Masterarbeit

Titel der Masterarbeit

„Adaptation Duration Dissociates Category-, Identity- and Image-specific Processes for Faces“

Verfasserin

Adriana Zbanț

angestrebter akademischer Grad

Master of Science (MSc)

Wien, 2015

Studienkennzahl lt. Studienblatt:	A 066 013
Studienrichtung lt. Studienblatt:	Joint Degree Programme MEi: CogSci Cognitive Science
Betreuer:	Professor Gyula Kovács

Acknowledgements

I would like to thank my supervisors, Gyula Kovács and Márta Zimmer, for their invaluable help and guidance.

Contents

Abstract

In the last decades several studies have demonstrated that the way we perceive faces can be biased by the prior presentation of another face, a phenomenon commonly referred to as face-related after-effect (FAE). This effect was linked to a neural signal-reduction at the occipito-temporal areas. This stimulus-specific signal reduction has been referred to as adaptation (ADA), repetition suppression, or neural priming. In case of faces, ADA can be observed in the amplitude modulation of the early event-related potential (ERP) components, such as the P100, N170, and P2. Recent studies suggest that manipulating the duration of the first face presentation provides an opportunity to selectively adapt neural processes at different stages of visual processing. Although rapid (< 1000 ms adaptation duration) ADA paradigms have found conflicting ERP results these findings indicate the adaptation of early, short-latency responses while for longer ADA durations a strong category-specific modulation of the N170 was observed. To date, only few studies have investigated the effects of varying adaptor durations. Therefore, the goal of this study was to uncover the effects of systematically varying adaptor durations on the behavioural and neuronal responses. To this end, in a 2AFC familiarity decision paradigm, we used five adaptor durations: 200, 1200, 2000, 3500, 5000 ms, and three face adaptor categories: Different Identity (Diff ID), different images of the Same Identity (Same ID), identical images of the same person - Repetition Suppression (RS). A Fourier phase-randomized adaptor image served as control (No). We defined three different types of effect: GENERIC ADAPTATION/PRIMING EFFECT as referring to the No versus Diff ID distinction; IDENTITY-SPECIFIC ADAPTATION/PRIMING EFFECT as referring to the Same ID versus Diff ID distinction; and IMAGE-SPECIFIC ADAPTATION/PRIMING EFFECT as referring to the Same ID versus RS distinction. The behavioural results show a strong priming effect both in the accuracy and in response times, mainly in case of RS condition. Our electrophysiological results indicate that by varying adaptor duration we can obtain different adaptation effects following different adapting durations, for each of the early face-related ERP components. The P100 and N170 reflect generic adaptation related to face perception, with a modulating effect of adaptor duration on the N170 that shows that generic adaptation takes place after 1200 ms. The P2 displays sensitivity to repetition after 1200 ms, while the N250 displayed generic, image and identity-specific adaptation at specific adaptor durations, showing that the activity of these components is also modulated by adaptor duration. Together these results show that for longer adaptor durations there is a dissociation between generic, image and identity-specific processes.

1. Introduction

1.1 Perception

Since the beginning of humanity, the world around us has been a topic of interest, either as a cause of concern or as a source of fascination. Throughout time philosophers have theorized with regard to our access to the world around us, passing from direct access to things as they are, all the way to only experiencing the *Phenomenon* but never the things in themselves (Kant, 1781). Our information of the world around us comes through perception and it is our perceptual experience that we have direct access to. But many a time has our perception deceived us. Even though it is our best bet at finding out information about our environment and thus surviving, our perceptual experience can also play tricks upon us. The “tricks” of perception however are far less common than its proper functioning, which is what guarantees our proper responses to the world surrounding us. But what if those “tricks” could tell us something about the way in which perception properly functions? Why do these perceptual distortions happen? And what better way to start than by looking at the world around us as it appears to us?

1.1.1 Spatial and Temporal Context

Our environment is ever-changing. As Heraclitus said, “you cannot step into the same river twice” (see Graham, 2011, for an analysis of the remaining fragments attributing the line to Heraclitus). No two states are identical and for us to be able to respond to this dynamic world, our perceptual abilities have to be in tune with our environment. This means that our brain has to constantly update its model of the world. But our experience of the world, even based on such a constantly-updating model, has to happen somewhere and it happens in a spatial and temporal context. Immanuel Kant was the one who showed that space and time are not entities that we perceive, but are the necessary conditions for our perceptual experiences (Kant, 1781, A26/B42; A32–33/B49; A28/B44, A34–35/B51–51). In other words, space and time structure our perception. Our perceptions of the things around us are not independent of the spatial and temporal context in which they find themselves, but on the contrary, this contextual information is what helps us make sense of the information that we receive from the environment. Every day we are surrounded by objects that cast shadows and have casted shadows upon them. When the shadow of a bigger building is projected upon a nearby smaller building, we judge the color of the smaller building to be more or less uniformly the same, despite the fact that the shadowed area appears darker. This is an example of built-in invariance. However, this is not the only example illustrating the way in which our brain uses contextual information to form an accurate perception of the world around us. Another such example is size invariance. When seeing objects, people and buildings from a high vantage point, we know of course that those objects are not so much smaller, but that they only appear smaller due to distance.

These are just a few examples of the way in which contextual information changes our perception of things. However, as mentioned before, there is a fine balance between using appropriate contextual information that is absolutely necessary for forming a percept and using redundant information that consumes both energy resources and time. Our brains manage to reach this fine balance on most occasions, but there are times when our perception of the world is distorted. The context in which stimuli present themselves to us in the environment affects all sense modalities, from audition (Oxenham, 2001) to olfaction (Kadohisa et al., 2006), gustation (Gent et al., 1978; Bujas et al., 1991) and somatosensory processing (Wallace et al., 2004) or vision (for brightness, Eagleman et al., 2004; for orientation, Bednar, 1997; for color, Engel, 2005; for motion Kohn and Movshon, 2004; for shape, Suzuki and Cavanagh, 1998).

Visual perception is perhaps one of the most studied topics in cognitive science, and for good reason since a great amount of the information we receive from the outside world comes through visual input. But despite the many investigations relating to it, there are still many unanswered questions. Some of the still not understood phenomena relate to the way in which our brain uses contextual information to form perceptions. This contextual information can influence not only low-level stimuli, such as oriented bars, which are processed in primary visual areas, but also more complex stimuli such as whole objects that are processed further along the visual system in higher-level visual areas. One such example of low-level characteristics of visual stimuli that are affected both by the spatial and the temporal context is orientation, which is portrayed by the tilt illusion (spatial context) or the tilt after-effect (temporal context) (Schwartz et al., 2007). An example of the tilt illusion can be seen in Figure 1. In this case two circles are nested into one another. The central nested circle (target) is filled with vertical black stripes on a white background, whereas the bigger circle that surrounds it is filled with the same black stripes that are tilted 15° clockwise from the vertical position. This causes the stripes inside the smaller circle to appear "repulsed away from the context" (Gibson and Radner, 1937), therefore tilted counter clockwise. In this way, the spatial context of the slightly tilted stripes affects the perception of the target. In the case of the tilt after-effect (Figure 2), a circle filled with tilted stripes (adaptor) is presented for at least 30 seconds before the target circle appears, which contains perfectly vertical stripes. However, due to the temporal context (the presentation in the recent past of the tilted stripes circle), the stripes in this target circle appear slightly tilted in the opposite direction from the ones in the adaptor.

Fig. 1 Tilt Illusion
The surrounding circle that serves as spatial context contains stripes that are tilted 15° clockwise, as opposed to the central circle's lines which are vertical. This creates the illusion that the stripes inside the central circle are actually tilted counterclockwise.

Fig. 2 Tilt After-Effect
The adaptor which contains clockwise tilted lines serves as temporal context for the test circle which contains vertical stripes. After the presentation of the adaptor for at least 30 seconds, the lines in the test circle appear slightly tilted in the opposite direction from the ones in the adaptor.

Besides the widely described adaptation to simple visual stimuli (such as a disc patterned with oriented lines) the types of illusions or after-effects can be observed for more complex shapes and visual properties as well (such as visual motion, simple geometric shapes or faces).

The spatial and temporal context are both equally important in understanding visual perception and despite being studied in separation the two are very likely to interact in order to produce our percepts. Because both timing and spatial localization are crucial for understanding the influence of spatial and temporal context, single-cell recording offers the best investigating tool, due to its very good spatial and temporal resolution. However, due to ethical reasons, the use of single-cell recording on humans only for experimental purposes is prohibited (human single-cell recording as part of an experiment is only allowed if there is a medical reason for which the skull of the person has to be opened up, such as the case of epilepsy and, under these conditions, the experimental manipulations are limited). Nonetheless, single-cell recording studies have been conducted on monkeys (Rhesus macaque) (Kohn and Movshon, 2003). However, despite the valuable information that we can get from these studies, generalizing these results to humans is a task made difficult by a number of factors that range from the difference in species (monkeys vs. humans) to difference in alertness (monkeys are anesthetized and immobilized, whereas humans are alert).

1.2 Face Perception

In our everyday life we encounter a countless number of faces and are able to rapidly process information about each of them on a variety of dimensions. Just by briefly looking at a face, you can tell the gender, age or emotional state, whether you recognize the person or not and if so, what is their relationship to you (whether they are genetically linked to you, Brédart and French, 1999). Moreover, you can also have access to a great amount of information about them and their personality (likes and dislikes, interests, relationship to other people, affiliation, social status etc.). Studies show that faces can offer an abundant array of information concerning many aspects, such as intelligence (Zebrowitz, et al., 2002; Zebrowitz and Rhodes, 2004), health (Kalick et al., 1998; Ilg et al., 2004), dominance (Berry, 1991b), extraversion (Borkenau & Liebler, 1992), and sexual availability (Gangestad et al.,1992), together with age (Berry, 1991a; Montepare and Zebrowitz-McArthur, 1988), sex (Berry, 1991a; Smith, 1979), sexual orientation (Ambady et al., 1999), and identity (Cutting and Kozlowski, 1977). There is a good reason for which we are so good at identifying and processing human faces. They are important visual stimuli on which a great amount of our social interaction is based. Being able to identify the emotional expression on a face, the gender and the age of a face is a basic ability for survival and reproduction. The more you can tell from a face, the greater are your chances of having a successful interaction with that person, even if that means running as fast as you can because you have encountered someone who poses a threat. Moreover, without the ability of processing all this information coming from a human face, our social interactions as we know them would be impossible. Think of how much information you lose when you talk to someone on the phone as opposed to when you are seeing them face-to-face. You have no access to their facial expression, so even though you might be able to recognize some emotions from their voice inflexions, you cannot really tell if they are frowning, if they seem bored because they are gazing out the window lost in a reverie and not paying attention to what you are saying or if they find what you are saying is unpleasant. You cannot really tell their age, so it is difficult to adjust your vocabulary or behavior according to that. These are just a few examples, but if the social situation becomes more complex, even more facial cues that you use to guide your own behavior are lost.

The complexity of features that are encoded in a human faces leads to another point worth considering when trying to understand face perception. In virtue of what information do we recognize faces? Do we need the whole set of information that can be coded about a face, or only a part? The current research results suggest that faces are special when comparing them to other non-face object categories. Whereas non-face object categories are processed in a feature-based manner, faces are processed holistically, as a configuration. That means that when you recognize a face as being that of a particular someone, your decision of attributing an identity to that face is a multidimensional one, as is evident from studies that investigate the face inversion effect (FIE), the Thatcher illusion or the Composite Face Effect. The FIE (Yin, 1969) refers to the decrease in recognition performance that is found when a face is inverted as opposed to upright, in relation to other types of objects presented in the same conditions. The inversion of a face eliminates the configural information of a face, leaving only the featural one and thus, the FIE stands as proof of a configural processing of faces.

Another effect that provides clear evidence in favour of configural face processing is the Thatcher illusion (Thompson, 1980), in which two images of the same face look similar when presented inverted, even though one of them has the eyes and mouth inverted (presented in upright position). When presented in upright position, one of the images looks like a grotesque version of the other (Figure 3). This illusion is also accounted for by the fact that inversion reduces the sensitivity to the relational information between the features of the face. However the effects observed for the Thatcher illusion can be explained as a feature of inversion.

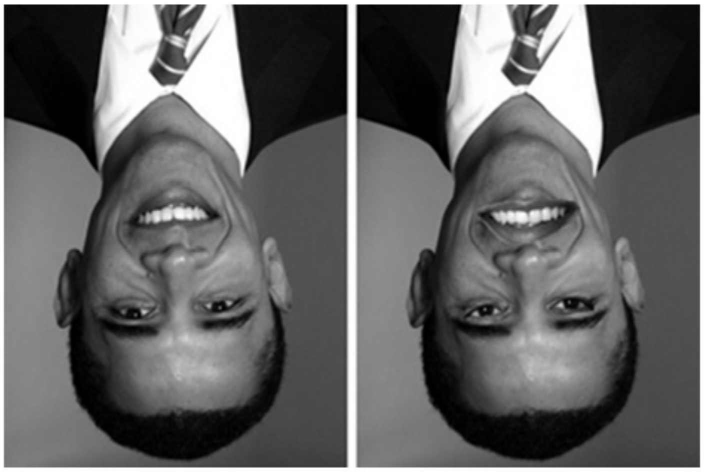

Fig. 3 Thatcher Illusion

Yet another face-specific effect accounting for the holistic processing of faces is the composite face effect (CFE) (Young et al., 1987) in which the top half of a face is joined with the bottom half of a different face (Figure 4). When presented side-by-side with the original face, the two faces seem to represent two different persons, because the information is automatically integrated, presumably due to configural processing of that face.

Fig. 4 The Composite Face Effect

1.2.1 Models of Face Perception

Perceiving and recognizing faces seems to involve the processing of many types of information. These processes are automatic and in most cases effortless. Moreover, the speed at which this information is processed also suggests that face perception processes may be parallel. The natural question to ask is “How does our brain manage to achieve this?”. Several models have been proposed for understanding face perception. Here, I shall focus on two of the most influential and relevant ones: the Bruce and Young (1986) model of face processing and Haxby’s model (2000).

1.2.1.1 The Bruce and Young Model

The Bruce and Young model, devised by Vicki Bruce and Andy Young, is based on the idea that the information one gets from a face serves a different number of purposes. This means that for each type of information that we get, there is a different and distinct process dedicated to it when it comes to face perception. These processes are dealt with separately by our brain. Since this model assumes that there are discrete and successive stages for face perception, then the process of face recognition can fail at any of these stages. Based on this idea of discrete and successive stages, Bruce and Young identify seven types of information, called ‘codes’ that are involved in face perception. **Pictorial codes** contain information concerning the details of a specific image that one is viewing and of the face within it. **Structural codes** are more abstract than the former and contain information that is necessary for the recognition of a face, in spite of changes in pose, gaze, expression and other variable dimensions. **Visually-derived semantic codes** contain information about the meaningfulness of a face for its perceiver (gender, age), whereas **Identity-specific semantic codes** contain more specific information concerning the person whose face is being perceived, such as occupation, interests, friends and others. Next in line are **Name codes** which code for the name of the person only. The necessary existence of such codes is made evident if we think of the fact that we can know someone’s name without knowing much else about them, but also access semantic information about someone, without remembering their name. **Expression codes** are the ones that reflect the emotional state of the person whose face we are viewing, whereas **Facial speech codes** refer to the movement of lips and tongue that affect the way in which we perceive speech.

Face processing is achieved by accessing information from each of these codes. As mentioned before, since this is a discrete, sequential process, there are separate steps for accessing this information (Figure 5).

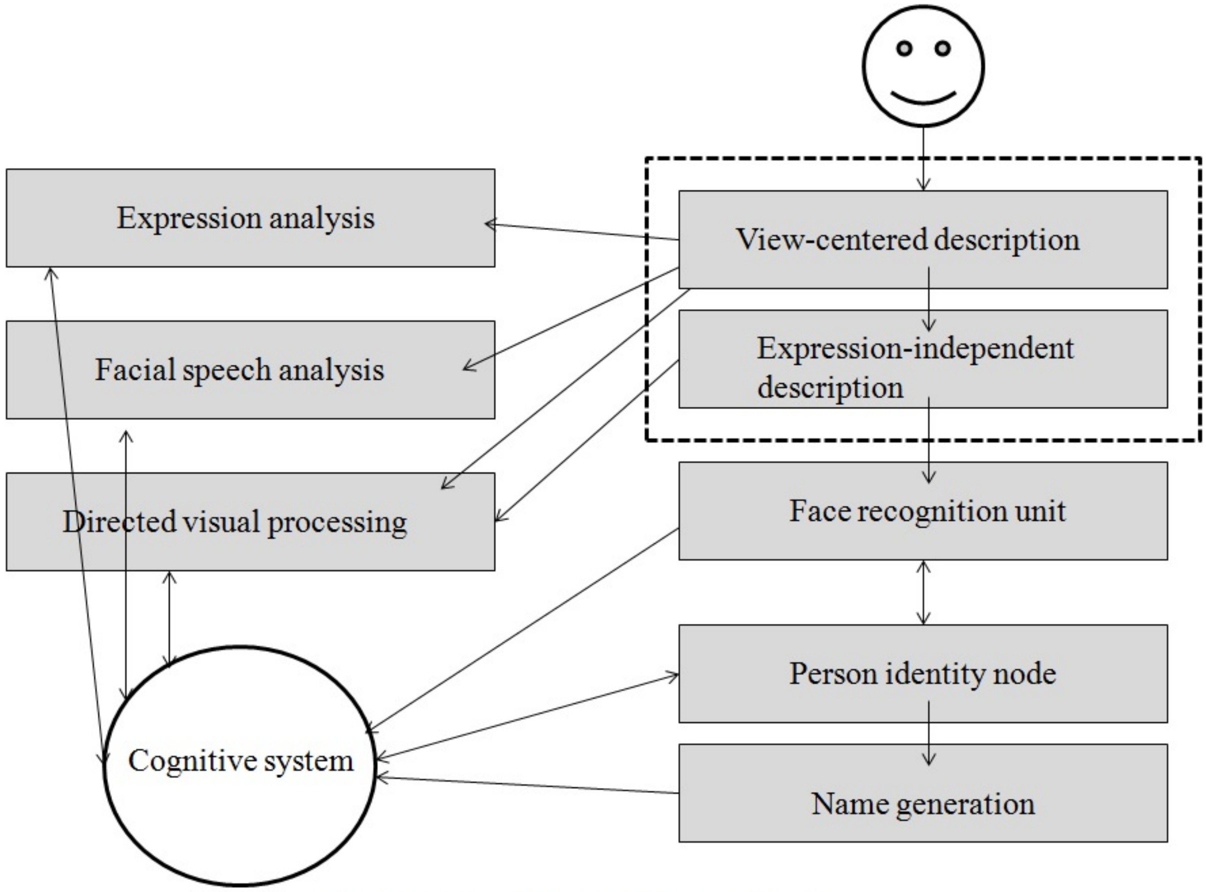

Fig. 5 Bruce and Young (1986) model of face recognition

The first step is the **initial encoding** of a face which leads to the formation of a distinct representation in the brain of that face. Second in line is the **structural encoding** of the face which is achieved by constructing many representations of that face, containing more view-point specific representations for some attributes and more view-point independent representations for others. If the face is familiar, then the **Face Recognition Unit (FRU)** is activated for that face, each face having its own FRU. **Person Identity Nodes (PIN)** are next in line, which are "modality-free" gateways towards semantic information connected to that face, such as voice or gait cues that can identify someone or aid in your recognition. Each FRU is associated to a PIN.

PINs in turn, activate the **Semantic Information Unit (SIU)** which contains information about the person who owns the face, such as occupation, relationship to others and to you, age etc. Lastly, SIUs activate the **Name Unit** that gives the associated name to that specific face.

1.2.1.2 Haxby's Model

One of the greatest challenges faced by the Bruce and Young model is the lack of neural information with regard to the precise localization of these coding steps in the brain. Other models, such as the one proposed by Haxby (Haxby et al., 2000), have taken into consideration the neural evidence that exists with regard to the brain areas involved in face processing. The Haxbyan model assumes that there are two systems in the brain that are involved in face perception: the core system and the extended system. The core system also works in a step-by-step manner, similarly to the Bruce and Young model. Its first stage is a pure sensory step, the **visual perception of a face** which takes place in the inferior occipital gyrus.

This information is then fed to the **recognition processes** which are in turn separated into two categories. The first ones are the **processes that deal with invariant aspects** of faces such as gender, age or the so-called first-order relations within a face. These aspects are crucial for the recognition of individuals. The area that is responsible for this processing stage is the fusiform gyrus, located in the temporal lobe, usually referred to as the fusiform face area (FFA). The second type of recognition processes is those involving the **variable aspects of faces**. This involves facial expression, emotion or eye gaze information. The brain area that processes all this information is the superior temporal sulcus (STS). After the core system has finished its processing, the information is fed into the extended system which does not deal with the pure sensory processing of faces, but with associated processes that can make use of facial stimuli, such as spatially directed attention, prelexical speech, emotional facial expression, person identity and semantic or biographical information (see Figure 6 for a schematic representation of Haxby's model). For each of these types of information, there is a separate brain area that processes it. Semantic and biographical information is processed in the anterior temporal lobe, as suggested by Haxby. Other studies (Turk et al., 2005) have shown that the FFA also responds to semantic information and that there is no other area that is specifically involved only in the processing of this category of information. Spatially directed attention refers to information connected to head orientation and gaze direction, which are cues that we use to see where a person is directing his/her attention. The intraparietal sulcus and the STS have been found to be involved in the processing of this kind of information (Hoffman and Haxby, 2000; Puce et al. 1998). Using information connected to prelexical speech production which is used in lip-reading is also a part of Haxby's model. This kind of processing takes place in the auditory cortex, which is the posterior section of the superior temporal gyrus (Calvert et al., 1997; Okada and Hickok, 2009, Wright et al., 2003). Finally, facial emotions are also processed separately by the amygdala, the insula and the limbic system, all areas believed to be involved in the processing of emotion (Fitzgerald et al., 2006; Calder et al., 2001).

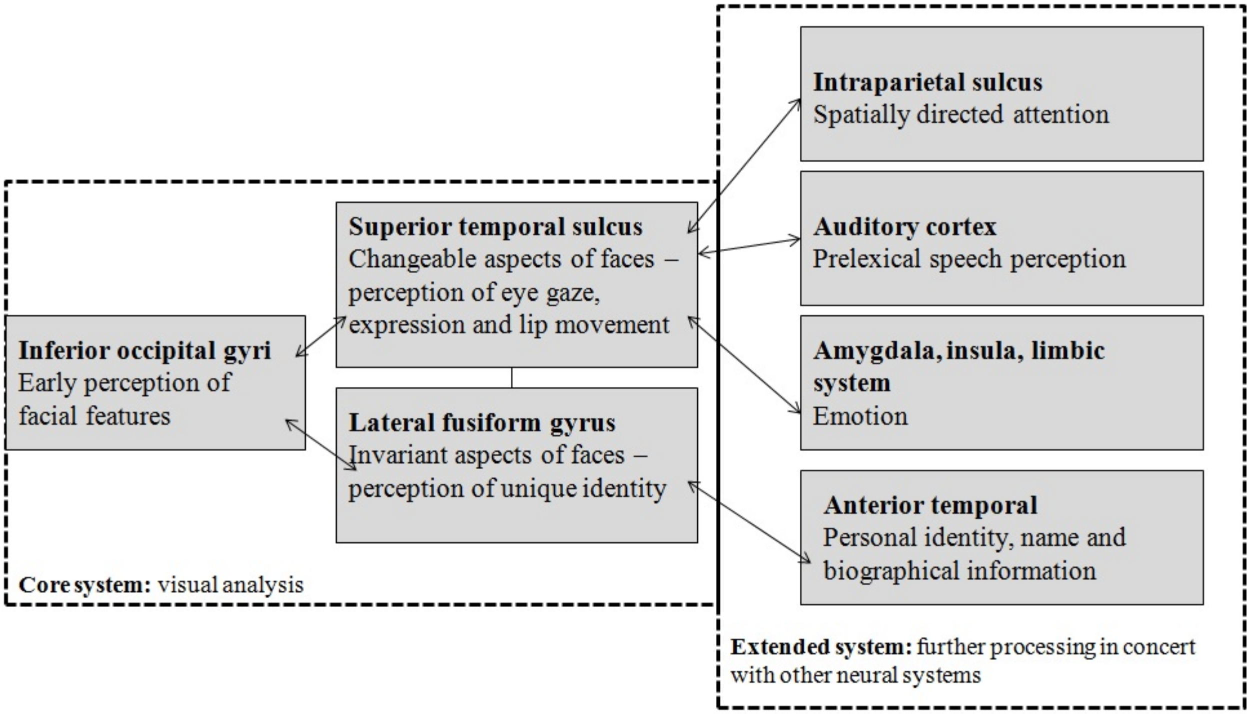

Fig. 6 Haxby's model of the distributed neural system for face perception (Haxby et al., 2000). The core system consists of three regions of occipitotemporal visual extrastriate, which deal with changeable and invariant aspects of the visual facial configuration. The extended system consists of regions that are also parts of neural systems for other cognitive functions, but that are also implicated in face perception to some extent. The regions in the extended system that are involved in the processing of the spatially directed attention of another person, speech-related mouth movements and facial expressions and identity.

1.2.2 Neural Correlates of Face Perception

1.2.2.1 Electrophysiological Correlates

Electroencephalography (EEG) is a method of recording electrical brain activity along the scalp. The neural generators of this electrical activity are the pyramidal cells of the cortex and the sources of the activity are the post-synaptic potentials (PSPs) of these types of neurons. By placing electrodes on the human scalp we can record the electrical activity of these cells in virtue of the fact that the PSPs form an extracellular cortical dipole layer which runs to the surface of the cortex and project toward it electrical polarities that are the opposite of those found in the innermost layers of the cortex. The electrodes measure the difference in voltage of these local extracellular currents and by multiple differential electrode recording combinations, an estimate of the activity at any single electrode site is obtained.

If one measures the electrical activity during one particular event (such as the presentation of a stimulus) and then averages this activity over a number of repeated trials, one would obtain an event-related potential (ERP). ERPs are averaged EEG responses that are timelocked to events and reflect specific psychological functions. ERPs can be divided into different components which can in turn be either positive (P) or negative (N). These components appear between specific time windows (they have a latency, expressed in ms) and have different amplitudes (expressed in μV). Different ERP components are linked to different cognitive functions and the following ERP components have been identified in relation to face processing (see Figure 7): P100, N170, P200, N250(r), N400 and other later components.

The earliest face-related ERP component is the P100 or P1 (~100ms after stimulus onset), which corresponds to the early pictorial encoding stage in the Bruce and Young model (Jacques and Rossion, 2007; Desjardins and Segalowitz, 2009; Hole and Bourne, 2010; Schweinberger, 2011). Although some studies (Itier and Taylor, 2004a; Hermann et al., 2005) have argued in favor of a face specificity of the P100, no clear evidence has been found to suggest this is the case. Therefore, the P1 component is not specific to faces only, but to visual stimuli in general.

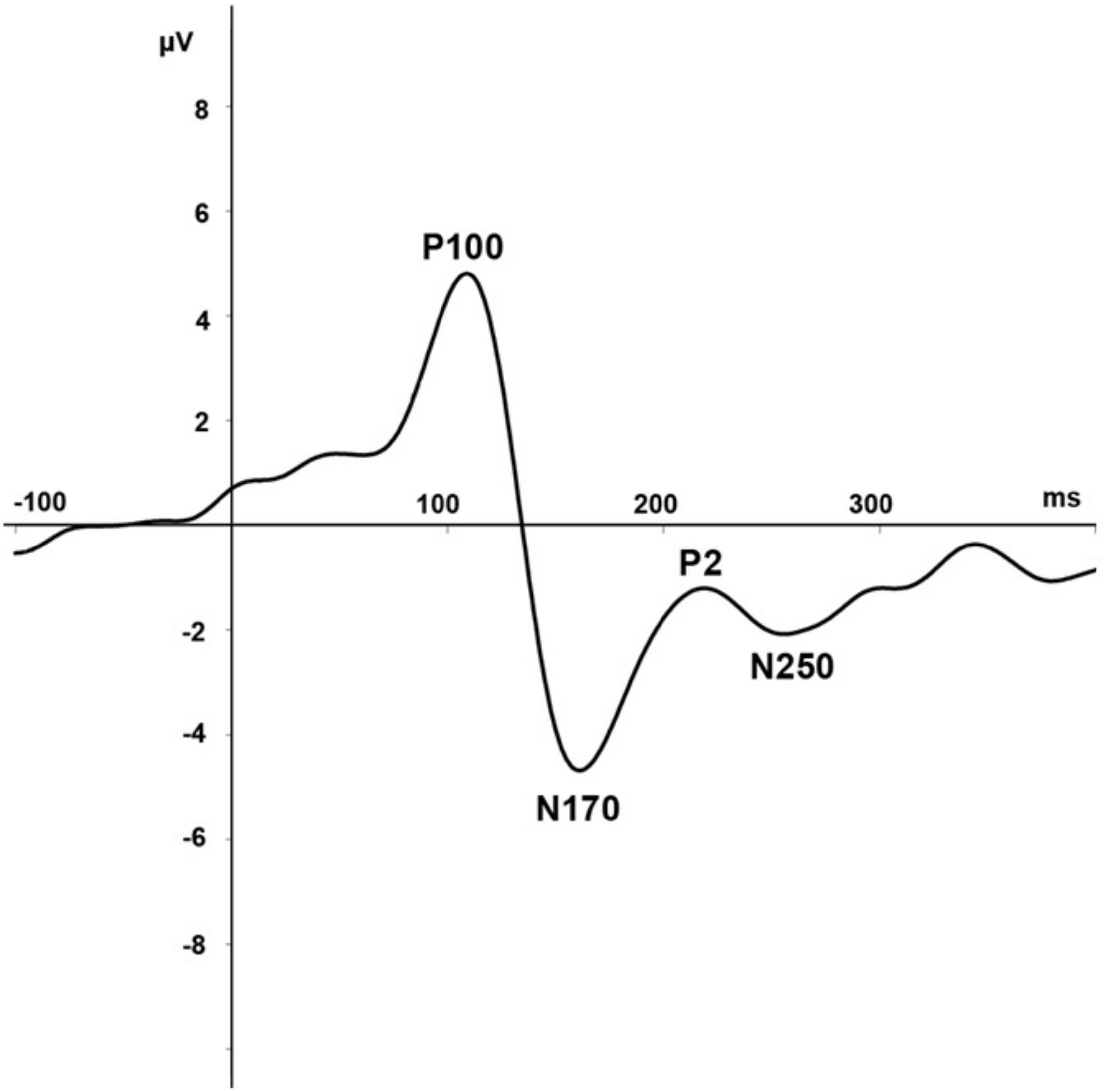

Fig. 7 Face-related early ERP components. The figure shows the 4 face-related ERP components: P100, N170, P2 and N250 as they would usually appear on an EEG wave. X axis shows time in ms. Y axis shows amplitude values in μV.

The N170 is the earliest face-specific ERP component, reflecting the structural encoding of faces in the Bruce and Young model and presents larger amplitudes in relation to faces as opposed to other types of stimuli (Jacques and Rossion, 2007; Hole and Bourne, 2010; Eimer, 2011; Schweinberger, 2011). Therefore, N170 displays category-specific effects. This is evident from studies involving the inversion of faces (Jacques and Rossion, 2007; Jacques et al. 2007, Rossion et al. 2000), Thatcherized faces (Carbon et al., 2005) or faces presented in photographic negative (Itier and Taylor, 2002). In the case of inverted faces, the amplitude of the N170 component is much larger and there is a ~10ms delay in the latency (Rossion et al., 1999). Familiarity effects are not usually associated with the N170, however some studies have found conflicting results, thus arguing in favour of a familiarity effect being reflected on the N170 (Caharel et al., 2002). Moreover, the N170 is also more enhanced in the right hemisphere, reflecting a hemispheric dominance for this component (Scott and Nelson, 2006). Source localization studies that used dipole fitting methods have found the N170 component to be linked both to the bilateral occipitotemporal cortex and posterior fusiform gyrus. More specifically, both OFA (Gauthier et al., 2000) and FFA (Kanwisher et al., 1997) were found likely to generate the N170 ERP component. Other source localization studies that estimated the cortical origin of the N170, computed the distributed brain activation patterns and found different results that suggest the STS as a source (Itier and Taylor, 2004b).

Another component specific to face processing is the P200 or P2 component which seems to be connected to a variety of processes that generally involve responses to face stimuli that are perceived as typical, and thus is influenced by expertise. It also reflects the processing of spatial relations between facial features of individual faces and is involved in the initiation of individual recognition mechanisms (Stahl et al., 2010), thus being modulated by face familiarity. P200 is also involved in the extraction of configural information from faces and reflects deeper processing of this category of stimuli.

The N250 component (also named N250r when used in repetition priming paradigms) appears linked to the processing of individual identity, showing a larger amplitude for familiar as opposed to unfamiliar faces. The N250 seems to be larger in response to repetitions involving the same image of a familiar face, even though there is a clear N250 response even for different images involving the same identity (see Schweinberger, 2011 for a review).

Later ERP components have also been linked to deeper processing of semantic information associated with faces. For example, the N400 component has been found to be connected to the processing of semantic information associated with faces or with a person and appears to be uninfluenced by the method of recognition (via names or faces). It is a marker for postperceptual processing stages in person recognition, as opposed to just face recognition (Schweinberger, 2011).

1.2.2.2 Neuroimaging

Neuroimaging data provides ample evidence that supports the idea that different parts of the brain are specialized in processing a specific type of information involved in the perception of human faces (see Figure 8). Functional Magnetic Resonance Imaging (fMRI) studies have provided us with consistent information regarding the brain areas that are involved in face processing. fMRI is a metabolic neuroimaging technique. This means that it does not show the actual electrical activity in the brain, but the increase in blood flow to areas of the brain that are more active. Since more active areas consume and require more oxygen, the blood flow to those areas is different when compared to other areas. The fMRI measures the blood oxygenation level dependent (BOLD) signal, which reflects this variability in blood flow. fMRI is made possible in virtue of the fact that oxygenated and deoxygenated blood have different magnetic properties which are detected by the fMRI scanner.

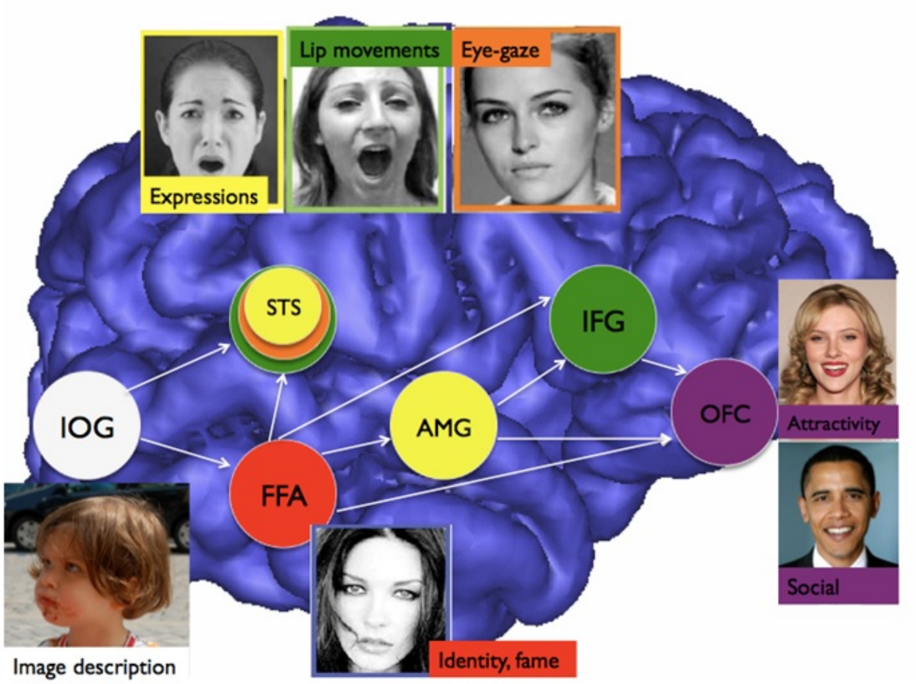

Fig. 8 Brain areas involved in face perception. Colored circles show the approximate location of that specific brain area, whereas the face images that have corresponding colored borders show the type of information that is processed in that brain area. Abbreviations stand for the following: IOG – Inferior Occipital Gyrus, FFA – Fusiform Face Area, STS – Superior Temporal Sulcus, AMG – Amygdala, IFG – Inferior Frontal Gyrus, and OFC – Orbitofrontal Cortex.

As Haxby's model suggests, it has been found through neuroimaging studies that both OFA and FFA are involved in the simple detection of a stimulus as a face. Andrews and Schluppeck (2004) found that Mooney faces (low-information two-tone pictures of faces) elicited more activation in the FFA when they were perceived as face-like, as opposed to when they were not. Moreover, the OFA and FFA seem to be unaffected by changes in view-point, as is to be expected if the FFA deals with the invariant properties of a face (Pourtois et al., 2005; Chen et al., 2007). Some studies (Rotshtein et al., 2005) have found different responses when comparing OFA and FFA. Whereas the OFA is more sensitive to physical aspects of the face than the FFA, the FFA is less responsive to inverted faces, compared to upright ones, than the OFA. Since inversion is believed to affect configural processes which make use of a face's overall configuration to identify it as a face, a smaller activation of the FFA for inverted faces indicates its involvement in the structural encoding of a face as a face. Other studies that were investigating subconscious face processing, by use of masking paradigms (Morris et al., 2007), have found that the FFA displayed higher activation when the stimulus was a masked face, as opposed to a masked object. This indicates also an involvement of the FFA in automatic face processes. The OFA and FFA also reflect processing of facial identity, together with the anterior temporal lobe, which can be seen in experiments that use a familiarity paradigm (Eger et al., 2005). However, data showing a differential response of the FFA to familiar and unfamiliar faces is contradictory (for a review see Kanwisher and Yovel, 2006).

Another brain area involved in the perception of human faces is the STS which displays a different pattern of activity when compared to the OFA and the FFA. As mentioned above, the STS has been linked to processing information connected to head orientation, gaze direction and facial expression (Puce et al. 1998; Hoffman and Haxby, 2000). The amygdala, insula and limbic system, as mentioned previously, are linked to the processing of facial emotions (Calder et al., 2001; Fitzgerald et al., 2006). Another type of information connected to face perception concerns lips movements, used in understanding speech. This processing takes place in the superior temporal gyrus and inferior frontal gyrus, both areas that are linked to speech comprehension and production as well (Calvert et al., 1997; Okada and Hickok, 2009, Wright et al., 2003). Other areas connect to face processing are those involved in assessing attractiveness, such as the orbitofrontal cortex (O'Doherty et al., 2003; Cloutier et al., 2008).

1.3 Faces in a Changing Environment

The majority of studies that investigate face perception present single instances of faces. This raises the issue of the ecological validity of these studies. In real-life situations, faces are not presented in a single, rather brief instance, but appear in an ever-changing environment. Fast and certain perception and recognition of these stimuli can be critical, among others, for the survival of our species. Recognizing if your baby is in need of help, because of a distressed or crying face, identifying expressions of fear or anger so that one can flee or prepare for a confrontation and recognizing signs of disease in faces are all crucial elements for ensuring our survival and that of our offsprings (Zebrowitz and Montepare, 2006).

Our perception of faces can be influenced both by relevant and irrelevant information that exists in the environment. Moreover, the previous perception of a face can modify the perception of a different, subsequent face as well. Thus, the exposure time to various faces shapes our perception of faces in general and is critical for comprehending the stages of visual processing. Understanding how our perception shifts following various perceptual experiences is essential for comprehending the mechanisms of face perception and visual perception in general.

By varying the exposure time to a stimulus, one can obtain significantly different behavioral and neural response upon presenting a second stimulus. If we look at the difference in behavioral responses we can find two major categories: improved performance or biased performance as a consequence of varying the temporal context. In the case of an improved performance we are dealing with priming. In the case of a biased performance the term "after-effects" is usually utilized to reflect the behavioral effects of adapting to a stimulus. These are examples of the way in which the temporal context can alter our perception and decision. Another way in which the temporal context can bias our perception is backward masking. Backward masking paradigms are often used to modify the perception of a stimulus presented before the mask and is achieved by immediately placing one stimulus where the previous one has appeared. If the mask is presented at the exact same location and within 100 ms of presentation, then the first stimulus is mentally erased by the superimposed mask (Sternberg, 2012). By backward masking the stimulus we can measure the effects that an unconscious processing of a type of stimulus has on the behavioral or neural response of subjects. Forward masking on the other hand happens when the target stimulus is preceded by another stimulus that biases or impairs the perception of the target. (Zimmer, 2010). The differences between backward and forward masking can be seen more clearly in Figure 9.

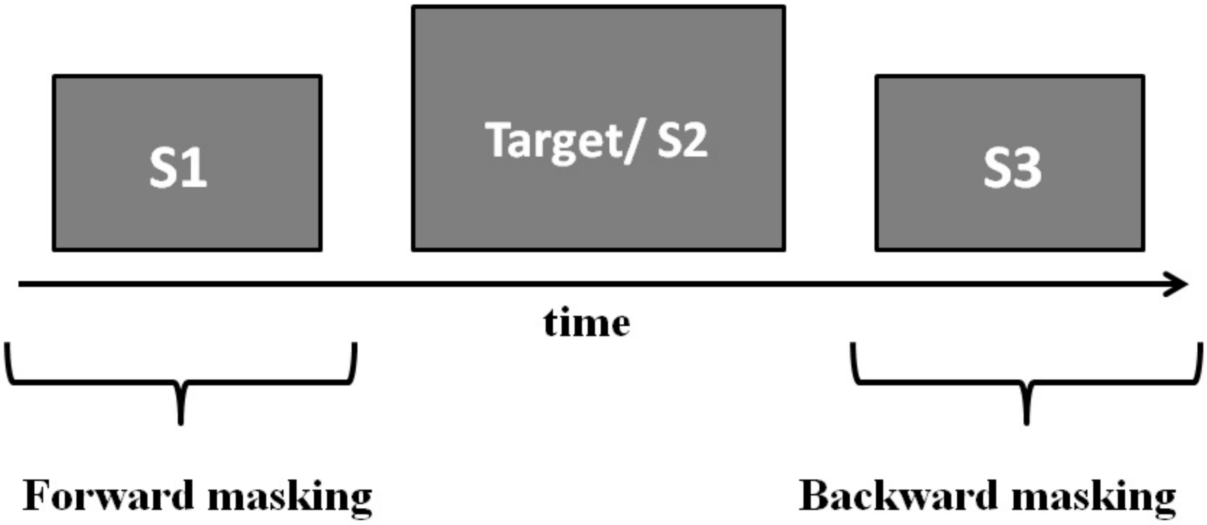

Fig. 9 Temporal Context in Experimental Design. Perception of the target image (Target) can be biased by a stimulus presented before it (S1). Likewise, perception of a stimulus (S2) can be influenced by a stimulus presented immediately after it (S3).

Many studies have already focused on adaptation-related after-effects in the case of human faces, finding a number of dimensions on which adaptation influences our perception of face, including distortion effects (Webster and MacLin, 1999), identity (Leopold et al., 2001), gender (Kovács et al., 2005, 2006, 2007), ethnicity (Webster et al., 2004), attractiveness (Rhodes et al., 2003), expression (Webster et al., 2004) or gaze (Schweinberger et al., 2007).

Repeating a stimulus can lead not only to different behavioral responses, relative to a baseline, but also to a different neuronal and haemodynamic activity. The term “repetition suppression” (RS) refers to a signal reduction or a reduction in activity to an exactly repeated versus an unrepeated stimulus, as measured by Positron Emission Tomography (PET) or fMRI (Henson, 2003; Grill-Spector et al., 2006). The same reduced response can also be observed at a neuronal level, in which case it bears the name of “response suppression”. Response suppression reflects a reduced firing rate of neurons as a consequence of repeating a stimulus. This reduction in firing rate is evident in single-cell recording or electroencephalography/magnetoencephalography (EEG/MEG).

The interesting point related to repetition or response suppression is that the same haemodynamic or neural response can be registered in both the case of priming and that of adaptation. However, one important question is what neuronal mechanisms lies at the root of repetition/response suppression. Three models of adaptation have been proposed to account for the reduced haemodynamic and neuronal activity.

1.3.1 Models of Adaptation

The Fatigue model (Miller & Desimone, 1994, Grill-Spector & Mallach, 2001, Grill-Spector et al., 2006) states, in short, that the firing amplitude of the neurons that are responsive to that particular stimulus decreases. This means that initially all neurons respond to a stimulus, but after repeated stimulation with the repeated presentation of that same stimulus, their activity reduces proportionally with the stimulation. In other words, the neurons become fatigued.

The Sharpening model (Desimone, 1996, Wiggs & Martin, 1998) states as well that all neurons initially respond to a stimulus, but, in contrast to the Fatigue model, the neurons “sharpen” their response and upon a second presentation of the same stimulus, only those neurons that code relevant features of the stimulus will respond. Thus, the reduced response is explained by the fact that at a repeated presentation, only the “sharpened” neurons respond, as compared to the initial presentation when all neurons, even those responding to irrelevant features, fire.

The Facilitation model (James & Gauthier, 2006, Henson & Rugg, 2003) predicts that by repeating a stimulus a faster processing of it ensues, which means that you obtain shorter latencies and shorter durations of neural firing. James & Gauthier’s (2006) accumulation model, for example, states that after repetition of a stimulus, information about it is gathered faster. Another version of the Facilitation model assumes that the cause of faster processing is synaptic potentiation, which occurs at several stages along the processing stream.

1.3.2 Adaptation to Faces

Face adaptation-related after-effects also modulated ERP components. The P100 ERP component for example, showed amplitude enhancement following face adaptation (Zimmer and Kovács, 2011a). However, some studies reported an identity-specific amplitude reduction for target images following adaptation to an identity-congruent adaptor (Walther et al., 2013).

The N170 ERP component shows category-specific adaptation effects for faces, most studies finding an amplitude reduction in the case of this component (Kovács et al., 2005; Walther et al., 2013; Zimmer and Kovács, 2011; Amihai et al., 2011). Other rapid-adaptation studies (Eimer et al., 2010, 2011) using face inversion experimental paradigms, showed N170 amplitude reductions for faces when compared to house adaptors. This shows that timing is an important factor in the strength of the adaptation effect.

In the case of the P2 component, a right hemisphere dominance was also found by some adaptation studies (Feuerriegel et al., 2015). This ERP component was also modulated by the inter-stimulus interval (ISI), but also by the adaptor duration and ISI (smaller amplitudes after 500 ms adaptation when compared to 200 ms for the 200 ms ISI). Other studies also found identity-specific amplitude reductions for the P2 component (Walther et al., 2013).

The N250 component showed significant amplitude reductions in repetition paradigms for familiar when compared to unfamiliar faces (Begleiter et al., 1995; Schweinberger et al., 1995; Pfütze et al., 2002). When repetitions happen in rapid succession, unfamiliar faces can also modulate the N250 component, although the effect is much smaller than in the case of familiar faces (Begleiter et al., 1995; Schweinberger et al., 1995; Herzmann et al., 2004;).

Taking all these into consideration, one notable question is whether one can distinguish a significant difference between priming and adaptation at a neuronal level. Even though the two are different in terms of behavioral responses, there are also considerable similarities between the two phenomena. Both priming and adaptation after-effects were reported to be independent of size (for priming: Brooks et al. 2002; for adaptation: Zhao and Chubb, 2001), viewpoint (for priming: Brooks et al. 2002; for adaptation: Jiang et al., 2006) and retinal position (for priming: Brooks et al. 2002; for adaptation: review by Kovács and Zimmer, 2011). Moreover, for both priming and adaptation, distortion and identity effects were found (for priming: Bindemann et al., 2008; for adaptation: Carbon and Ditye, 2012; Hills et al., 2010). Priming and adaptation after-effects were also found to be equally long-lasting, with effects that are visible even after 7 days delay between S1 and S2 (for priming: Cave, 1997; for adaptation: Carbon and Ditye, 2011). All these make it difficult to say whether there is a clear-cut difference between priming and adaptation at a neuronal level. In order to investigate the difference between these two phenomena, several studies have looked at the way in which varying experimental parameters can pinpoint wherein the difference lies.

Some studies have kept the timing parameters constant. For example, Kovács et al. (2007, 2008) investigated adaptation-related after-effects for gender discrimination after a relatively short adaptor duration (500ms) which would be closer to the shorter S1 durations used in priming experiments as compared to ones studying adaptation. Despite the short adaptation duration, significant after-effects were found. In a familiar face identification task, Walther et al. (2013) explored the possibility of an influence of stimulus ambiguity on whether one observes priming or adaptation after-effects. They have found that short-term repetition priming and after-effects can be obtained in the same temporal context for the same task, with more ambiguous S2 stimuli eliciting adaptation effects and less ambiguous ones leading to a priming effect.

Other studies have looked into varying the timing parameters and observing whether different effects were elicited. Daelli et al. (2010) presented prototypical S1s, followed by ambiguous S2s and found aftereffects when the inter-stimulus interval (ISI) was short (50 ms), but priming effects when the ISI was long (3100 ms). A magnetoencephalography (MEG) study by Harris and Nakayama (2007) also investigated the different effects elicited by a varying ISI (100, 200, 300 and 600 ms) and found that the M170 response (which is the correlated component of N170 for MEG) to the second face presented decreased in a linear manner with decreasing ISI. This shows that adaptation depends on ISI, even though this effect is short-lived. By an ISI of 800 ms there was no difference between adapted and non-adapted conditions.

The effects of varying the adaptor duration in adaptation studies have also been investigated in studies that were looking into coding mechanisms for faces. A study by Kovács et al. (2007) showed that for shorter adaptor durations (500 ms) the adaptation effect was entirely position independent, whereas for longer durations (5000 ms), the effect was both position invariant and position dependent.

Varying the adaptor time has led to a number of recent adaptation studies that make use of a so-called “rapid adaptation paradigm” in which the adaptor is presented for short durations centered around 200 ms. A previous study by Kovács et al. (2006) found category-specific adaptation effects on the N170 ERP component for faces following prolonged adaptation (5000 ms). The subsequent rapid adaptation studies wanted to investigate the category specificity of face adaptation effects at shorter adaptor durations. Some of these studies focused on the problem of configural processing of faces and the role that eyes play in the perception of human faces. The main focus of these studies was the N170 ERP component for electrophysiological studies (Eimer et al., 2010, Eimer et al., 2011, Nemrodov and Itier, 2011) or the M170 for MEG studies (Harris and Nakayama, 2007, 2008). The reason for focusing on these components is that they are the most relevant when studying the perception of faces versus other object categories since the N170 and M170 reflect the structural encoding of faces and appear to be the earliest ERP components that are specific only to faces. In the case of all of these studies, the adaptor duration was 200 ms. The problems with these studies concerned the results, which though roughly in line with some of the previous findings, seemed rather inconclusive. For example, in one of the experiments of the Eimer et al. study, they investigated the possibility that the differential N170 electrophysiological response to upright versus inverted faces (enhanced amplitude for inverted faces), suggests an additional recruitment of object selective neurons in the case of the inverted face. If this hypothesis is true, in an adaptation paradigm, the N170 should have a reduced amplitude for inverted face adaptors followed by inverted face test stimuli as compared to other types of face adaptors or object adaptors, such as houses. The interesting finding of this experiment was that upright and inverted house adaptors had almost no significant effect on the N170 when the test stimulus was a house, but had a very strong and consistent effect in response to inverted faces.

Because of the shortcomings of their previous studies and the inconclusive results of other rapid adaptation paradigm studies, Nemrodov and Itier (2012) tried to investigate whether the rapid adaptation paradigm is a valid tool for studying face perception. Their findings showed that this paradigm is too rapid to obtain any kind of specific effects. For their study they used all possible combinations of adaptor and test images for upright faces, houses, chairs and car stimuli and found no interaction between any of these. Their results thus showed that this paradigm does not produce any category specific adaptation effects in the 170 - 200 ms window after test stimulus onset, specific for the N170. This kind of category specific adaptation effect is essential for interpreting the adaptation results of the studies that investigate face perception by relying on the N170 component. Therefore, their conclusion was that the rapid categorical adaptation paradigm does not work.

The rapid adaptation paradigm studies, together with the Nemrodov and Itier study (2012) showed that adaptor duration is an important factor in understanding adaptation effects in the case of faces. Different adaptor durations lead to significantly different adaptation effects at the electrophysiological level and in single cell recordings in monkeys (Kohn and Movshon, 2003). Few studies have however investigated the effect that different adaptor durations have on the processes involved in face processing and on the major ERP components specific to face processing. Those that have looked into the matter have found inconclusive results. Feuerriegel et al. (2015) investigated the category specificity of adaptation over a range of adaptor durations (200, 500, 1000 ms) and ISIs (200, 500 ms). However, their results indicated that at the level of N170 there was no category adaptation for faces. Face adaptors led to the smallest N170 amplitudes for both target faces and chairs, after 500 ms adaptor duration. This comes in contrast with the previous studies that found category adaptation at the level of N170, but is similar to the results obtained by Nemrodov and Itier. Their study however, showed that adaptor duration and ISI have different effects on neural adaptation over various stages of visual processing. Nonetheless, the question remains whether the N170 is category dependent at longer adaptor durations, since Feuerriegel et al. only used relatively short adaptor durations.

The goal of the present investigations for my master thesis was to test whether systematically varying the adaptor duration affects the neural response at the level of known face-selective ERP components, thus reflecting different effects on the various stages of visual processing. By varying the adaptor duration along a broader interval we expected to obtain clearer and stronger results than by using short intervals of variation such as those employed by previous studies (Feuerriegel et al., 2015). By manipulating adaptation duration we should be able to dissociate different subgroups of neurons within the posterior inferior-temporal region that code the image-based, identity-based or generic (category-based) information separately.

This investigation is made possible by making use of an interdisciplinary approach to the topic of human visual perception that is of psychological, neuroscientific and philosophical interest.

Starting from a more general, philosophical question regarding the way in which our visual perception of the world is shaped by the temporal and spatial context and moving towards a more specific question involving adaptation to human faces, my thesis investigations try to offer an answer that is not bound to a single discipline. Through the use of knowledge from neuroscience of vision (structural and functional brain organization), cognitive psychology (perceptual processes), social psychology (importance of face stimuli in our everyday interactions), electrophysiology (event-related potential correlates) and psychophysics, I will try to give an answer to the question of whether we can obtain significantly different behavioral and electrophysiological effects by manipulating adaptor duration and type, in the case of face perception.

2. Materials and Methods

2.1 Participants

Sixteen naïve healthy-volunteers (16 right-handed and one ambidextrous, 6 females, mean age = 22.69 years, ± 4.83 years SD) participated in the study. They received course credits for their participation and gave signed, informed consent in accordance with the Ethical Committee of the Budapest University of Technology and Economics prior to testing. All participants had normal or corrected-to-normal visual acuity, no previous history of any neurological or ophthalmological diseases and were not under any medication. One additional participant was excluded from the behavioural and electrophysiological analysis (right-handed 22 years old male) due to an insufficient number of recognized familiar faces and a high number of recognized unfamiliar faces, which was evident in the post-testing questionnaire.

2.2 Stimuli

Grayscale images of familiar and unfamiliar faces were used, with sixteen different identities (eight female) for each category. Familiar faces were digital images of famous persons, ranging from Hollywood celebrities to politicians that Hungarian students were likely to recognize, whereas unfamiliar faces were digital images of less-known persons that were unlikely to be recognized by the participants (such as a Finnish politician or an actress from Iceland). Two different images portraying the same person were used for each identity, equalling a number of thirty-two images in total. All images were downloaded from freely available websites and converted into grayscale (8 bit) using Adobe Photoshop CS3 Extended 10.0 (Adobe Systems Inc.). Images were then cropped to reveal only the contour of the face, including hair. Since previous studies have shown that early ERP components, such as P1, are sensitive to luminance (Johannes et al., 1995) and that neural processes are sensitive to luminance histogram skewness (Olman et al., 2008), stimuli were equated in luminance and their histograms were matched using the lummatch and histmatch functions of the MATLAB (Mathworks, Natick Massachusetts, USA) SHINE toolbox (Willenbockel et al., 2010).

For the adaptors, three different images were used: an image that was identical to the test stimulus /repetition suppression (RS) condition/, a different image that depicted the same identity as the test stimulus /same identity (SameID) condition/, and an image depicting a different identity than the test stimulus /different identity (DiffID) condition/. It is worth noting, however, that in these cases the familiarity of the adaptor and target image was also different. For the control condition, sixteen Fourier phase-randomized images were created from the face images used in the study and used as adaptors /non-adapted (No) condition/.

Stimuli were presented centrally on a uniform grey background. An LG Flatron W2600 HP monitor (resolution: 1280 x 960 pixels, refresh rate: 60 Hz) was used for stimulus presentation, while viewing distance (57cm) was maintained constant using a chinrest. Stimulus presentation was controlled using MATLAB 2008a Psychtoolbox 3.0.9 (Brainard, 1997; Pelli, 1997) and custom-made scripts.

2.3 Procedure

Subjects were instructed to perform a two-alternative forced-choice (2AFC) familiarity task for faces by pressing the key labelled ‘7’ on the computer keyboard when the face was perceived as familiar and the key labelled ‘8’ when it was perceived as unfamiliar. A green fixation cross presented in the centre of the screen indicated the presence of the target stimulus to the subject. Prior to the presentation of the target, a grey screen was presented for a random period of time between 500 and 700 ms, followed by the adaptor image. The duration of the adaptor image varied randomly between one of five values: 200, 1200, 2000, 3500 and 5000 ms. The adaptor was followed by a 500 ms grey screen after which the target stimulus appeared for 200 ms. (Figure10). To ensure that the subjects were also focusing on the adaptor image, a yellow fixation cross directed their attention to the centre of the screen during the presentation of the adaptor. Subjects were also instructed to refrain from movements during the experiment and from blinking during the presentation of the target stimulus. Each subject completed a total of 640 trials [2 (familiarity: familiar (F) vs. unfamiliar (UF)) × 4 (adaptor category: No, RS, Same ID, Diff ID) × 5 (adaptor duration: 200, 1200, 2000, 3500, 5000 ms) × 16 (identity)] with five breaks in between testing blocks. Adaptor categories and durations were intermixed and presented in random order. An experimental session lasted approximately 50 minutes.

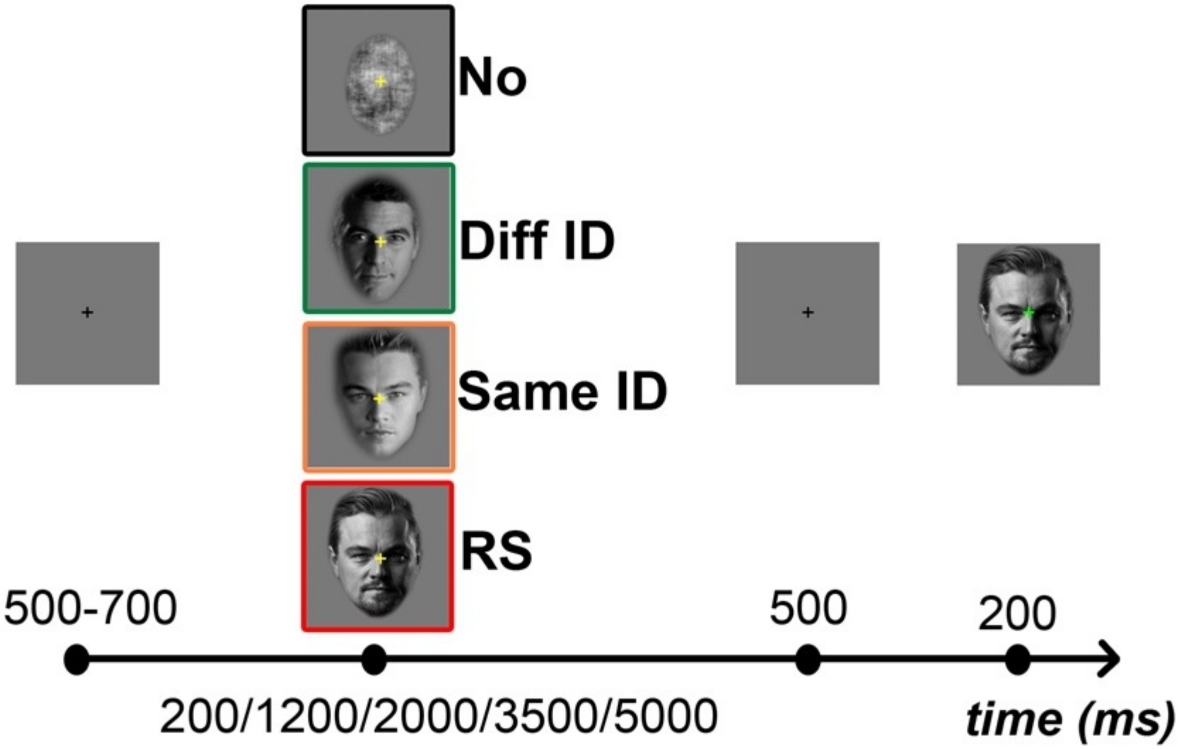

Fig. 10 Example of stimulus sequence presentation. The arrow indicates time direction. A blank grey screen was present between test stimulus and adaptor for a randomized period of time between 500 and 700 ms. Following this, a randomly chosen adaptor from one of the four adaptor categories (No, Diff ID, Same ID, RS) was presented for a random period of time chosen from the five adaptor durations (200, 1200, 2000, 3500 and 5000 ms). Subsequently, a blank grey screen was presented for 500 ms, after which the test stimulus appeared, lasting for 200 ms.

At the end of the session the subject had to answer a questionnaire that verified his familiarity with the identities used in the experiment. The questionnaire consisted of presenting the subject with each of the identities used and asking him/her to identify the familiar ones by naming them (or at least giving some correct information in terms of the given person verifying that he/she recognized that person). In case the subject did not recognize one or more of the faces belonging to the familiar category or recognized faces belonging to the unfamiliar category, the trials containing those identities were removed from the statistical analysis for both behavioural and electrophysiological data.

2.4 Behavioural Data Analysis

Accuracy and response times (RTs) were recorded during the experiment. Accuracies and RTs were analysed with a 2 × 4 × 5 repeated measures ANOVA with familiarity (2; familiarity: F vs. UF), adaptor category (4; No, RS, Same ID, Diff ID) and adaptor duration (5; 200, 1200, 2000, 3500, 5000 ms) as within-subject factors. All analyses involved Greenhouse - Geisser adjusted degrees of freedom for correction for non-sphericity. Post-hoc-t-statistics were performed by Tukey's HSD tests.

2.5 Electrophysiological Recording and Analysis

2.5.1 EEG Acquisition and Processing

Electroencephalography (EEG) data was recorded using a Brain-Amp (BrainProducts GmbH, Munich, Germany) amplifier from 60 Ag/AgCl scalp electrodes placed according to the international 10/10 electrode system (Chatrian et al., 1985) and mounted on an EC80 Easy Cap (Easycap, HerrschingBreitbrunn, Germany) (see Figure 11 for electrode placement).

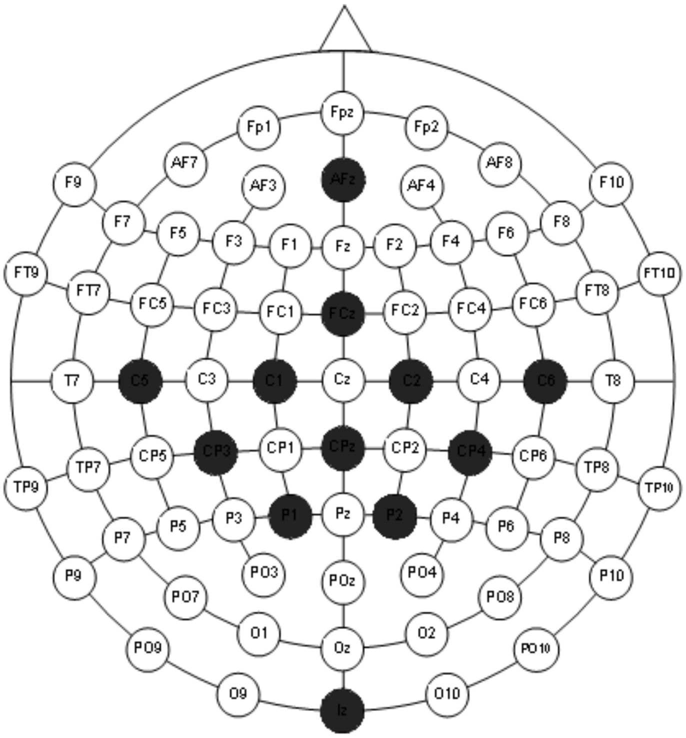

Fig. 11 Electrode placement used in the experiment. Covered with a dark-grey color are electrode positions that were not used (no electrode was placed there).

Eye movements were recorded using two electrodes placed on the outer canthi of the eyes and one electrode placed on the infraorbital ridge of the right eye. All channels were referenced online to an average of the activity recorded at the two reference electrodes placed on the left and right earlobe and digitally transformed to a common averaged reference offline. The ground electrode was placed on the forehead and all input impedances were kept below 8 kΩ. EEG was digitized at 1000 Hz sampling rate (with an analog bandpass filter of 0.016 - 1000 Hz).

2.5.2 ERP Data Analysis

EEG data were analysed using Brain Vision Analyzer 1.05.0002 (BrainProducts GmbH., Munich, Germany). After correcting ocular movement artefacts and digitally re-referencing to a common average, the EEG was segmented offline into 700 ms long epochs starting 100 ms prior to target stimulus onset and ending 600 ms after target stimulus onset. DC trend correction was applied, and a semi-automatic artefact rejection was implemented. Segments containing blinks, movement artefacts and baseline drifts were rejected on the basis of visual inspection. After cleaning the EEG data approximately 70% of the trials remained available for further analysis. It is worth noting, however, that the reason for removing a given segment in most cases was that the familiarity of the given person was misjudged by the subject. EEG epochs were averaged separately for each condition and participant. Averages were band-pass filtered (Butterworth zero phase filter; 0.1 – 30 Hz; slope: 12 dB/oct) and baseline corrected using a 100 ms pre-stimulus baseline. The peak amplitude and latency of the individually averaged ERPs were extracted using a semiautomatic detection algorithm that identified the global maxima separately for each selected channels in a specific time window as follows. P1 was defined as a main positive deflection in the 80-130 ms time window, whereas the N170 was defined as a negative component in the 135-190ms time interval. P2 was the second positive component in the 195-250 ms time window, while N250 was defined as the second negative component at around 230-330 ms.

P1 amplitude was measured over O1 (left hemisphere, LH) and O2 (right hemisphere, RH) electrode positions (Herrmann et al., 2005a and Herrmann et al., 2005b). For the N170, the standard posterior-occipito-temporal sites that correspond to the P7, P9 and PO9 (LH) and P8, P10 and PO10 (RH) channels were used (Wong et al., 2009). P2 amplitude was measured over O1, PO3 and PO7 (LH) and O2, PO4 and PO8 (RH) (Wang et al., 2014), while the amplitude of the N250 component was measured over P7, P9, PO9 and TP9 (LH) and P8, P10, PO10 and TP10 (RH) (Schweinberger et al., 2002). Five-way repeated-measure ANOVA was conducted for both amplitude and latency values of the pooled values of the relevant electrodes with familiarity (2; F vs. UF), adaptor category (4; No, RS, Same ID, Diff ID), adaptation duration (5; 200, 1200, 2000, 3500, 5000 ms), hemisphere (2; LH vs. RH) and electrode (2, 3 or 4) as within-subject factors separately for each component. It is worth noting that in case of the P100 component we ran a four-way repeated-measures ANOVA since we used only two electrodes, one for the LH and the other for the RH recordings. The Greenhouse - Geisser correction was applied to correct for violations of sphericity, while Post-hoc-t-statistics were computed using Tukey's HSD tests.

Moreover, we correlated the behavioural and electrophysiological effects. First, we calculated the magnitude of behavioural adaptation/priming effect by subtracting either the accuracy or the response time values in each adapted condition (RS, Same ID and Diff ID after 5 different adaptation durations) from that of the control condition (No). Moreover, we defined three different types of effect: GENERIC ADAPTATION/PRIMING EFFECT as referring to the No versus Diff ID distinction; IDENTITY-SPECIFIC ADAPTATION/PRIMING EFFECT as referring to the Same ID versus Diff ID distinction; and IMAGE-SPECIFIC ADAPTATION/PRIMING EFFECT as referring to the Same ID versus RS distinction. The electrophysiological adaptation/priming effect was defined as the absolute value of the differences in amplitude that were calculated by subtracting the P100, N170, P2 and N250 amplitudes obtained during the adapted conditions from that of the No condition. These effects were then correlated to each other by Pearsons tests.

Finally, we tested whether different types of adaptation effects modify the strength of the adaptation effect differently reflected on the early face-related ERP components separately for both hemispheres. Therefore a four-way repeated-measure ANOVA was conducted for the strength of adaptation indices based on the amplitude difference values with adaptation effect (3; GENERIC, IDENTITY-SPECIFIC, IMAGE-SPECIFIC), component (4; P100, N170, P2, N250), hemisphere (2; LH vs. RH) and duration (5; 200, 1200, 2000, 3500, 5000 ms) as within-subject factors. The Greenhouse - Geisser correction was applied to correct for violations of sphericity, while Post-hoc-t-statistics were computed using Tukey's HSD tests.

3. Results

3.1 Behavioral Results

Figure 12 shows the behavioral results for both accuracy and response times.

3.1.1 Accuracy

Main effect of CONDITION was observed ($F(1.1,16.6)=5.05$, $p=0.004$, $\eta_p^2=0.25$). Better performance was found in case of RS and Same ID conditions when compared to Diff ID condition (post-hoc p values: 0.005 and 0.014, respectively). No other comparisons between conditions were significant (all ps > 0.14). Better performance was observed in case of the longest (5000 ms) adaptation duration when compared to 3500 ms adaptation duration (main effect of DURATION: $F(4,60)=2.74$, $p=0.037$, $\eta_p^2=0.15$; post-hoc $p=0.03$). No other duration effect was found (all ps > 0.1). A significant CONDITION × DURATION interaction ($F(3.26,48.9)=2.38$, $p=0.007$, $\eta_p^2=0.14$) shows that the performance of the subjects was the worst in case of Diff ID conditions when compared to RS (all ps < 0.00005) and to Same ID (all ps < 0.004) conditions for almost all adaptation durations, however these effects are missing in case of the longest (5000 ms) adaptation duration (all ps > 0.15). In case of 200 ms and 1200 ms adaptation duration better performance was found in case of No when compared to Diff ID condition ($p<0.00004$ for 200 ms and $p<0.02$ for 1200 ms respectively). Significant CONDITION × FAMILIARITY interaction was observed ($F(1.99,29.92)=3.9$, $p=0.015$, $\eta_p^2=0.21$). The subjects' decisions were better in No condition when compared to RS or to Diff ID but only for familiar faces. Moreover, better performance was observed for unfamiliar faces when compared to familiar ones in case of Diff ID condition. These latter two effects were modified by DURATION (significant 3-way interaction: $F(4.02,60.36)=1.93$, $p=0.03$, $\eta_p^2=0.11$) in a way that better performance in No versus Diff ID was more pronounced in case of shorter durations (such as 200 and 1200 ms) while better performance for unfamiliar faces in Diff ID condition was found only in case of 1200 and 5000 ms adaptation durations.

3.1.2 Response Times

Faster decisions were observed for familiar faces when compared to unfamiliar ones (main effect of FAMILIARITY: $F(1,15)=5.27$, $p=0.037$, $\eta_p^2=0.26$). Main effect of CONDITION was found

($F(3,45)=61.54$, $p<0.0001$, $\eta_p^2=0.8$) in a step-by-step manner. Fastest decisions were observed in case of RS (all ps < 0.0005) followed by Same ID condition (all ps < 0.0005), however no significant difference was found between No and Diff ID conditions ($p=0.72$). Although we have found that FAMILIARITY modifies the main effect of CONDITION (significant FAMILIARITY × CONDITION interaction: $F(2.19,32.84)=12.09$, $p<0.0001$, $\eta_p^2=0.45$), the only relevant difference between the speed of decision is a faster decision in case of RS and Same ID conditions for familiar faces when compared to unfamiliar ones ($p=0.0002$ and $p=0.0008$, respectively). Any other significant difference can be interpreted by the significant main effect of condition. Adaptation duration also modified the main effect of condition (significant DURATION × CONDITION interaction: $F(12,180)=2.76$, $p=0.002$, $\eta_p^2=0.16$). We have observed smaller RT values in case of 2000 ms adaptation duration when compared to 3500 ms ($p=0.0044$) and to 5000 ms ($p=0.02$) in the Same ID condition. Interestingly, in case of 2000 ms adaptation duration we did not observe a significant difference between RS and Same ID conditions ($p=0.99$), as was the case for all other adaptation durations. Any other significant difference can be interpreted by the significant main effect of condition.

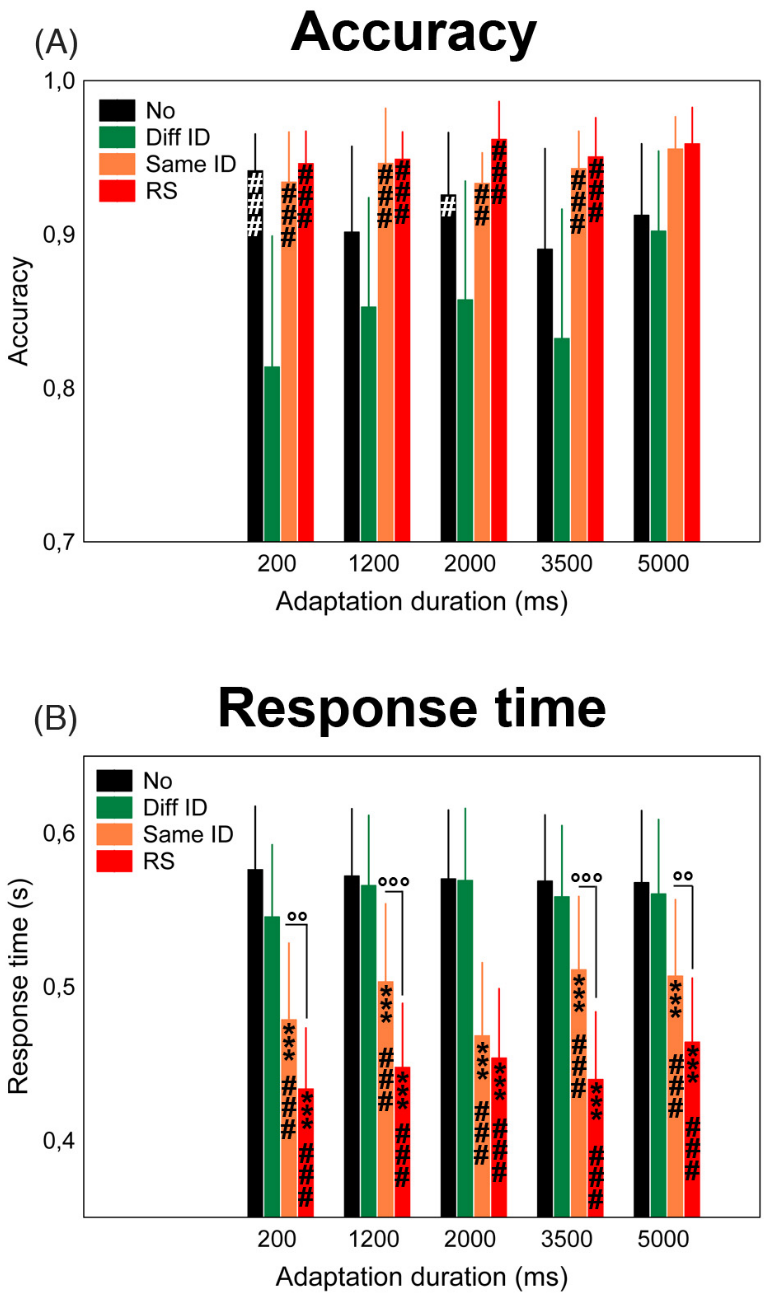

Fig. 12 Behavioral Results. Effect of varying adaptor duration on the accuracy (A) and response times (B) in the 2 AFC familiarity decision task for the control condition and the three adaptor categories: No (black), Diff ID (green), Same ID (orange), RS (red). X axis shows the five adaptor durations in ms (200, 1200, 2000, 3500, 5000). '#' shows significant differences when compared to Diff ID condition. '*' shows significant differences when compared to No. 'o' shows significant differences when comparing Same ID and RS. One sign indicates $p<0.05$, two signs $p<0.005$, three signs $p<0.0001$.

3.2 Electrophysiological Results

Clearly identifiable face-related ERP components, such as the P100, N170 and P2 were measured at occipital and posterior-occipital electrode sites (N250). Figures 15, 17 and 19 show the grand averages of the amplitudes of P100, N170, P2 and N250.

3.2.1 P100

Larger P100s were observed in all adapted conditions when compared to the control (No) (main effect of CONDITION: $F(3,45)=9.83$, $p<0.0001$, $\eta_p^2=0.4$, all post-hoc $ps<0.001$). No other significant difference between conditions was found (all $ps>0.9$). There was a right hemisphere dominance in the amplitude of P100s (main effect of HEMISPHERE: $F(1,15)=5.75$, $p=0.03$, $\eta_p^2=0.28$). In case of the shorter adaptation duration (namely in case of 200 ms and 1200 ms) smaller P100s were measured when compared to longer adaptation durations (namely 2000 ms, 3500 ms, and 5000 ms) (main effect of DURATION: $F(4,60)=12.09$, $p<0.0001$, $\eta_p^2=0.45$, post-hoc comparisons show all $ps>0.023$). No other effect of duration was observed (all other $ps>0.27$). Both familiarity and hemisphere modify the main effect of condition, however most of the significant post-hoc comparison can be interpreted by the main effect of condition (significant CONDITION × FAMILIARITY interaction: $F(3,45)=3.44$, $p=0.025$, $\eta_p^2=0.19$; significant CONDITION × HEMISPHERE interaction: $F(3,45)=3.83$, $p=0.016$, $\eta_p^2=0.2$). The only exception is that significantly larger P100 in case of Same ID condition when compared to control (No) is solely observed for familiar faces and not for unfamiliar ones (post-hoc $p=0.0004$ for familiar faces but $p=0.68$ for unfamiliar faces). Figure 13 shows the amplitude values of P100 for all conditions and adaptor durations.

The latency of the P100 was significantly longer at longest adaptation duration (5000 ms) when compared to the shortest ones (namely 200 ms and 1200 ms). Longer latencies were also observed in case of 3500 ms adaptation duration when compared to 1200 ms duration (main effect of DURATION: $F(4,60)=5.2$, $p=0.001$, $\eta_p^2=0.26$, 200 vs 5000 post-hoc $p=0.02$, 1200 vs 5000 post-hoc $p=0.003$, and 1200 vs 3500 post-hoc $p=0.02$, respectively).

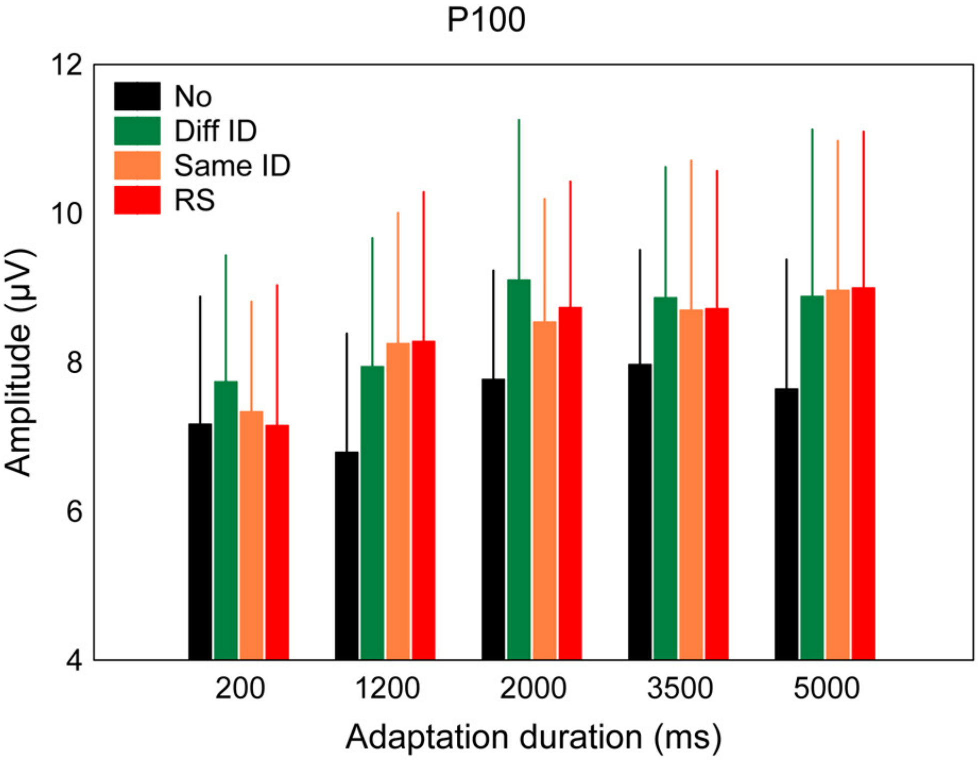

Fig. 13 Mean (±SD) of the amplitudes of the P100 for the three adaptor categories: No (black), Diff ID (green), Same ID (orange), RS (red). X axis shows the five adaptor durations in ms (200, 1200, 2000, 3500, 5000). Y axis shows the amplitude values in µV. There were no significant differences between conditions at any of the adaptor durations.

The observed GENERIC ADAPTATION/PRIMING EFFECT (No versus Diff ID) at the behavioural level correlated with the electrophysiological effect on the P100 amplitude both in case of 2000 ms adaptation duration in both hemispheres (LH: $r=0.7$, $p<0.05$ and RH: $r=0.79$, $p<0.05$, respectively) and in case of the longest adaptation duration (5000 ms) as well (LH: $r=0.76$, $p<0.05$ and RH: $r=0.79$, $p<0.05$, respectively). This latter effect was also observed for the response times (LH: $r=0.55$, $p<0.05$ and RH: $r=0.55$, $p<0.05$, respectively). The IMAGE-SPECIFIC BEHAVIOURAL ADAPTATION/PRIMING EFFECT (Same ID versus RS) correlated with the amplitude values of the P100 components in case of 1200 ms adaptation duration ($r=0.79$, $p<0.05$) and in case of 3500 ms adaptation duration ($r=0.73$, $p<0.05$) but only in the RH. The only significant correlation between the IDENTITY-SPECIFIC ADAPTATION/PRIMING EFFECT (Same versus Diff ID) and the P100 amplitudes was observed in case of 2000 ms adaptation duration in the RH ($r=0.78$, $p<0.05$).

3.2.2 N170

A clear right hemisphere dominance was observed (main effect of HEMISPHERE: F(1,15)=7.58, p=0.015, η_p^2=0.34). Unfamiliar faces evoked larger N170s when compared to familiar ones suggested by the main effect of FAMILIARITY (F(1,15)=8.94, p=0.009, η_p^2=0.37). N170 showed a significant main effect of CONDITION (F(3,45)=47.12, p<0.0001, η_p^2=0.76) due to the N170 amplitudes in the No condition being more negative than those in all other conditions (all ps<0.002). Post-hoc comparisons suggest that the relatively smallest (but significant) adaptation effect was observed in case of Diff ID conditions (No vs Diff Id p=0.00017, Same ID vs Diff ID p=0.018, and RS vs Diff ID p=0.0057, respectively). Although the amplitude decrease was more pronounced in case of RS and Same ID these two conditions did not differ significantly from each other (p=0.97). It is worth noting, however, that Diff ID was more negative when compared to Same ID in the right hemisphere (RH) suggested by the significant interaction of CONDITION and HEMISPHERE (F(3,45)=5.45, p=0.003, η_p^2=0.27, post-hoc test: Same ID vs Diff ID p=0.0008 in the RH but p=0.49 for the LH). Adaptation duration modified the main effect of condition (significant CONDITION × DURATION interaction: F(6.27,93.99)=3.33, p=0.0002, η_p^2=0.18). Interestingly, larger N170s were found in No for longer adaptation duration (namely in case of 2000, 3500, and 5000 ms durations when compared to the shortest 200 ms duration, all ps<0.004). For shortest adaptation duration the only significant amplitude reduction was observed in case of Same ID (No vs Same ID p=0.008) while no other adaptation effect appeared. In case of 1200 and 2000 ms adaptation duration significant adaptation effects were found in all adapted conditions when compared to the control (No) (all ps<0.002 for 1200 ms, and all ps<0.0006 for 2000 ms, respectively), however the amplitude values of N170s were not affected by the type of adaptor (all ps>0.62 in case of 1200 ms duration, and all ps>0.79 for 2000 ms duration, respectively). Furthermore, for 3500 ms adaptation duration, a strong tendency was observed when comparing RS and Diff ID conditions suggesting that the reduction of the N170 is more pronounced in case of RS (p=0.055). This tendency reached the level of significance in case of longest adaptation duration (5000 ms) (p=0.0008). For other comparisons the pattern of the effects was the same when compared to shorter adaptation durations. Figure 14 shows the amplitude values of N170 for all conditions and adaptor durations, while figure 15 shows the grand averages of the event-related potentials.

Longer latencies were observed for unfamiliar faces when compared to familiar ones (main effect of FAMILIARITY: F(1,15)(13.73, p=0.002, η_p^2=0.48). N170s were evoked earlier in case of No and RS when compared to the Same ID and Diff ID conditions (main effect of CONDITION: F(3,45)=8.75, p=0.0001, η_p^2=0.37, post-hoc p-values: No vs Same ID: p=0.03, No vs Diff ID: p=0.01, RS vs Same ID: p=0.002, and RS vs Diff ID: p=0.0008, respectively). Neither No and RS (p=0.75) nor Same ID and Diff ID (p=0.98) differed from each other. Main effect of DURATION (F(4,60)=6.15, p=0.0003, η_p^2=0.29) suggests that after 1200 and 2000 ms adaptation N170s appeared earlier when compared to the shortest (200 ms) and longest (5000 ms) durations (all significant ps<0.033 while other ps>0.18). Significant CONDITION × DURATION interaction was found (F(5.7,85.6)=1.82, p=0.047, η_p^2=0.11) suggesting that in case of shortest adaptation duration (200 ms) N170s were evoked later in case of Diff ID when compared to control (Diff ID vs No: p=0.02). Longer latencies were also found for Same ID when compared to either No or RS conditions for 200 ms adaptation duration (Same ID vs No p=0.0001, and Same ID vs RS: p=0.0005, respectively). In case of 1200 ms and 2000 ms adaptation durations, Same ID adapted target faces evoked slightly earlier N170s when compared to 200 ms adaptation duration time (200 vs 1200: p=0.0008, and 200 vs 2000: p=0.017, respectively). This pattern was modified differently by left and right hemispheres suggested by a 3-way CONDITION × DURATION × HEMISPHERE interaction (F(12,180)=1.85, p=0.04, η_p^2=0.11). The significant difference between Same ID and RS for the shortest adaptation duration was only observed in the left hemisphere (p=0.0005) and not in the RH (p=0.57) while the difference between the Diff ID condition and the control for 200 ms adaptation duration was only observed in the RH (p=0.0001) and not in the LH (p=0.9).

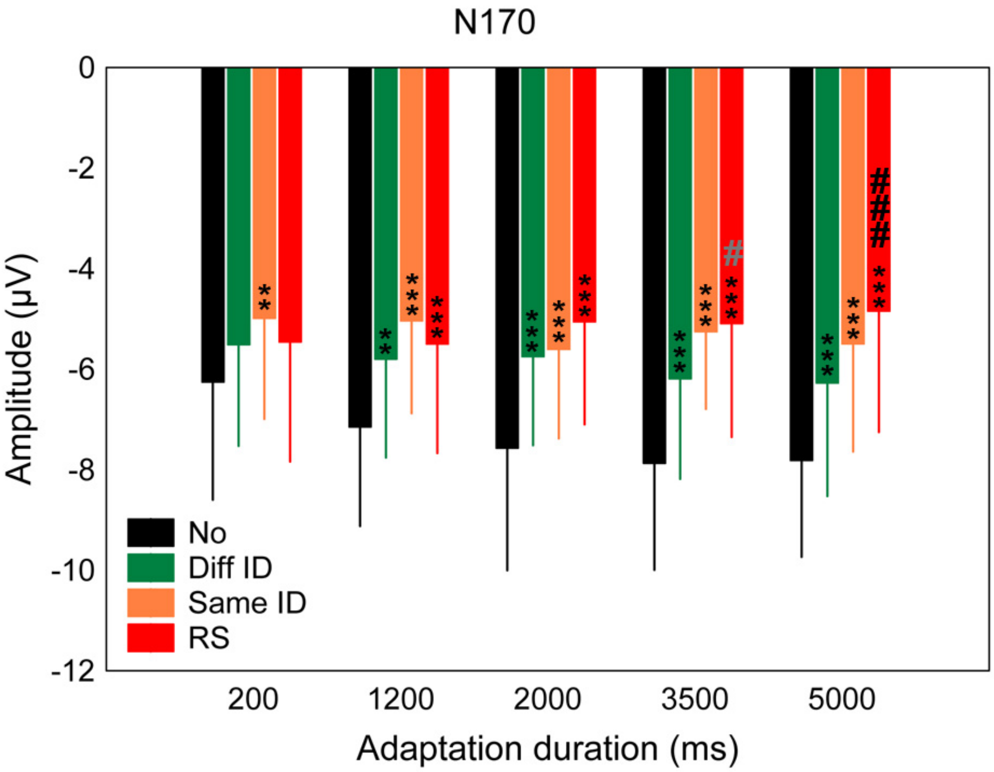

Fig. 14 Mean (±SD) of the amplitudes of the N170 for the three adaptor categories: No (black), Diff ID (green), Same ID (orange), RS (red). X axis shows the five adaptor durations in ms (200, 1200, 2000, 3500, 5000). Y axis shows the amplitude values in µV. Black‘#’ shows significant differences when compared to Diff ID condition. Grey ‘#’ shows the strong tendency effect (p = 0.054 or 0.05). ‘*’ shows significant differences when compared to No. One sign indicates p<0.05, two signs p<0.005, three signs p<0.0001. No significant differences were found when comparing Same ID and RS.

The IMAGE-SPECIFIC BEHAVIOURAL ADAPTATION/PRIMING EFFECT (Same ID versus Diff ID) correlated with the amplitude values of the N170 components in case of the longest adaptation duration (5000 ms) in the RH (r=0.51, p<0.05). The observed IDENTITY-SPECIFIC ADAPTATION/PRIMING EFFECT (Same ID versus RS) at the behavioural level correlated with electrophysiological effect on the N170 amplitude both in case of the shortest adaptation duration (200 ms) (r=0.51, p<0.05) and in case of the longest duration (r=0.5, p<0.05) but only in the LH.

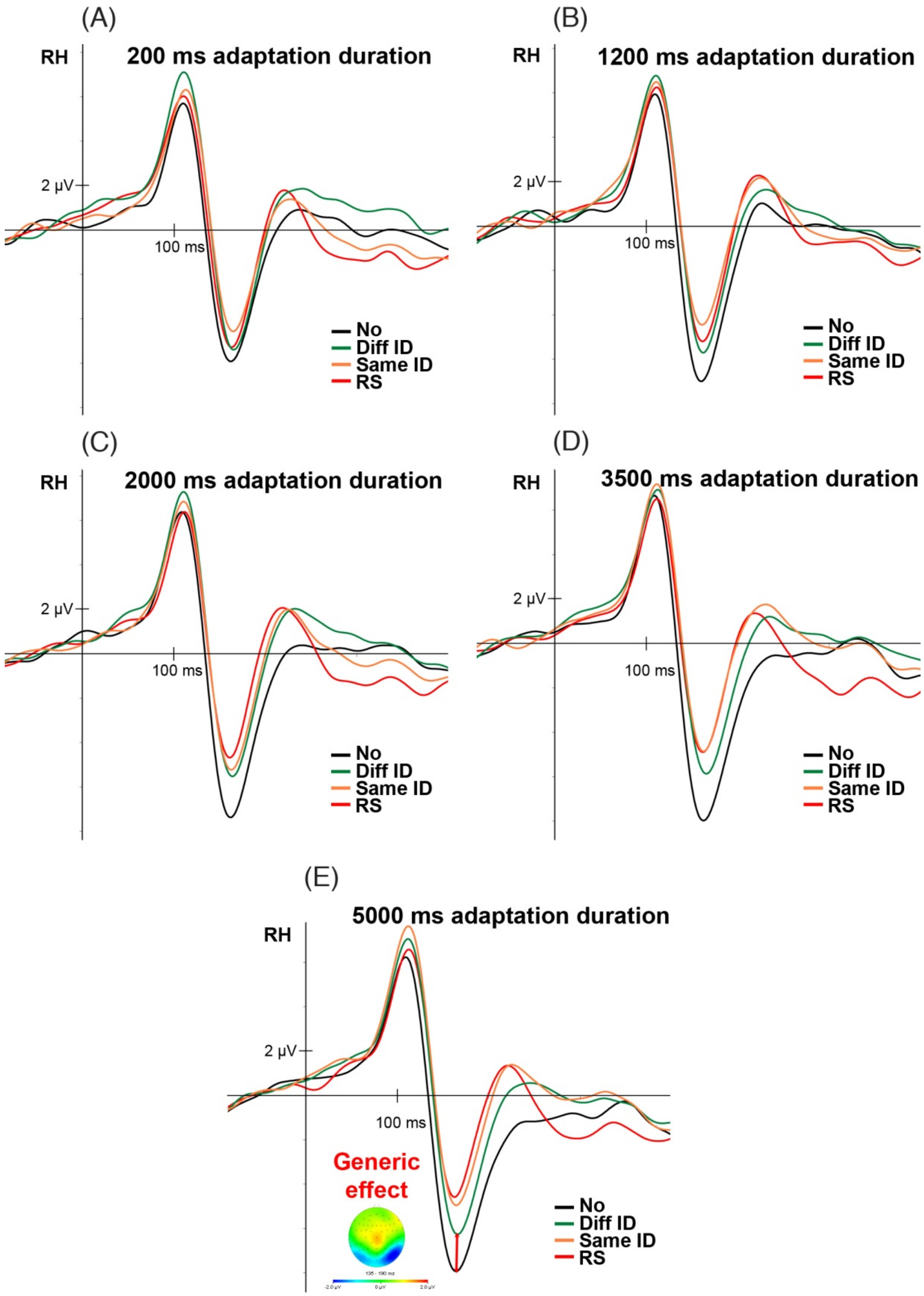

Fig. 15 Grand average N170 event-related potentials (ERPs) displayed between -100 and 400 ms of the pooled occipitotemporal recording sites of right hemisphere for the control condition and the three adaptor categories: No (black), Diff ID (green), Same ID (orange), RS (red). X axis shows time in ms. Y axis shows the amplitude values in µV. The figure shows ERPs for each adaptor duration: (A)- 200 ms, (B)- 1200 ms, (C)- 2000 ms, (D)- 3500 ms, (E)- 5000 ms. (E) shows a topographical voltage map for the GENERIC adaptation effect.

3.2.3 P2

Faces evoked larger P2s in the RH than in the LH (main effect of HEMISPHERE: F(1,15)=12.56, p=0.003, η_p^2=0.46). After adaptation to the same identity (Same ID) or to the same image (RS) larger P2s were observed when compared to the control (No) (main effect of CONDITION: F(2.19,32.8)=12.63, p<0.0001, η_p^2=0.46, Same ID vs No: p=0.002, and RS vs No: p=0.0002, respectively). Moreover, larger P2s were found in case of RS when compared to Diff ID (p=0.002). This main effect was modified by adaptation duration (significant CONDITION × DURATION interaction: F(6.37,95.58)=2.4, p=0.007, η_p^2=0.14). In case of the shortest adaptation duration there was no significant effect reflected on the amplitude of the component (all ps>0.99). In all other cases there was a signal enhancement in RS when compared to the control (ps<0.0005). This was also the case for the RS versus Diff ID comparisons (all ps<0.036) except for 2000 ms adaptation duration where these conditions did not differ from each other (p=0.87). In case of 3500 ms adaptation duration Same ID condition also evoked larger P2s when compared to the control (p=0.00005). Furthermore, right hemisphere data suggest that there is a step-by-step differentiation among No, Diff ID, Same ID, and RS conditions in an ascending manner (significant CONDITION × HEMISPHERE interaction: F(3,45)=2.97, p=0.042, η_p^2=0.17), however this effect was cancelled in case of the LH since the comparisons between Same ID vs RS and Same ID vs Diff ID did not reach the level of significance (p=0.11). Figure 16 shows the amplitude values of P2 for all conditions and adaptor durations, while figure 17 shows the grand averages of the event-related potentials.

Longer latencies were measured at PO3/4 electrode sites when compared to either PO7/8 or O1/2 recording sites (main effect of ELECTRODE: F(2,30)=6.09, p=0.006, η_p^2=0.29). In case of 1200 ms adaptation duration P2s were evoked later for unfamiliar faces than for familiar ones (significant DURATION × FAMILIARITY interaction: F(4,60)=3.16, p=0.02, η_p^2=0.17). No other significant main effect or interaction was observed.

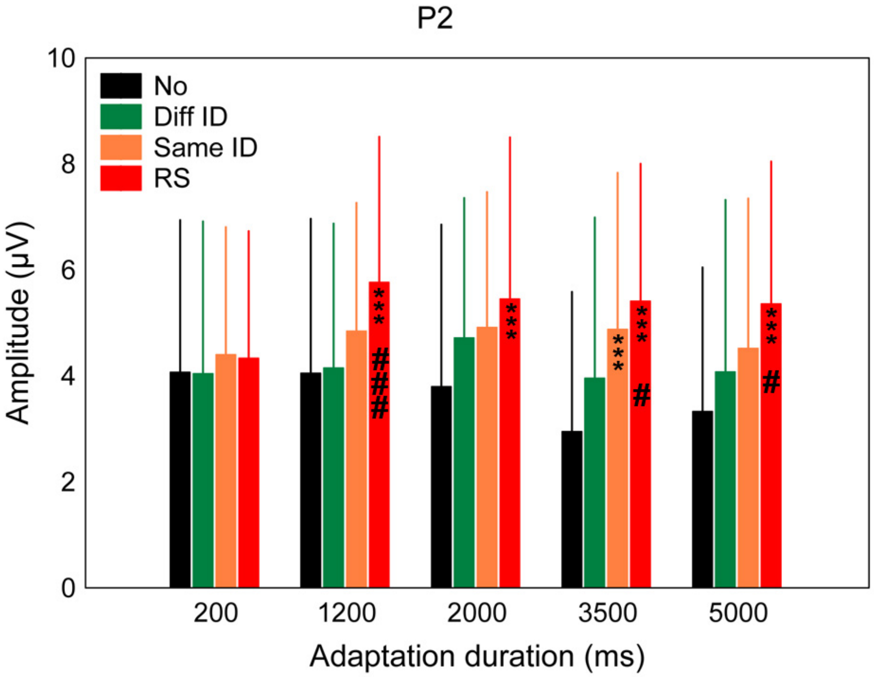

Fig. 16 Mean (±SD) of the amplitudes of the P2 for the three adaptor categories: No (black), Diff ID (green), Same ID (orange), RS (red). X axis shows the five adaptor durations in ms (200, 1200, 2000, 3500, 5000). Y axis shows the amplitude values in µV. '#' shows significant differences when compared to Diff ID condition.). '*' shows significant differences when compared to No. One sign indicates $p<0.05$, two signs $p<0.005$, three signs $p<0.0001$. No significant differences were found when comparing Same ID and RS.

The observed GENERIC ADAPTATION/PRIMING EFFECT (No versus Diff ID) at the behavioural level correlated with the electrophysiological effect on the P2 amplitude both in case of 1200 ms adaptation duration in the LH ($r=-0.53$, $p<0.05$) and in case of 3500 ms adaptation duration in the RH (RH: $r=0.53$, $p<0.05$, respectively). This latter effect was also observed for the response times in both hemispheres (LH: $r=0.59$, $p<0.05$ and RH: $r=0.5$, $p<0.05$, respectively). In case of the longer adaptation durations (3500 ms and 5000 ms) the IDENTITY-SPECIFIC ADAPTATION/PRIMING EFFECT (Same versus RS) that were calculated by the response time values and the P2 amplitudes correlated with each other in the LH (3500 ms: $r=0.77$, $p<0.05$, 5000 ms: $r=0.56$, $p<0.05$). This effect was also appeared in the accuracy data in case of 3500 ms adaptation duration in the LH ($r=0.6$, $p<0.05$). In case of the response time values the IMAGE-SPECIFIC ADAPTATION/PRIMING EFFECT (Same ID versus Diff ID) correlated with the amplitude values of the P2 components in case of 3500 ms adaptation duration in the LH (r=0.59, p<0.05).

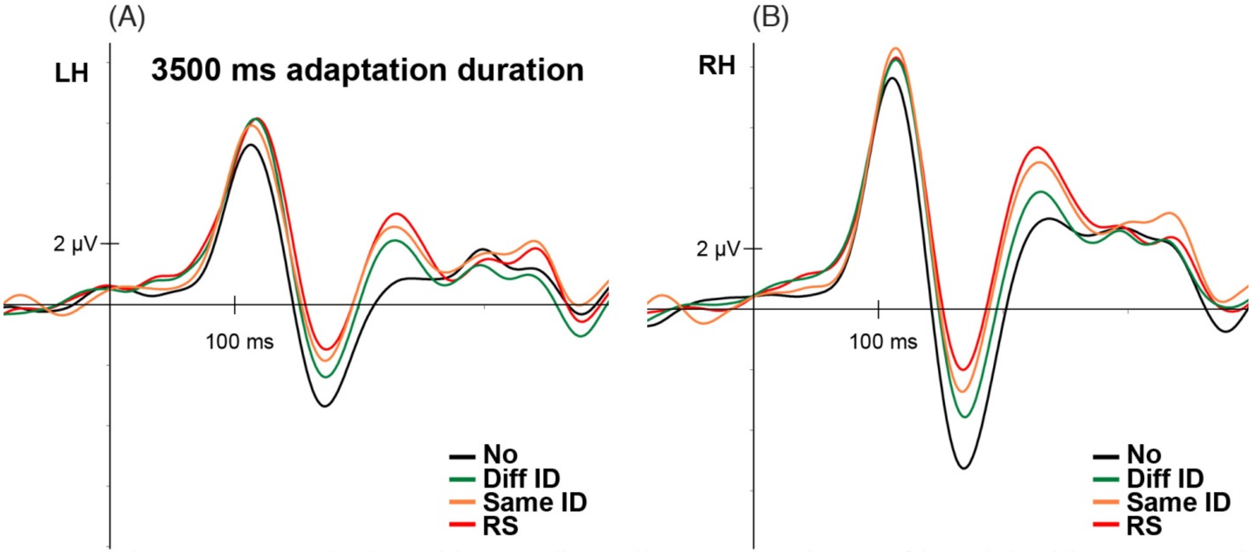

Fig. 17 Grand average P2 event-related potentials (ERPs) displayed between -100 and 400 ms of the pooled occipitotemporal recording sites of right hemisphere (A) and of left hemisphere (B) for the control condition and the three adaptor categories: No (black), Diff ID (green), Same ID (orange), RS (red) at 3500 ms adaptor duration. X axis shows time in ms. Y axis shows the amplitude values in µV. (A) shows the left hemisphere data, whereas (B) shows the right hemisphere data.

3.2.4 N250

The most negative N250s were observed in RS when compared to all other conditions (main effect of CONDITION: F(1.89,28.33)=11.94, p<0.0001, η_p^2=0.44, all ps<0.02). Moreover, more negative N250s were measured in control (No) condition than in Diff ID (p=0.025). N250s evoked by target faces were larger in case of the longest adaptation duration (5000 ms) conditions when compared to the shortest (200 ms) duration (main effect of DURATION: F(2.44,36.66)=3.02, p=0.025, η_p^2=0.17, post-hoc comparison: p=0.02). As we expected, familiar faces evoked larger (more negative) N250s (main effect of FAMILIARITY: F(1,15)=14.48, p=0.0017, η_p^2=0.49). The only relevant finding that came from the significant three-way CONDITION × DURATION × HEMISPHERE interaction (F(4.67,70.1)=2.15, p=0.016, η_p^2=0.13) is that for all adaptation duration a more negative N250 was found in RS when compared to Diff ID in both hemispheres (all ps<0.007), except for 1200 ms duration RH data (p=0.7).

Significant DURATION × HEMISPHERE interaction was found (F(2.12,31.83)=3.23, p=0.018, η_p^2=0.18) suggesting on the one hand that in case of the shortest (200 ms) adaptation duration N250s were evoked later in the RH than in the LH (p=0.013). On the other hand there was a duration effect that appeared only in the RH, namely after the shortest adaptation duration N250s were evoked later than in case of the longest one (p=0.044). In case of the LH data N250s were evoked later for 2000 ms duration when compared to either 3500 ms (p=0.039) or to 5000 ms (p=0.0016). Figure 18 shows the amplitude values of N250 for all conditions and adaptor durations, while figure 19 shows the grand averages of the event-related potentials.

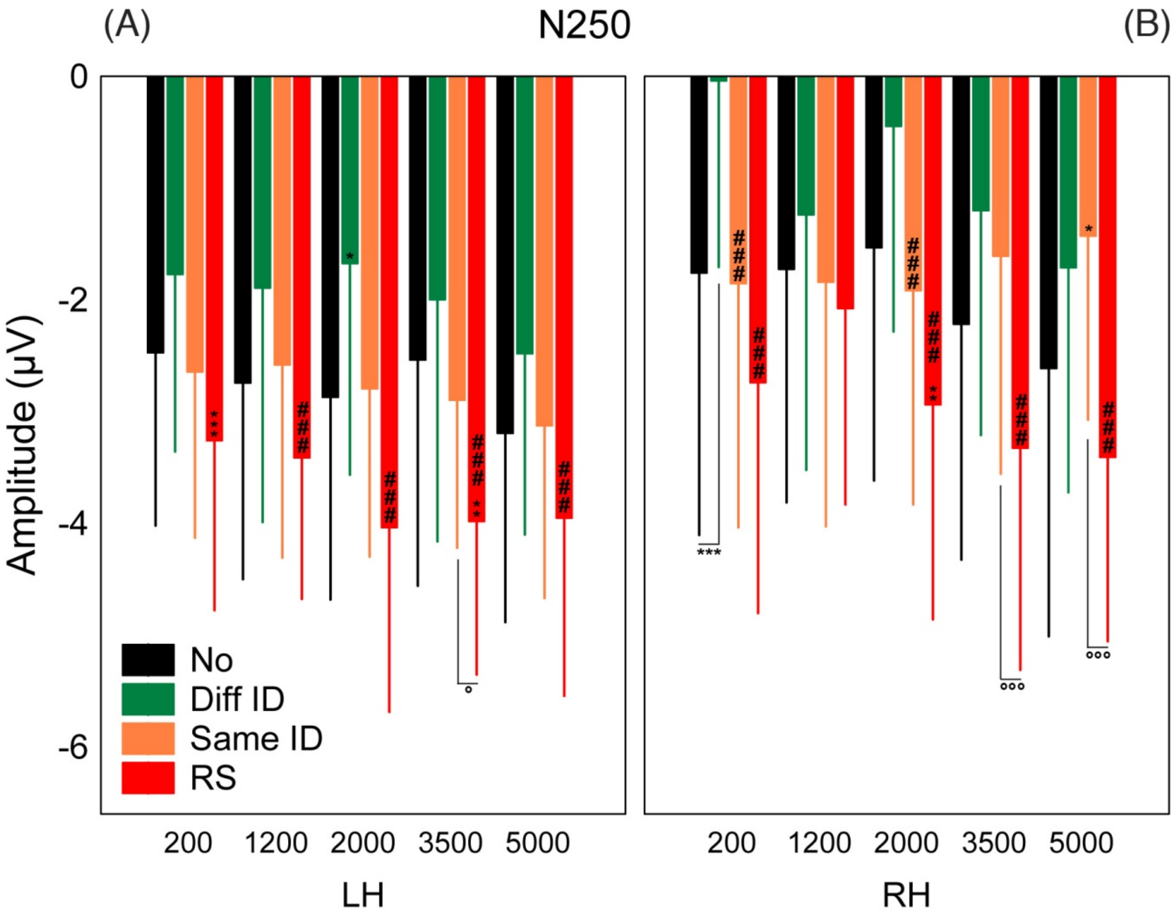

Fig. 18 Mean (±SD) of the amplitudes of the N250 for the three adaptor categories: No (black), Diff ID (green), Same ID (orange), RS (red). X axis shows the five adaptor durations in ms (200, 1200, 2000, 3500, 5000). Y axis shows the amplitude values in µV. '#' shows significant differences when compared to Diff ID condition.). '*' shows significant differences when compared to No. 'o' shows significant differences when comparing Same ID and RS. One sign indicates p<0.05, two signs p<0.005, three signs p<0.0001. (A) shows the amplitude values for the left hemisphere (LH) while (B) shows the values for the right hemisphere (RH).

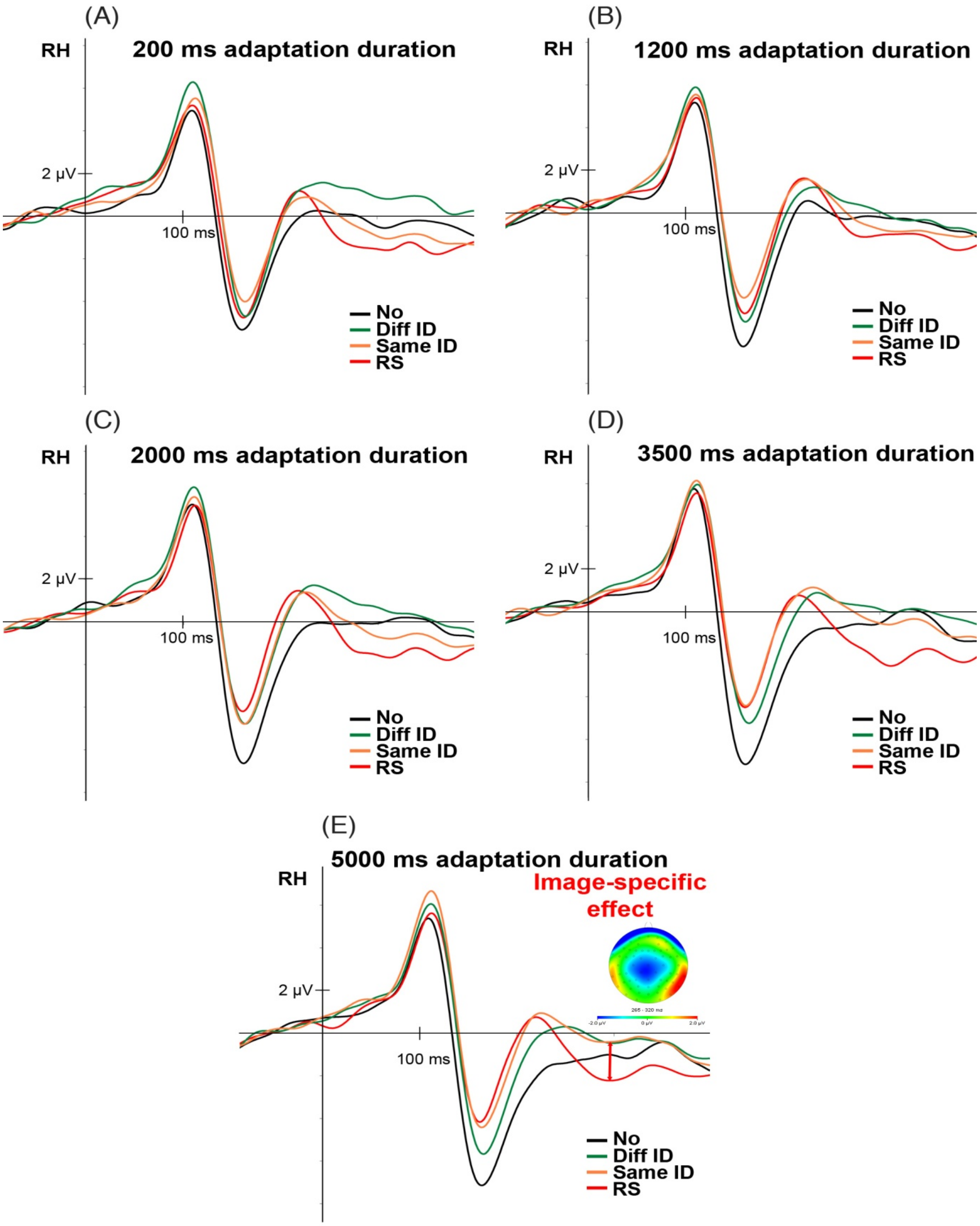

Fig. 19 Grand average N250 event-related potentials (ERPs) displayed between -100 and 400 ms of the pooled occipitotemporal recording sites of right hemisphere for the control condition and the three adaptor categories: No (black), Diff ID (green), Same ID (orange), RS (red). X axis shows time in ms. Y axis shows the amplitude values in µV. The figure shows ERPs for each adaptor duration: (A)- 200 ms, (B)- 1200 ms, (C)- 2000 ms, (D)- 3500 ms, (E)- 5000 ms. (E) shows a topographical voltage map for the IMAGE-specific adaptation effect.

The observed GENERIC ADAPTATION/PRIMING EFFECT (No versus Diff ID) at the behavioural level correlated with electrophysiological effect on the N250 amplitude in case of the shortest adaptation duration (200 ms) in the LH ($r=0.68$, $p<0.05$). Interestingly, the IDENTITY-SPECIFIC ADAPTATION/PRIMING EFFECT (Same versus RS) that was calculated by the response time values and the N250 amplitudes correlated negatively with each other in the RH ($r=-0.51$, $p<0.05$).

By running a meta-analysis based on different types of adaptation effects we can say that altogether larger adaptation effect was observed in case of GENERIC adaptation when compared to the IDENTITY-SPECIFIC adaptation (main effect of ADAPTATION EFFECT: $F(2,30)=3.97$, $p=0.03$, $\eta_p^2=0.21$, post-hoc comparison: $p=0.026$). This effect was the most pronounced in case of the 2000 ms adaptation duration suggested by the significant ADAPTATION EFFECT × DURATION interaction ($F(8,120)=2.21$, $p=0.03$, $\eta_p^2=0.13$, post-hoc comparison: $p=0.0035$). The results of the meta-analysis also emphasize the right hemisphere dominance of the N170 component, mainly in case of GENERIC adaptation effect (main effect of HEMISPHERE: $F(1,15)=5.15$, $p=0.038$, $\eta_p^2=0.26$ and significant COMPONENT × HEMISPHERE interaction: $F(3,45)=6.64$, $p=0.0008$, $\eta_p^2=0.31$, post-hoc comparison: $p=0.0007$). Interestingly, the significant three-way ADAPTATION EFFECT × COMPONENT × HEMISPHERE interaction ($F(2.87,43)=2.62$, $p=0.022$, $\eta_p^2=0.15$) draw our attention to the role of the two negative face-related ERP components in adaptation paradigms. In case of the earlier N170 component we can say that GENERIC ADAPTATION EFFECT was larger than either the IDENTITY-SPECIFIC ($p=0.0045$) or the IMAGE-SPECIFIC ADAPTATION effect ($p=0.008$) in the RH. On the one hand the GENERIC ADAPTATION EFFECT observed on the N170 was much larger when compared to the effect reflected on the later N250 in the RH ($p=0.0004$). On the other hand the IDENTITY-SPECIFC ADAPTATION EFFECT observed on the N250 was larger when compared to the effect reflected on the earlier N170 in the LH ($p=0.005$).

4. Discussion

The goal of the present study was to investigate the behavioral and neuronal effects of systematically varying adaptor duration and whether this variation will lead to a differentiation between various stages in the visual processing of faces. By using a broader interval for the variation of the adaptor duration we expected to find a differentiation between generic, image and identity-specific processes. We have found that indeed by varying adaptor duration we can obtain significantly different adaptation effects following different adapting durations. Our results show that for longer adaptor durations there is a dissociation between generic, image and identity-specific processes.

4.1 Behavioral Results

The behavioral results indicated a better performance and reaction times overall for RS and Same ID conditions, when compared to Diff ID condition, showing that there was a strong priming effect in this case. This was to be expected since the stimuli used in our experiment were unequivocal and thus the task difficulty was not so high. As such, we were expecting a priming effect at the behavioral level, as opposed to after-effects. Walther et al. (2013) found that ambiguity of the stimuli used plays an important role in differentiating between priming effects and after-effects. Their results show that ambiguous, morphed S2 stimuli elicited after-effects, whereas unambiguous S2s led to priming effects. Moreover, in the case of RTs we found a familiarity main effect, showing that faster RTs were recorded for familiar faces, which is in line with previous studies (Tong and Nakayama, 1999) that showed that familiar faces are processed much faster than unfamiliar ones.

4.2 Electrophysiological Results

4.2.1 P100

In case of the P100 ERP components we have found larger amplitudes for all adapted conditions when compared to control (No), indicating a signal enhancement in the case of this component. This main effect of condition suggests a generic adaptation effect at the level of P100. This is in line with previous studies that have found a signal enhancement for the P100 component in the case of face perception (Zimmer and Kovács, 2011a). This finding shows that there are different modulating effects on P100 (signal enhancement) when compared to the later N170 (signal reduction) as a consequence of adaptation, suggesting separate mechanisms that elicit these components and different roles that they play in face perception. No other significant difference was found between the adapted conditions. Also, no significant condition and duration interaction was found either, suggesting that at the level of this component there are no modulating effects of adaptor duration. This was to be expected since the P100 ERP component reflects early visual encoding processes and responds equally to different types of face stimuli (Kovács et al., 2007; Schweinberger et al., 2007; Zimmer and Kovács, 2011). A main effect of duration showed that larger P100 components were recorded for shorter adaptor durations when compared to longer ones. This effect could be due to the fact that at shorter adaptor durations (200, 1200 ms) one cannot separate the two images (adaptor and target image), and thus the two faces perceived as one elicit a stronger response.

For the investigations on whether the electrophysiological data reflect the behavioral performance (either the accuracy or the speed of decision). In the case of the behavioral and electrophysiological correlations, for all ERP components, we have chosen to focus only on the data that are significant behaviorally as well. For accuracy data the only significant difference was found between Diff ID and all other conditions. As such, we were interested in the No vs. Diff ID (GENERIC) and Same ID vs. Diff ID (IDENTITY) comparisons. Behavioral generic adaptation effects were found for 200 and 2000 ms adaptor durations, whereas identity-specific adaptation was found for all adaptor durations between 200 and 3500 ms adaptor durations. In the case of RT data, we found identity-specific adaptation for all adaptor durations, while image-specific adaptation was found only for 200, 1200, 3500 and 5000 ms.

The significant generic and identity-specific adaptation effect found for the P100 at 2000 ms in the RH could reflect the processing of low-level information when comparing two identities. These low-level differences between adaptor stimuli could lead to the signal enhancement of the P100, which was correlated with better performance (better accuracies) for Same ID condition.

4.2.2 N170

The N170 ERP component demonstrated strong right hemisphere (RH) dominance, in line with results of previous experiments (Puce et al., 1996, 1998). This RH dominance was also evident in the results of the meta-analysis that showed the RH dominance of the component, as evident from the component and hemisphere interaction for generic adaptation. All adapted conditions displayed a signal reduction (less negative amplitudes) of the N170 component when compared to control, indicating that adaptation to face stimuli reduces the amplitude of this component. The main effect of condition showed no significant differences between the adaptor categories, but suggests, as in the case of the P100, a generic adaptation effect at the level of the N170 ERP component. These findings show that the adaptation effect reflected on these two early face-related components is a generic one. Therefore, we can hypothesize that the stages of face perception reflected in these ERP components are rather linked to a purely sensory processing that is insensitive to the identity information within the adaptor stimulus. In addition to this, there was an interaction effect at the level of the N170 between condition and adaptor duration, indicating that the generic effect is stronger for adaptor durations that are longer than 1200 ms. No identity- or image-specific effects were found at the level of the N170. It is worth noting however, that in case of 200 ms adaptation duration, there is a positive correlation between behavioral identity-specific effect and N170 LH data, meaning that the better the accuracy of the subjects is, the larger the amplitude of the N170 is. Specifically, our data show that at the shortest adaptation duration the adaptation effect was larger for Same ID when compared to Diff ID. This could be interpreted if we take into account the fact that the left hemisphere is generally associated with feature-based processing of faces, while the right hemisphere is connected to holistic face processing (Leehey et al., 1978; Rapazynski and Erlichman, 1979; Fairweather et al., 1982; Rhodes, 1993).Since the fit between the adaptor image and the target image (feature-by-feature) is much better in case of Same ID condition when compared to Diff ID, this could explain both the larger amplitude values and the lateralization to the LH, which processes information in a feature-by-feature manner. If we do not have enough time to process the image deeper, as is the case for the shortest adaptor duration, then this fit between features can be used as a pop-up cue, to establish whether it is the same person or not.

The generic adaptation reflected on the N170 is in line with previous studies (Kovács et al., 2006, 2007; Zimmer and Kovács, 2011a, 2011b) that showed reduced amplitude of this component after adaptation to faces. Recently, Feuerriegel et al. (2015) also varied adaptor duration systematically and found no generic (category-specific) adaptation on the N170 component. In light of our findings, their results can be explained by the fact that they used relatively shorter adaptor durations (200-1000 ms) which do not affect this component in the same way as longer durations (>1200 ms). In our study, neither the generic-, image- nor identity-specific adaptation effects are apparent before 1200 ms, showing that in order to elicit a strong-enough response on the N170, longer exposure time to a stimulus is needed. Our results also support the claims of Nemrodov and Itier (2012) regarding the validity of rapid adaptation paradigms. In accordance with their findings, our results show that for adaptation-durations <1200 ms for N170 one cannot obtain any kind of specific effects at the level of this ERP component.

4.2.3. P2

The P2 ERP component also displayed a right hemisphere dominance and an overall signal enhancement for RS when compared to control (No) and Diff ID conditions, both in line with previous studies (Feuerriegel et al., 2015). The hypersensitivity of P2 in the case of RS vs. No was found only for adaptor durations >1200 ms, whereas in the case of RS vs. Diff ID the significant difference in signal enhancement was found for 1200, 3500 and 5000 ms only. Even though the authors of some of the previous studies (Kovács et al., 2007; Zimmer and Kovács, 2011a, 2011b) did not concentrate on this component, the enhancement of the P2 after adaptation is evident in the grand averages figures for the ERP components investigated in these studies. Whereas P100 and N170 ERP components are linked to special and well-defined stages of face processing, this does not hold true for the later P2 component. Some studies linked this component to task-difficulty (Philiastides et al., 2006), while in other studies the authors emphasized the role of P2 in face-related tasks for which we have expertise (own race effect versus other race effect) (Stahl et al., 2008). P2 enhancement has also been found in previous studies (Bankó et al., 2011; Németh et al., 2014) investigating the effect of phase noise and task difficulty on this component. Even though the lateral occipital cortex (LOC) is believed to be an object-selective area, some studies (Bankó et al. 2011, Nagy et al., 2012) have found that the caudal-dorsal part of it, the lateral occipital (LO) is also responsive to faces and seems to modulate face perception. Indeed, Nagy et al. (2012) have found bidirectional connections between LO and the OFA-FFA complex that is involved in face processing, with faces modulating the LO-FFA connection and objects modulating the LO-OFA. And since the LOC is also the neural generator of both P100 and P2, one would expect a similar behaviour of these two components - an enhancement, rather than a reduction, especially for repetitions of exactly the same image (RS). This is indeed the case, as Bankó et al. (2011) have shown by investigating the effects of phase noise and task difficulty on early face-related ERPs. Their results indicated that the P2 is not modulated by task difficulty, but by noisy stimuli, which lead to an enhanced amplitude of this component. If the task requires deeper processing, as is the case with a task in which the faces have added noise, then the processing demands are increased, which would in turn trigger re-entrant visual cortical processing mechanisms that are reflected on the P2 component. Németh et al. (2014) have also investigated the effect of phase noise on early ERP components and found that the P2 component is enhanced for both noisy faces and cars.

In addition to the general sensitivity for the RS condition, the difference between RS and Diff ID conditions could suggest that at the stage of processing reflected by the P2, we can process identity information. Moreover, the fact that no generic adaptation effect was observed at the level of the P2 also suggests that the role of this ERP component in face processing is different than that of the N170, for which the generic effect was the most pronounced. The P2 could thus be involved in the early processing of identity information.

The correlation analysis revealed an identity-specific adaptation for the LH at 3500 ms adaptor duration, in the case of accuracy results, while the correlation with the RTs revealed an identity-specific adaptation at 3500 and 5000 ms adaptor durations and an image-specific adaptation at 3500 ms, both in the LH. The RTs correlations are dominant in the case of this component suggesting an independence from sensory processing and more of a connection with the speed of decision, since the faster the decision is, the larger the signal enhancement on P2 can be observed. Regarding the LH dominance, one could speculate that this is the case due to the processing of semantic information involved in identity-specific processes. However, at the level of this ERP component, the largest adaptation effect was the image-specific one. Considering again that the LOC is the neural generator of the P2 component, one could speculate that after adapting to a specific image of a given identity at the level of OFA-FFA complex and analyzing face-related information, including identity, there is increased difficulty in distinguishing between RS and Same ID condition, that is, in saying whether it is the exact same image or a different image of the same person. This could cause a reactivation in the connection between OFA-FFA and LOC, feeding information back to the LOC so that this distinction can be realized. Since dissociating between same image and a different image of same identity is not necessarily a face-related process, the LOC could be responsible for this processing, which would lead to an increased activity of this area. This increased activity would, in turn, be reflected in the signal enhancement of the P2.

4.2.4. N250

At the level of the N250 generic-, image- and identity-specific adaptation effects were found, but only for specific adaptation durations. This effect also displayed hemispheric asymmetries. The interaction between condition and adaptor duration showed a generic effect at 200 ms for the RH and at 2000 ms for the LH. Identity-specific adaptation effects were found at the same adaptor durations as generic ones, but only in the RH. In the case of image adaptation effects there was again a hemispheric difference, with the LH showing adaptation at 2000 ms and the RH at 3500 and 5000 ms respectively. These findings show that generic-, image- and identity-specific adaptation happen in parallel and are not independent of one another, since the longer the duration is, the stronger the effect of adaptation when comparing these three types of adaptation effects within the same time window (that is, on the same ERP component – N250).

The idea of parallel processing in the case of face perception has already been investigated in relation to Bruce and Young's model of face perception. Previous studies have looked at Bruce and Young's claim that identity and expression are analyzed by independent but parallel processes. The results of many of these studies (for example: Tranel et al., 1988; Young et al., 1993; Haxby et al., 2000) support the Bruce and Young model of face perception, while others (for a review, see Calder and Young, 2005) disputed the independence of these processes (the parallel-contingent model of Schweinberger et al's, 1999 and Martens et al.'s, parallel-dependent model for face recognition, 2010). Despite the fact that we did not investigate differences between identity and emotion, our results with regard to the N250 component support the idea of parallel processing of information that involves generic, image and identity-specific processes in face perception.

The behavioral and electrophysiological correlations showed a generic adaptation effect at 200 ms adaptor duration, for accuracy data, this effect being lateralized to the LH. The behavioral data show a worse performance for Diff ID when compared to the control condition (No). This information, together with the ERP results showing a larger amplitude (more negative) for RS condition (two exact images of same identity) when compared to Diff ID can be explained by the fact that the N250 is involved in processing identity information (see Schweinberger, 2011 for a review). It was found (see Schweinberger, 2011 for a review) that the N250 is larger (more negative) for repetitions of an image depicting the same identity (as is the case with RS). Having a more positive N250 for Diff ID condition that shows two different identities is thus not surprising. Moreover, since this effect is observed for the shortest duration and only in the LH, it could also be explained by the difference in the types of information processed by the two hemispheres. As mentioned before, it is generally believed that the LH processes information in a feature-by-feature manner which could mean that at shorter durations, when deeper processing is impossible in order to ascertain identity, we could rely on feature-based information. Therefore, this could explain why this effect is only apparent at the shortest adaptor duration and is lateralized to the LH.

4.2.5 Meta-analysis Results

The meta-analysis can shed more light on the adaptation-related processes of the two negative ERP components. Whereas the N170 displayed the strongest generic adaptation effect, the N250 showed a stronger identity-specific adaptation when compared to the N170. However, both of these effects were lateralized in opposite hemispheres: the N170 has a stronger generic adaptation effect in the RH when compared to the N250, whereas the N250 has a stronger identity-specific adaptation in the LH when compared to the N170. This suggests that these components may reflect different stages in the processing of faces and that specific types of information are processed differently in the two hemispheres – identity information being specific for the N250 LH, while generic face information being specific for the N170 RH.

4.3 Concluding Remarks

Our results show that the P100, N170, P2 and N250 reflect generic adaptation effects related to face perception (category-specific processes) that are modulated by adaptor duration. Since the experimental paradigm used in our study did not include cross-category adaptor and test image, stronger results showing generic adaptation could be obtained with a cross-category paradigm in future studies. Since Feuerriegel et al. (2015) also found modulating effects of ISI, it would perhaps also be interesting to see if there are any such effects at longer adaptor durations, i.e. whether the ERP components' amplitude is affected differently depending on the duration of the gap between adaptor and test stimuli.

In conclusion, the present study was the first to investigate the relation between systematically varying adaptor duration along a broader interval and the behavioral and neuronal response elicited by the adaptor stimuli. Our results indicate that by varying adaptor duration we can obtain different adaptation effects following different adapting durations, for each of the early face-related ERP components. The P100 and N170 reflect generic adaptation related to face perception, with a modulating effect of adaptor duration on the N170 that shows that generic adaptation takes place after 1200 ms. The P2 displays sensitivity to repetition after 1200 ms, while the N250 displayed generic, image and identity-specific adaptation at specific adaptor durations, showing that the activity of these components is also modulated by adaptor duration. Together these results show that for longer adaptor durations there is a dissociation between generic, image and identity-specific processes. Understanding how quickly our visual system adjusts to the surrounding environment is essential for comprehending the relationship between neuronal events and behavior and this study sheds more light onto face-related adaptation effects.

5. References

1. Ambady, N., Hallahan, M., & Conner, B. (1999). Accuracy of judgments of sexual orientation from thin slices of behavior. *Journal of Personality and Social Psychology 77*, 538-547.
2. Amihai, I., Deouell, L.Y., & Bentin, S. (2011) Neural adaptation is related to face repetition irrespective of identity: a reappraisal of the N170 effect. Experimental *Brain Research 209*, 193 -204.
3. Andrews, T.J., & Schluppeck, D. (2004) Neural responses to Mooney images reveal a modular representation of faces in human visual cortex. *Neuroimage 21(1),* 91-98.
4. Bankó, E.M., Gál, V., Körtvélyes, J., Kovács, G., & Vidnyánszky, Z. (2011) Dissociating the Effect of Noise on Sensory Processing and Overall Decision Difficulty. *The Journal of Neuroscience 31 (7),* 2663-2674.
5. Bednar, J.A. (1997) Tilt Aftereffects in a Self-Organizing Model of the Primary Visual Cortex. PhD thesis. University of Texas at Austin, Austin, USA.
6. Begleiter, H., Porjesz, B., & Wand, W.Y. (1995) Event-related brain potentials differentiate priming and recognition to familiar and unfamiliar faces. *Electroencephalography and Clinical Neurophysiology 94*, 41-49.
7. Berry, D.S. (1991a). Child and adult sensitivity to gender information in patterns of facial motion. *Ecological Psychology 3*, 349-366.
8. Berry, D.S. (1991b). Accuracy in social perception. Contributions of facial and vocal information. *Journal of Personality and Social Psychology 61*, 298-307.
9. Bindemann, M., Burton, A.M., Leuthold, H., & Schweinberger, S.R. (2008) Brain potential correlates of face recognition: Geometric distortions and the N250r brain response to stimulus repetitions. *Psychophysiology 45(4*), 535-544.
10. Borkenau, P., & Liebler, A. (1992). Trait inferences: Sources of validity at zero acquaintance. *Journal of Personality and Social Psychology 62,* 645-657.
11. Brainard, D.H. (1997) The psychophysics toolbox. *Spatial Vision 10*, 433–436.
12. Brédart, S., & French, R.M. (1999) Do babies resemble their fathers more than their mothers? A failure to replicate Christenfeld & Hill (1995). *Evolution and Human Behavior 20,* 129-135.
13. Brooks, B.E., Rosielle, L.J., & Cooper, E.E. (2002) The priming of face recognition after metric transformations. *Perception 3(3),* 297-313.
14. Bruce, V., & Young, A. (1986) Understanding face recognition. *British Journal of Psychology 77,* 305-327.
15. Bujas, Z., Szabo, S., Ajudvić, D., & Mayer, D. (1991) Time course of recovery from gustatory adaptation to NaCl. *Perception and Psychophysics 49(6),* 517-521.
16. Caharel, S., Poiroux, S., & Bernard, C. (2002) ERPs associated with familiarity and degree of familiarity during face recognition. *International Journal of Neuroscience 112*, 1499-1512.
17. Calder, A. J., & Young, A. W. (2005). Understanding the recognition of facial identity and facial expression. *Nature Reviews Neuroscience 6*,641–651.
18. Calder, A.J., Lawrence, A.D., & Young, A.W. (2001) Neuropsychology of fear and loathing. *Nature Reviews Neuroscience 2(5),* 352-363.
19. Calvert, G.A., Bullmore, E.T., Brammer, M.J., et al. (1997) Activation of auditory cortex during silent lipreading. *Science 276 (5312),* 593-596.

20. Carbon, C.C., & Ditye, T. (2011) Sustained effects of adaptation on the perception of familiar faces. *Journal of Experimental Psychology-Human Perception and Performance 37(3)*, 615-625.
21. Carbon, C.C., & Ditye, T. (2012) Face adaptation effects show strong and long-lasting transfer from lab to more ecological contexts. *Frontiers in Perception Science 3*, 1-6
22. Carbon, C.C., Schweinberger, S.R., Kaufmann, J.M., et al. (2005) The Thatcher illusion seen by the brain: an event-related brain potentials study. *Cognitive Brain Research 24(3),* 544-555.
23. Cave, C.B. (1997) Very long-lasting priming in picture naming. *Psychological Science 8(4),* 322-325.
24. Chatrian, G.E., Wirch, A.L., Edwards, K.H., Turella, G.S., Kaufman, M.A., & Snyder, J.M.(1985) Cochlear summating potential to broadband clicks detected from the human external auditory meatus. A study of subjects with normal hearing for age. *Ear and Hearing 6,* 130–138.
25. Chen, C.C., Kao, K.L.C., & Tyler, C.W. (2007) Face configuration processing in the human brain: the role of symmetry. *Cerebral Cortex 17(6),* 1423-1432.
26. Cloutier, J., Heatherton, T.F., Whalen, P.J., & Kelley, W.M. (2008) Are Attractive People Rewarding? Sex Differences in the Neural Substrates of Facial Attractiveness. *Journal of Cognitive Neuroscience 20 (6),* 941-951.
27. Cutting, J.E., & Kozlowski, L.T. (1977). Recognizing friends by their walk: Gait perception without familiarity cues. *Bulletin of the Psychonomic Society 9,* 353-356.
28. Daelli, V., van Rijsbergen, N.J., & Treves, A. (2010) How recent experience affects the perception of ambiguous objects. *Brain Research 1322,* 81-91.
29. Desimone, R. (1996) Neural mechanisms for visual memory and their role in attention. *PNAS 93,* 13494-13499.
30. Desjardins, J., & Segalowitz, S.J. (2009) Deconstructing the P1 and N170 face-effect using independent component analysis, *Psychophysiology 46*, S24.
31. Eagleman, D.M., Jacobson, J.E., & Sejnowski, T.J. (2004) Perceived luminance depends on temporal context. *Nature 428*, 854-856.
32. Eger, E., Schweinberger, S.R., Dolan, R.J., et al. (2005) Familiarity enhances invariance of face representations in human ventral visual cortex: fMRI evidence. *NeuroImage 26(4*), 1128-1139.
33. Eimer, M. (2011) The face-sensitive N170 component of the event-related brain potential. In A. J. Calder, G. Rhodes, M. H. Johnson, J. V. Haxby (eds.), *Oxford Handbook of Face Perception*, Oxford, New York: Oxford University Press, 329-344.
34. Eimer, M., Gosling, A., Nicholas, S., & Kiss, M. (2011) "The N170 component and its links to configural face processing: A rapid neural adaptation study". *Brain Research 1376*, 76-87.
35. Eimer, M., Kiss, M., & Nicholas, S. (2010) "Response Profile of the Face-Sensitive N170 Component: A Rapid Adaptation Study". *Cerebral Cortex 20*, 2442-2452.
36. Engel, S.A. (2005) Adaptation of Oriented and Unoriented Color-Selective Neurons in Human Visual Areas. *Neuron 45*, 613-623.
37. Fairweather, H., Brizzolara, D., Tabossi, P. et al. (1982) Functional cerebral lateralization-dichotomy or plurality. *Cortex 18(1),* 51-65.

38. Feuerriegel, D., Churches, O.F., & Keage, H.A.D. (2015) “Is the neural adaptation of the N170 category-specific? Effects of adaptor stimulus duration and interstimulus interval”, *International Journal of Psychophysiology 96*, 8-15.
39. Fitzgerald, D.A., Angstadt, M. Jelsone, L.M., et al. (2006) Beyond threat: amygdale reactivity across multiple expressions of facial affect. *NeuroImage 30(4),* 1441-1448.
40. Gangestad, S.W., Simpson, J.A., DiGeronimo, K., & Biek, M. (1992). Differential accuracy in person perception across traits: Examination of a functional hypothesis. *Journal of Personality and Social Psychology 62*, 688-698.
41. Gauthier, I., Tarr, M.J., Moylan, J., Skudlarski, P., Gore, J.C., & Anderson, A.W. (2000) The Fusiform Face Area is Part of a Network that Processes Faces at the Individual Level. *Journal of Cognitive Neuroscience 12 (3),* 495-504.
42. Gent, J.F., & McBurney, D.H. (1978) Time course of gustatory adaptation. *Perception and Psychophysics 23(2),* 171-175.
43. Gibson, J.J., & Radner, M. (1937) Adaptation, After-effect and Contrast in the Perception of Tilted Lines. I. Quantitative Studies. Journal of Experimental *Psychology 20(5),* 453-467.
44. Graham, D.W. (2011) "Heraclitus". The Stanford Encyclopedia of Philosophy .Edward N. Zalta (ed.), URL = <http://plato.stanford.edu/archives/sum2011/entries/heraclitus/>.
45. Grill-Spector, K., & Malach, R. (2001) fMR-adaptation: a tool for studying the functional properties of cortical neurons. *Acta Psychologica 107*, 293-321.
46. Grill-Spector, K., Henson, R., & Martin, A. (2006) “Repetition and the brain: neural models of stimulus-specific effects”. *TRENDS in Cognitive Sciences 10 (1),* 14-23.
47. Harris, A., & Nakayama, K. (2007) “Rapid Face-Selective Adaptation of an Early Extrastriate Component in MEG”. *Cerebral Cortex 17,* 63-70.
48. Harris, A., & Nakayama, K. (2008) “Rapid Adaptation of the M170 Response: Importance of Face Parts”. *Cerebral Cortex 18*, 467-476.
49. Haxby, J.V., Hoffman, E.A., & Gobbini, M. I. (2000) The distributed human neural system for face perception. *Trends in Cognitive Sciences 4(6),* 223-233.
50. Henson, R.N.A. (2003) “Neuroimaging Studies of Priming”. Progress in *Neurobiology 70*, 53-81.
51. Henson, R.N.A., & Rugg, M.D. (2003) Neural response suppression, haemodynamic repetition effects, and behavioural priming. *Neuropsychologia 41*, 263-270.
52. Hermann, M.J., Ehlis, A.C., Ellgring, H., & Fallgatter, A.J. (2005) Early stages (P100) of face perception in humans as measured with event-related potentials (ERPs). *Journal of Neural Transmission 112*, 1073-1081.
53. Herrmann, M.J., Ehlis, A.-C., Ellgring, H., & Fallgatter, A.J. (2005a) Early stages (P100) of face perception in humans as measured with event-related potentials (ERPs). *Journal of Neural Transmission 112 (8*), 1073-1081.
54. Herrmann, M.J., Ehlis, A.-C., Muehlberger, A., & Fallgatter, A.J. (2005b) Source Localization of Early Stages of Face Processing. *Brain Topography 18(2),* 77-85.
55. Herzmann, G., Schweinberger, S.R., Sommer, W., & Jentzsch, I. (2004) What’s special about personally familiar faces? A multimodal approach. *Psychophysiology 41*, 688-701.

56. Hills, P.J., Elward, R.L., & Lewis, M.B. (2010) Cross-modal face identity aftereffects and their relation to priming. *Journal of Experimental Psychology Human Perception and Performance 36(4),* 876-891.
57. Hoffman, E.A., & Haxby, J.V. (2000) Distinct representations of eye gaze and identity in the distributed human neural system for face perception. *Nature Neuroscience 3*, 80-84.
58. Hole, G., & Bourne, V. (2010) Face Processing. Psychological, Neuropsychological, and Applied Perspectives. Oxford & New York, Oxford University Press.
59. Ilg, W., Golla, H. Thier, H.P., & Geise, M.A. (2004). Influences of cerebellar diseases on gait – quantification of the spatio-temporal characteristics of walking in cerebellar patients. Unpublished manuscript. Laboratory for Action Representation and Learning, Hertie Center for Clinical Brain Research. University Clinic Tubingen, Germany.
60. Itier, R.J., & Taylor, M.J. (2002) Inversion and contrast polarity reversal affect both encoding and recognition processes of unfamiliar faces: a repetition study using ERPs. *Neuroimage 15(2),* 353-372.
61. Itier, R.J., & Taylor, M.J. (2004a) N170 or N1? Spatiotemporal Differences between Object and Face Processing Using ERPs. *Cerebral Cortex 13*, 132-142.
62. Itier, R.J., & Taylor, M.J. (2004b) Source analysis of the N170 to faces and objects. *NeuroReport 15 (8),* 1261-1265.
63. Jacques, C., & Rossion, B. (2006) The speed of individual face categorization. *Psychological Science 17(6),* 485-492.
64. Jacques, C., & Rossion, B. (2007) Early Electrophysiological Responses to Multiple Face Orientations Correlate with Individual Discrimination Performance in Human. *Neuroimage 36 (3),* 863-876.
65. Jacques, C., d'Arripe, O., & Rossion, B. (2007) The time course of the inversion effect during individual face discrimination. *Journal of Vision 7(8),* 1-9.
66. James, T.W., & Gauthier, I. (2006) Repetition-Induced Changes in BOLD Response Reflect Accumulation of Neural Activity. *Human Brain Mapping 27*, 37-46.
67. Jiang. F., Blanz, V., & O'Toole, A.J. (2006) Probing the visual representation of faces with adaptation- A view from the other side of the mean. *Psychological Science 17(6),* 493-500.
68. Johannes, S., Munte, T.F., Heinze, H.J.,, & Mangun, G.R. (1995) Luminance and spatial attention effects on early visual processing. *Cognitive Brain Research 2*, 189–205.
69. Kadohisa, M., & Wilson, D.A. (2006) Olfactory Cortical Adaptation Facilitates Detection of Odors Against Background. *Journal of Neurophysiology 9,* 1888-1896.
70. Kalick, S.M., Zebrowitz, L.A., Langlois, J.H., & Johnson, R.M. (1998). Does human facial attractiveness honestly advertise health? Longitudinal data on an evolutionary question. *Psychological Science 9*, 8-13.
71. Kant, I. (1781) *Critique of Pure Reason*, translated by Paul Guyer and Allen Wood. Cambridge: Cambridge University Press, 1998.
72. Kanwisher, N., & Yovel, G. (2006) The fusiform face area: a cortical region specialized for the perception of faces. *Philosophical Transcations of the Royal Society of London. Series B, Biological Sciences, 361 (1476),* 2109-2128.

73. Kanwisher, N., McDermott, J., & Chun, M.M. (1997) The fusiform face area: a module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience 17 (1)*, 4302-4311.
74. Kohn, A., & Movshon, J.A. (2003) Neuronal Adaptation to Visual Motion in Area MT of the Macaque. *Neuron 39*, 681-691.
75. Kohn, A., & Movshon, J.A. (2004) Adaptation changes the direction tuning of macaque MT neurons. *Nature Neuroscience 7,* 764-772.
76. Kovács, G., Zimmer, M., Harza, I., & Vidnyánszky, Z. (2007) Adaptation duration affects the spatial selectivity of facial aftereffects. *Vision Research 47 (25).*
77. Kovács. G., Zimmer, M., Bankó, É., Harza, I., Antal, A., & Vidnyánszky, Z. (2005) Position specificity of facial adaptation. *NeuroReport 16 (17).*
78. Kovács. G., Zimmer, M., Bankó, É., Harza, I., Antal, A., & Vidnyánszky, Z. (2006) Electrophysiological Correlates of Visual Adaptation to Faces and Body Parts in Humans. *Cerebral Cortex 16 (5).*
79. Leehey, S.C., Carey, S., Diamond, R., et al. (1978) Upright and inverted faces: the right hemisphere knows the difference. *Cortex 14*, 411-419.
80. Leopold, D.A., O'Toole, A. J., Vetter, T., & Blanz, V. (2001) Prototype-referenced shape encoding revealed by high-level aftereffects. *Nature Neuroscience 4 (1)*, 89-94.
81. Martens, U., Leuthold, H., & Schweinberger, S.R. (2010) Parallel Processing in Face Perception. *Journal of Experimental Psychology: Human Perception and Performance 36 (1),* 103-121.
82. Miller, E.K., & Desimone, R. (1994) Parallel neuronal mechanisms for short-term memory. *Science 263*, 520-522
83. Montepare, J.M., & Zebrowitz-McArthur, L. (1988). Impressions of people created by age related qualities of their gaits. *Journal of Personality and Social Psychology 55,* 547-556.
84. Morris, J.P., Pelphrey, K.A, & McCarthy, G. (2007) Face processing without awareness in the right fusiform gyrus. *Neuropsychologia 45(13),* 3087-3091.
85. Nagy, K., Greenlee, M.W., & Kovács, G. (2012) The lateral occipital cortex in the face perception network: an effective connectivity study. *Frontiers in Psychology 3*, 1-12.
86. Németh, K., Kovács, P., Vakli, P., Kovács, G., & Zimmer, M. (2014) Phase noise reveals early category-specific modulation of the event-related potentials. *Frontiers in Psychology 5*, 1-12.
87. Nemrodov, D., & Itier, R.J. (2011) The role of eyes in early face processing: A rapid adaptation study of the inversion effect. *The British Journal of Psychology 102 (4),* 783-798.
88. Nemrodov, D., & Itier, R.J. (2012) Is the rapid adaptation paradigm too rapid? Implications for face and object processing. *NeuroImage 61,* 812 -822.
89. O'Doherty, J., Winston, J., Critchley, H., Perrett, D., Burt, D.M., & Dolan, R.J. (2003) Beauty in a smile: the role of medial orbitofrontal cortex in facial attractiveness. *Neuropsychologia 41*, 147-155.
90. Okada, K., & Hickok, G. (2009) Two cortical mechanisms support the integration of visual and auditory speech: a hypothesis and preliminary data. *Neuroscience Letters 452 (3)*, 219-223.

91. Olman, C., Boyaci, H., Fang, F., & Doerschner, K.(2008) V1 responses to different types of luminance histogram contrast [Abstract]. *Journal of Vision. 8*, 345a.

92. Oxenham, A. J. (2001) Forward masking: adaptation or integration? *Journal of the Acoustical Society of America 109,* 732-741.

93. Pelli, D.G. (1997) The Video Toolbox software for visual psychophysics: transforming numbers into movies. *Spatial Vision 10*, 437–442.

94. Pfütze E.M., Sommer W., & Schweinberger S.R. (2002). Age-related slowing in face and name recognition: evidence from event-related brain potentials. *Psychology and Aging 17,* 140–160

95. Philiastides, M.G., & Sajda, P. (2007) EEG-informed fMRI reveals spatiotemporal characteristics of perceptual decision making. *Journal of Neuroscience* 27,13082–13091.

96. Pourtois, G., Schwartz, S., Seghier, M.L., et al. (2005) View-independent coding of face identity in frontal and temporal cortices is modulated by familiarity: an event-related fMI study. *Neuroimage 24(4),* 1214-1224.

97. Puce, A., Allison, T., Asgari, M., et al. (!996) Differential sensitivity of human visual cortex to face, letterstrings, and textures: a functional magnetic resonance imaging study. *Journal of Neuroscience 16(6*), 5205-5215.

98. Puce, A., Allison, T., Bentin, S., et al. (1998) Temporal cortex activation in humans viewing eye and mouth movements. *Journal of Neuroscience 18(6),* 2188-2199.

99. Rapaczynski, W., & Ehrlichman, H. (1979) Opposite visual hemifield superiorities in face recognition as a function of cognitive style. *Neuropsychologia 17*, 645-652.

100. Rhodes, G. (1993) Configural coding, expertise, and the right hemisphere advantage for face recognition. *Brain and Cognition 22*, 19-41.

101. Rhodes, G. Jeffery, L., Watson T.L., Clifford, C.W.G., & Nakayama, K. (2003) Fitting the mind to the world: face adaptation and attractiveness aftereffects. *Psychological Science 14 (6).*

102. Rossion, B., Campanella, S., Gomez, C. M., et al. (1999), Task Modulation of Brain Activity Related to Familiar and Unfamiliar Face Processing: an ERP study. *Clinical Neuropsychology 110 (3),* 449-462.

103. Rossion, B., Gauthier, I., Tarr, M.J., Despland, P., Bruyer, R., Linotte, S., & Crommelinck, M. (2000) The N170 occipito-temporal component is delayed and enhanced to inverted faces but not to inverted objects: an electrophysiological account of face-specific processes in the human brain. *Neuroreport 11(1),* 69-74.

104. Rotshtein P., Henson R.N., Treves A., Driver J., & Dolan R.J. (2005) Morphing Marilyn into Maggie dissociates physical and identity face representations in the brain. *Nature Neuroscience 8,*107–113.

105. Schwartz, O., Hsu, A., & Dayan, P. (2007) Space and time in visual context. *Nature Reviews 8*, 522-535.

106. Schweinberger, S. (2011) Covert recognition and the neural system for face processing. In A. J. Calder, G. Rhodes, M. H. Johnson, J. V. Haxby (eds.), *Oxford Handbook of Face Perception*, Oxford, New York: Oxford University Press, 345-366.

107. Schweinberger, S.R., Burton, A.M., & Kelly, S.W. (1999). Asymmetric relationship between identity and emotion perception: Experiments with morphed faces. *Perception & Psychophysics 61*, 1102–1115.

108. Schweinberger, S.R., Kloth, N., & Jenkins, R. (2007) “Are you looking at me? Neural correlates of gaze adaptation”. *NeuroReport 18 (7).*

109. Schweinberger, S.R., Pfütze, E.M., & Sommer, W. (1995) Repetition priming and associative priming of face recognition: evidence from event-related potentials. *Journal of Experimental Psychology, Learning, Memory and Cognition 21,* 722 – 736.

110. Schweinberger, S.R., Pickering, E.C., Burton, A.M., & Kaufmann, J.M. (2002) Human brain potential correlates of repetition priming in face and name recognition. *Neuropsychologia 40*, 2057-2073.

111. Scott, L.S., & Nelson, C.A. (2006) Featural and configural face processing in adults and infants: a behavioral and electrophysiological investigation. *Perception 35 (8),* 1107-1128.

112. Smith, P. (1979) Sex markers in speech. In K.R. Scherer and H. Giles (eds.) *Social markers in speech,* Cambridge: Cambridge University Pres.

113. Stahl, J., Wiese, H., & Schweinberger, S.R. (2008) Expertise and own-race bias in face processing: an event-related potential study. *Neuroreport 19*, 583-587.

114. Stahl, J., Wiese, H., & Schweinberger, S.R. (2010) Learning task affects ERP-correlates of the own-race bias, but not recognition memory performance. *Neuropsychologia 48*, 2027-2040.

115. Sternberg, R.J. (2012) *Cognitive Psychology, 6th Edition*. Belmont: Wadsworth Cengage Learning.

116. Suzuki, S., & Cavanagh, P. (1998) A shape-contrast effect for briefly presented stimuli. *Journal of Experimental Psychology: Human Perception and Performance 24(5),* 1315-1341.

117. Thompson, P. (1980) Margaret Thatcher: a new illusion. *Perception 9*, 483-484.

118. Tong, F., & Nakayama, K. (1999) Robust representations for faces: Evidence from visual search. *Journal of Experimental Psychology: Human Perception and Performance 25(4),* 1016-1035

119. Tranel, D., Damasio, A.R., & Damasio, H. (1988). Intact facial recognition of facial expression, gender and age in patients with impaired recognition of face identity. *Neurology 38*, 690–696.

120. Turk, D.J., Rosenblum, A.C., Gazzaniga, M.S., et al. (2005) Seeing John Malkovich:the neural substrates of person categorization. NeuroImage 24(4), 1147-1153.

121. Wallace, M.T., Roberson, G.E., Hairston, W.D., Stein, B.E., Vaughan, J.W., & Schirillo, J.A. (2004) *Unifying multisensory signals across time and space. Experimental Brain Research 158*, 252-258.

122. Walther, C., Schweinberger, S.R., Kaiser, D., & Kovács, G. (2013) Neural correlates of priming and adaptation in familiar face perception. *Cortex 49*, 1963-1977.

123. Wang, W., Miao, D., & Zhao, L. (2014). Visual MMN elicited by orientation changes of faces. *Journal of Integrative Neuroscience, 13,* 485-495.

124. Webster, M.A., & MacLin O.H. (1999) Figural aftereffects in the perception of faces. *Psychonomic Bulletin & Review 6 (4).*

125. Webster, M.A., Kaping, D., Mizokami, Y., & Duhamel, P. (2004) Adaptation to natural facial categories. *Nature 428.*

126. Wiggs, C.L., & Martin, A. (1998) Properties and mechanisms of perceptual priming. *Current Opinion in Neurobiology 8*, 227-233.
127. Willenbockel, V., Sadr, J., Fiset, D., Horne, G.O., Gosselin, F., & Tanaka, J.W. (2010) Controlling low-level image properties: the SHINE toolbox. *Behavior Research Methods 42*, 671–684.
128. Wong, S., Baltuch, G.H., Jaggi, J.L., & Danish, S.F. (2009) Functional localization and visualization of the subthalamic nucleus from microelectrode recordings acquired during DBS surgery with unsupervised machine learning. *Journal of Neural Engineering 6(2).*
129. Wright, C.I., Martis, B., Schwartz, C.E., et al. (2003) Novelty responses and differential effects of order in the amygdale, substantia innominata, and inferior temporal cortex. *Neuroimage 18(3),* 660-669.
130. Yin, R.K. (1969) Looking at upside-down faces. *Journal of Experimental Psychology 81 (1)*, 141-145.
131. Young, A., Hellawell, D., & Hay, D.C., (1987) Configurational Information in Face Perception. *Perception 16*, 737 -759.
132. Young, A.W., Newcombe, F., de Haan, E.H.F., Small, M., & Hay, D.C. (1993). Face perception after brain injury: Selective impairments affecting identity and expression. *Brain 116*, 941–959.
133. Zebrowitz, L. A., Hall, J.A., Murphy, N.A., & Rhodes, G. (2002) Looking smart and looking good: Facial cues to intelligence and their origins. Personality and Social *Psychology Bulletin 28*, 238-249.
134. Zebrowitz, L.A., & Montepare, J.M. (2006). The ecological approach to person perception: Evolutionary roots and contemporary offshoots. In M. Schaller, J.A. Simpson, & D.T. Kenrick (eds.) *Evolution and Social Psychology*. New York: Psychology Press.
135. Zebrowitz, L.A., & Rhodes, G. (2004) Senitivity to 'bad genes' and the anomalous face overgeneralization effect: Accuracy, cue valiidity and cue utlilization in judging intelligence and health. *Journal of Nonverbal Behavior*, 167-186.
136. Zhao, L., & Chubb, C. (2001) The size-tuning of the face-distortion aftereffect. *Vision Research 41(23),* 2979-2994.
137. Zimmer, M. (2010) The behavioural and electrophysiological aspects of the temporal context of face processing. Phd Thesis, Budapest University of Techonology and Economics, Department of Cognitive Sciences, Psychology Doctoral School, Budapest.
138. Zimmer, M., & Kovács. G. (2011a) Electrophysiological correlates of face distortion after-effects. *The Quarterly Journal of Experimental Psychology 64 (3).*
139. Zimmer, M., & Kovács. G. (2011b) Position specificity of adaptation-related face aftereffects. *Philosophical Transactions of the Royal Society B 366.*

Curriculum Vitae

Personal details:

Family Name: Zbanț

Surname: Adriana

Education and qualifications:

- B.A. in Philosophy (Theoretical Philosophy), University of Bucharest, June 2013.
- Neuroscience Course, University of Medicine and Pharmacology „Carol Davila", March –June 2012.
- *George Coșbuc* Billingual High School, 2010.
- Cambridge Certificate in Advanced English, Grade A, 2009.

Published works:

- Zimmer, M., Zbanț, A., Németh, K., Kovács, G. "Adaptation Duration Dissociates Category-, Image- and Identity-specific Face Processing Steps", Frontiers in Psychology, section Perception Science (in review).
- Zbanț, A. (2015) "Adaptation Duration Dissociates Category- and Image-Specific Processes for Faces". In *Proceedings of the MEi: CogSci Conference 2015,* Ljubljana, Slovenia (forthcoming).
- Zbanț, A. (2014)" Unconscious Processing of Human Faces. A Subcortical Pathway for Disgust?". In *Proceedings of the MEi: CogSci Conference 2014*, Krakow, Poland, p. 110.
- Zbanț, A. (2013) "Can Quantum Mechanics Explain Consciousness? The Limits of Wigner and Stapp's Theories". In Vacariu, G. & Ștefanov, Gh. (eds). *The Mind – Brain Problem In the Neuroscience of Cognition.* Bucharest University Press, 113 -126.
- Zbanț, A. (2012) "Ethical Perspectives on Abortion". In *Morphe –Students' Philosophy Publication (1)*.

Conference Participation:

- *MEi:CogSci Conference*, Ljubljana, June 2015: "Adaptation Duration Dissociates Category- and Image-Specific Processes for Faces".
- *MEi:CogSci Conference*, Krakow, June 2014: "Unconscious Processing of Human Faces. A Subcortical Pathway for Disgust? ".
- *The Mind-Brain Relationship in the Neuroscience of Cognition Symposium,* April 2012, organized by the Department of Theoretical Philosophy at the University of Bucharest: "Schrödinger and Emergence Theories – Searle and Frith".

Other works:

- "Proper Names and Definite Description". In *The Journal of the Department of Theoretical Philosophy, <http://filosofieteoretica.wordpress.com/>,* 2013.
- "Consciousness and Its Place in Nature". *Ibid.* 2012.
- "In Defense of Knowing-How. An Answer to the Critiques of Stanley and Williamson". *Ibid*. 2011.

Awarded Scholarships:

- CEEPUS (CIII – AT -0103), March 2013

Summer Schools Participation:

- *Leibniz and Modern Thought* Summer School, held at Sâmbăta de Sus, organized by University of Craiova, July 2012.
- *Science, Religion and Philosophy* Summer Course, organized by University of Bucharest, September 2011.

Additional information:

- Language skills: Advanced knowlegede of English, Intermediate knowledge of French and Basic knowledge of Spanish.
- Computer Programming Languages: Python.
- Statistical Analysis software knowledge: SPSS, R.
- Electrophysiological Data Recording and Analysis knowledge: Brain Vision Analyzer 1.05.0002, BrainProducts GmbH.