vestluspartneri hetkeseisundist, tema hoiakutest ja arvamustest vaatleja suhtes. Seega on sotsiaalselt tähtis ära tunda ja töömälus hästi eristada näoilmeid. See, kui hästi või halvasti inimeste töömälu näoilmete eristamisega toime tuleb sõltub paljudest teguritest, millest mõnesid siinne doktoritöö uuris.

Esimene uuring keskendus stiimuli omaduste mõju uurimisele. Eesti Laste Isiksuse, Käitumise ja Tervise Uuringus (ELIKTU) osalenud 507 täiskasvanud inimesel tehtud eksperimendis uurisime, kas ja kuivõrd mõjutavad näoilmete füüsikalised tunnused (nt vihasel näol on allapoole viltune kulmukaar ja allapoole suunatud suunurgad) seda, kuidas näoilmeid omavahel töömälus eristatakse. Peamine küsimus oli see, kas inimesed otsustavad emotsioone väljendavate nägude sarnasuse ja erinevuse üle näo kujundliku väljanägemise või selle emotsionaalse sisu põhjal. Uuringust nähtus, et see, kui erinevad on skemaatilised näoilmed tunnuste arvu poolest (nt erinev suu, erinev kulmukaar jne) ennustab palju paremini sooritust kui see, millise emotsiooniväljendusega oli tegu (kurb, kuri, salakaval, rõõmus, neutraalne). Siiski, leidus ka tõendeid, et emotsionaalne sisu võib omada positiivset mõju töömälu täpsusele. Eelkõige siis, kui tuleb võrrelda rõõmsat näoilmet mälus oleva neutraalse näoilmega.

Teine uuring sisaldas kolme käitumuslikku eksperimenti (n1=117, n2=69, n3=53 inimest), mille abil uurisime fotodel esitatud emotsionaalsete näoilmete peidetud (implitsiitset) mõju neutraalsete sõnade meeldejätmisele. Kui esimeses uuringus selgus, et rõõmsad näoilmed soodustavad "sama" vastamise kallet, aga ka vähesel määral töömälu täpsust, siis teine uuring kinnitas rõõmsa näoilme positiivset mõju implitsiitsele mälule. Uuenduslikum osa oli rõõmsate nägude tähenduse muutmine lihtsa operantse tingimise ülesandega, kus nägudele omistati negatiivne, neutraalne või positiivne tähendus. Ilmnes, et näoilmete emotsionaalne sisu on tähtis. Negatiivse tähendusega rõõmsad näod ei soodustanud implitsiitset mälu, küll aga soodustasid seda positiivse tähendusega täpselt samad rõõmsad näod. Järeldasin, et positiivne motiveeriv kontekst aitab neutraalset teavet paremini meelde jätta.

Kolmas uuring kirjeldas kahe geenimarkeri koosmõju emotsiooniväljenduste tajule (ELIKTU andmetel). Kasutasime skemaatiliste näoilmetega lihtsa reaktsiooniaja eksperimenti. Reaktsiooniajad jagasin Posneri tähelepanuprotsesside järgi kahte gruppi: kiired ja aeglased. Hierarhilised statistilised mudelid (segamudelid) kirjeldasid mõlemat protsessi eraldi. Noradrenaliini süsteemi markerina kasutasime *ADRA2A* C-1291G geenivarianti ja dopamiini süsteemi markerina kasutasime *COMT* Val158Met geenivarianti. Tulemused näitasid, et see, kui kiiresti inimesed näoilmetele reageerivad, sõltub nende kahe geenivariandi ja soo koosmõjust. Naised, kellel oli lisaks ka tähelepanematuse riski ennustav geenialleel (G-alleel) ja kõrgem dopamiini tase (Met-alleel) reageerisid aeglasemalt tugevat aktivatsiooni tekitavale (salakavalale) näoilmele. Meestel oli seos vastupidine.

Neljas uuring keskendus kahe geenimarkeri koosmõju uurimisele näoilmetega töömälu ülesandes (ELIKTU andmetel). Siin vaatlesime dopamiini ja serotoniini süsteemide markerite koosmõju üldisemalt näoilmete töömälu tõhususele (st õigete vastuste reaktsiooniaegadele). *COMT* Val158Met genotüüp ja vereliistakute monoamiini oksüdaasi aktiivsus (vMAO) kui dopamiini ja serotoniini süsteemi markerid ennustasid koosmõjus töömälu tõhusust. Selgus, et madala vMAO aktiivsus, mida üldiselt peetakse riskiteguriks, võib olla kasulik just kiirust nõudvas ülesandes, kuid ainult siis, kui dopamiinisüsteemi kodeerib Val/Met genotüüp (keskmine dopamiini tase prefrontaalkoores). Samas Met/Met genotüübi (kõrge dopamiini tase prefrontaalkoores) puhul tuleb töömälu ülesandes kasuks, vastupidi, kõrge vMAO aktiivsus. Soolisi erinevusi sellest uuringust selgelt ei ilmnenud.

Viies uuring kirjeldas depressiivsuse, ärevuse ja nende koosesinemise mõjusid emotsionaalsete näoilmete töömälu sooritusele võrdluses sobitatud kontrollgrupiga (alamvalim ELIKTU andmetest). Huvitav tulemus oli see, et kõrge depressiivsus, aga mitte kõrge ärevus, seostus madalama töömälusooritusega katsetingimuses, kus oli tarvis meenutada neutraalset näoilmet ja võrrelda seda rõõmsa näoga. Selline rõõmsast näost tingitud töömälu halvenemine võib viidata sellele, et depressiivsemad inimesed väldivad rõõmsaid nägusid, mistõttu teevad ka vigu ülesandes, kus neid tuleb neutraalse näoilmega võrrelda.

Kuues uuring oli jätk viiendale. Uurisime sotsiaalärevuse diagnoosiga inimestel näoilmete töömälu sooritust (alamvalim ELIKTU andmetest). Valimisse kuulusid need, kellel oli sotsiaalärevus diagnoositud varasemalt, kuid olid tervenenud, need, kes olid katse ajal sotsiaalärevuse diagnoosiga ja kontrollrühm. Tulemused näitasid, et üldiselt oli näoilmete äratundmine töömälus parem neil, kellel oli katse ajal sotsiaalärevuse episood. See kinnitas akuutse sotsiaalärevuse puhul näoväljenduste aktiveeriva mõju (*heightened attentional vigilance*) hüpoteesi. Varasem sotsiaalärevusega grupp erines nii kontrollgrupist kui akuutsest grupist eelkõige vihase näoilme äratundmisel: varasema sotsiaalärevusega inimesed tegid oluliselt rohkem vigu vihase näo äratundmisel kui need, kellel oli parajasti sotsiaalärevus või kellel polnud kunagi olnud sotsiaalärevuse diagnoosi.

Kokkuvõtteks saab doktoritööst järeldada, et emotsionaalsete näoilmete taju ja töömälu sooritus sõltub paljude tegurite koostoimest. Ei saa väita, et on olemas lihtne “retsept” või üks kindel geeni-alleel, mis määratleks selle, kui hästi inimene teiste näoilmeid ära tunneb või mälus olevaga võrrelda suudab. Võib öelda, et emotsiooniväljenduste mõju oli oodatust väiksem. Saab järeldada, et positiivsed näoilmed pigem soodustavad töömälu sooritust, kuid mitte depressiivsetel. Lisaks mõjutab näoilmete taju ja töömälu protsesse noradrenaliini, dopamiini ja serotoniini süsteemide ja soo koostoime. Töös pakkusin välja teoreetilise mudeli nende tulemuste kirjeldamiseks ning arutlesin mõningate võimalike rakenduste ja tulevikusuundade üle.

PUBLICATIONS

CURRICULUM VITAE

Name: Gerly Tamm
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Education

2011–2021 Doctoral studies, University of Tartu, Department of Psychology
2017–2020 Academic leave (maternity)
2013–2015 Doctoral studies as a visiting research fellow, University of Missouri, Department of Psychological Sciences
2008–2010 Master's studies in psychology (*cum laude*), University of Tartu, Department of Psychology
2005–2008 Bachelor's studies in psychology (minor: economics), University of Tartu, Department of Psychology
2003–2005 High school studies (mathematics and physics class, *diploma with commendation),* Hugo Treffner Gymnasium

Career

02.10.2018–... University of Tartu, Center for Applied Social Sciences (CASS), data analyst – project manager (0,50)
01.09.2015–01.10.2018
University of Tartu, Center for Applied Social Sciences (CASS), data analyst – project manager (1,00)
2013–2015 University of Missouri, Working Memory Lab, visiting research scholar (1,00)
2011–2013 and 2016–2017
Foundation Tartu Center of Mental Health, rehabilitation specialist – psychologist and research project manager (0,20)
01.01.2016–31.12.2016
University of Tartu, Department of Psychology, project manager (part-time)
20.09.2010–31.12.2014
University of Tartu, Department of Psychology, project manager (0,50)
2010–2014 Valga Hospital, psychologist (0,20)
2010–… University of Tartu, Department of Psychology, research assistant, lecturer, and thesis advisor (temporary part-time jobs)

Fields of research

Experimental psychology, behavioural and cognitive neuroscience

Publications and conference proceedings in peer-reviewed journals

Tamm, G., Kreegipuu, K., Harro, J. (2021). Platelet MAO activity and COMT Val158Met genotype interaction predicts visual working memory updating efficiency. *Behavioural Brain Research, 47,* 113255. DOI: 10.1016/j.bbr.2021.113255.

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Peer-reviewed conference presentations and posters (selection)

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Tamm, G., Rahe; T., Palu-Laeks, M., Salakka, S., Cowan, N. (2016). The Effect of Age on Visual Working Memory, Metamemory, and Behavioural Inhibition in 18–50 Years Old Women and Men. *24th Biennial Meeting of the International Society for the Study of Behavioural Development*, Lithuania, Vilnius.

Tamm, G., Kreegipuu, K., Harro, J. (2015). Individual Differences in Visual Information Processing: The Interaction of DBH and Gender. 87th Annual Meeting of the Midwestern Psychological Association, Chicago, 114–114.

Kukk, G., Kreegipuu, K., Harro, J., Cowan, N. (2014). *Is Working Memory Accuracy Affected by the Valence and Arousal? 86th Annual Meeting of the Midwestern Psychological Association,* USA, Chicago, 81–81.

Kukk, G., Kreegipuu, K. (2011). The Emotional Load and Perceptual Differences of Schematic Faces and Objects. *Rovereto Attention Workshop Attention and Objects*, Italy, Rovereto.

Other publications (selection)

Tamm, Gerly (2021). "*Käpp ja Käsi" programmiga sarnased loomi kaasavad sekkumised ja nende mõju õigusrikkujatele: teaduskirjanduse süstemaatiline analüüs*. NGO Käpp ja Käsi. 1–25.

Espenberg, S., Juurik, M., Lõuk, K., Parder, M.L., Remmik, M., Sutrop, M., Tamm, G. (2020). *Teaduseetika järelevalve ja toetamise riikliku süsteemi loomine Eestis.* Tartu: Tartu Ülikooli sotsiaalteaduslike rakendusuuringute keskus RAKE ja Tartu Ülikooli Eetikakeskus.

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Tamm, G., Kõiv, K., Zagura, N., Rozgonjuk, D., Türk, Ü., Taimalu, M., Külmoja, I., Podberjoznaja, G., Agajev, S., Konstabel, K. (2016). *Õpetajate enesetõhususega seotud mõõtevahendi kohandamine (inglise keelest eesti ja vene keelde).* The National Institute for Health Development.

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2008–2010 Magistriõpingud psühholoogias (*cum laude*), Tartu Ülikool, Psühholoogia Instituut
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Teenistuskäik

02.10.2018–... Tartu Ülikool, Sotsiaalteaduslike Rakendusuuringute Keskus (RAKE), analüütik – projektijuht
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2010–… Tartu Ülikool, Psühholoogia Instituut, eksperimentaator, lektor ja seminarijuhendaja, uurimistööde juhendaja (ajutised osaajaga tööd)

Teadustöö põhisuunad

Eksperimentaalpsühholoogia, käitumuslik ja kognitiivne neuroteadus

Publikatsioonid ja publitseeritud konverentsiteesid teadusajakirjades

Tamm, G., Kreegipuu, K., Harro, J. (2021). Platelet MAO activity and COMT Val158Met genotype interaction predicts visual working memory updating efficiency. *Behavioural Brain Research, 47,*113255. DOI: 10.1016/j.bbr.2021.113255.

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Eelretsenseeritud konverentsiettekanded ja postrid (valik)

Tamm, G. (2020). Present Vs Past Diagnosis of Social Anxiety Disorder: Differences in Recognition of Emotional Schematic Facial Expressions in Working Memory. *32nd Association for Psychological Science Annual Convention: 32nd Association for Psychological Science Annual Convention.* USA, online conference.

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Tamm, G., Cowan, N. (2015). Fluctuations in emotional state during cognitive tasks: preliminary results. *Annual Conference of the Doctoral School for Behavioural, Social and Health Sciences.* Estonia.

Tamm, G., Rahe; T., Palu-Laeks, M., Salakka, S., Cowan, N. (2016). The Effect of Age on Visual Working Memory, Metamemory, and Behavioural Inhibition in 18–50 Years Old Women and Men. *24th Biennial Meeting of the International Society for the Study of Behavioural Development*, Lithuania, Vilnius.

Tamm, G., Kreegipuu, K., Harro, J. (2015). Individual Differences in Visual Information Processing: The Interaction of DBH and Gender. 87th Annual Meeting of the Midwestern Psychological Association, Chicago, 114–114.

Kukk, G., Kreegipuu, K., Harro, J., Cowan, N. (2014). *Is Working Memory Accuracy Affected by the Valence and Arousal? 86th Annual Meeting of the Midwestern Psychological Association,* USA, Chicago, 81–81.

Kukk, G., Kreegipuu, K. (2011). The Emotional Load and Perceptual Differences of Schematic Faces and Objects. *Rovereto Attention Workshop Attention and Objects*, Italy, Rovereto.

Muud publikatsioonid (valik)

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