

Effects of Sexually Dimorphic Shape Cues on Neurophysiological Correlates of Women's Face Processing

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Abstract Sexual dimorphism (i.e., masculinity in males and femininity in females) is known to affect social perceptions that are important for both mate choice and intrasexual competition, such as attractiveness and dominance. Little is known, however, about the neurophysiological underpinnings mediating sexual dimorphism's effects on face processing. Here we investigate the neurological correlates of processing sexually dimorphic faces using event-related potentials (ERPs). We employed image transformation techniques to enhance and reduce the sexually dimorphic shape features of male and female faces viewed by women performing a sex categorization task. Sexual dimorphism modulated superior-central N250 magnitude and the peak latency of the N170 and P200. The sex of the face further modulated the amplitude of the P200. These findings extend prior work linking the superior-central N250 to social categorization processes triggered by face shape, and strengthen its functional interpretation in terms of coarse- versus fine-grained categorical judgements. We conclude that ERPs can illuminate the cognitive mechanisms (i.e., mental processes) underlying behavioral responses to sexual dimorphism.

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Introduction

Perceptions of physical attractiveness affect many aspects of our lives, such as who we reproduce with (Gangestad, 1993; Gangestad & Buss, 1993), employ (Chiu & Babcock, 2002), and vote for (Klein & Ohr, 2000; Little et al., 2007a), as well as other fundamental aspects of human care (e.g., Bordieri, Solodky, & Mikos, 1985; Dion, 1972; Kurdahi Badr & Abdallah, 2001; Stephan & Langlois, 1984). Facial attractiveness, specifically, may be particularly important in person perception (see, e.g., Little, Jones, & DeBruine, 2011; Thornhill & Gangestad, 1999), although not the only important element involved in prosocial biases toward attractive people (see Maestripieri, Henry, & Nickels, 2017). Evidence suggests that the face is processed differently than the body, beginning at a very early age. For example, the configural processing of faces, which emerges very early in infancy (Le Grand, Mondloch, Maurer, & Brent, 2003; Walton & Bower, 1993), develops earlier than the configural processing of bodies (Slaughter, Heron, & Sim, 2002). Brain imaging studies (e.g., Allison, Puce, Spencer, & McCarthy, 1999; Eimer, 2000; Halit, de Haan, & Johnson, 2000; Kanwisher, McDermott, & Chun, 1997; McCarthy, Puce, Belger, & Allison, 1999; Puce, Allison, & McCarthy, 1999) and single-cell recording studies (Perrett, Hietanen, Oram, & Benson, 1992) show greater activity in certain brain regions (e.g., the fusiform gyrus, Kanwisher et al., 1997) when processing faces compared to other types of stimuli, further suggesting that face processing may play a particularly important role in overall person perception.

Certain facial traits, including bilateral symmetry, facial averageness, color cues to health, and sexual dimorphism (i.e., masculinity in males and femininity in females), are related to attributions of attractiveness with relative consistency across cultures (reviewed in, e.g., Little et al., 2011; Mogilski & Welling, 2017). However, compared to the consistently high preferences for female facial femininity among men (e.g., Perrett et al., 1998; Welling et al., 2008a), preference for male masculinity among women is considerably more variable, with some studies reporting a high preference for relatively masculine men (e.g., Johnston, Hagel, Franklin, Fink, & Grammer, 2001) and others reporting a high preference for relatively feminine men (e.g., Welling et al., 2007). Given that masculinity is associated with measures of long-term health (reviewed in Thornhill & Gangestad, 2006) and negative personality traits (e.g., dishonesty; Perrett et al., 1998), it is likely that women's preferences for masculinity reflect how women resolve the tradeoff between the benefits (e.g., genetic immunocompetence that may be passed on to offspring) versus costs (e.g., less investment) of choosing a masculine partner. Certainly, preferences for male masculinity appear to be relatively context-specific, whereby preferences for masculinity are higher in conditions where genetic fitness should be prioritized. For example, women prefer masculine men more when environmental conditions are harsher (DeBruine, Jones, Crawford, Welling, & Little, 2010; DeBruine, Jones, Little, Crawford, & Welling, 2011; Little et al., 2007b), when considering men for short-term (i.e., purely sexual) relationships (Little, Jones, Penton-Voak, Burt, & Perrett, 2002), and when conception is more likely (e.g., Gildersleeve, Haselton, & Fales, 2014; Penton-Voak et al., 1999; Welling et al., 2007).

Thus, various adaptive functions may be served when social behavior is influenced by others' sexually dimorphic features (Rhodes, Chan, Zebrowitz, & Simmons, 2003; Thornhill & Gangestad, 1999), but little is known about the brain's response to these features.

Relatively few studies have examined how event-related potentials (ERPs) are influenced by face shape during face processing, although some work has been done on the brain's response to another socially important facial cue – that of race. Recently, Balas and Nelson (2010) investigated the effect on White participants of manipulating own-race (White) and other-race (Black) face shape and skin pigmentation within images viewed in a simple orientation discrimination task. They found that the N170, an early-processing component in face recognition (e.g., Bentin & Deouell, 2000; Herzmann, Schweinberger, Sommer, & Jentzsch, 2004; Itier & Taylor, 2004a, 2004b), and a superior-central N250 component were modulated by skin color, independent of face shape, such that the N170 amplitude was larger (i.e., more negative) and the latency shorter to Black faces than to White faces, and that the N250 amplitude was larger for White faces than to Black faces (with no N250 differences in latency in response to skin color). However, only the superior-central N250 exhibited sensitivity to face shape, whereby White face shape made N250 magnitudes less negative compared to Black face shape. As concluded by Balas and Nelson (2010), the superior-central N250 may reflect greater experience with face shapes of own- compared to other-race individuals, although it is possible that this component may relate to the ease of processing face shape more generally. With respect to facial masculinity, although the neurophysiological correlates of perceived sex of the face have been investigated (Mouchetant-Rostaing & Giard, 2003; Schyns, Bonnar, & Gosselin, 2002; Xu, Liu, & Kanwisher, 2005), only one study has investigated perception of sexually dimorphic face shape using ERPs. Cellerino et al. (2007) presented participants with profile views of gender-ambiguous faces and investigated perceptual masculinity based on a sex categorization task. They found that the right parieto-temporal N170 latency positively correlated with perceived masculinity, suggesting that the right parieto-temporal region plays a role in processing sexually dimorphic cues. However, given that the images were intentionally gender-ambiguous, the manipulation used by Cellerino et al. (2007) may not have been sufficiently salient to properly capture the encoding of sexually dimorphic face shape. Similarly, profile views of faces may not provide enough structural information related to sexually dimorphic shape because important dimorphic features are obscured or not fully visible (e.g., jaw width; Penton-Voak et al., 2001).

ERPs allow brain activity to be tracked with high temporal resolution and provide researchers with a way to study the brain's response to facial manipulations in real-time (i.e., as they happen), thereby offering important insight into the electrophysiology underlying perception. Here, given the importance of sexually dimorphic traits in person perception, we investigate how these cues are processed in the brain using ERPs. We demonstrate that neurophysiological correlates of face processing in women are sensitive to sexually dimorphic cues in male and female faces, providing novel insight into cognitive mechanisms (i.e., mental processes) mediating adaptive responses to facial sexual dimorphism. Given that most behavioral studies on facial sexual dimorphism have focused on women's responses and given that preferences for sexually dimorphic traits are less consistent across women as compared to men, ERPs were recorded from a sample of young adult women as they categorized faces

manipulated in sexually dimorphic shape as male or female. This work builds upon previous research (Cellerino et al., 2007) by using stronger manipulations of sexually dimorphic face shape. We predicted sexual dimorphism effects upon the right parieto-temporal N170, and further predicted effects upon the superior-central N250, on the assumption that processes reflected by this component are not exclusively tuned to race-specific structure (i.e., that this component may reflect expertise with faces more generally). We additionally examined whether sexual dimorphism manipulations trigger different neurophysiological responses (as measured by differences in ERP amplitude and latency) as a function of sex, indicating functionally distinct processing of sexually dimorphic cues in male versus female faces.

Methods

Stimuli

We manipulated images using prototype-based image transformation techniques. First, prototype male and female face images were made by averaging the shape, color, and texture of a group of male and a group of female faces (for more information, see Rowland & Perrett, 1995; Tiddeman, Burt, & Perrett, 2001). Next, 50% of the linear differences in 2D shape between these prototype faces were added to or subtracted from 40 unfamiliar male and 40 unfamiliar female face identities (all with neutral expressions). This generated 40 pairs of male faces and 40 pairs of female faces, with each pair consisting of a version enhanced and a version reduced in sexual dimorphism (see, e.g., Buckingham et al., 2006; Little et al., 2007b; Welling, DeBruine, Little, & Jones, 2009; see also Figure 1). Previous studies have verified that manipulating sexual dimorphism in this way influences perceptions in the predicted manner (DeBruine et al., 2006; Welling et al., 2007). Importantly, the masculine and feminine versions of each image differed equally in 2D shape from the original image, and pairs of images were matched in other regards (e.g., texture, color, and identity). Also, the image manipulation applied to male and female faces was identical.

The experiment was implemented using *Presentation 9.13*, with 4 randomized blocks of 40 trials, each containing 20 of the 80 face pairs (half female). Each image (20 male and 20 female) was presented once within each block in a random order.

Procedure

Heterosexual female participants ($N = 17$ adult White women, $M_{age} = 21$ years, $SD = 2.89$ years) were recruited through the Psychology Subject Pool at the University of Aberdeen (Scotland, United Kingdom) and participated in exchange for course credit. All participants had normal or corrected to normal vision and reported being right-handed. These women classified faces as male or female using a response box while electroencephalogram (EEG) was recorded in an electrically and acoustically shielded chamber. Participants responded *right button = female* and *left button = male* during blocks 1 and 3 and the opposite during blocks 2 and 4, as quickly as possible. Each face was presented for 200 ms, followed by a 600 ms blank screen, and then a 500 ms fixation cross followed by a 700–1700 msec blank screen. Trial durations were

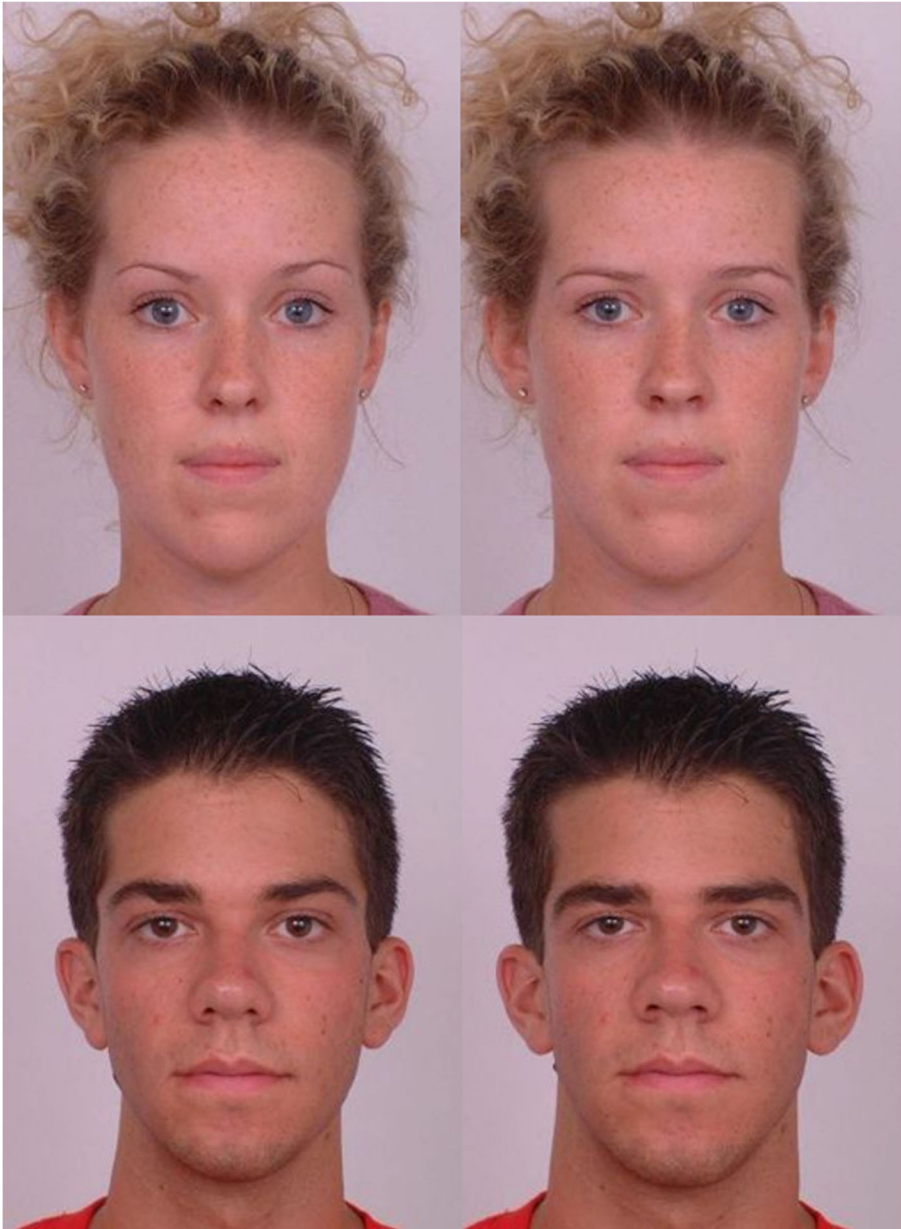


Fig. 1 Examples of female (top row) and male (bottom row) manipulated faces. Feminized versions are on the left and masculinized versions are on the right. Masculinized and feminized versions differ only in 2D shape and are identical in other regards (e.g., color, texture, and identity). Differences from average face shape are also constrained to be mathematically equivalent for each particular masculinized and feminized individual image. The manipulation therefore produces equivalently atypical, (i.e., distinctive) versions of each base identity

randomly set at 2000–3000 ms, in 200 ms jumps. This task allows us to measure categorical discrimination based on biological sex, as well as the influence of relevant fine-grained details (i.e., sexually dimorphic traits) in sex categorization, and how these details potentially correlate with ERP components involved in face processing.

ERP Derivation

Sixty-four-channel EEG data files were converted via the Polyrex conversion programme to a 16-bit resolution (gain .05) for processing in *Neuroscan Edit 4.3*. Following ocular artefact correction, data were bandpass filtered (.1 to 30 Hz), re-referenced to the common average, then epoched (100 ms pre- to 800 ms post-stimulus) and baseline corrected. Trials containing drift or saturation artefacts were rejected and data were smoothed using a 5-point binomial filter. ERPs were created from correct-response trials for the enhanced-male ($M_{\text{trials}} = 35.7$), reduced-male ($M_{\text{trials}} = 34.8$), enhanced-female ($M_{\text{trials}} = 34.9$), and reduced-female ($M_{\text{trials}} = 34.4$) conditions (i.e., masculinized male, feminized male, feminized female, and masculinized female, respectively).

Results

Behavioral Data

One-sample *t*-tests revealed that participants categorized faces in all conditions more accurately than chance (all $t > 40.66$, all $p < .001$, see Figure 2). Repeated-measures ANOVA [within-subjects factors: *sex of face* (male, female); *sexual dimorphism* (enhanced, reduced)] revealed only a main effect of *sexual dimorphism* upon sex discrimination ($F_{1,16} = 5.88$, $p = .03$, $\eta_p^2 = .269$), whereby enhanced sexual dimorphism faces were categorized with more accuracy than reduced sexual dimorphism faces (all other $p > .39$). Reaction time (RT) analyses (from trials where $RT > 150$ ms, see Kaufmann, Schweinberger, & Burton, 2009) revealed a main effect of *sexual dimorphism* ($F_{1,16} = 9.61$, $p = .007$, $\eta_p^2 = .375$), whereby enhanced sexual dimorphism faces were categorized faster. A marginal main effect of *sex of face* ($F_{1,16} = 4.12$, $p = .06$, $\eta_p^2 = .205$) emerged, reflecting faster identification of male versus female faces, and a *sex of face* by *sexual dimorphism* interaction ($F_{1,16} = 10.41$, $p = .005$, $\eta_p^2 = .394$). RTs were slower for masculinized female faces than for feminized female faces ($t_{16} = 5.14$, $p < .001$), with no equivalent effect for male faces ($p = .83$).

ERP Data

Figure 3 shows ERPs at left and right lateral inferior sites P7/P8 and the superior-central Pz site where the primary components of interest (N170 and superior-central N250) are located. Repeated-measures ANOVA of N170 mean amplitude (150–180 msec) [within-subject factors: *sex of face* (male, female); *sexual dimorphism* (enhanced, reduced); *site* (P7, P8)] produced no significant main effects or interactions (all $p > .08$). However, repeating this analysis using N250 mean amplitude data (230–270 msec) at Pz produced a main effect of *sexual dimorphism* ($F_{1,16} = 5.67$, $p = .03$, $\eta_p^2 = .262$) because superior-

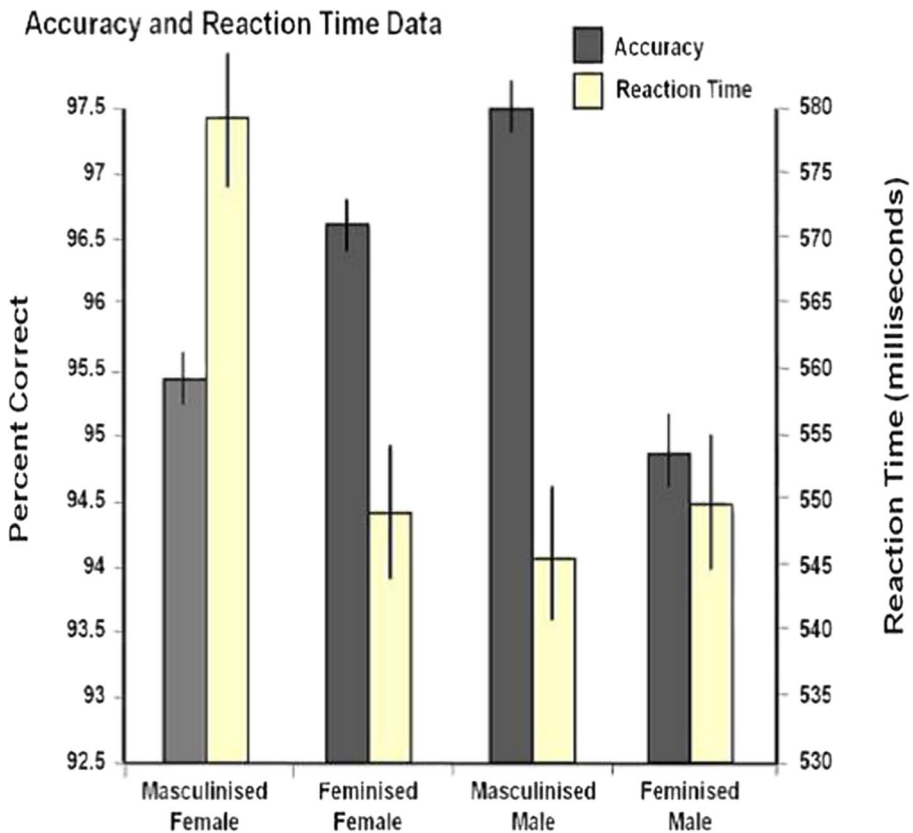


Fig. 2 Mean percent accuracy (out of 40, grey bars) and mean RTs (milliseconds, yellow bars) for all four conditions. Faces enhanced in sexual dimorphism (i.e., masculine male faces and feminine female faces) were categorized more accurately ($M = 97.1\%$, $SD = .04$) and faster ($M = 550$ msec, $SD = 82$) than reduced sexual dimorphism faces ($M = 95.1\%$, $SD = .04$; $M = 564$ msec, $SD = 94$). Male faces were also identified faster ($M = 546$ msec, $SD = 95$) than female faces ($M = 564$ msec, $SD = 83$). RTs were slower for female faces reduced in sexual dimorphism ($M = 580$ msec, $SD = 81$) than for female faces enhanced in sexual dimorphism ($M = 548$ msec, $SD = 84$), with no equivalent effect for male faces

central N250 amplitude was larger for reduced versus enhanced sexual dimorphism images (see Figure 4a), with no other effects (all $p > .65$). Inspection of Fig. 3 shows further differentiation between positive ERPs in each condition at the lateral inferior sites during the 230–270 msec interval. We analyzed this effect using repeated-measures ANOVA with the above factors, which gave only a main effect of *sex of face* ($F_{1,16} = 10.25$, $p < .008$, $\eta_p^2 = .390$; see Figure 4b) due to increased positivity of ERPs evoked by female versus male images (all other effects $p > .6$).

Analyses of lateral inferior peak latency data revealed sexual dimorphism by site interactions both for the N170 ($F_{1,16} = 6.39$, $p = .022$, $\eta_p^2 = .285$) and (marginally) the subsequent 230–270 msec positivity ($F_{1,16} = 4.23$, $p = .056$, $\eta_p^2 = .209$). ERPs peaked faster over the left hemiscalp at P7 for faces enhanced in sexual dimorphism (N170: 163 msec versus 166 msec, $t_{17} = 2.18$, $p < .05$; 230–270 msec positivity: 251 msec versus 258 msec,

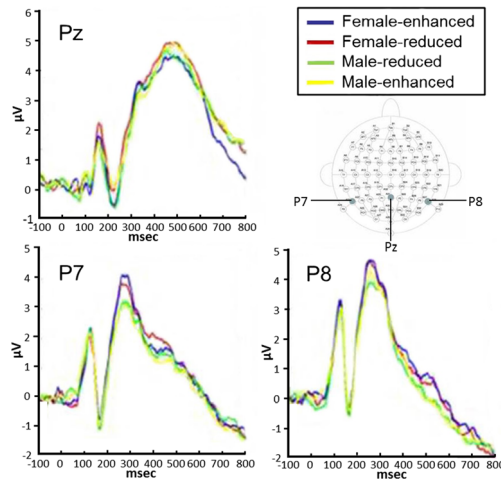


Fig. 3 Grand average ERPs contrasting all four image conditions at the superior-central Pz site and the lateral inferior P7 and P8 sites. Scalp locations are indicated on the inset. Clear lateral inferior N170 and superior-central N250 are evident and, in addition, a lateral inferior positivity enhanced for female versus male images

$t_{17} = 2.16, p < .05$). Note that prominent superior-central N250 peaks could not be identified reliably in all participants, as was the case in Balas and Nelson’s (2010) study, and so we too cannot provide superior-central N250 latency analyses.

Superior-central N250 Sexual Dimorphism Effect

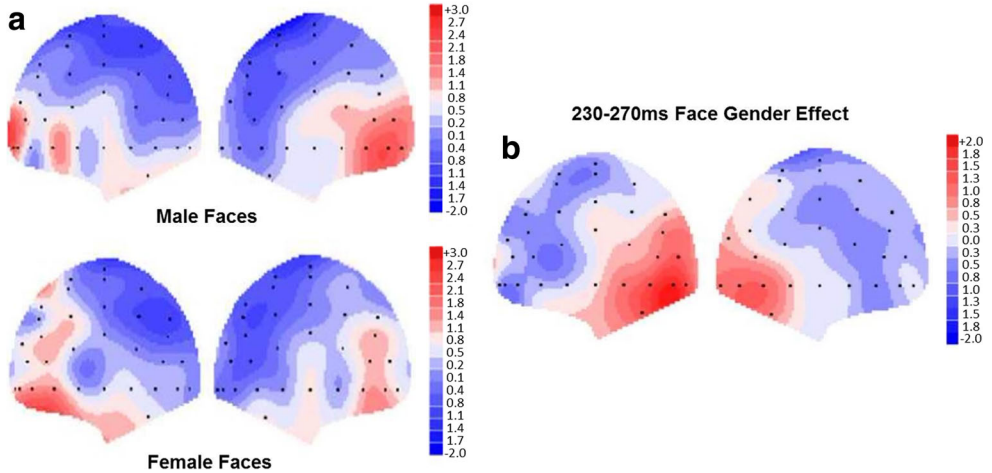


Fig. 4 (a) Topographic maps depicting left and right hemi-scalp as viewed from the side, illustrating the effect of sexual dimorphism upon the superior-central N250 during the 230–270 msec interval separately for male (top) and female (bottom) faces. Each map was created by subtracting ERPs in the enhanced conditions (i.e., masculinized male and feminized female) from ERPs in the respective reduced conditions (i.e., feminized male and masculinized female). (b) Topographic map of the lateral inferior face gender positivity observed during the 230–270 msec interval, created by subtracting ERPs evoked by male faces (average of the reduced and enhanced male face ERPs) from ERPs evoked by female faces (average of the reduced and enhanced female face ERPs). Electrode sites are shown as black squares, and the voltage range for each map is given in the color scales

Discussion

Reduced sexual dimorphism resulted in decreased overall accuracy and, for female faces, increased reaction times, suggesting that this manipulation affected within-category (i.e., within-sex) discrimination of facial features that signal biological sex. In other words, sexually dimorphic faces were easier to correctly categorize as male or female, especially for female faces. These behavioral data add to our ERP data; our key finding was that the superior-central N250 was largest for reduced sexual dimorphism faces regardless of their sex, extending Balas and Nelson's (2010) work by showing that superior-central N250 sensitivity is not limited to racial characteristics of face shape. In line with Balas and Nelson's (2010) expertise account of the superior-central N250 (see also Scott, Tanaka, Sheinberg, & Curran, 2006, 2008; Tanaka, Curran, Porterfield, & Collins, 2006), our findings suggest that correct categorization of faces with reduced sexual dimorphism requires sensitivity to fine-grained facial features that signal sex. Thus, faces that are less sex-typical (i.e., less sexually dimorphic) are more difficult to categorize with respect to biological sex, as suggested by our behavioral data, and this task difficulty is apparently reflected in enhanced N250 negativity in response to faces with reduced sexual dimorphism. Moreover, previous fMRI work investigating effects of sexual dimorphism on face perception (Rupp et al., 2009) identified five brain regions (i.e., superior temporal gyrus, precentral gyrus, anterior and posterior cingulate, and inferior parietal neocortex) previously related to either face or risk processing that showed increased activation to masculinized versus feminized male faces in women. Our findings complement this work by revealing neurophysiological correlates of face perception processes sensitive to sexual dimorphism, and by showing that common responses can be triggered in response to sexually dimorphic manipulations within male and female faces. These findings yield novel information regarding how features relevant to mate preferences and sex categorization are encoded in the brain.

Participants in our sample were quicker at categorizing male faces than female faces. It is possible that this categorical difference is reflected in the inferior lateral positivity observed during the 230–270 msec interval, which showed reduced positivity to male versus female faces. This positivity could be a P200 effect related to social categorization that is enhanced for same-sex versus opposite-sex images. Similar research has found enhanced P200 effects for “in-group” versus “out-group” individuals in terms of ethnicity (Ito & Urland, 2003, 2005; see also Kubota & Ito, 2007; Stahl, Wiese, & Schweinberger, 2010) and age (Wiese, Schweinberger, & Hansen, 2008). In support of this conclusion, Latinus and Taylor (2006) previously demonstrated faster P200 latency for upright faces when compared to inverted faces, Mooney faces, and non-face stimuli, and this was coupled with faster N170 peak latency. Correspondingly, we find that the peak latencies of the N170 and the subsequent putative P200 over the left hemi-scalp are similarly affected by sexual dimorphism. Although Cellerino et al. (2007) found longer N170 latency to faces perceived as masculine, they used gender-ambiguous faces, which may have been more complex to process. Here we used sex-typical faces that varied in the degree of sexual dimorphism and found that enhanced (i.e., more sex-typical) faces were related to earlier N170 peak latencies, perhaps suggesting, as our behavioral data suggests, that they are easier to process than faces with reduced sexual dimorphism. Alternatively, differences in the observed inferior lateral positivity may

reflect greater ease of perceptual processing for mating-relevant (i.e., male) faces, but this interpretation is highly speculative and additional work would be needed to investigate the mate choice specificity of this component. Regardless, because the superior-central and lateral inferior ERP modulations were differentially sensitive to sexual dimorphism and sex, we suggest that these two effects could reflect the concurrent activation of functionally distinct processes (i.e., shape processing versus sex categorization).

There are several limitations of the current work. First, our sample consisted of only 17 women. However, we note that small sample sizes are commonplace in the ERP literature and similar research has made use of comparable participant numbers (i.e., $N = 14$, 12 female, Balas & Nelson, 2010; $N = 20$, 10 female, Cellerino et al., 2007). Still, future work could use a larger sample with more varied demographic characteristics (e.g., different ethnicities or sexual orientations). Similarly, future work could test males so that inferences can be made about whether differences between male and female stimuli reflect properties of male versus female faces or same- versus different-sex expertise in face processing. Researchers could also have participants rate or categorize faces for attractiveness within short-term and long-term mating contexts, which has been shown to influence preferences for sexually dimorphic face shape (e.g., Little et al., 2002). Male and female participants could rate the attractiveness of both sexes to assess whether more attractive faces are processed more quickly. Finally, although our results aligned well with the race-related face shape findings reported by Balas and Nelson (2010), suggesting that the N250 component may reflect expertise in correctly categorizing faces based on subtle aspects of face shape, we did not test other aspects of expertise in faces or other stimuli. Future research could include additional conditions related to face shape (e.g., ethnicity) and/or a non-face condition to see whether results are relatively specific to dimorphic face shape or if they generalize to expertise in other domains.

Sexually dimorphic facial cues are important both for women's mate preferences and for assessing same-sex competitor mate-quality (e.g., Perrett et al., 1998). Therefore, sexual dimorphism manipulations may trigger an evaluative response in regard to mate quality that is common to male and female faces, although perception of mate quality was not directly tested in the current study. Our data are consistent with this conclusion, revealing identical ERP effects (increases in superior-central N250 magnitude and alterations in left lateral inferior ERP peak latencies) triggered by reduced versus enhanced sexual dimorphism in male and female faces. A necessary caveat is that neural generators independently sensitive to male versus female sexual dimorphism may co-exist within the same regions, producing the similar male and female ERP effects related to sexual dimorphism observed here. Importantly, future ERP work can now explore the various individual difference factors (e.g., Jones et al., 2005; Vukovic et al., 2009; Welling et al. 2007, 2008b, 2008c) that influence female sexual dimorphism preferences, which may allow sexual dimorphism effects triggered by male and female faces to be neurally dissociated. This, in turn, should lead to a better functional characterization of the cognitive mechanisms underlying adaptive behavioral responses to sexual dimorphism. These same techniques can later be applied to investigate how other cues to mate quality and attractiveness (e.g., averageness, symmetry, color cues to health; see, e.g., Little et al., 2011; Mogilski & Welling, 2017) are processed in the brain. Furthermore, eventual research could investigate how ERP components

associated with sexual dimorphism and other cues to mate quality are influenced by different contexts where cues to genetic fitness should be prioritized, such as under harsher environmental conditions (DeBruine et al., 2010, 2011; Little et al., 2007b), thereby bridging the evolutionary psychology and perceptual neurology literatures.

Compliance with ethical standards

Conflict of Interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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