While some researchers have suggested that preferences for attractive faces are the result of a domain-specific beauty detection module, others argue these preferences develop based on averages of stimuli through a domain-general learning mechanism. We tested whether cognitive and perceptual mechanisms sensitive to experience underlie facial preferences by familiarizing participants with human, chimpanzee, or morphed faces (60%-chimp/40%-human). Results indicated that participants familiarized with human-chimp morphs showed greater zygomaticus major activity, a physiological correlate of positive affect (Study 1), and higher explicit attractiveness ratings (Study 2) to faces morphed to some degree with chimpanzees. These results demonstrate that experience shifts attractiveness preferences away from the normative average, and suggest that a domain-general cognitive mechanism better accounts for facial preferences than a domain-specific innate beauty-detector.

Both children and adults agree on which faces are attractive or unattractive within and between different cultures. Moreover, even young infants prefer attractive faces (Langlois et al., 1987, 2000; Langlois, Ritter, Roggman, & Vaughn, 1991). These findings have led some researchers to conclude that humans and other animals come equipped with a beauty-detecting mechanism such that attractiveness preferences are innate, present at birth, and the result of evolved reproductive advantage because attractiveness is thought to be an honest signal of health, fitness, and mate value (Møller & Zamora-Muñoz, 1997; Symons, 1995; Thornhill &
Gangestad, 1999). Rather than an innate template, evolution may have provided a domain-general information processing mechanism to cognitively average across exemplars of a category. The central tendency of a category, called a prototype, is often preferred over exemplars distant from the central tendency and is developed through experience (Reed, 1972; Rosch, 1973). Research shows that faces created by averaging individual faces together are attractive (e.g., Langlois & Roggman, 1990; Rhodes, Halberstadt, Jeffery, & Palermo, 2005). Thus, evolutionary and cognitive theories of attractiveness differ regarding what has evolved (domain-specific vs. domain-general mechanisms of beauty detection) and the role of experience in preferences for attractive faces.

We sought to determine whether cognitive and perceptual mechanisms sensitive to the environment underlie preferences for attractive faces by manipulating exposure to faces. If facial preferences are the product of an information processing mechanism sensitive to the environment, experience should influence such preferences; if facial preferences are based on an innate domain-specific beauty template necessarily tied to mate value, experience should make little difference. The following sections briefly elucidate the predictions made by domain-specific and domain-general theories of facial attractiveness regarding the effect of experience, followed by the description of a methodology that could provide support for either hypothesis.

DOMAIN-SPECIFIC VERSUS DOMAIN-GENERAL THEORIES OF FACIAL PREFERENCE ORIGIN

Domain-specific accounts of facial preference maintain that attractive faces are preferred because they advertise good health and mate value. Thornhill and Gangestad (1999) argue that certain facial features (e.g., clear eyes, smooth skin) are linked with health, reproductive fitness, and superior immune functioning. Furthermore, male facial attractiveness has been linked to the quality of their semen (Soler et al., 2003); it is assumed—though unproven—that better sperm carry better genes that produce healthy progeny. Thus, facial cues associated with better genes should be preferred over time.

Alternatively, a domain-general mechanism such as cognitive averaging theory asserts that attractive faces are preferred because they are closer to the central tendency of the category and thus more prototypical (Langlois & Roggman, 1990). Preferences for prototypes are consistently found for several categories including dot patterns (Bomba & Siqueland, 1983; Winkielman, Halberstadt, Fazendeiro, & Catty, 2006), colors (Martindale & Moore, 1988), birds, fish, and cars (Halberstadt & Rhodes, 2003). Langlois and Roggman (1990) created a prototype1 face by mathematically averaging the pixel values of different facial images on a computer. They discovered that the novel averaged face was rated as more attractive than most of its individual faces. Studies have since demonstrated that attractive faces cluster near the averaged prototype face in face-space (a geometric model of per-

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1. Although there is debate in the cognitive psychology literature regarding whether prototypes are abstracted or exemplars are stored in memory, it is not relevant for our purposes (see Rubenstein, Kalakanis, & Langlois, 1999 for a discussion). In this article we use the term prototype as shorthand to refer to the average facial configuration of the population.
ceptual similarities), providing evidence that attractive faces are preferred because they are prototypical (e.g., Potter & Corneille, 2008).

Although domain-specific mate-selection theories of facial attractiveness do not exclude the possibility that humans should be sensitive to their surroundings (indeed, this would be a disadvantageous design), if these mechanisms evolved to enhance mate selection, facial preferences should not change when confronted with faces that dramatically violate categorical norms. For example, we would expect that a person whose experience was limited to Caucasian faces would prefer Caucasian faces to Asian faces; however, upon moving to Asia, both mate-selection and cognitive averaging theories would predict that this person’s facial preferences would shift: the former because it is no longer advantageous to mate with a Caucasian—who are few and far between—and the latter because an environment of primarily Asian faces would have shifted the person’s central tendency toward an Asian exemplar. On the other hand, these two theories’ predictions should diverge when target faces shift toward a disadvantageous mating option (e.g., a non-human).

Thus, to test the effect of experience we exposed study participants to morphs of human and chimpanzee faces. If people have an innate beauty template tied to reproductive fitness, experience should not significantly shift preferences toward a simian face because this option represents a poor mate choice. On the other hand, if facial preferences are the result of a domain-general learning mechanism, preferences should reflect prior exposure even in the extreme case of a normatively unattractive face.

ELECTROPHYSIOLOGICAL CORRELATES OF AFFECT
AS A PROXY FOR PREFERENCE

Because stimuli that differ in attractiveness and prototypicality are known to elicit differential physiological affective responses (e.g., Principe & Langlois, 2011; Winkielman et al., 2006), we assessed affect using facial electromyography (EMG). Particular muscle activity indicates valenced affect; for example, activation of the zygomaticus major (ZM) is positively correlated with liking ratings ($r = .52$; Larsen, Norris, & Cacioppo, 2003). Although ZM is generally sensitive to only strong changes in valence (Larsen & Norris, 2009), it has been used successfully to detect prototypicality differences in dot patterns (Winkielman et al., 2006).

STUDY 1

METHOD

Participants and Familiarization Stimuli. We recruited 72 adults (26 male) through a research participation course requirement. We did not use data for participants in which experimenter error ($n = 4$), or equipment error ($n = 4$) occurred, leaving a final sample of 64 participants. We randomly assigned participants to three groups. Control Group 1 ($n = 20$; 7 male) viewed 15 human faces (7 male), posed with neutral facial expressions and clothing cues obscured; Control Group 2 ($n =$
15; 5 male) viewed 15 chimpanzee faces retrieved from a Google image search of “chimpanzees”; and Experience Manipulation Group (n = 29; 10 male) viewed 15 chimp-human morphs (60%-chimp/40%-human). We reasoned that because all participants should come into the lab with pre-existing categories of human and of chimp faces (but not a preformed category of chimp-human morphs), we did not expect to find evidence of a prototype or preference shift for either of these complementary control groups. A nonsignificant repeated-measures ANOVA with group as the between-subjects factor and degree of humanness as the within-subject factor supported this hypothesis (p > .25); thus, we collapsed across Control Groups 1 and 2—henceforth referred to as the Control Group.

Test Stimuli. After each group was familiarized with their respective group of 15 faces, all participants viewed 10 test faces. Three of the 10 test faces included: a 100% Caucasian female 32-face average, a 100% Caucasian male 32-face average, and a 100% chimp 32-face average (see Figure 1). The other seven test faces were morphed faces created by combining either the male or female 32-face average with the chimp 32-face average in 10% increments from 10%-chimp/90%-human to 70%-chimp/30%-human (see Figure 2).

Procedure. Participants sat 1.5 m away from a monitor. Two experimenters placed nine Ag/AgCl electrodes on the left side of the face including the zygomaticus major (see Fridlund and Cacioppo, 1986 for electrode locations). We reported additional electrophysiological data in a separate publication (see Principe & Langlois, 2011). Participants first saw a face-sized black dot to serve as a psychological baseline. After the baseline, we displayed each of the 15 familiarization-phase faces in a random order for 2 s each, with a variable ISI of 4–8 s. Ten test faces, also presented in a random order, immediately followed these faces.

Data Acquisition and Treatment. A Biopac MP150 acquisition system with shielded bipolar leads recorded data. We amplified the signal 5,000x with a high-pass filter of 10 Hz, digitized at 1,000 Hz. We video recorded participants to identify and discard movement artifacts (e.g., a sneeze) associated with the presentation of stimuli. The index of EMG activity was the root-mean squared activity of the 2-s stimulus event minus 2 s of baseline activity (see Fridlund & Cacioppo, 1986 for data processing options). Given the nested structure of our data (stimuli within participants) and the fact that not all participants saw all stimuli, we used hierarchical linear modeling to determine the relationships between Level 1 variables (stimuli-related—i.e., ZM activity, attractiveness, degree of humanness) with...
Level 2 variables (participant-related—i.e., sex). For the sake of brevity, we report only the final significant model using the notation established by Raudenbush and Bryk (2002).

Predictions. We predicted that participants familiarized to human-chimp morphs would show significantly less ZM activity to 100% human averages and greater ZM activity in response to simian averages compared with participants familiarized to 100% humans or to 100% chimps. Importantly, we did not expect that a short lab exposure would entirely override years of experience with human faces; in other words, exposing participants to ambiguous facial stimuli should not result in greater liking for ambiguous stimuli (e.g., 50/50 or 60/40 morphs) compared with prototypical human faces. Instead, preferences should shift toward faces with a small influence of “chimpiness”; thus, we confined our major analyses to test faces with 0%, 10%, 20%, or 30% degrees of chimp influence. Note that cognitive averaging theory also suggests that people should have preferences for prototypical chimp faces and experience with faces that deviate from chimp prototypes should also shift preferences away from these faces; however, because we know of no theory that specifically states that preferences for attractive animals are related to fundamental issues of genetic survival, we examined only prototype shifts away from the human norm. Previous work has demonstrated that perceptions shift after familiarization to non-prototypical faces (see Anzures, Mondloch, & Lackner, 2009; Cooper & Maurer, 2008; and Rhodes, Jeffery, Watson, Clifford, & Nakayama, 2003 for a discussion of perceptual aftereffects in faces) and that experience with faces enhances liking (e.g., Shimojo, Simion, Shimojo, & Scheier, 2003); no study, however, has examined whether preferences will change for the averaged/prototype face itself after exposure to non-prototypical faces. Furthermore, although Winkielman et al. (2006) used EMG to measure changes in physiological positive affect associated with changes in the prototypicality of dot patterns and shapes, this study is the first to use the same method for changes in facial prototypicality.

Finally, if ZM activity is elicited not only as a correlate of general positivity and liking for prototypes, but also as an attractiveness indicator, we should see a face-sex by participant-sex interaction such that female participants will have greater ZM activity to male faces, whereas male participants will have greater ZM activity to female faces regardless of the degree of divergence from the prototype.
As expected, an HLM analysis revealed a significant interaction between experience and degree of humanness, $\beta = 0.04$, $t(301) = 2.21$, $p = .03$ (see Figure 3). Participants exposed to chimp-human morphs showed greater ZM activity to 10%-chimp/90%-human and 20%-chimp/80%-human morphs compared with the original 100% human average. Participants whose experience was confined to known facial categories (i.e., humans or chimps) did the reverse and elicited higher ZM activity to 100% human faces compared with the morphs.

In addition to the interaction between experience and degree of humanness variables, we also found a significant interaction between face-sex and participant-sex, such that female participants showed higher ZM activity to male faces and male participants showed higher ZM activity to female faces, regardless of degree of humanness, $\beta = -0.10$, $t(304) = -2.51$, $p = .01$. Finally, the full HLM model had a significant random intercept, signifying a large amount of variability in our data is attributable to individual differences in ZM responses ($\rho = .57$; i.e., 57% of the variability between participants is explained by individual differences in affectivity—however, these differences did not differ across stimuli). Equation 1 shows the full significant model.

Formula: $ZM$ activity $= \beta_0 + \beta_1(Humanness) + \beta_2(Face-Sex) + \beta_3(Participant-Sex) + \beta_4(Experience) + \beta_5(Face-Sex*Participant-Sex) + \beta_6(Humanness*Experience) + \varepsilon$

where $\beta_0 = \gamma_{00} + u_0$

(1)

A key limitation of Study 1 is that, although ZM activity may be an implicit marker of positive affect and attractiveness judgments, this muscle response is not an explicit indictor of changes in preference. Thus, we conducted a second study to provide additional evidence that experience directly influences facial preferences.

STUDY 2

METHOD

Participants and Stimuli. We recruited 49 undergraduate adults (12 male) to provide explicit attractiveness ratings of the same faces used in Study 1. Participants received course credit in exchange for volunteering for this study.
Procedure. Participants sat 1.5 m from a computer screen with a keyboard. Based on the results of Study 1, we randomly divided participants into two groups. Group 1 saw 15 human faces \( (n = 13) \) or 15 chimp faces \( (n = 12) \); Group 2 saw 15 60/40 chimp-human morphs \( (n = 24) \). In individual sessions, we presented 15 faces on the computer one at a time in a random order. Participants rated each face for attractiveness on a 7-point scale by pressing the key that corresponded to their rating. After making each rating, the next face immediately appeared. Following the 15th face, participants rated, in a random order, the test faces from Study 1.

Predictions. Because Study 2 participants made conscious attractiveness judgments for faces that had been morphed with chimpanzees, we expected that the effects found in Study 1 would be reduced (i.e., participants exposed to 60/40 chimp-human morphs may not rate a 20/80 chimp-human morph as significantly more attractive than the 100% human face); however, we still expected that differential experience would predict how the prototype-morphed test faces would be rated. Specifically, participants exposed to 60/40 morphs should rate prototype-morphed faces significantly higher than the group exposed to only human or chimp faces. In addition, those who saw humans or chimps in the first set of faces should rate the 100% human prototypes as more attractive than the group of participants exposed to human/chimp morphs.

RESULTS AND DISCUSSION

Despite the fact that participants provided explicit attractiveness judgments of images morphed across species, experience once again significantly interacted with the degree to which the prototype test face had been morphed with a chimpanzee, \( \beta = .01, t(338) = 2.86, p < .01 \). As the prototype-morphed test faces decreased in
humanness, the disparity of attractiveness ratings between groups of participants differing in exposure increased such that those exposed to 60/40 morphs rated prototyped-morphed faces higher than participants exposed to human or chimp faces (see Figure 4). Unlike Study 1, participants who were exposed to 60/40 chimp-human morphs did not significantly prefer any of the prototype-morphed test faces to the 100% human average (although the mean difference between the prototype and the 10/90 chimp-human morph approached significance; \( p = .12; dz = 0.15 \)).

As in Study 1, we also found a significant interaction between face-sex and participant-sex, \( \beta = -0.53, t(338) = -2.44, p = .02 \). Regardless of degree of humanness, both male and female participants rated female faces more attractive than male faces; however, male participants rated female faces more attractive and male faces less attractive than female participants. The finding that female faces were rated more attractive in general is typical of the attractiveness literature (e.g., Ramsey, Langlois, & Marti, 2005). Additionally, we found an interaction between the degree of humanness and face sex such that although female faces were rated as more attractive than male faces, as the degree of humanness decreased, ratings for female faces decreased at a much faster rate than male faces. This result is likely due to the fact that chimp morphs increase the perception of masculinity in faces (i.e., large brows and wide jaws). Previous facial attractiveness research has shown conclusively that increasing the masculinity of female faces significant decreases their attractiveness compared to masculine male faces (e.g., Hoss, Ramsey, Griffin, & Langlois, 2005). Finally, the full HLM model had a significant random intercept, signifying that a large amount of variability in our data is attributable to individual differences in attractiveness responses (\( \rho = .55; i.e., 55% \) of the variability between participants is explained by individual differences in how they used the 7-point scale—however, these differences did not change across stimuli). Equation 2 shows the full significant model.
The results of these studies revealed that experience influences physiological affect and explicit attractiveness judgments, even in the extreme case of faces morphed with chimpanzees. Combined, these findings suggest that experience and affect are mechanisms that underlie attractiveness preferences. Although *zygomaticus major* (ZM) activity is typically regarded as a correlate of a generalized positive affective response rather than a specific response to attractiveness, there are complementary findings that support the supposition that ZM is an indicator of affective preferences for facial attractiveness. First, as mentioned previously, Winkielman and colleagues (2006) showed that more prototypical dot patterns are judged as more attractive and elicit more ZM activity. Furthermore, we discovered that female participants exhibit more ZM activity to male faces, whereas male participants showed more ZM activity to female faces. Although the Winkielman finding could indicate general liking, combined with the sex differences in our study, the ZM might also respond specifically to attractiveness. Furthermore, although Study 1’s effect was attenuated in Study 2, we nevertheless demonstrated that explicit attractiveness ratings follow the same pattern, providing evidence that the ZM responds to differences in attractiveness perception.

Theoretically, our results better conform to a domain-general explanation of attractiveness preferences than to a domain-specific mate selection explanation because if responses to attractiveness are based on cues to good health and good genes, they should not be triggered by stimuli that are (a) artificially invented; (b) not viable; and (c) normatively less attractive to humans. Note that one could possibly argue the reverse of our position: that facial preference mechanisms are based on health and mate value and because this mechanism is so important to the propagation of the species, it has been co-opted by non-human stimuli. We argue, however, that if such a mechanism functions across domains, it is necessarily (and currently) a domain-general mechanism and that our results support the conclusion that experience with non-human faces shifts prototype-based preferences. Put another way, we cannot know whether the mechanism that underlies facial attractiveness evolved as a mate-detector or as a general information processor; however, our data support the theory that, in practice, the modern brain functions as the latter.

Although not directly observed, we conjecture that the results of Studies 1 and 2 are based on a domain-general learning mechanism that incorporates recent experiences into either a human-face prototype or triggers non-human exemplars from memory. Past research has demonstrated that in spite of nearly universal rank order agreement about who is and is not attractive both within and across cultures (Langlois et al., 2000), there are mean differences in attractiveness preferences based on local environments (e.g., the Other-Race Effect [ORE]; see Kelly et
al., 2007). The current research suggests that the differences in facial preference seen in the ORE are the result of experience and a flexible information processing mechanism. Indeed, the idea of a constantly updated facial prototype is consistent with recent work suggesting that central tendencies are extracted from visual stimuli, such as two-dimensional black discs, across time (Albrecht & Scholl, 2010).

Interestingly, there may be a threshold effect of experience. For example, even with differential experience, affect significantly decreased when humanness was less than 80% (Study 1; see Figure 3) and explicit attractiveness ratings decreased when humanness was less than 90% (Study 2; see Figure 4). Furthermore, there was no significant relationship between experience and humanness for test faces with more than 30%-chimp influence ($p > .25$). Future research should attempt to replicate whether there is a threshold effect in other stimuli domains. If such a threshold exists, this finding may indicate that there is a categorical boundary beyond which prototype shifts are unlikely. For example, Study 1 participants may have been able to incorporate 20% of the chimpanzee average into their cognitive central tendency, but at 30% the face no longer fit into the human face category. Studies in this vein may help ascertain new information regarding how people categorize and under what conditions. The threshold concept may be particularly interesting in stereotyping studies (e.g., how many degrees away from an in-group prototype member can one be before one is no longer in the in-group?)

In some respects, the question of whether humans are born with a beauty detector is an attractiveness-specific version of the debate concerning the “specialness” of facial stimuli. Much research has shown that facial recognition processes are different from non-face object recognition processes (e.g., Farah, 1996; Grill-Spector, Knouf, & Kanwisher, 2004). Two theories provide different explanations for this phenomenon. One theory suggests that the way faces are processed is unique to faces (e.g., Kanwisher, 2000; Robbins & McKone, 2007). Alternatively, others have argued that objects with which a person has expertise can mimic “special” facial processing (e.g., Gauthier & Bukach, 2007; Wong, Palmeri, & Gauthier, 2009).

Although cognitive mechanisms that recognize faces are likely closely related to those that recognize facial attractiveness, they may not be identical; thus, we cannot say that our results provide direct support for the expertise hypothesis. Nevertheless, if facial processing were governed by a domain-specific mechanism responsive only to faces, it is unlikely that brief exposure to non-prototypical animal-morphs would have altered facial preferences. Furthermore, our results match previous findings that show physiological affect changes with respect to typicality in dot patterns and shapes (Winkielman et al., 2006) and supports recent work demonstrating that experience alters perceptions of prototypicality in novel categories based on a general learning mechanism (Davis & Love, 2010).

One limitation of this research is that we cannot know whether affective response is merely a correlate of facial processing and experience, or whether it is causative in attractiveness judgments. Future studies should investigate the specific role affect plays in attractiveness judgments and as a potential precursor or outcome of other stereotype-related cognitions and perceptions.
REFERENCES


