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The behavioural and electrophysiological aspects of the temporal context of face processing

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I. Antecendents and Aims of the present study

From a mathematical perspective we may consider the world around us an enormous set of information (set of objects end events). Most of these pieces of information are unimportant to us a given point of time, while other, much smaller amount of them is essential for some reason. For the sake of effective information processing we are armed with special sensory systems, which obtain the important information of the environment and translate it to the language of the nervous system [Sekuler & Blake, 2002].

In everyday life to see an object (or other visual stimulus) in isolation from its environment is very unlikely - objects mostly appear within their specific context. The context itself may be temporal or spatial and both have an impact on object processing. Literature is available concerning the effect of spatial context both on the electrophysiological and the behavioural level in humans and primates. From the perspective of the nervous system one stage of the ventral visual pathway, the inferior-temporal cortex (IT) is important [Logothetis et al., 1996; Rolls et al. 2003].

In this dissertation I will focus on the effects of the temporal context of face processing that has been broadly investigated in the past decades. Temporal context means the effects of a preceding or subsequent stimulus on the test stimulus. Experimental designs using a preceding stimulus are referred to as forward masking, priming and adaptation, while the name backward masking is used in subsequent stimulus presentation.

Adaptation effect is detectable on several stages of the visual processing, such as tilt after-effect [Gibson & Radner, 1937], motion after-effect [Mather et al., 1998]. For measuring these effects stimuli on different levels of complexity were used, ranging from very simple (for example a line with a given orientation) to highly complex. The most complex visual stimuli, in case of which adaptation effect was demonstrated, are human faces [Webster &

MacLin, 1999; Leopold et al., 2001]. This adaptation effect takes place both at the behavioural and the neuronal level. At the behavioural level we experience that our visual system gets accustomed (adapts) to the repeated or prolonged exposure to a stimulus. Due to this effect the behavioural response to the new stimuli changes, the thresholds of psychometrical function shift. Similarly to the behavioural effects, neural changes also take place. Due to repeated stimulus presentation, activity reduction can be measured with electrophysiological and imaging methods [Li et al., 1993; Gruber & Müller, 2005; Sayre & Grill-Spector, 2006].

After summarizing the theoretical background (1st chapter) in the second half of the dissertation I will review the behavioural and event-related potential (ERP) results of our adaptation experiments. We also applied transcranial Direct Current Stimulation (tDCS) with the help of which we could change the activity of different brain regions locally and reversibly in a non-invasive manner. We tested in a separate experiment the effects of this method on adaptation.

Our results suggest that the neuronal representation of surrounding objects is not fixed, it is recalibrating from second to second. While perceiving a stimulus our perceptual system considers the given stimulus as a norm and detects the deviation from it [Valentine, 1991; Rhodes et al. 2003]. Moreover, our results suggest that adaptation is not specific to lower level visual areas but it appears on the higher level, more complex visual areas as well.

Interestingly, post-stimulus presentation can also modify stimulus perception. For example detection and identification of the test stimulus can be modified by another (mask) stimulus. Masking effect can be triggered both by preceding and subsequent mask presentation. The latter phenomenon is called backward masking. It has different types in function of the spatial overlap of the test stimulus and the mask as well as the temporal difference between test and stimulus presentation (the latter is called stimulus onset asynchrony - SOA). In the last part of this dissertation I will present a backward masking experiment using facial expressions. Our behavioural and ERP results show that masking effects change in accordance with the type of mask and the SOA as it is shown by the behavioural results and early and late ERP components.

Main questions:

1. **Which are the levels of visual processing that object-selective after-effects can be linked to?**
2. **Is there category specificity in adaptation?**
3. **Are there hemispheric asymmetries in the strength of the adaptation effect (both in the behavioural and the electrophysiological domains)?**
4. **What role does the duration of adaptation play in shape-selective after-effects?**
5. **Which level of face processing can be regarded as being reflected in consciousness?**

II. Research Methods

Participants

Altogether 77 naive, healthy subjects with normal or corrected-to-normal vision took part (34 female, mean age=21.47 years) in the reviewed psychophysical, electrophysiological and transcranial direct current stimulation experiments.

Adaptation experiments

We used the morphed[1] versions of faces and hands as stimuli (modified by WinMorph 3.01) from a database created by our own laboratory. Experimental paradigms in all the adaptation experiments were rather similar: after a short period of randomized fixation (fixation duration changed between 500 – 700 ms) the adaptation stimuli were presented (long term adaptation lasted for 5000 ms (1. – 6. publications), while short term adaptation was 500 ms long (4. publication)). After a short break (at the beginning 200ms, later 500 ms) the test stimuli emerged for 200 ms. Participants had to carry out a two-alternative forced choice discrimination task. (gender discrimination 1. – 5. publications, direction of distortion – 6. publication). In the central stimulus presentation experiments (1., 3., 5. & 6. publications) a single adaptor and test stimuli was presented centrally on a screen. In the peripheral experiments (2. and 4. publications) both the adaptor and the test stimulus were presented in pairs 5 degrees left and right from the fixation mark. In these experiments the fixation of the individuals was controlled by an eye tracker (infra red camera – iView X Red, SMI). Stimuli were presented using a self programmed experiment under MATLAB Psychtoolbox [Pelli, 19979. The behavioural adaptation effect can be detected via the shift of the psychometrical function. For example in case of gender discrimination after adapting with a female face an androgynous face will be judged as more masculine compared to the control condition (Control condition – Fourier phase randomized version of faces as adaptors).

[1] The animated transformation of one image into another by gradually distorting the first image so as to move certain chosen points to the position of corresponding points in the second image.

Backward masking experiments

Emotional faces served as stimuli (fearful and neutral faces). The experimental paradigm was the following: after a short, randomized fixation period (500 – 700 ms) a test stimulus emerged for only 23.5 ms, afterwards the mask was presented for 500 ms. The visibility of the test stimulus was manipulated by the modulation of temporal differences between the test stimulus and the mask (stimulus onset asynchrony – SOA). Besides, we examined the effect of different types of masks (Fourier phase randomized images[2], neutral faces, inverted neutral faces). Both the effects of different masks in case of the shortest SOA and the effects of normal neutral faces with different SOA-s were significant and reflected behavioural and neural changes.

Electrophysiological measurements

Parallel with the behavioural data ERPs were also recorded via 23 electrodes placed according to the international 10/20 system. The registered data were analysed off-line with the Brain VisionAnalizer program (Brain Products GmbH, Munich, Germany). In the reviewed experiments we focused on the brain areas responsible for face processing, focusing separately in early, face specific components such as P100 on O1 and O2 electrodes and in N170 on P7/P8, PO7/PO8, TP7/TP8 & PO9/PO10 electrodes, respectively. After the statistical analysis of latencies and amplitude values both components showed significant differences between adapted and non-adapted conditions.

In our transcranial Direct Current Stimulation (tDCS) experiment using a battery-driven stimulator (Schneider Electronic, Gleichen, Germany) we temporally, non-invasively and reversibly changed the excitability of a given brain area. We stimulated the right posterior-occipito-temporal area with 1mA current, running between an active and a reference electrode (anodal stimulation depolarises, while cathodal hyperpolarises). The electrodes were 12 cm^2 plastic electrodes placed in wet sponge. Due to the DC stimulation the extent of the after-effects changed.

[2] An algorithm [Nasanen, 1999] based on function transformation that replaces the phase spectrum with random values (ranging from 0 to 360 deg), leaving the amplitude spectrum of the image intact, while removing any shape information.

III. New scientific results

Brief summary

Our results support that the perception and processing of a given visual stimulus strongly depend on its temporal context. This effect is visible both at the behavioural (shift of the threshold) and the neural level (latency and amplitude changes of ERPs). Results support that neurons responsible for after-effects and for their visual consciousness are localized in the posterior-occipito-temporal areas.

Summary of Results

- Electrophysiological and transcranial Direct Current experiments suggest that shape-selective after-effects are the result of higher-level processing and not due to the stimulus particles individual adaptations.
- Adaptation effects are category-specific – no cross-categorical effects were found.
- Right hemispherical asymmetries were discovered in adaptation supported by behavioural and electrophysiological data.
- The duration of adaptation is a key factor in shape-selective after-effects, there is no position-specific adaptation effect in case of short term adaptation
- The early face-specific ERP components are independent of the visibility of the stimulus however, 200 ms after stimulus onset the processing of the stimulus becomes strongly dependent on the visibility of faces and their conscious perception.

Detailed summary

1. Lower versus higher adaptation mechanisms in shape-selective after-effects.

Our data suggests that in the background of face and hand adaptation there are higher-level processes (3. publication). Both in case of face and hand adaptation we found size and orientation invariance. This fact supports the hypothesis that adaptation is not simply a sum of the adaptations of lower features', but an after-effect of higher level, non-retinotopic and shape-selective mechanisms.

In a following experiment (2. publication) we showed adaptation triggered by both normal and inverted faces presented peripherally has a position-invariant and a position-specific component. Adaptation effect is the strongest when the adaptor and the test stimulus overlap but in non-overlapping conditions the differences between adapted and control conditions are still significant. These adaptation effects can be measured on the early face specific ERP components – P100 and N170 – as well [Roisson et al., 1999]. P100 showed a significant increase in the amplitude, while the amplitudes of the N170 decreased strongly for both hand and face adaptation (3. publication). However, the effect was larger if the adaptor and the test were situated in the same hemifield (2. publication). Our face perception Direct Current Stimulation experiment also supports the existence of higher-level processing in adaptation (5. publication). According to our results anodal stimulation of the right posterior-occipito-temporal cortex decreased the adaptation effect, while, the transcranial stimulation of the primary visual cortex did not caused any changes. Previous face adaptation experiments supported our findings in proving that face adaptation is size [Zhao & Chubb, 2001], position [Leopold et al., 2001] and orientation [Rhodes et al., 2003] invariant. These results also suggest that the background neural mechanisms are linked to the higher levels of face processing.

2. The category specificity of shape-selective after-effects

The gender decision on the opponent category, after presenting human faces and hands as adaptors, were not shifted compared to the control (3. publication). Supporting the behavioural data the amplitude and latency of N170 did not show adaptation effect for different category adaptor and test stimuli. These findings were supported by a pilot study using houses as adaptors, while experimental task was gender discrimination (1. publication). Fang and He [Fang & He, 2005] found similar effects in a viewpoint after-effect experiment, where no cross-categorical adaptation were found for different classes of objects (faces, cars and paper clip like objects).

3. Hemispherical asymmetries in shape-selective after-effects

It is widely known that the right hemisphere plays a crucial role in face perception [Rossion et al., 2003 a, b]. In our face distortion after-effect experiment (6. publication) we found that the amplitude of the N170 component decreased only in the right hemisphere. This effect was stronger in the case of distorted adaptors compared to veridical ones. Right hemisphere dominance is also supported by our data adapting with overlapping and non-overlapping adaptors. The strongest adaptation effect in the amplitude of the N170 component could be observed when the adaptor was presented on the left side while registration was contralateral, namely on the right hemisphere (2. and 4. publications).

4. The temporal dynamics of face adaptation

We described that long term face adaptation (5000 ms) contains position variant and invariant components. Using a female adaptor androgynous faces were judged more masculine by participants if the adaptor and the test were presented in the same retinal position than when presented in non-overlapping positions. In case of short term adaptation (500 ms) we found position invariance in both overlapping and non-overlapping trials. In accordance with our behavioural data the amplitude of the N170 component has a position specific effect only after long term adaptation. These results suggest that both long and short term adaptation trigger the position-invariant face-selective mechanisms of adaptation. In contrast position-specific adaptation requires long adaptation time. Consequently, the manipulation of the adaptation time is a useful tool for selectively examining shape-specific adaptation and its stimulus selectivity.

5. Correlates of consciousness in face processing

The results of our backward masking experiment suggest that emotional face processing has two stages (7. publication). The first step of processing - approximately the first 200 ms after stimulus presentation – is independent from the stimulus visibility. After 200 ms stimulus processing is strongly influenced by the stimulus becoming conscious. 220 ms after stimulus presentation the amplitude of the negative ERP component (N2) (registered from the face processing areas) correlates with the conscious perception of the stimulus.

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