Face adaptation effects: Reviewing the impact of adapting information, time, and transfer

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Abstract (186 words)

The ability to adapt is essential to live and survive in an ever-changing environment such as the human ecosystem. Here we review the literature on adaptation effects of face stimuli to give an overview of existing findings in this area, highlight gaps in its research literature, initiate new directions in face adaptation research and help to design future adaptation studies. Furthermore, this review should lead to better understanding of the processing characteristics as well as the mental representations of face-relevant information. The review systematises studies at a behavioral level in respect of a framework which includes 3 dimensions representing the major characteristics of studies in this field of research. These dimensions comprise (1) the specificity of adapting face information, e.g. identity, gender or age aspects of the material to be adapted to, (2) aspects of timing (e.g., the sustainability of adaptation effects), and (3) transfer relations between face images presented during adaptation and adaptation tests (e.g., images of the same or different identities). The review concludes with options for how to combine findings across different dimensions to demonstrate the relevance of our framework for future studies.

Face adaptation effects:

Reviewing the impact of adapting information, time, and transfer

The term *adaptation* refers to the ability to adjust to novel information and experiences. This ability to adapt is essential for living and surviving in an ever-changing environment such as the human ecosystem (Carbon & Ditye, 2012). Visual adaptation in particular is an effect of the processes by which the visual system encodes and represents information, and includes a process by which the visual system (passively or actively) alters its function in response to the lack of fit between mental representations and perceived objects (e.g., Clifford & Rhodes, 2005; Clifford, Wenderoth, & Spehar, 2000). Such responses result in adaptation effects. In experimental situations, such adaptation effects are typically assessed in an adaptation test phase after an adaptation phase. Intensive investigations of these adaptation effects provides an excellent opportunity for an exploration and deeper understanding of the processing architecture as well as the representation of particular stimuli (Li, Tzen, Yadgarova, & Zaidi, 2008; Webster, 2011).

The present paper includes a systematic review about the literature on adaptation effects of face stimuli[1]:

Please, insert Footnote 1 here.

Which areas does this review on face adaptation cover and which areas does it negotiate? This review focuses on empirical studies that investigate face adaptation effects on a behavioral level; this is typically realised by an overt categorisation of face stimuli in a test phase. In fact, we focus on adaptation under optimal conditions in a fully developed and (more or less) optimally functioning cognitive system; i.e. we review findings of studies typically investigating adaptation effects in younger adults possessing face recognition skills that are

particularly impressive, for instance the fact that normal persons can discriminate thousands of faces (Jeffery & Rhodes, 2011) when they reach so-called "face expertise" (Schwaninger, Carbon, & Leder, 2003). This focus on complex objects of the face category is realised in an exclusive and extensive way; that is, we do not relate findings in the area of face adaptation effects to other visual coding mechanisms such as colour coding as realised in previous work (Webster, 2011; Webster & MacLeod, 2011). By reviewing face issues exclusively, we assume to provide the main aim of this review most efficiently: we aim to clearly highlight and systematise existing findings as well as gaps in the research literature in the area of face adaptation effects. This systematisation should stimulate new directions in face adaptation research and help to design future adaptation studies. In contrast to what we provide, we do not include results about the adaptation of neural processes to face stimuli: for instance, studies on modulations of the N170 as a result of prior adaptation (e.g., Kloth, Schweinberger, & Kovács, 2010; Kovács et al., 2006) as questions regarding this area of research refer to further dimensions and use different theoretical frameworks, mostly based on specific brain processes and structures. In addition, we omit research from developmental and evolutionary perspectives on face adaptation effects as they were already the major aim of recent alternative review papers (Jeffery & Rhodes, 2011; Leopold & Rhodes, 2010).

We start this review by presenting a framework that enables a systematic organisation of findings in the field of face adaptation effects. This framework includes dimensions representing the major characteristics of studies (i.e., experimental manipulations) or operational parameters in this field. As discussed in detail in a later section, the dimensions enable a categorisation of the (1) various adapting face information, (2) timing characteristics of adaptation effects (e.g., the delay between adaptation and adaptation test phases), and (3) transfer relations between face images presented during these phases (e.g., images of the same or different identities). In the main section of the present review, we discuss the research literature specifically towards each of the framework's dimensions. Finally, we present

options for how to combine findings across different dimensions to demonstrate the relevance of our framework for future studies.

Investigations on adaptation effects in faces are very relevant for the progress of cognitive research, since these effects offer a window into the processes and dynamics of highly complex object processing. First of all, faces are arguably the most important social stimuli since they are the primary means by which we perceive identity information, emotional information etc. (see below). This expertise and its investigation in adaptation effects provide an essential tool or window for dissecting different levels of neural code and the visual pathway in face processing. This latter fact is also the motivation for a close look at timing and additionally the transfer characteristics of adaptation effects in faces. As research on adaptation effects in faces is moreover a broad and elaborated field today, represented by a great number of adaptation studies employing different procedures and aiming at different research questions, this research field also offers an excellent opportunity for taking a more general perspective on the found effects in the form of a review.

Framework to conceptualise research on face adaptation effects

As illustrated in Figure 1, we integrate findings in the field of face adaptation research into a conceptual framework that includes three dimensions. The first dimension of this framework represents different types of potential facial information which are susceptible to adaptation; we call this dimension *adapting information*. Instances of adapting information are identity information (e.g., Jiang, Blanz, & O'Toole, 2006; Leopold, O'Toole, Vetter, & Blanz, 2001), configural information (e.g., Carbon, Strobach et al., 2007; Little, DeBruine, Jones, & Waitt, 2008), gaze information (e.g., Jenkins, Beaver, & Calder, 2006), emotional information (e.g., Adams, Gray, Garner, & Graf, 2010; Ng, Boynton, & Fine, 2008; Webster, Kaping, Mizokami, & Duhamel, 2004), age information (e.g., Schweinberger et al., 2010), gender information (e.g., Bestelmeyer et al., 2008; Kovács, Zimmer, Harza, & Vidnyánszky, 2007), ethnicity information (e.g., Jaquet, Rhodes, & Hayward, 2008; Ng et al., 2008),

attractiveness information (e.g., Anzures, Mondloch, & Lackner, 2009), or viewpoint information (e.g., Chen, Yang, Wang, & Fang, 2010). The present list of adapting information is completed by face information investigated in the context of face distortion after-effects (FDAEs; e.g., Webster & MacLin, 1999). This method of manipulating faces may affect types of facial information that are listed above (e.g., configural information, age, identity, gender; please see also later sections). However, FDAEs are realised by unique manipulation algorithms (i.e., distortions by expanding or contracting the frontal-view original face image relative to a midpoint on the nose). Further, these algorithms relax the controlling of which specific information types are affected. For example, manipulating faces in the context of FDAEs affect facial features (e.g., eyes, mouth etc.) while manipulations of configural information (i.e., spatial distances between these features) rather leave these features unaffected. Generally, these different types of instances of adapting information realise different levels of ecological validity. While differences in age, viewpoint, gaze, or emotion are plausible and realistic in an ecological context, manipulations of identity or configural information have less validity since such changes do not typically occur in the ecosystem.

The second dimension of the present framework, *time*, orders adaptation effects according to different types of temporal information. The first information type, *delay,* is related to the robustness and sustainability of adaptation effects; basically, the time interval between an adaptation and an adaptation test phase. Delays range from milliseconds (e.g., Leopold et al., 2001; Rhodes, Jeffery, Watson, Clifford, & Nakayama, 2003) to minutes (e.g., Carbon & Leder, 2006; Kloth & Schweinberger, 2008), but also include days and even weeks under typical laboratory (e.g., Carbon & Ditye, 2011; Carbon, Strobach et al., 2007) as well as ecologically more valid test contexts (Carbon & Ditye, 2012). The delay characteristics of adaptation effects are essential for providing useful information about the decay of adaptation effects and thus the "re-calibration" and "re-adaptation" abilities of the visual system (Carbon & Ditye, 2011). Furthermore, they allow inferences about the robustness and consistency of

perceptual information in general. In parallel to the "time" information *delay,* we focus on *adaptation duration*, the time span during which the adapting stimulus is presented (e.g., Strobach, Ditye, & Carbon, 2011). Adaptation duration information provides insights into how this time span can modulate the adaptation effect size or the adaptability of faces. Moreover, this type of time information was compared with simple adaptation effects (e.g., with tilt information; Leopold, Rhodes, Müller, & Jeffery, 2005; Rhodes, Jeffery, Clifford, & Leopold, 2007) to explore the dynamics of adaptation effects at different levels of cortical visual hierarchy. Finally, we focus on "time" information of the *test duration* type, establishing the time span during which the test stimulus is presented (e.g., Rhodes et al., 2007). Similar to the adaptation duration, test duration can give insights into to the dynamics of adaptation in face stimuli in contrast to simple adaptation effects.

The third dimension in the present framework is associated with the transfer of adaptation effects. This *transfer* dimension reflects the range and limits of adaptation transfer effects providing important inferences about the nature of processing being linked with specific adapted stimuli or being of more general quality. In this way, the investigation of adaptation is a tool (rather than a topic) for localising the plasticity and pointing out common coding principles of various levels of visual processing (from retinotopic to high and possibly face-specific levels of visual processing; Webster, 2011; Webster & MacLeod, 2011). There exists two systems of structuring transfer effects: Transferring between different (manipulated) image versions of the identical identity during adaptation and test phases (e.g., variations in size or orientation) enables exclusive low-level perceptual effects of adaptation (e.g., on a retinal level; Zhao & Chubb, 2001) to be excluded. Additionally, as proposed by Carbon et al. (2007), adaptation transfer can be systematically tested with face images used in the adaptation and test phases showing the same images of the same identity vs. different images of the same identity vs. different images of different identities.[2]

Please, insert Footnote 2 here.

The approach can be extended by investigating transfer effects, inter alia, across family members, gender, and/ or ethnicity.

As will be seen later, not all studies in the field of face adaptation research allow a localisation of its research in all dimensions of the applied framework. For example, many studies apply sets of face images of different identities during adaption and the identical set of images during a following test phase (e.g., Buckingham et al., 2006; Chen et al., 2010). Such a procedure prevents conclusions about the transferability of adaptation effects, since potential effects in an adaptation test phase may originate from the presentation of the identical image and / or the presentation of other identities' images during the adaptation phase.

Please, insert Figure 1 here.

Investigating the adaptation effects of different types of face information – the adapting information dimension

Basically, the result patterns in studies on adaptation effects showed an *adaptation bias* and were thus consistent in the following way: values of adaptation test ratings tend towards the (typically extreme) values of adapting information presented during the adaptation phase; in other words, average or neutral faces are perceptually biased away from the adapting face. After introducing findings in the context of FDAEs, we show findings of facial information loosely ordered with increasing abstractedness.

FDAEs: Webster and MacLin (1999) investigated FDAEs within face images of a single identity by presenting adaptation images that were distorted by expanding or contracting the frontal-view original face image relative to a midpoint on the nose. After viewing distorted faces during adaptation (e.g., contracted face images), original faces appear distorted in the direction opposite to the distraction (e.g., expanded face images). In contrast to this effect after adaptations to distorted faces, no such adaptation effect followed the presentation of original face images (i.e., distorted faces still appeared distorted). In this way, Webster and MacLin provided among the first evidence for adaptation effects in complex, natural objects, suggesting that adaptation may play an important normalising role in face perception and adaptation effects may strongly influence form perception (see also Burkhardt et al., 2010; Hills, Holland, & Lewis, 2010; Jaquet & Rhodes, 2008; Jaquet, Rhodes, & Hayward, 2007; Jaquet et al., 2008; Jeffery, Rhodes, & Busey, 2006, 2007; Morikawa, 2005; Robbins, McKone, & Edwards, 2007; Yamashita, Hardy, De Valois, & Webster, 2005; Zhao & Chubb, 2001); such a "complex" adaptation phenomenon was recently transferred to animals, trees, or every-day objects (e.g., light bulb; Daelli, van Rijsbergen, & Treves, 2010).

However, the FDAE enables no specification of which types of facial information are precisely involved in face adaptation. For example, the usage of FDAEs simultaneously affects feature information such as mouth, eyes, or eyebrows (e.g., Cabeza & Kato, 2000; Tanaka & Sengco, 1997), configural information such as nose-mouth distance (Leder & Carbon, 2006; Rhodes, 1988; Young, Hellawell, & Hay, 1987), as well as holistic information referring to face processing "as a whole" (e.g., Leder & Carbon, 2005; Tanaka & Farah, 1993). As a consequence, it is essential to systematically vary distinct face information between adaptation and test phases in order to generate precise conclusions about the mechanisms of face adaptation effects, a fact that is not necessarily granted in the context of FDAEs.

Configural information: Carbon and colleagues (Carbon & Ditye, 2011; Carbon & Leder, 2005; Carbon, Strobach et al., 2007; Strobach et al., 2011) aimed instead at investigating adaptation effects of distorted configural information on subsequent adaptation tests. Participants were either presented face images during adaptation of familiar identities with decreased eyes-mouth distance or face images with increased eyes-mouth distance relative to the original. In a subsequent test phase participants were asked to select the veridical version (1) out of a series of versions of gradually altered eyes-mouth distances, or (2) from one original and one slightly altered version (e.g., slightly decreased or increased eyes-mouth distance). The results showed a bias in participants' selections in the direction of the respective manipulations, e.g. after viewing face images with extremely decreased eyes-mouth distance there was an increased likelihood of selecting a version with slightly decreased distances (for similar results with exclusive shifting the eyes in the vertical axis see Walton & Hills, 2012). Thus, these studies demonstrated adaptation effects of configural information. Similar results are demonstrated by Little and colleagues (Little, DeBruine, & Jones, 2005; Little et al., 2008) following the inspection of manipulated eyes-spacing: Inspecting faces with extreme narrow or wide eye distances resulted in increased normality rating for subsequently presented face images with moderately manipulated distances. These latter findings demonstrate the generalisation of adaptation effects after exposure to manipulated configural information.

Gaze and viewpoint information: Adaptation to a consistent leftward or rightward gaze produces ratings that demonstrate an elimination of observers' perception of the gaze in the adapted direction (Jenkins et al., 2006; Schweinberger, Kloth, & Jenkins, 2007). That is, a gaze to the adapted side was subsequently seen as pointing straight. Leftward and rightward viewpoint adaptation resulted in similar adaptation effects (Chen et al., 2010; Fang, Ijichi, & He, 2007); thus, a face turned to the adapted side was subsequently seen as pointing straight. Again, these effects can be interpreted as a re-calibration mechanism: probably the best

heuristic to use if one constantly lacks a straight viewpoint is to retune the processing of gaze direction or viewpoint.

Emotional and attractiveness information: Another example for testing adaptation effects is represented by investigations on the effects of different facial expressions. For instance, after perceiving a happy face, a previously ambiguous happy-angry face appeared distinctly angry, and thus the boundary between happy and angry faces was shifted towards the happy expression (Fox & Barton, 2007; Juricevic & Webster, 2012; Webster et al., 2004). Such shifted emotion categorisation was even evident with adapting stimuli having been suppressed from awareness (Adams et al., 2010; Benton & Burgess, 2008) illustrating the fast and automatic processing of such expressions. Attractiveness adaptation effects demonstrated that viewing consistently distorted faces shifts attractiveness preferences toward the adapting stimuli; for instance, contracted face images (Webster & MacLin, 1999) appeared more attractive after adapting to contracted faces than after adapting to expanded faces (Anzures et al., 2009; Carbon, Leder, & Ditye, 2007; MacLin & Webster, 2001; Rhodes et al., 2003). Similarly, faces with left-right asymmetries appeared more attractive when asymmetrical faces were presented during adaptation (Rhodes, Louw, & Evangelista, 2009).

Gender information: Adaptation to either masculine or feminine faces increases preferences for novel faces that are (gender-wise) similar to those that were recently seen (Buckingham et al., 2006), as well as increasing the femininity and masculinity ratings of test faces, respectively (see also Kovács et al., 2007; Ng et al., 2008; 2006; Webster et al., 2004). An alternative measurement of gender adaptation effects demonstrated that adapting to a male/ female face selectively enhances discrimination for male/ female faces (Yang, Shen, Chen, & Fang, 2011).

Age and ethnicity information: When participants viewed young or old adult faces (i.e, adults of different ages), their "young/ old boundary" was biased towards the age of the adapting face (O'Neil & Webster, 2011). Consistently, test faces appeared older or younger

when the adapting faces were young or old, respectively (Schweinberger et al., 2010).

Therefore, there is evidence for an adaptation bias for facial age as well (see also Lai, Oruc, & Barton, 2012). An analogue bias also exists for face ethnicity, exemplarily shown for Caucasian vs. Asian faces: Adaptation to an average Asian or Caucasian face reduced identification thresholds for faces from the adapted relative to the unadapted ethnicity (Rhodes, Watson, Jeffery, & Clifford, 2010; Webster et al., 2004).

Identity information: Leopold et al. (2001) provided evidence for increased sensitivity for particular face identities after adaptation, as investigated in the context of face identity aftereffects (FIAEs). Based on the ideas of a "face space" (e.g., a multidimensional representation of faces as their distance to a prototypical "center" face, Valentine, 2001), the authors were able to explain the effect in the theoretical framework of a computationally derived mental representation (Figure 2). After perceiving an "anti-face" (located opposite an original face of an identity, on a trajectory crossing this original face and a face-space average), adaptation specifically shifted perception along a trajectory passing through the adapting anti-face and average face away from the original face, selectively facilitating recognition of a test face lying on this trajectory. Such adaptation effects on the identity level were replicated in a number of studies and variations (Anderson & Wilson, 2005; Hurlbert, 2001; Leopold et al., 2005; Palermo, Rivolta, Wilson, & Jeffery, 2011; Rhodes, Evangelista, & Jeffery, 2009; Rhodes et al., 2011; Rhodes & Jeffery, 2006; Rhodes et al., 2010) and are often explicitly referred to as changes of the face space.

In sum, this section demonstrates adaptation effects of numerous facial attributes. To our knowledge there are no attributes that don't show any such effects in the research literature, which indicates that adult face coding systems are more flexible than was previously thought (Bruce, 1994). At this point it is essential to stress again, that the class of faces is the only object class that allows investigating and reviewing this large number of information types.

Please, insert Figure 2 & Table 1 here.

Investigating temporal characteristics of adaptation effects – the time dimension

Delay

Face adaptation effects are typically tested with a delay interval of only a few seconds or even less (Benton & Burgess, 2008; Bestelmeyer et al., 2008; Carbon & Ditye, 2011; Leopold et al., 2001; Rhodes et al., 2003; Webster & MacLin, 1999). Given these constraints, the studies mainly show that (A) adapting face information such as face identity occurs on a perceptual level, and (B) there is no recalibration of the visual system after this delay. In sum, they allow conclusions about neither adaptation effects on the representational level nor on the robustness of visual system recalibration. One of the first systematic investigations of adaptation effects and their delay characteristics focused on gaze information (Kloth & Schweinberger, 2008); Table 2 gives an overview of studies testing adaptation effects with short and long delays. This study demonstrated a decrease in the gaze adaptation effect over time but this effect was still measureable up to 385 s after the end of the adaptation phase. This is evidence for the idea that adaptation effects are not completely perceptually-based. Also it suggests that there is no complete "return to normal" ("recalibration", see Carbon & Ditye, 2011) of the visual system, associated to gaze processing, within this time range of more than six minutes. Consequently, adaptation effects are "stickier" than many of the traditional low level adaptation effects (e.g., Köhler & Wallach, 1944) and can be initially interpreted as evidence of representation-based effects.

Carbon and colleagues systematically extended research on effects of adaptation to manipulated configural information of famous faces. These studies demonstrated adaptation effects after five minutes (Carbon & Leder, 2005; Carbon, Strobach et al., 2007; Strobach et

al., 2011), 80 min (Carbon & Leder, 2006), 24 hours (Carbon & Ditye, 2011; Carbon, Strobach et al., 2007; Strobach et al., 2011), and even one week (Carbon & Ditye, 2011). Therefore, adaptation seems to be very robust and refers to effects on the functional level of representations. According to Carbon et al.'s research, it takes at least one week for the visual system to return to its original state before adaptation (i.e., to recalibrate to its pre-adaptation state), at least in terms of adaptation effects for configural facial information.

To sum up, regarding the delay dimension, a series of recent experiments revealed relatively long-lasting adaptation effects. This evidence is related to face attributes of gaze information (Kloth & Schweinberger, 2007), and configural information (e.g., Carbon et al., 2007). It illustrates aspects of face processing that are related to an increased participation of representations and do not only rely on simple iconic traces or simple visual aftereffects (Carbon et al., 2007). To learn about mental representations, these findings of long-lasting adaptation effects demonstrate that the investigated types of facial information (i.e., gaze information, configural information) are not exclusively processed and coded at a perceptual level. One may speculate that such processing and coding involves long-term memory functions. However, there are no investigations of "delay" effects on facial information aspects of age, attractiveness, emotion, ethnicity, gender, FIAEs or viewpoint information. Such investigations are essential to assess the functional level (representation level and/ or perceptual level), the robustness / sustainability and the time needed for recalibrations of adaptation effects of these types of information. We will come back to this immense gap in the adaptation literature in a later section.

Please, insert Table 2 here.

Adaptation duration

The increase in the time interval for presenting visual adaptation material typically results in an increase of simple perceptual adaptation effects demonstrating the adaptability of tilt, motion or shape information (Rhodes et al., 2007). In fact, this relation is characterised by a logarithmic function between adaptation duration and effect size. A comparable relation was found in faces. Rhodes, Leopold, Jeffery and colleagues (Leopold et al., 2005; Rhodes et al., 2007) tested the FDAEs as well as FIAEs after varying presentation times of adapting face stimuli; in fact, test stimuli appeared immediately after adaptation material was presented between 1,000 and 16,000 ms. Independent of size relations between adaptation and test faces, FDAEs and FIAEs increased with adaptation time. The relationship between adaptation duration and effect is thus comparable in simple perceptual information as well as complex face objects, illustrating common coding principles at different levels of cortical visual hierarchy.

There were however no, or very short, time delays between adaptation and test phases in these prior studies (Leopold et al., 2005; Rhodes et al., 2007) and thus it is likely that adaptation effects were investigated at the perceptual level only. In contrast, Carbon et al (2007) introduced delays of 5 min to 24 h between these phases, allowing investigation of the effects of adaptation delay on the adaptation of memory face representations (in this case, the adapting information was configural information). On the basis of this argument, Strobach, Ditye, and Carbon (2011) performed multiple regression analyses on the individual adaptation duration and their adaptation effects after both 5 min and 24 h. Positive relations between both measures (i.e., longer presentation times of adaptation faces resulted in increased adaptation effects) demonstrated an impact of the adaptation time on the effect size, extending findings on the perceptual level to findings demonstrating mechanisms instead on a memory level.

There is a lack of studies that explicitly investigate the effects of adaptation time for facial attributes other than FDAEs, FIAEs, and configural information – e.g. for age, gender, and attractiveness. Such investigations would provide elaborated knowledge about the coding principles of face-specific and simple visual information.

Test duration

Similarly to changes in the magnitude of adaptation effects following variability in adaptation duration, the time span of presenting a test stimulus modulates the magnitude of these effects (Leopold et al., 2005; Rhodes et al., 2007). In fact, test faces were presented for 100, 200, 400, 800, or 1,600 ms and the adaptation effects, as measured in paradigms of FDAEs and FIAEs, reduced with increasing test time. Since similar effects are evident with simple after-effects, face and simple perceptual information (i.e., tilt, orientation) illustrate common coding principles at different levels of cortical visual hierarchy. However, what is clearly lacking in this domain is research on the question of whether the test duration has an effect when adaptation effects are tested on a memory rather than on a perceptual level. That is to say, it is an open issue in the literature whether the negative relation of test duration and adaptation effect (e.g., increasing test duration and decreasing adaptation effects) is evident after a delay of minutes, hours, or days. Furthermore, this negative relationship was established for FDAEs and FIAEs. However, it is lacking for alternative facial information and such tests should be attempted in future studies. They are essential to establish a more elaborate knowledge of the coding principles of face-specific types of information.

Investigating the transferability of adaptation effects – the transfer dimension

After reviewing adaptation effects of different face information and time characteristics (e.g., the sustainability of adaptation effects), it is essential to review the relationship between the adapting and test face images; i.e., to test transfers of adaptation effects to new face images (or new image versions) not presented during adaptation. Here, we review findings that investigated transfer effects between the same image of one identity

(identical images or images differing in viewpoint, orientation or size between adapting and test images) and different images of the same identity. Additionally, we also discuss adaptation transfer effects between images of different identities. As illustrated in Table 3, we test these transfer effects at the *pictorial level* (identical face image during adaptation and test), *identity level* (different face images of the same identity during adaptation and test), and *novel level* (different face images of different identities during adaptation and test, Carbon & Ditye, 2011). In the following section, we primarily discuss types of adapting face information that demonstrate transfer effects. We followed this strategy because, for the remaining types of face information (e.g., gaze, emotion), there was (A) no investigation of transfer effects and/ or (B) no conclusive evidence for such effects.

Please, insert Table 3 here.

When focusing on FIAEs, Hole (2011) demonstrated adaptation effects with identical face images during adaptation and testing which also transfer onto new image versions changed in viewpoints, orientation, and vertically stretched versions from the adapting face images when using familiar; this confirmed Jiang et al.'s (2006) finding of viewpoint invariance of FIAEs who also added evidence of their transfers across shape and surface reflectance information. Anderson and Wilson (2005) supported Hole's finding of size independent transfer with unfamiliar, synthetic faces while their study provided no support of a viewpoint-invariant FIAE for this face type. Guo et al. (2009) revealed limits to the transferability of the FIAEs by showing that this effect exclusively works from upright to inverted orientation, but not vice versa with unfamiliar faces. With familiar faces, however, Hole showed that the FIAE produced by inverted adaptation faces and upright test faces was similar to that produced by upright adapting faces. Furthermore, this type of adaptation effect

seems to be gender-specific since there is an effect from adaptation to test faces when these faces are related via a gender-specific prototype, whereas there was no such effect with an androgynous face (i.e., combined male and female prototype; Rhodes et al., 2011). Leopold and colleagues (Leopold et al., 2001, 2005) showed that relations between a facial prototype and the individual faces in face space could be manipulated by face adaptations of different identities. In other words, this manipulation includes face images during adaptation that are not located on a trajectory crossing an original face and a face-space average (similar to Figure 1); thus, there is evidence for FIAEs on the *novel level*. This conclusion is consistent with the fact that FIAEs are rather high-level perceptual effects: composite faces (different views of a composite face comprised of the top half of a famous face and the bottom half of a non-famous face) either did or did not produce a FIAE depending on whether or not the famous face is explicitly recognized before the post-adaptation test phase (Laurence & Hole, 2012).

Conversely, adaptation to facial expressions (i.e., emotional information) was partly independent from the represented identities. That is, adaptation effects with a focus on facial expressions were transferred to different faces and thus include at least portions of novel-level processing (Fox & Barton, 2007). Interestingly, the above discussed FIAE is not affected by expressional information. That is, FIAEs were not modulated by congruency of facial expression during adaptation and test phases (i.e., same expression vs. different expression; Fox, Oruc, & Barton, 2008). Thus, expressional adaptation and FIAEs tend towards asymmetry with impact of identity information on expression adaptation, but there is no reverse effect.

For facial gender, Yang et al. (2005, 2011) demonstrated that gender discrimination enhancement induced by face adaptation can transfer across a substantial change in three-dimensional facial orientation. Additionally, gender-adaptation effects are position invariant effects (Kovács et al., 2007). These effects also seem to be age-independent, since Barrett and

O'Toole (2009) demonstrated an effect of gender adaptation within sets of children's and adults' faces and also between these sets of faces. These age-independent effects also demonstrate that gender adaptation effects may work on a *novel level* since adaptation and test faces were derived from different identities. However, this novel level is limited to the orientation of faces; that is, adaptation effects work independently with upright and inverted face presentations (Watson & Clifford, 2006). Alternatively, the limitation of emotion adaptation effects is set at race boundaries: Adapting to one type of emotion in, for instance, a Caucasian face, affects the later processing of an alternative Caucasian face but not that of an alternative ethnicity (i.e., black faces; Otten & Banaji, 2012).

The adaptation effect realised in the form of viewpoint adaptation (i.e., adaptation to left or right-turned faces) occurs at the *novel level* as demonstrated by transfer effects across different identities, different gender, and different vertical orientations (Fang et al., 2007). In the case of face normality ratings and their adaptation effects, there exists evidence for at least orientation-transferable adaptation effects, i.e. between upright and inverted orientations of face images (Rhodes et al., 2003).

Transfer effects of adapting configural information are not only in action at the *pictorial* and *identity* levels, but also at the *novel* level (i.e., different face images of different identities during adaptation and test; Carbon & Ditye, 2011; Carbon, Strobach et al., 2007); even though the effect was slightly reduced compared with pictorial and identity conditions. This was demonstrated by the transfer effects of adapting configural information in combinations of identical adaptation and test facial images, of different adaptation and test facial images from the same identity and transfers to new identities, i.e. transfers to test face images of identities not presented during prior adaptation (Walton & Hills, 2012, for comparable results with exclusive eyes shifts in the vertical axis). Little et al. (2008) assumed that such transfer effects are gender-specific. FDAEs are not transferable to images mirrored after the adaptation phase (Morikawa, 2005), but there is evidence of the transfer of such

effects to different ethnicities (Jaquet et al., 2007), between different viewpoints (Jeffery et al., 2006, 2007), different orientations of upright and inverted faces (e.g., adapting face is oriented 45° from vertically upright and the test face 45° in the opposite direction; Watson & Clifford, 2003) between different identities and orientations (Webster & MacLin, 1999) as well as different facial image sizes (Yamashita et al., 2005; Zhao & Chubb, 2001). Consequently, FDAEs occur up to the *novel level*. Consistently, adaptation effects of facial age on a *novel level* are demonstrated by transfers between different genders (O'Neil & Webster, 2011) and identities (Schweinberger et al., 2010).

In sum, there is clear evidence for adaptation effects across different identities for a first set of face information (e.g., gender, age, configural information), i.e. transfer effects on a *novel level*. Adaptation of this set of information seems to affect the high-order visual system and/ or memory representations. In contrast to these transferable adaptation effects, there is no clear evidence of transfer effects for other face information, such as attractiveness. Furthermore, there is evidence that some face information is only transferable between different identities when the specific subgroups are not changed simultaneously (e.g., FDAE transfers are gender-specific). To learn about processing characteristics and mental representations of faces, this section indicates that face coding is hierarchically structured with an orchestration of common underlying structures. This common structure was demonstrated at the novel level and maybe theoretically represented in a prototype in face space (Valentine, 2001). However, the processing of some facial aspects is characterised by and related to specific modules (e.g., gender-specific modules of FDAEs) potentially working in parallel to a general face space prototype.

Future investigations of face adaptation effects

A summarizing overview of existing and lacking research in the field of face adaptation effects is illustrated in Table 4. Future studies may apply the present framework's dimensions or operational parameters (adapting information, time, and transfer) for a

systematic continuation of investigating face adaptation effects. For instance, for a number of adapting information types (e.g., emotion, age, attractiveness, gender) there exists no test for the robustness of adaptation effects; that is, adaptation effects of these types of face information are demonstrated after short delays between adaptation and adaptation test phases. However, there are no studies that test these adaptation effects after long delays and their decay over time. To present one specific example, in accordance with time intervals applied by Carbon and colleagues (Carbon & Ditye, 2011; Carbon, Strobach et al., 2007), the adaptation effect of facial age should be tested after time intervals of five minutes, 24 hours and one week in order to cover a broad range of time periods and to test the robustness of the age adaptation effect. Likewise, testing the impact of adaptation and test time should be extended to forms of facial information beyond phenomena investigated in the context of FDAEs (Leopold et al., 2005; Rhodes et al., 2007). As illustrated, a first extension of investigations on adaptation time occurs in the context of adaptation of configural information (Strobach et al., 2011), but other contexts are definitely needed to generate a broader picture of timing aspects in face adaptation. In this way, our framework is able to characterise gaps in the adaptation research literature while combining findings along the dimension adaptation information and delay.

Please, insert Table 4 here.

Similarly, such an expansion of tests should also be performed on the transfer dimension since this type of test is essential for investigating the functional level of adaptation effects and increasing the ecological validity of these studies. While transfer tests on the same face image of the same identity (e.g., varying orientation or context during adaptation and test; Carbon & Ditye, 2012) enable investigations on picture or "iconic" processing (Carbon, 2008), and thus not necessarily on face processing per se, transfer tests on different face

images of the same identity as well as different identities' face images allow for conclusions about the characteristics of face representations. So far, these two types of transfer tests (i.e., (1) different face images of the same identity, (2) different face images of different identities) were separately conducted in most studies. Future studies may combine these two transfer types.

An additional way to continue face adaptation research, in terms of gaining knowledge on the basis of adaptation effects, is to combine aspects (i.e., our framework's dimensions) of time and transfer. For instance, future studies should systemically investigate the effects of manipulating face information across different delays between adaptation and test phases, combined with tests for the different transfer levels between adaptation and test faces. Additionally, the effects of gender adaptation can be investigated after relatively short and long delays between faces of the same or different age groups, ethnicities or gaze points. A related investigation focused on transfer effects between different emotional expressions and gender in the context of FDAEs (Tillman & Webster, 2012). This systematic investigation of the interplay of delay and transfer may provide conclusions about the range of adaptation effects and their origin from similar or different methods of neural coding.

Additionally, future studies should relate investigations on the functional level of face adaptation effects to concepts applied to other types of processes or skills. One option might be in relation to improved skills acquired during cognitive training (e.g., working memory training) and their range of transferability. Existing studies on this issue (Karbach & Kray, 2009; S.-C. Li et al., 2008; Strobach, Frensch, & Schubert, 2012; Strobach, Frensch, Soutschek, & Schubert, 2012) categorise the range of skill transfer into near transfer (transfer between situations with common basic characteristics) and far transfer (transfer between situations with structural differences). Conversely, near transfer tests could investigate the adaptation effects of facial images on other facial images, while far transfer tests investigate adaptation effects on facial images after prior adaptation to specific properties of cars

(Carbon, 2010) or adaptations to mental sets due to the presentation of gender-typical objects (e.g., lipstick vs. motor bike, Javadi & Wee, 2012). For instance, one could test whether there is a transfer of adaptation effects of configural information (i.e., spatial relations between features) from face stimuli to car stimuli (i.e., far transfer). In particular, front views of cars with a similar setting of parts as can be found in faces are favourable for performing such transfer tests (see Windhager et al., 2010). In fact, this type of future transfer study would cross boundaries between different types of visual objects and may show similarities and differences in these general object characteristics.

Footnotes

Footnote 1.   We refer to face adaptation effects as aftereffects (Köhler & Wallach, 1944) at higher perceptual and cognitive levels (Carbon & Ditye, 2011).

Footnote 2.   In the present work, we define that different facial images can originate from the same identity. For example, the same identity can produce face images differing in emotionality. In contrast, the same facial image of the same identity can produce different versions that vary in size or orientation.

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Figure 1.JPEG

Figures

Figure 1.   Framework to review face adaptation effects including dimensions for

different types of adapting information, transfer effects, and timing between adaptation and
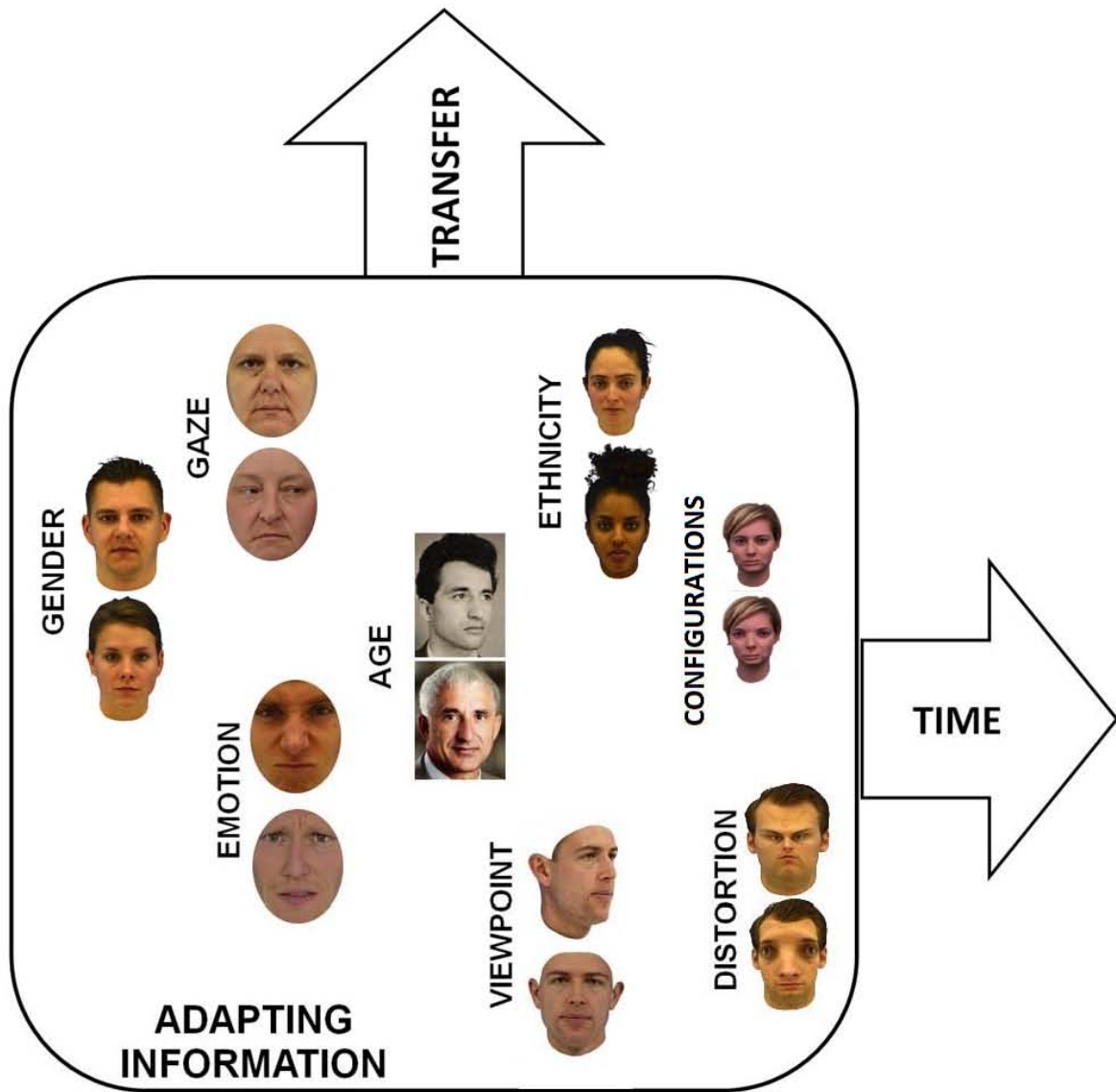
adaptation test phases.

Figure 2.   Computationally derived face space in which the stimuli were generated

to investigate face identity adaptation effects (FIAE). The original faces (green ellipses) are

connected to the average face (blue ellipse) by an 'identity trajectory.' Numbers refer to the

'identity strength' possessed by the given face (taken from Leopold et al., 2001).