

# Neural Correlates of Generic versus Gender-specific Face Adaptation

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## Abstract

■ The perception of facial gender has been found to be adaptively recalibrated: adaptation to male faces causes participants to perceive subsequent faces as more feminine and vice versa [Webster, M. A., Kaping, D., Mizokami, Y., & Duhamel, P. Adaptation to natural facial categories. *Nature*, 428, 557–561, 2004]. In an event-related brain potential (ERP) study, Kovács et al. [Kovács, G., Zimmer, M., Banko, E., Harza, I., Antal, A., & Vidnyanszky, Z. Electrophysiological correlates of visual adaptation to faces and body parts in humans. *Cerebral Cortex*, 16, 742–753, 2006] reported reduced N170 amplitudes and increased latencies for test faces following female gender adaptation compared to control stimulus (a phase randomized face) adaptation. We examined whether this N170 attenuation to test faces was related to the adaptor's gender, or to adaptation to

face exposure in general. We compared N170 effects after adaptation to either male or androgynous faces. Additionally, we investigated cross-modal adaptation for the same test faces following male or androgynous voice adaptors. Visual adaptation to face gender replicated previously reported aftereffects in classifying androgynous faces, and a similar trend was observed following adaptation to voice gender. Strikingly, N170 amplitudes were dramatically reduced for faces following face adaptors (relative to those following voice adaptors), whereas only minimal gender-specific adaptation effects were seen in the N170. By contrast, strong gender-specific adaptation effects appeared in a centroparietal P3-like component (~400–600 msec), which in the context of adaptation may reflect a neural correlate of the detection of perceptual novelty. ■

## INTRODUCTION

Although the investigation of adaptation to simple stimulus attributes (e.g., motion or color) has a very long tradition, it has been a striking novel discovery within the past decade that adaptive recalibration also governs the perception of very complex visual stimuli such as human faces. Webster and MacLin (1999) were the first to report visual aftereffects in face perception: They found that adaptation to distorted (e.g., contracted) faces led to a perception of veridical faces as being distorted in the direction opposite to the adaptor (e.g., expanded). Since then, similar contrastive aftereffects have been reported to follow adaptation to facial identity (Löffler, Yourganov, Wilkinson, & Wilson, 2005; Leopold, O'Toole, Vetter, & Blanz, 2001), eye gaze direction (Jenkins, Beaver, & Calder, 2006; Seyama & Nagayama, 2006), viewpoint (Fang, Ijichi, & He, 2007), ethnicity (Webster, Kaping, Mizokami, & Duhamel, 2004), and emotional expression (Butler, Oruc, Fox, & Barton, 2008; Fox & Barton, 2007; Webster et al., 2004). Such high-level visual aftereffects have been shown to be largely size invariant (e.g., Zhao & Chubb, 2001), suggesting that they do not mainly reflect adaptation to single features on low levels of visual

processing, even though they are similar in other respects to low-level adaptation effects, for instance, in time course (Kloth & Schweinberger, 2008; Leopold, Rhodes, Muller, & Jeffery, 2005).

Of special interest for the present study are aftereffects in the perception of facial gender. Following the prolonged viewing of a female (or male) face, participants tend to classify subsequently presented androgynous faces as distinctively male (or female; Webster et al., 2004), suggesting that distinct neural populations selectively code aspects of femaleness and maleness in faces. In line with this idea, it has been shown more recently that simultaneous opposite aftereffects of adaptation can be elicited for male and female faces (Bestelmeyer et al., 2008; Little, DeBruine, & Jones, 2005).

Despite the large number of studies investigating the nature of behavioral aftereffects, the neural correlates of human face adaptation are only beginning to be investigated by electrophysiological and functional imaging methods (Kovács, Cziraki, Vidnyanszky, Schweinberger, & Greenlee, 2008; Kovács et al., 2006). At the same time, when considering the substantial research studying ERPs in face perception, the investigation of ERP correlates of face adaptation should provide important information; both with respect to the stages of face processing that are affected by adaptation and with respect to the level of neural processing reflected in a specific component.

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The successful combination of face adaptation paradigms and ERP recordings is illustrated by Kovács et al. (2006), who investigated the electrophysiological correlates of gender adaptation. This study focused on the face-sensitive N170 component (Bentin, Allison, Puce, Perez, & McCarthy, 1996), which is thought to be a correlate of the structural encoding of faces (Rossion et al., 2000; Bentin et al., 1996), and which was hypothesized to be the major ERP component affected by selective adaptation to gender stimuli. Further, Kovács et al. investigated high-level gender adaptation in the perception of human hands, and included cross-categorical adaptation conditions, as participants adapted to photographs of female faces, female hands, or control stimuli (Fourier phase randomized versions of the adaptors). In line with the findings by Webster et al. (2004), adaptation to female faces as compared to control adaptation stimuli led to a bias to perceive subsequently presented faces as more masculine. Interestingly, although hands appeared to be comparatively weaker cues for a person's gender, qualitatively similar adaptation effects were observed for hands. By contrast, Kovács et al. did not find evidence for cross-categorical aftereffects, strongly suggesting that gender adaptation effects are category-specific. Paralleling these perceptual aftereffects, the analysis of the N170 revealed that adaptation to both female hands and female faces resulted in a strong attenuation of this component only when adaptors were of the same category as test stimuli. N170 amplitude to test stimuli was reduced, and latency increased, after adaptation to faces and hands as compared to control stimuli. Consequently, the authors suggested this modulation as being the primary correlate of shape-selective facial gender adaptation in humans. However, it is not immediately evident how this interpretation can be reconciled with other studies which found the N170 to be insensitive to facial gender processing (Mouchetant-Rostaing & Giard, 2003; Mouchetant-Rostaing, Giard, Bentin, Aguera, & Pernier, 2000).

Similar to the findings of Kovács et al. (2006), pronounced effects of adaptation on N170 amplitude and latency were also reported in an ERP study on gaze direction adaptation (Schweinberger, Kloth, & Jenkins, 2007). Irrespective of the direction of prior adaptation (gaze directed to the left or right, respectively) reduced N170 amplitudes and increased latencies were found in response to test faces that followed adaptation to faces with directional gaze, as compared to test faces presented without prior adaptors. However, although the N170 adaptation effect was completely independent of the adaptor's gaze direction, this study found the perceptual bias in gaze perception to strongly depend on the adaptor's gaze direction (see also Jenkins et al., 2006). This suggests that the N170 effect may reflect adaptation to generic face exposure, rather than adaptation to a specific gaze direction.

We therefore considered the possibility that the previously found N170 adaptation effects (Kovács et al., 2006) might at least partially have been affected by the choice of the control adaptor condition (Fourier phase randomized

images). Not only did the control adaptor lack any gender-specific information, it also lacked any shape-specific information characteristic of either faces or hands. In the present study, we aim at disentangling the respective influences of stimulus category repetition and gender adaptation on N170. Although we used the same test faces and a similar experimental design as Kovács et al. (2006), we used androgynous adaptor faces as control stimuli, which therefore should lack any adaptive power with respect to gender perception (cf. Webster & MacLin, 1999).

The most influential theoretical model (Bruce & Young, 1986) makes little reference to neurophysiological processes mediating various aspects of face perception, whereas more recent models make an attempt to integrate experimental, electrophysiological, and neuroimaging findings (e.g., Schweinberger & Burton, 2003; Haxby, Hoffman, & Gobbini, 2000). In terms of these models, we expect the present study to be informative for the question of whether the N170 attenuation reflects adaptation at an early level of "face detection" (i.e., the detection of a generic facial configuration in early perceptual processing), or instead at a more advanced stage of structural encoding of invariant facial information about gender (cf. Haxby et al., 2000).

A second aim of the present study was to test whether the previously observed category specificity of the gender adaptation effect (Kovács et al., 2006) would also hold for an auditory–visual cross-modal condition. Whereas we are unaware of strong reasons to expect a similar perceptual integration for faces and hands, our idea of an auditory–visual adaptation condition was prompted by recent evidence for strong perceptual integration of faces and voices (e.g., von Kriegstein et al., 2008), which is currently being considered in models of person perception (Campanella & Belin, 2007). Of particular relevance, an auditory influence on the perception of face gender was recently reported by Smith, Grabowecy, and Suzuki (2007). In this study, androgynous faces were perceived as more male when simultaneously combined with pure tones in the fundamental frequency range of male voices, whereas the same faces were perceived as more female when combined with tones in the female fundamental frequency range.

We considered a cross-modal voice–face adaptation condition as a particularly strong test for the hypothesis of category specificity of adaptation effects on the perception of facial gender. In the present study, we therefore used additional conditions with naturalistic male or androgynous voices as adaptors, in analogy to the conditions with male or androgynous face adaptors.

## METHODS

### Participants

Nineteen naïve and healthy participants (3 men, age range = 19–28 years,  $M = 22.9$  years) contributed data. They all reported normal or corrected-to-normal vision and were right-handed according to the Edinburgh Handedness

Inventory (Oldfield, 1971). Participants gave their written informed consent prior to data acquisition. The study was conducted in accordance to the ethical guidelines of the Declaration of Helsinki.

## Stimuli

Face stimuli were derived from grayscale full-front digital photographs of four young men and four young women (e.g., Kovács et al., 2006). Faces had no visible gender-specific features such as facial hair, jewellery, or make up and did not wear glasses. They were fitted behind an oval mask hiding the outer contours of the faces. Morphs were generated by entering male–female pairs into a morphing algorithm (Winmorph 3.1; for details of the morphing procedure please, see Kovács et al., 2006). For each pairing, the morphing procedure resulted in 100 face images, varying gradually on a male–female axis. From these images, four androgynous face images (50% male/50% female) and four male face images (98% male/2% female) were chosen to serve as androgynous and male adaptors, respectively. Four faces with different morph levels (20%:80%, 40%:60%, 60%:40%, and 80%:20% male:female ratio) were chosen from each male–female pair and served as the 16 test stimuli (see Figure 1). Both visual test and adaptation stimuli measured  $6.5 \times 6.5$  cm. All face stimuli were presented on a black screen at a viewing distance of  $\sim 87$  cm, which was kept constant using a chin rest.

Voice stimuli were generated on the basis of high-quality audio recordings obtained from four male and four female speakers pronouncing the vowel–consonant–vowel (VCV) combination /aba/. All of them were native speakers of German with age ranging from 20 to 27 years. Voices were recorded at a resolution of 16 bit and a sampling rate of 44,100 Hz. Using Adobe Audition stimuli, stimuli were normalized for average amplitude and timing and edited to a uniform duration of 886 msec, containing the normalized 686 msec utterance of the VCV plus 100 msec silence at the beginning and the end, respectively. These preprocessed voices were combined to four male–female voice pairs, which were entered into a morphing algorithm (Kawahara & Matsui, 2003). Pairings were matched according to maximal similarity in intensity patterns in the spectrogram in order to optimize morph quality. From each morphed series, four androgynous utterances (50% male:50% fe-

male) and four male utterances (100% male) were chosen to serve as androgynous and male acoustic adaptors, respectively. Each VCV utterance was repeated four times to form one single voice adaptor, which led to a total duration of 3544 msec for one acoustic adaptor (for more details concerning the voice stimuli used in this study, please see Schweinberger et al., 2008). Acoustic stimuli were presented via Sennheiser headphones with an approximate intensity of 60 dB along with a black screen.

## Task and Procedure

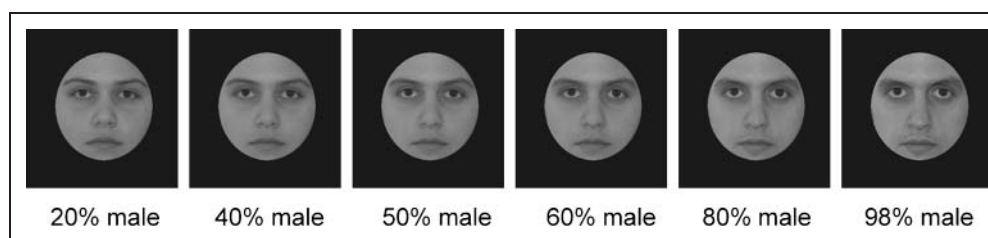
In a within-subjects design, participants underwent four adaptation conditions which were either unimodal (face adaptors) or cross-modal (voice adaptors) and either contained ambiguous (androgynous adaptation) or unambiguous gender information (male adaptation). The four different adaptation conditions were tested in separate blocks with the order of modality and gender of adaptation stimuli counterbalanced across participants. In each of the four conditions, eight repetitions of each of the four morph levels derived from the four identity pairings were presented, resulting in a total of 128 trials per condition.

In each trial, the adaptor was first presented for 3544 msec (see Figure 2). It was then replaced by a white question mark on black screen for 800 msec indicating that participants had to respond to the following test face which was presented for 200 msec. After that, a black screen was shown for 2000 msec, during which participants responded. Participants were asked to determine the gender of the test faces, classifying them as either male or female by pressing one of two marked keys (labeled “M” and “F”) on a standard keyboard (please see Figure 2, for an overview of the procedure).

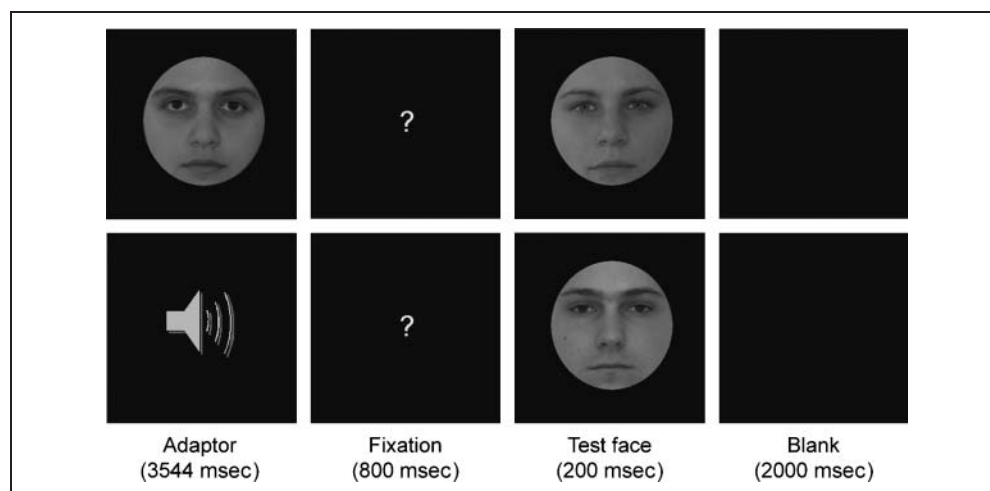
## Electrophysiological Recordings

The EEG was recorded from 32 Ag/AgCl electrodes (AC, 0.05–40 Hz, 250 Hz sampling rate) at locations Fz, Cz, Pz, Iz, Fp1, Fp2, F3, F4, C3, C4, P3, P4, O1, O2, F7, F8, T7, T8, P7, P8, F9, F10, FT9, FT10, TP9, TP10, P9, P10, PO9, and PO10, with TP10 as initial common reference, using an Easy-Cap. Electrode impedances were kept below 10 k $\Omega$ . The horizontal EOG was recorded from the outer canthi of both eyes, and the vertical EOG was monitored bipolarly

**Figure 1.** Examples for test stimuli (20%, 40%, 60%, and 80% male) and androgynous (50% male) and male (98% male) adaptation stimuli derived from the morphing continuum of one female/male pairing.



**Figure 2.** Trial procedure in face adaptation (top) and voice adaptation (bottom) trials. Please note that both voice and face adaptors could either be of male or androgynous gender.



from above and below the right eye. Off-line, trials with nonocular artifacts were discarded. For all other trials, the EEG was corrected for contributions of vertical and horizontal eye movements using BESA's automatic EOG artifact correction based on an adaptive artifact correction (Ille, Berg, & Scherg, 2002). Data were segmented into trials of 1200 msec (200 msec prestimulus baseline), digitally low-pass filtered at 20 Hz (zero phase shift, 12 dB/oct), and recalculated to average reference.

### ERP Analyses

Three components were analyzed: the early visual components P1 and N170 as well as the late positive component (P3) in the time interval of 400 to 600 msec.

For P1, we calculated mean amplitudes<sup>1</sup> in response to test faces in the time segment 100–140 msec at eight occipito-temporal electrode locations (O1, O2, P9, P10, PO9, PO10, TP9, and TP10). For N170, mean amplitudes for the time segment 150–190 msec were analyzed at eight posterior electrode locations (P7, P8, TP9, TP10, P9, P10, PO9, and PO10). These time segments were defined by the interval of  $\pm 20$  msec placed around the peak latency of the grand mean (defined at the electrode where the respective ERP component was maximal). Finally, effects in the late positive component were analyzed using mean amplitudes between 400 and 600 msec at nine electrodes (F3, F4, C3, C4, P3, P4, Fz, Cz, and Pz).

Where appropriate, epsilon corrections for heterogeneity of covariances were performed (Huynh & Feldt, 1976). All post hoc *t* tests were corrected according to the Bonferroni procedure ( $\alpha = .05$ ).

### Statistical Analyses

For the analysis of the behavioral data, mean percentages of "male" responses were analyzed in an analysis of variance (ANOVA) with the factors adaptor modality (visual vs. acous-

tic), adaptor gender (androgynous vs. male), and morph level of test stimulus (20%:80%, 40%:60%, 60%:40%, and 80%:20% male:female ratio).

Effects of adaptation on the ERP components (mean amplitudes in the respective time intervals obtained at the relevant electrodes) were examined in an analysis including the factors electrode locations, laterality, adaptor modality, and adaptor gender. Please note that in analogy to and for an easier comparison with the gender adaptation study by Kovács et al. (2006), the morph level of test faces has not been included as a factor in the analysis of the ERP data.

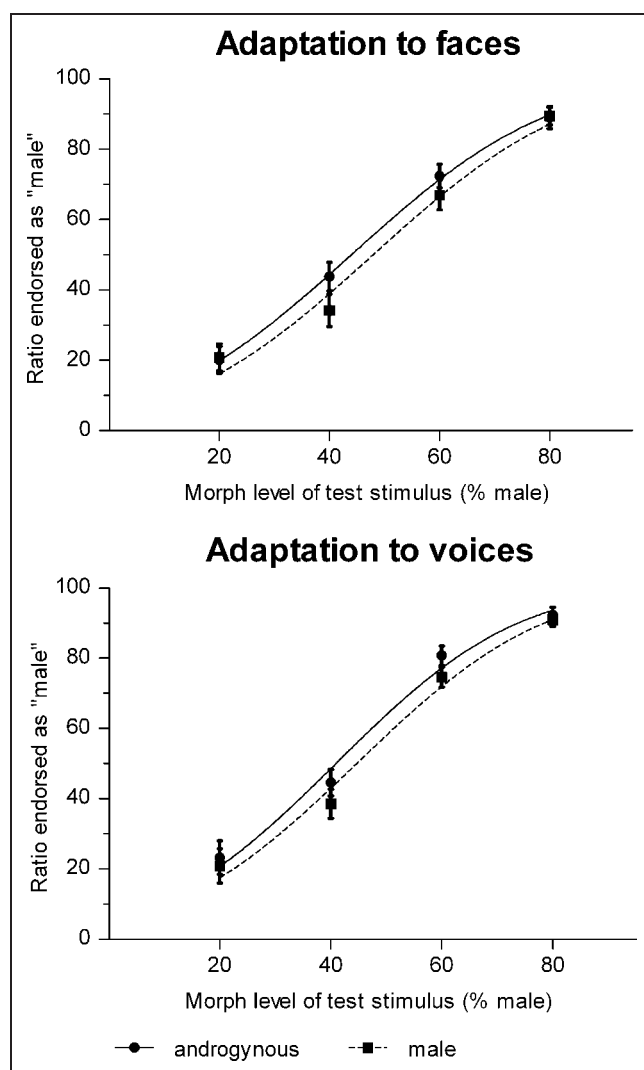
## RESULTS

### Behavioral Results

The  $2 \times 2 \times 4$  ANOVA (for details, please see Methods section) revealed a significant main effect of morph level [ $F(3, 54) = 180.43, p < .001$ ], which had to be expected. In addition, contrastive aftereffects of adaptation were reflected in a main effect of adaptor gender [ $F(1, 18) = 5.08, p < .05$ ], which was qualified by a significant interaction with morph level [ $F(3, 54) = 4.50, p < .01$ ]. This interaction resulted from the fact that adaptation, in line with previous observations (cf. Afraz & Cavanagh, 2008; Kovács et al., 2006; Leopold et al., 2001), induced larger aftereffects for intermediate morph levels [*t* tests for 40%:60% and 60%:40% male/female ratio:  $t(18) > 2.52, p < .05$  for both levels] than for stimuli with less ambiguous gender information (*t* tests for 20%:80% and 80%:20% male:female: all *ps*  $> .70$ ; see Figure 3 and Table 1).

No further effects were significant, in particular, the interaction of adaptor modality and adaptor gender [ $F(1, 18) < 1$ ], and adaptor modality, adaptor gender, and morph level [ $F(3, 54) = 1.12, p > .30$ ], although there was a trend for an interaction of adaptor modality and morph level [ $F(3, 54) = 2.55, p = .066$ ].





**Figure 3.** Mean ratios of "male" classifications ( $\pm$ SEM) across morph levels, and cumulative Gaussian functions fitted to these data. Top: Effects of adaptation to face gender. Bottom: Effects of adaptation to voice gender. Solid lines represent results of adaptation to androgynous gender, dashed lines represent results of adaptation to male gender.

**Table 1.** Proportion of Mean "Male" Classifications and Size of the Aftereffect (Difference between Number of Male Classifications following Androgynous and Male Adaptation) Depending on the Morph Level of the Test Stimulus (20% Male, 40% Male, 60% Male, and 80% Male) and the Adaptation Condition (Androgynous Face, Male Face, Androgynous Voice, and Male Voice)

Adaptation Stimulus	Morph Level of Test Stimulus (% Male)			
	20%	40%	60%	80%
Androgynous face	20.2 (3.8)	43.8 (4.0)	72.4 (4.3)	89.0 (3.1)
Male face	20.9 (3.8)	34.2 (4.6)	66.9 (4.2)	89.4 (2.5)
<b>Size of aftereffect for face adaptation</b>	<b>-0.7</b>	<b>9.6</b>	<b>5.5</b>	<b>-0.4</b>
Androgynous voice	23.2 (4.8)	44.6 (3.8)	80.8 (2.8)	92.3 (2.3)
Male voice	20.9 (4.9)	38.5 (4.2)	74.6 (2.8)	90.9 (1.9)
<b>Size of aftereffect for cross-modal adaptation</b>	<b>2.3</b>	<b>6.1</b>	<b>6.2</b>	<b>1.4</b>

As earlier studies did not find cross-categorical (Kovács et al., 2006) or cross-modal (Schweinberger et al., 2008) effects in gender adaptation paradigms, the mere absence of a significant interaction with adaptor modality may not provide sufficient evidence to demonstrate the existence of cross-modal adaptation effects. To determine whether cross-modal voice–face adaptation would be reliable as a separate, we performed independent ANOVAs for each adaptor modality, with adaptor gender and morph level as factors. For face adaptation trials, there was a significant interaction of adaptor gender and morph level [ $F(3, 54) = 4.87, p < .01$ ], supporting the fact that the visually presented face adaptor differently biases gender discrimination at the various morph levels. Indeed, individual  $t$  tests at the different morph levels revealed that this effect was significant at the ambiguous morph level 40%:60% [ $t(18) = -3.54, p < .01$ ], whereas the smaller differences at the other morph levels (see Table 1) failed to reach significance ( $p > .20$ ).

For voice adaptation trials, there was a trend toward a main effect of adaptor gender [ $F(1, 18) = 3.05, p = .098$ ], but no significant interaction of adaptor gender and morph level [ $F(3, 54) = 1.37, p > .20$ ]. Nevertheless,  $t$  tests at individual morph levels indicated an adaptation effect at the ambiguous morph level 60%:40% [ $t(18) = -2.70, p < .05$ ], whereas differences at the other morph levels (see Table 1) failed to reach significance ( $p > .08$ ), similar to the face adaptation condition.

## Electrophysiological Results

### P1

The ANOVA of P1 amplitudes with the factors electrode location, laterality, adaptor modality, and adaptor gender revealed main effects of electrode location [ $F(3, 54) = 58.19, p < .001$ ] and adaptor modality [ $F(1, 18) = 78.91, p < .001$ ], as well as an interaction of electrode location and adaptor modality [ $F(3, 54) = 24.65, p < .001$ ]. In short,

P1 amplitudes were much larger in trials following face adaptors compared with those following voice adaptors, and this difference was most pronounced at those electrodes at which P1 was more prominent (cf. Figure 4). The interaction between adaptor modality and adaptor gender was also significant [ $F(1, 18) = 15.52, p < .01$ ]. P1 responses to test faces following face adaptors were slightly but significantly larger following adaptation to androgynous than male adaptors [ $M = 3.19$  vs.  $2.95 \mu\text{V}$ ;  $t(18) = 3.69, p < .01$ ]. For test faces following voice adaptors, P1 was slightly smaller following androgynous than male adaptors [ $M = 1.45$  vs.  $1.67 \mu\text{V}$ ;  $t(18) = -2.89, p < .05$ ].

P1 peak latencies at O1 and O2 were evaluated in an ANOVA with laterality, adaptor modality, and adaptor gender as factors. The only significant effect was adaptor modality [ $F(1, 18) = 13.81, p < .01$ ], with somewhat longer latencies in trials following face than in trials following voice adaptors ( $M = 118.5$  vs.  $113.6$  msec, respectively).

#### N170

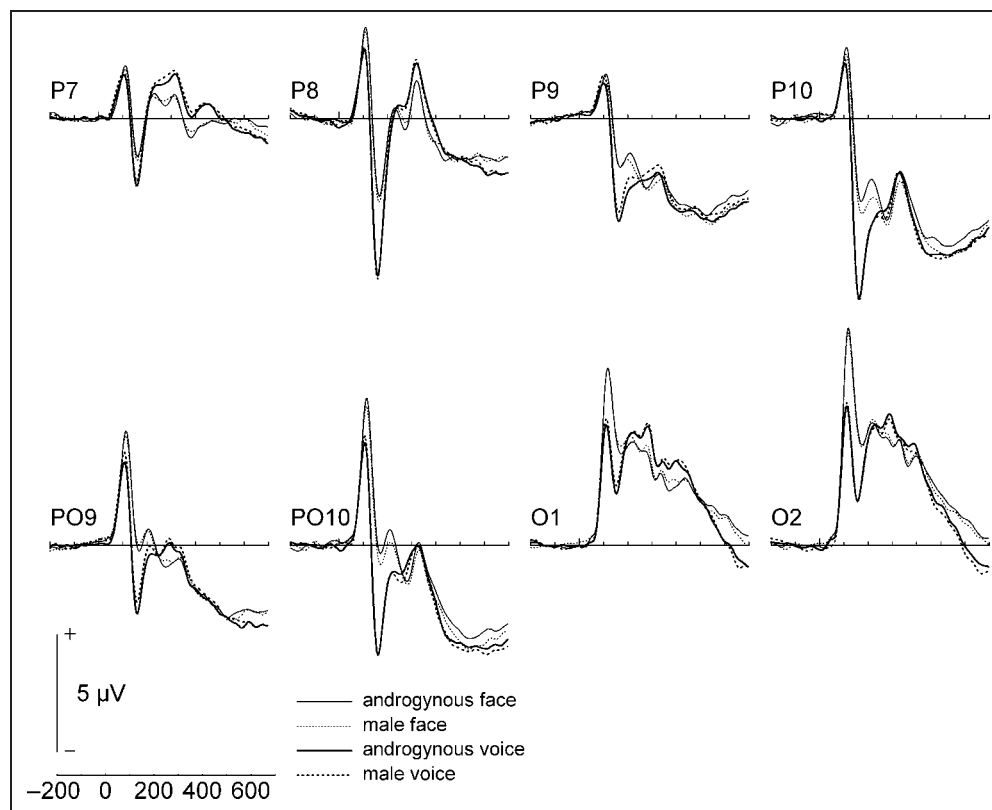
An ANOVA on N170 mean amplitudes with the factors electrode location, laterality, adaptor modality, and adaptor gender revealed significant main effects of electrode location [ $F(3, 54) = 8.03, p < .01$ ] and laterality [ $F(1, 18) = 5.60, p < .05$ ], reflecting the typical N170 topography (cf. Figure 4). Most importantly, there was a prominent effect

of adaptor modality [ $F(1, 18) = 114.96, p < .001$ ], which was further qualified by interactions with electrode location [ $F(3, 54) = 11.89, p < .001$ ] and with laterality [ $F(1, 18) = 13.01, p < .01$ ]. As can be seen in Figure 4, the effect of adaptor modality reflects substantially larger N170 amplitudes in response to test faces preceded by voice adaptors ( $M = -3.86 \mu\text{V}$ ) as compared to when the same test faces were preceded by face adaptors ( $M = -1.78 \mu\text{V}$ ). Although measurable at each of the electrode locations, the adaptor modality effect was more pronounced at electrode sites P7/P8, P9/P10, and PO9/PO10 than at TP9/TP10, and was more distinct over right than left hemispheric electrodes [ $M_{\text{diff}} = 2.80$  vs.  $1.35 \mu\text{V}$ , respectively;  $t(18) = 3.61, p < .01$ ].

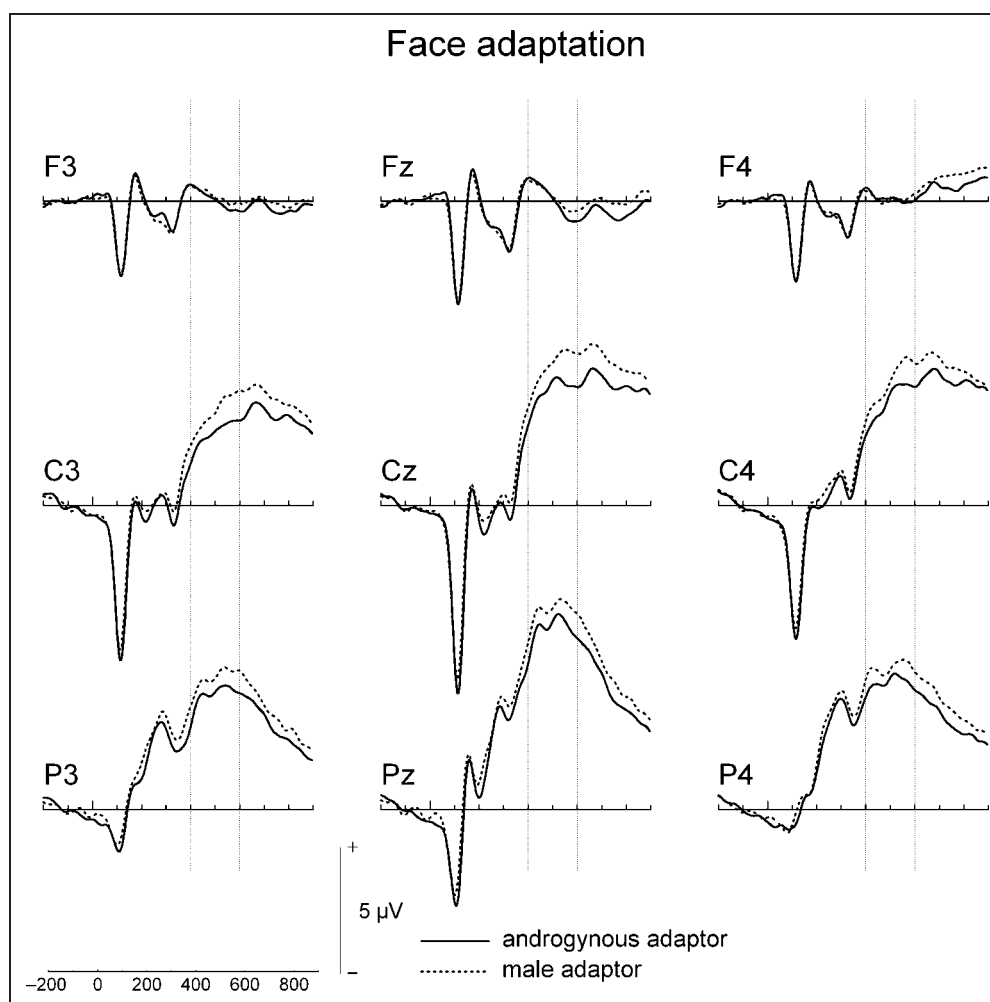
In addition to those prominent effects of adaptor modality on the N170, Figure 4 suggests only a very small gender-specific adaptation effect. The analysis revealed an interaction of laterality and adaptor gender [ $F(1, 18) = 5.47, p < .05$ ], and a three-way interaction of electrode location, laterality, and adaptor gender [ $F(3, 54) = 4.54, p < .01$ ]. The effect of adaptor gender was only significant at PO9 [ $F(1, 18) = 5.32, p < .05$ ], with smaller amplitudes after male than androgynous adaptation ( $M = -0.72$  vs.  $-1.06 \mu\text{V}$ , respectively).<sup>2</sup>

An analogous ANOVA on peak amplitudes replicated the above findings, except for an additional four-way interaction of electrode location, laterality, adaptor modality, and adaptor gender [ $F(3, 54) = 3.60, p < .05$ ]. Separate comparisons between male and androgynous

**Figure 4.** ERPs to test faces either preceded by adaptor faces (thin) or voices (bold) of androgynous (solid) or male gender (dotted lines).



**Figure 5.** Effects of adaptation to facial gender in the time interval between 400 and 600 msec (vertical lines). ERPs in response to test faces following androgynous (solid) or male (dotted) face gender adaptation, respectively.



adaptors for each electrode location and adaptor modality were suggestive of somewhat reduced N170 following male versus androgynous voice adaptors at P9 and PO9, and somewhat increased N170 following male versus androgynous adaptors at PO10; however, none of these differences were significant after correcting for multiple comparisons ( $p > .05$ ).

The analysis of N170 peak latencies revealed significantly longer N170 latencies [ $F(1, 18) = 10.87, p < .01$ ] in trials following face adaptors than in trials following voice adaptors ( $M = 165.1$  vs.  $161.9$  msec; see Figure 4).

#### Late Positive Component (P3)

An ANOVA revealed main effects of electrode location [ $F(2, 36) = 75.45, p < .001$ ] and laterality [ $F(2, 36) = 16.31, p < .001$ ], and an interaction between electrode location and laterality [ $F(4, 72) = 17.81, p < .001$ ]. There was also a three-way interaction between electrode location, adaptor modality, and adaptor gender [ $F(2, 36) = 3.91, p < .05$ ], which was further examined in separate

analyses for frontal, central, and parietal electrodes, respectively. These analyses revealed significant interactions of adaptor modality and adaptor gender for parietal electrodes [ $F(1, 18) = 5.00, p < .05$ ] and a strong trend for central electrodes [ $F(1, 18) = 4.21, p = .05$ ]. In trials following face adaptors only, more positive amplitudes were seen following male than androgynous adaptors [ $t(18) = 2.41, p < .05$ ;  $t(18) = 2.33, p < .05$ , for central and parietal electrodes, respectively; see Figure 5]. No such effects of adaptor gender were found in trials following voice adaptors (all  $ps > .40$ ; see Figure 6).

We hypothesized that these differences in the late positive component might reflect a P3 effect, with larger amplitudes arising in response to test faces deviating from the “context” set by the preceding face adaptors (cf. Donchin & Coles, 1988). Specifically, we reasoned that because an identical set of (androgynous, on average) test faces was either preceded by androgynous or male adaptor faces, the net deviance from the previously seen faces (the adaptors) was larger in the male adaptor condition, and this might have led to a more positive P3 component in this condition. This explanation would predict that the larger P3 in the male adaptor condition should be more pronounced

specifically for female test faces for which this deviance from the male adaptors is largest.

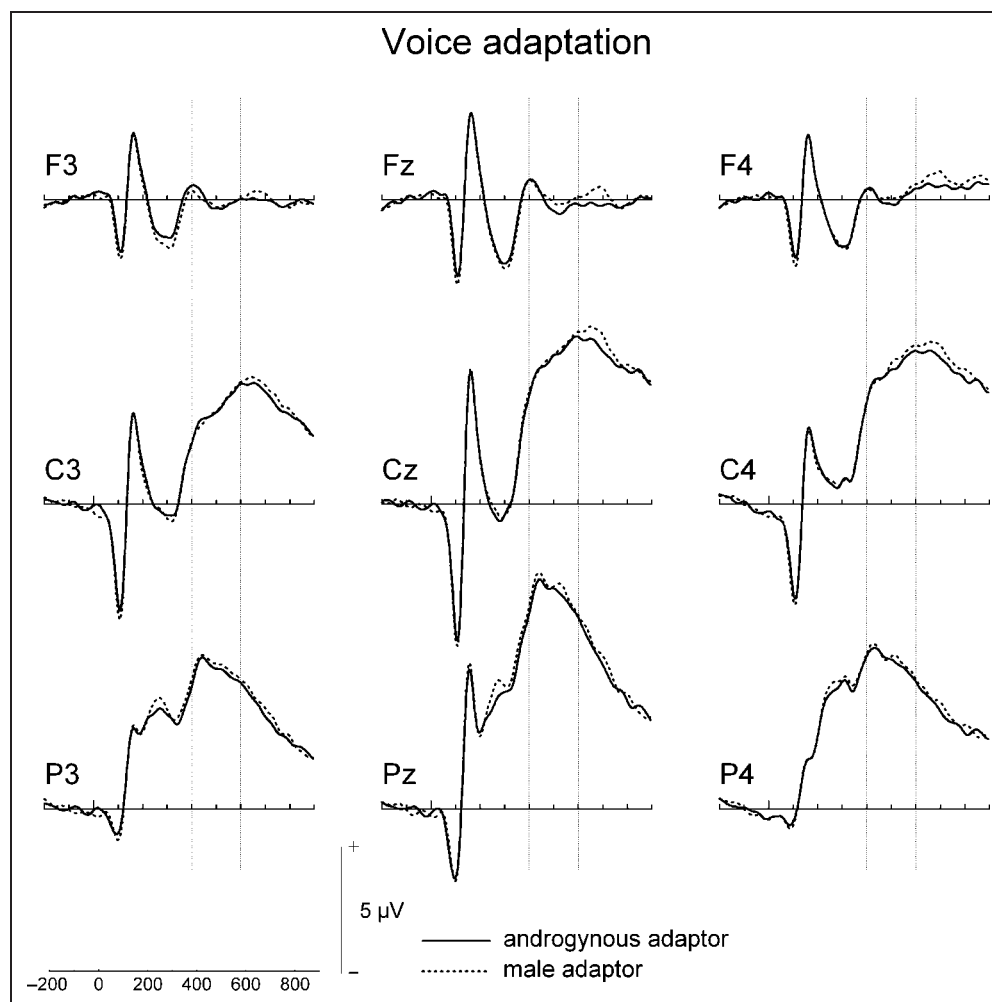
To test this prediction, we performed an additional ANOVA on mean amplitudes in the 400–600 msec interval, considering central and parietal electrodes only (C3, Cz, C4, P3, Pz, and P4) with adaptor gender and morph level (4) as factors. Crucially, this ANOVA yielded a significant interaction of adaptor gender and morph level [ $F(3, 54) = 4.99, p < .01$ ]. Indeed, the larger positivity following male than androgynous face adaptation was seen only for the most female test faces of the 20%:80% morph level [ $t(18) = 3.84, p < .01$ ]. By contrast, no significant differences between androgynous and male adapted trials were seen for any of the three other morph levels (all  $ps > .10$ ). Figure 7 shows that, compared to the other morph levels, the most female test faces elicited a distinctly larger positivity following male but not androgynous face adaptation. Post hoc  $t$  tests for ERPs in the male adaptation condition confirmed larger P3 amplitudes in the 20%:80% morph level when compared to each of the other morph levels [ $ts(18) = 5.42, 5.92, \text{ and } 4.90, \text{ respectively, all } ps < .001$ ]. Moreover, the numerical (albeit not significant) differences between morph levels in each adaptation condition are in

line with the idea that P3 amplitudes were larger the more test faces deviated perceptually from the context provided by the adaptor faces.

## DISCUSSION

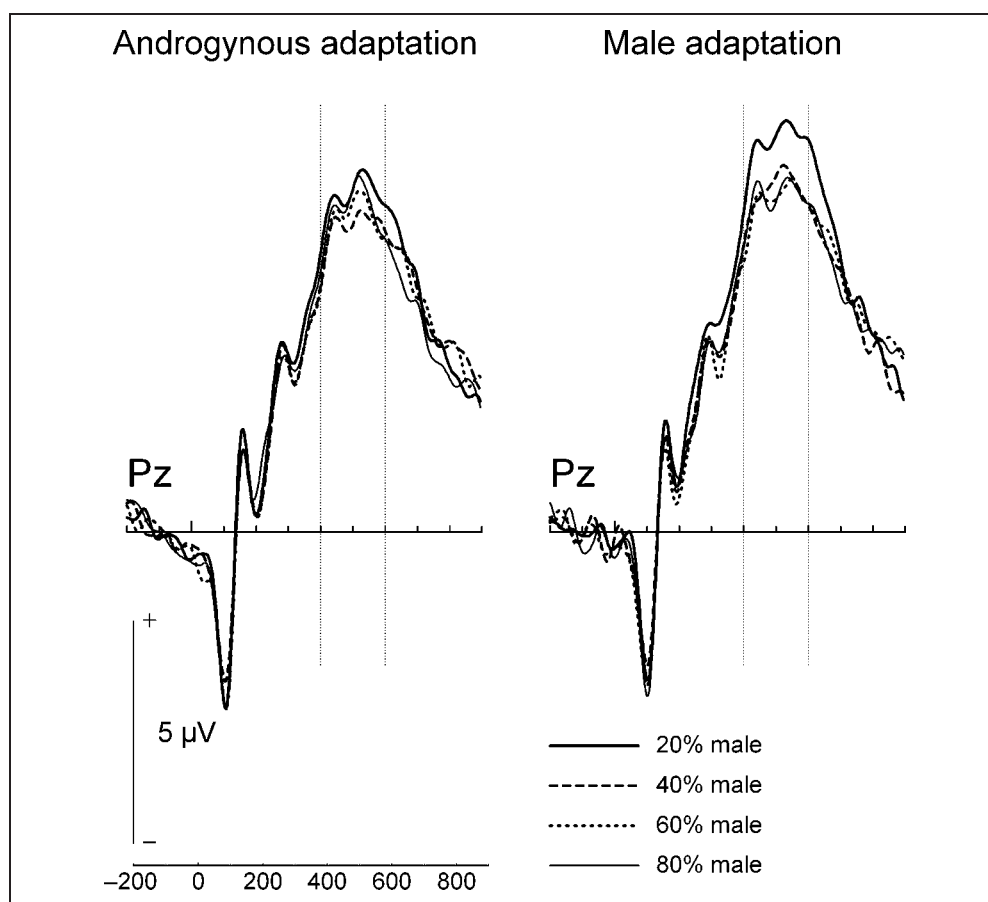
The present study demonstrates that adaptation to male faces elicits a strong aftereffect on the perceived gender of subsequent faces, in line with earlier findings (Kovács et al., 2006; Webster et al., 2004). Most importantly, although we also replicated the N170 attenuation following face adaptation that has been first reported by Kovács et al. (2006), the pattern of the present results suggests a different interpretation of the effect. Specifically, the N170 attenuation effect in that study was found in comparison to a control adaptation condition involving nonface adaptors, and has been interpreted as being a specific neural correlate of gender adaptation. We tested this claim of a gender-specific attenuation of the N170 by comparing ERPs to test faces preceded by either male or gender-neutral (androgynous) adaptor faces. Critically, this ensured that faces were used as adaptors throughout, and

**Figure 6.** Effects of adaptation to voice gender in the time interval between 400 and 600 msec (vertical lines). ERPs in response to test faces following androgynous (solid) or male (dotted lines) voice gender adaptation, respectively.





**Figure 7.** Late positive effect at electrode Pz. ERPs in response to test faces of the different morph levels are depicted in separate plots for trials following androgynous (left) or male face adaptation (right).



that differences between the control and the male adaptors were limited to gender information. In that situation, the prominent N170 adaptation effect for gender-specific versus neutral adaptation conditions was virtually abolished. In line with preliminary findings from earlier research on eye gaze adaptation (Schweinberger et al., 2007), this result is consistent with the idea that the N170 attenuation reflects adaptation to the category of faces per se, rather than adaptation to gender-specific information in faces.

This interpretation is strongly corroborated by a comparison of ERPs to face-adapted test faces with those to voice-adapted test faces. Independent of adaptor gender, the N170 to face-adapted test faces was greatly attenuated when compared with the same test faces after voice adaptation. From the present data alone, it might be argued that this N170 attenuation was not caused by face adaptors per se, but might have been caused by other visual adaptors containing complex shapes as well. However, that interpretation is not supported by the pattern of results found by Kovács et al. (2006), who observed a prominent attenuation of N170 in face-adapted trials when compared with hand-adapted trials. Moreover, the present N170 modality effect was of comparable magnitude as the N170 effect observed by Kovács et al.. Overall, we conclude that the N170 attenuation in the current study was strongly driven by adaptation to the *category* of faces, irrespective of gender. Our conclusion is in line with a very recent study reporting

category-level habituation of the N170 for faces (but not for words; cf. Maurer, Rossion, & McCandliss, 2008), although the influence of facial gender was not systematically investigated in that study. Thus, it appears that N170 attenuation reflects adaptation at the level of detecting generic facial configurations in early perceptual processing, rather than at a more advanced stage of encoding gender-specific information (cf. Haxby et al., 2000).

Although category-level attenuation was the prominent factor driving the N170 adaptation effect, smaller, gender-specific adaptation effects were also seen in both the N170 and in the preceding P1 components. Specifically, the N170 tended to be reduced over the left hemisphere following male versus androgynous adaptation, whereas it tended to be increased over the right hemisphere in the same condition. In principle, such findings might be reconciled with the suggestion that the two hemispheres differentially process facial gender (Parente & Tommasi, 2008). However, it needs to be noted that gender-specific adaptation effects on the N170 were extremely small numerically (cf. Figure 4) and did not consistently reach conventional levels of statistical significance. Although we therefore do not wish to make strong claims about a sensitivity of the N170 to gender-specific adaptation, we believe that any such effects are small at best, particularly so when contrasted with the prominent N170 attenuation effect (i.e., in the region of 3–4  $\mu$ V) driven by adaptor category and

modality. Although a tentative link at present, the lack of consistent effects of adaptation to facial gender across images in the occipito-temporal N170 ERP may be reconciled with a very recent fMRI study, which surprisingly failed to reveal image-invariant adaptation to facial identity in occipito-temporal cortex (Davies-Thompson, Gouws, & Andrews, 2009).

Whereas there was therefore only marginal evidence for a sensitivity of the N170 for gender-specific adaptation, larger and more systematic effects of adaptor gender were observed in the late positive component (400–600 msec) over central and parietal electrodes. These effects were restricted to unimodal (face-to-face) adaptation trials in which test stimuli preceded by male adaptors elicited significantly more positive amplitudes than those preceded by androgynous adaptors. The latency and topography of this component suggest that it reflects a P3 (Sutton, Braren, Zubin, & John, 1965; for a recent review, see Polich, 2007). P3 amplitude is highly sensitive to stimulus probability, and is typically large for relatively rare stimuli (Polich & Bondurant, 1997; Duncan-Johnson & Donchin, 1977). The most prominent theoretical explanation of the P3 effect is *context updating* (Donchin & Coles, 1988; Donchin, 1981; but see also Verleger, 1988). This framework proposes that the P3 reflects a comparison between the representation of a previous event in working memory and the current event. P3 amplitude is thought to be proportional to the degree of context updating required by the current event, which in turn depends on the discrepancy between this event and the context set by the previous stimuli. When applied to the paradigm of perceptual adaptation, it is reasonable to assume that the degree of context updating depends on the perceptual dissimilarity between adaptor and test stimuli.

We suggest that the adaptation effect in the P3 reflects the larger degree of context updating for test faces that least resembled the context set by the adaptor faces. Because the overall deviance of adaptor and test faces was smaller in the androgynous than in the male adaptation condition, the larger P3 in the latter condition is in line with such an interpretation. This conclusion received further support by a more detailed analysis of responses for the different morph levels of test stimuli. A distinct P3 was seen specifically in the condition exhibiting the largest perceptual deviance between the test face and the preceding adaptor faces (see Figure 7). This pattern of gender-specific adaptation effects in the P3 therefore may be considered as one of the neural correlates of enhanced “novelty detection” as a consequence of contrastive after-effects induced by adaptation. Indeed, recent theories relate adaptation and novelty to each other in the sense that adaptation improves the detectability or discriminability of novel stimuli by decreasing the magnitude of the response to the more frequent (less deviant) stimuli, and thereby increasing the relative magnitude of the response evoked by the novel or more deviant stimuli (Kohn, 2007). This differential processing of recent (adapted) and novel stim-

uli might explain the observed difference in the ERP at the P3 time window.

To date, however, there are only very few studies on ERP correlates of face adaptation, none of which reported results for the P3 component (Ganis & Schendan, 2008; Jacques, d’Arripe, & Rossion, 2007; Kovács, Zimmer, Harza, & Vidnyanszky, 2007; Kovács et al., 2006; Kovács, Zimmer, Harza, Antal, & Vidnyanszky, 2005). It is therefore difficult to directly relate the gender-specific adaptation effect in the 400–600 msec segment to prior work. We note, however, that the earliest ERP repetition effects in the context of stimulus repetition designs generally emerge earlier (from ~170 to 200 msec). Crucially, these effects typically accompany exact image repetition, whereas repetition across different views of faces or objects elicit ERP effects only at a later latency, and often include both an N250r (Bindemann, Burton, Leuthold, & Schweinberger, 2008; Schweinberger, Pickering, Jentsch, Burton, & Kaufmann, 2002) and a P3-like modulation (e.g., Schendan & Kutas, 2003; for a recent review, see Grill-Spector, Henson, & Martin, 2006). Although the relationship between these results and our data must remain tentative at present, there is clearly a need for an integrated account of the neurocognitive mechanisms that mediate positive priming on the one hand and negative aftereffects on the other (cf. Huber, 2008). One of the challenges for future research will be to understand in more detail the circumstances in which repetition leads to facilitation of processing, or to biased perception.

Turning to the behavioral data, we replicated earlier findings of a negative aftereffect following adaptation to male faces (Webster et al., 2004). Intriguingly, the present experiment generated some evidence for cross-modal gender adaptation, such that adaptation to male voices appeared to influence the subsequent perception of an ambiguous face’s gender. We believe that these effects should be interpreted with caution because, although they were not significantly reduced relative to the intramodal effects, they failed to consistently reach conventional levels of significance when tested as a separate. If substantiated, such effects would add to recent evidence that sensory information from other modalities, including smell (Kovács et al., 2004) and audition (Smith et al., 2007), may have an impact on the perception of facial gender. In line with recent models (Campanella & Belin, 2007), such an effect could be facilitated by cross-modal face–voice integration of gender information. It is important to keep in mind that audiovisual integration studies typically use simultaneous bimodal presentation of stimuli, and that temporal synchronicity might, in fact, be an important prerequisite for cross-modal integration to occur (Munhall, Gribble, Sacco, & Ward, 1996). By contrast, in the few cases in which cross-modal adaptation effects were investigated for complex stimuli, they were typically absent (Schweinberger et al., 2008; Fox & Barton, 2007). Nevertheless, we consider further research into possible mechanisms of cross-modal voice–face adaptation promising. Specifically, one interesting

question for the future may be whether bimodal adaptors can elicit aftereffects over and above those caused by unimodal adaptors (Bertelson, Vroomen, & de Gelder, 2003).

In summary, the present study investigated the neural correlates of perceptual adaptation to facial and vocal gender using ERPs. Our results demonstrate a dramatic N170 attenuation effect. Importantly, this effect was clearly related to adaptation to face exposure in general, whereas the contribution of gender-specific aftereffects was minimal at best. Accordingly, rather than reflecting the specific processing of facial gender, the N170 appears to be mainly driven by the detection of a facial configuration. More systematic gender-specific aftereffects were observed in a centro-parietal P3 component, which we suggest to reflect an adaptation-induced detection of perceptual novelty.

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### Notes

1. For the clearly pronounced P1 and N170 components, all analyses were also performed on peak amplitudes. For P1, individual peak amplitudes were measured at electrodes O1 and O2 as largest positivities in the time window of 90–130 msec. For N170, peak amplitudes were individually determined for each participant and hemisphere as amplitudes at the latency of the maximal negative peak between 150 and 200 msec within electrodes P7, P9, PO9, and TP9 as well as P8, P10, PO10, and TP10. Unless stated otherwise, these analyses led to the same effects as those on mean amplitudes reported here.

2. We present N170 effects collapsed across morph levels, consistent with the analysis reported by Kovács et al. (2006), ensuring comparability across studies. However, we also performed additional analyses including morph level as a factor, to control for the possibility that the negative findings in the N170 (i.e., no or little gender-specific adaptation) were driven by those morph levels showing no behavioral adaptation effects. Although the result confirmed that the effect of adaptor modality was highly significant independent of morph level, there was no significant interaction of adaptor gender and morph level [ $F(3, 54) < 1$ ]. Moreover, the small gender-specific adaptation effect seen in the original analysis at PO9 failed to reach significance in the analysis including morph level as a factor. This confirms that any effect of adaptor gender was very minor at best, relative to the prominent effects of adaptor modality.

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