Neural Mechanisms Underlying Visual Short-Term Memory for Facial Attributes

Theses of the *Ph.D.* Dissertation

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1 Introduction and aims

Face processing is one of the most researched fields of cognitive neuroscience, since the majority of socially relevant information is conveyed by the face, rendering it as a stimulus of exquisite importance. The development of reliable computational face recognition algorithms is also a key issue in computer vision. Despite the extensive research effort, we have yet to see a system that is effective in an unconstrained setting with variability in imaging parameters such as sensor noise, viewing distance, illumination and in facial expressions that has a huge impact on the configural layout of the particular face. The only system that does the work in spite of all these challenges is the human visual system itself. Therefore, advancing the understanding of the strategies this biological system employs is not only invaluable for a better insight of how the brain works but also a first step towards eventually translating them into machine-based algorithms (for review see [10]).

Faces are considered a special class of stimuli with dedicated neural processing mechanisms that differ from that of other nonface objects. Opinions differ on the reason underlying their special status: one group of researchers claims that faces are processed by cortical areas entirely dedicated to face processing [11, 12], while others argue that the specific responses obtained for faces is a result of the type of judgment we are required to make whenever viewing a face: differentiating that individual face from the rest (i.e. subordinate-level of categorization) and also the level of expertise with which we make these categorization judgments [13, 14]. Within the processing circuits there is evidence for a certain degree of separation between changeable (such as expression, lipspeech and eye gaze) and invariant facial attributes (such as identity and gender), the former being coded/processed predominantly in the superior temporal sulcus (STS), the later in the fusiform face area (FFA) [15]. This separation is not exclusive however, since there is significant overlap [16].

Independent of the fine details, if faces represent a class of stimuli of special importance, it is not only the neural mechanisms underlying processing of facial attributes that needs to be fine-tuned. The same should hold true for higher cognitive processes dealing with faces. Memory seems to be an especially important mechanism among these, since in every social encounter efficient processing of the faces in itself is not enough if we cannot remember who the person that we encountered is. More faces can be encoded and stored in visual short-term memory (VSTM) than inverted faces or other complex nonface objects [17] and this VSTM difference between upright and inverted faces is present only when the facial configural information has to be encoded and stored as opposed to the null effect of orientation in cases when only featural information changes [18]. Morover, there is no decay in discrimination performance of these gross featural/configural changes over time up to 10 seconds [18].

However, the time-scale of VSTM capacity for realistic fine changes is not known, which has evolutionary significance in monitoring continuously changing facial features such as facial mimic conveying important emotional information. Our goal was to investigate in a series of experiments how efficiently humans could store facial emotional expressions in visual short term memory. In addition, we also aimed at testing the prediction that short term memory for information related to changeable facial emotional expressions might be more efficient than that related to invariant facial attributes, such as identity. Furthermore, we aimed at resolving the question whether short-term memory for facial emotional expressions was based on the same neural mechanisms at different retention durations, or alternatively, encoding and retrieval processes were changing depending on how long emotional information had to be stored in visual short-term memory.

2 Methods Used in the Experiments

Throughout the course of my work I have used a wide array of experimental methods applicable in cognitive neuroscience research. This includes psychophysics, electrophysiology with classical ERP and more advanced mathematical analytical approaches and functional magnetic resonance imaging. For writing experimental presentations and scripts for analyzing the results I used Matlab 7.1 (The MathWorks Inc., Natick, MA, USA) with various toolboxes for presentation (Psychtoolbox 2.54 - [19, 20]) and for data analysis (Psignifit - [21]) alongside other commercial software (BrainVision Analyzer 1.05 - EEG preprocessing, Brainproducts GmbH., Munich, Germany; BESA 5.2 - source localization, MEGIS Software GmbH., Gräfelfing, Germany; BrainVoyager 1.91 - *f*MRI preprocessing and data analysis, Brain Innovation, Maastricht, The Netherlands). I have implemented the bootstrap bias-corrected and adjusted (BCa) analysis and the lateralized readiness potential (LRP) analysis in Matlab based on directions in the literature ([22] and [23, 24] for BCa and LRP, respectively). I recorded EEG with a BrainAmp MR amplifier (Brainproducts GmbH., Munich, Germany) with 64 Ag/AgCl electrodes mounted in an EasyCap (Easycap GmbH, Herrsching-Breitbrunn, Germany). The *f*MRI data were collected at the MR Research Center of Szentágothai Knowledge Center, (Semmelweis University, Budapest, Hungary) on a 3.0 Tesla Philips Achieva (Best, The Netherlands) scanner equipped with an eight-channel SENSE head coil.

3 New Scientific Results

1. Thesis: I have characterized the efficiency of short-term memory storage of different facial attributes, namely emotional expression and identity in a facial attribute discrimination task revealing a high-fidelity storage for both. Furthermore, I have proved that this storage is based on holistic processing of faces focused on the given attribute as opposed to the mere processing of local features.

Published in [1], [3].

Among many of its important functions, facial emotions are used to express the general emotional state (e.g. happy or sad); to show liking or dislike in everyday life situations or to signal a possible source of danger. Therefore, it is not surprising that humans are remarkably good at monitoring and detecting subtle changes in emotional expressions. To be able to efficiently monitor emotional expressions they must be continuously attended to and memorized. In contrast, there are facial attributes - such as identity or gender - that on the short and intermediate timescale are invariant [15, 16]. Therefore, invariant facial attributes do not require constant online monitoring during social interaction. Using a two interval forced choice facial attribute discrimination task we measured how increasing the delay between the subsequently presented face stimuli affected facial emotion and facial identity discrimination.

> *1.1. I have shown that people posses a high-fidelity visual short-term memory for facial emotional expression and identity, since emotion discrimination is not impaired when the faces to be compared are separated by several seconds, requiring storage of fine-grained emotion-related information in short-term memory. Likewise, in contrast to my prediction, I found no significant effect of increasing the delay between the sample and the test face in the case of facial identity discrimination.*

Observers performed delayed discrimination of three different facial attributes: happiness, fear and identity. In all three discrimination conditions reaction times were longer by approximately 150-200 ms in the 6-s delay than in the 1-s delay conditions providing support for the involvement of short term memory processes in delayed facial attribute discrimination in the case of 6-s delay condition. Increasing the delay between the face images to be compared had only a small non-significant effect on observers' performance in the identity discrimination condition revealed by a slight increase in the just noticeable difference (JND) value between the two faces. On the other hand, discrimination of facial emotions was not affected by the delay (Fig.1). These results suggest that fine-grained information about both facial emotions and identity can be stored with high precision, without any loss in VSTM.

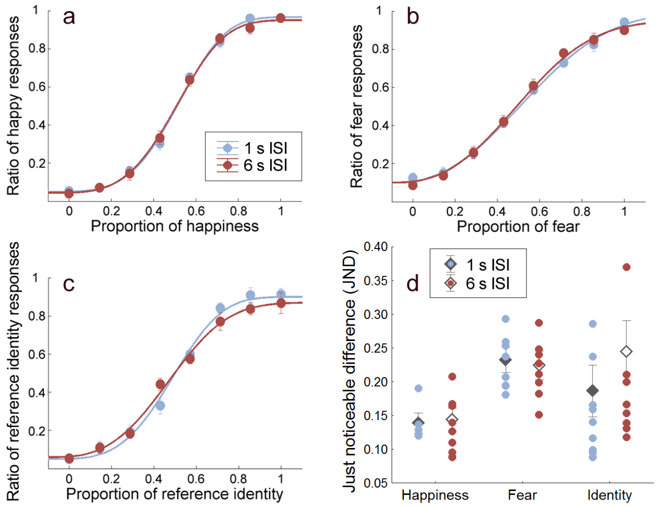

Figure 1: Effect of ISI on the performance of facial emotion and identity discrimination. Weibull psychometric functions fit onto (a) happiness, (b) fear and (c) identity discrimination performance. (d) The obtained just noticeable differences (JNDs). (Diamonds represent mean JNDs in each condition while circles indicate individual data for short (blue) and long (brown) delays. Error bars indicate $\pm SEM$ $(N = 10)$.)

1.2. Furthermore, I have corroborated my findings on a large sample size of 160 subjects revealing flawless short-term memory for both facial emotions and facial identity also when the discrimination task was performed with novel faces. I have also shown that practice and familiarity of faces affected performance in the facial identity discrimination task but not in the facial emotion discrimination task, which did not require learning.

To test whether high-precision visual short term memory for facial emotions also extends to situations where the faces and the delayed discrimination task are novel to the observers we conducted an experiment, where each participant (N=160) performed only two trials of delayed emotion (happiness) discrimination and another two trials of delayed identity discrimination. For half of the participants the sample and test faces were separated by a 1-s delay while for the other half of participants the delay was 10 s. The results revealed that subjects' emotion and identity discrimination performance was not affected by the delay between the face stimuli to be compared, even though the faces were novel (Fig.2). It also excludes the possibility that the present attribute discrimination is based on the representation of the whole range of the task-relevant feature information that builds up during the course of the experiment, as suggested by the Lages and Treisman's criterion-setting theory [25]. Instead it is based on the perceptual memory representation of the sample stimulus similarly to other delayed discrimination tasks [26, 27].

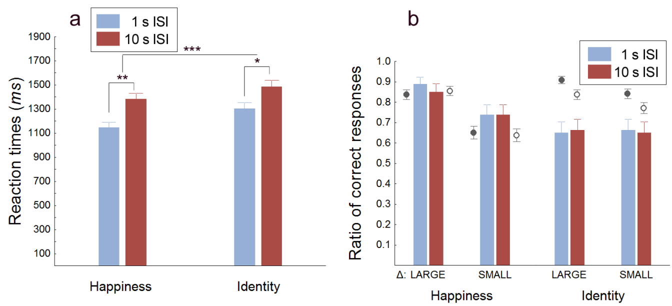

Figure 2: Reaction times and discrimination performance. (a) There was a significant RT increase in the 10-s compared to the 1-s delay condition in the case of both attributes (Valid number of measurements: $N = 74$ and $N = 60$ for the 1-s and the 10-s delay condition, respectively). (b) Performance did not show any significant drop from 1 s to 10 s delay (blue and brown bars, respectively) in either discrimination conditions, neither for face pairs with large nor with small difference. For comparison of the overall discrimination performance between this and the first experiment, grey circles represent the mean performance in the first experiment for the corresponding face pairs in the 1-s (filled circles) and 6-s (circles) delay conditions. Error bars indicate $\pm SEM$ ($N = 160$ and 10 for the current and the first experiment, respectively).

1.3. I have confirmed that the discrimination performance depended on holistic facial processing and could not be based solely on the processing of local features. In accordance with this I have proved that discrimination of fine-grained emotional expressions involved processing of high-level facial emotional attributes.

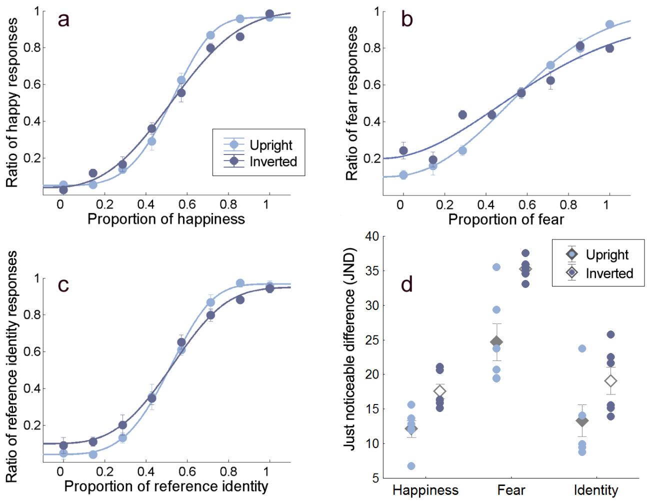

Figure 3: Effect of inversion on the performance of facial emotion and identity discrimination. Weibull psychometric functions fit onto (a) happiness, (b) fear and (c) identity discrimination performance. (d) Just noticeable differences (JNDs) obtained in the experiment. (Diamonds represent mean JNDs in each condition while circles indicate individual data for upright (light blue) and inverted (dark blue) presentation. Error bars indicate $\pm SEM$ $(N = 6)$).

It was crucial to show that performance in our facial attribute discrimination task was indeed based on high-level, face-specific attributes or attribute configurations as opposed to some intermediate or low level feature properties of the face images (e.g. local contour information, luminance intensity). In an experiment with the face stimuli presented in an inverted position where the configural feature was taken away leaving the low level features unaltered [28, 29] we found a significant drop in performance for all three attributes (i.e. increased JND values), which was most pronounced for upside-down fear discrimination, therefore proving holistic processing (Fig.3).

Furthermore, we have confirmed that the emotion discrimination in our short-term memory paradigm involved high-level processing of facial emotional attributes by performing an *f*MRI experiment and contrasting trials where subjects made decisions based on the emotional content of the stimuli with those based on identity content. We found no brain regions where activation was higher in the identity compared to the emotion discrimination condition. However, our analysis revealed significantly higher activations in the case of emotion compared to identity discrimination in the right posterior superior temporal sulcus (pSTS) among others (Fig.4). This is in agreement with previous studies showing that increased *f*MRI responses in the pSTS during tasks requiring perceptual responses to facial emotions compared to those to facial identity can be considered as a marker for processing of emotion-related facial information [30, 31].

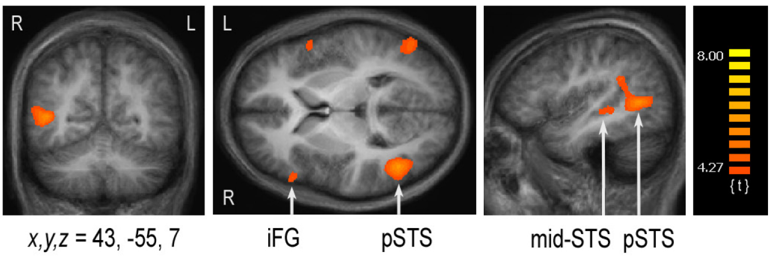

Figure 4: *f*MRI responses. Emotion vs. identity contrast revealed significantly stronger responses during emotion than identity discrimination within bilateral superior temporal sulcus (STS), and bilateral inferior frontal gyrus (iFG). (Coordinates are given in Talairach space, $N = 10$)

2. Thesis: I have shown that different neural mechanisms underlay high-fidelity short-term memory for emotional expressions depending on whether information had to be stored for one or for several seconds, which has been an unresolved question. This result was not confounded by differences in sensory processing demands or overall task difficulty which otherwise might offer alternative explanations to the above findings.

Published in [2], [3].

Previous research has implicated that during VSTM tasks encoding and retrieval processes were changing depending on how long the information has to be stored in VSTM. Patients with medial temporal lobe (MTL) lesions were impaired on VSTM tasks only when information had to be stored for several seconds but no VSTM deficits were found in the same tasks when retention duration was very short, 1 s [32, 33]. Moreover, studies investigating delayed discrimination of basic visual dimensions [34, 35, 36] found a significant increase in reaction times (RT) at delays longer than 3 s as compared to shorter, 1-s delays. Therefore, the goal of the present study was to directly compare short-term memory processes for facial expressions (happiness) when the faces to be compared were separated by one or by six seconds. We recorded event related potentials (ERP) while participants performed the same delayed emotion discrimination task with a 1-s or a 6-s ISI and found that several ERP response components are strongly modulated by retention duration both during encoding and retrieval of facial emotional information.

2.1. During encoding I found significant differences in the early P100 and N170 components of the event-related potential (ERP) responses between the delay conditions in a delayed emotion discrimination task. Furthermore, the memory-related late P3b ERP component was significantly reduced in the 1-s delay condition, which based on source-modeling results primarily originated from the right prefrontal cortex.

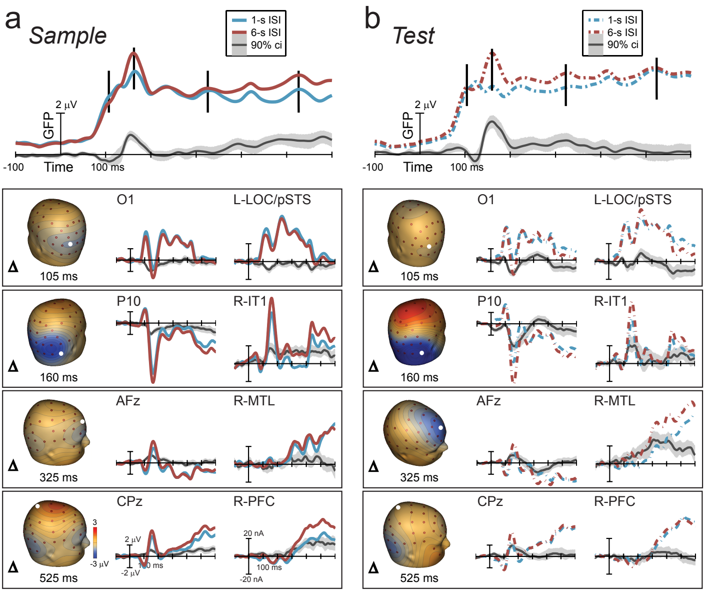

Figure 5: Delay effects observed in memory (a) encoding and (b) retrieval. Mean global field power (GFP) waveforms at 1-s and 6-s delays in the case of sample (solid blue and brown lines, respectively) and test faces (dashed blue and brown lines, respectively). GFP maxima of interest are marked with black lines and the corresponding topographic difference voltage maps of the 6-s vs. 1-s ISI conditions are depicted underneath with the ERPs on representative electrodes. Alongside are the time courses of possible cortical generators. Electrode locations are marked on scalp topographies with white dots. On all time courses gray bands indicate 90% BCa bootstrap derived confidence intervals of the 6-s vs. 1-s delay differences (dark gray lines).

Delay affected global field power (GFP) activity in the encoding phase already in a very early time window, peaking around 110 ms, corresponding to the P100 ERP component: activity of the scalp electrodes and sources related to the P100 component was significantly higher in the 1-s delay than in the 6-s delay condition (Fig.5a). On the other hand, GFP was higher in the 6-s delay than in the 1-s delay condition between 140-200 ms, in a time interval corresponding to the N170 ERP component. Activity of the scalp electrodes and sources related to N170 was modulated by delay correspondingly, being larger at 6 s than at 1 s delay.

Furthermore, GFP was also larger in the 6-s delay than in the 1-s delay condition in a later time interval, lasting from 375-600 ms, corresponding to the P3b component. This modulation pattern was consistent only with one source in our source model, namely with right ventral prefrontal cortex (PFC), which suggests PFC as the primary generator of this signal difference. This was also consistent with other findings [31] showing that modulation of the P3b component by memory load originated from the prefrontal cortex.

> *2.2. During retrieval, on the other hand, I found significantly stronger anterior medial temporal lobe (MTL) source activity peaking at 325 ms in the 6-s compared to the 1-s delay condition, which is evidence for MTL - possibly hippocampus - involvement during memory retrieval if faces are stored for several seconds.*

Bootstrap statistics revealed significantly higher GFP in the 6-s delay than in the 1-s delay condition in a time interval corresponding to the N170 ERP component (Fig.5b) in the case of the retrieval phase. Source modeling suggested this modulation might have been due to a strongly reduced transient inferior-temporal cortical neural response at 1-s delay as a possible contamination by adaptation effect. However, significantly higher GFP in the 6-s delay than in the 1-s delay condition was also found in a later time window, peaking around 325 ms. Source localization results suggested that this later delay-related modulation might have primarily originated from the right anterior MTL. The involvement of anterior MTL structures in face processing is supported by several lines of evidence coming form previous studies using intracranial ERP recordings [37, 38] as well as *f*MRI [32, 31, 39]. The results of the current study suggest that the retrieval phase of delayed discrimination of facial emotions at 6-s delay might be based on MTL processes to a larger extent than that of at 1-s delay, which is in line with several neuropsychologic studies [32, 33].

4 Possible Applications

The findings of the above series of studies reveal that humans possess flawless visual short-term memory for facial emotional expressions and facial identity. Such high-fidelity short term memory is inevitable for the ability to efficiently monitor emotional expressions and it is tempting to propose that impairment of such high-precision short-term memory storage of emotional information might be one of the possible causes of the deficits of emotional processing found in psychiatric disorders including depression, autism and schizophrenia [40, 41, 42].

The results of the present study provide the first evidence that different neural encoding and retrieval processes underlie flawless, high-resolution short-term memory for facial emotional expressions depending on whether information has to be stored for one or several seconds. Our findings therefore imply that models of short-term memory - which treat storage of sensory information over a period of time ranging from one up to several seconds as a unitary process (for review see [43]) - should be revised to include retention interval as an important factor affecting neural processes of memory encoding.

5 Acknowledgements

"Knowledge is in the end based on acknowledgment."
(Ludwig Wittgenstein)

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6 Publications

6.1 The Author's Journal Publications

[1] **É. M. Bankó**, V. Gál, and Z. Vidnyánszky, "Flawless visual short-term memory for facial emotional expressions," *Journal of Vision*, vol. 9, no. 1, pp. 12.1–13, 2009.

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6.2 The Author's International Conference Publications

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6.3 The Author's Other Journal and Conference Publications

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Cummulative Impact Factor of international journal papers: **17.516**; Number of independent citations: **29.**

6.4 Selected Publications Cited in the Dissertation

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