Research Article

Psychological Science
24(11) 2297–2305

DOI: 10.1177/0956797613493293
pss.sagepub.com

Adaptation to Faces and Voices: Unimodal, Cross-Modal, and Sex-Specific Effects

Anthony C. Little[1], David R. Feinberg[2], Lisa M. DeBruine[3], and Benedict C. Jones[3]
[1]Division of Psychology, School of Natural Sciences, University of Stirling; [2]Department of Psychology, Neuroscience and Behaviour, McMaster University; and [3]Institute of Neuroscience and Psychology, University of Glasgow

Abstract

Exposure, or adaptation, to faces or voices biases perceptions of subsequent stimuli, for example, causing faces to appear more normal than they would be otherwise if they are similar to the previously presented stimuli. Studies also suggest that there may be cross-modal adaptation between sound and vision, although the evidence is inconsistent. We examined adaptation effects within and across voices and faces and also tested whether adaptation crosses between male and female stimuli. We exposed participants to sex-typical or sex-atypical stimuli and measured the perceived normality of subsequent stimuli. Exposure to female faces or voices altered perceptions of subsequent female stimuli, and these adaptation effects crossed modality; exposure to voices influenced judgments of faces, and vice versa. We also found that exposure to female stimuli did not influence perception of subsequent male stimuli. Our data demonstrate that recent experience of faces and voices changes subsequent perception and that mental representations of faces and voices may not be modality dependent. Both unimodal and cross-modal adaptation effects appear to be relatively sex-specific.

Keywords

aftereffects, experience, face and voice processing, prototypes, categories, auditory perception, face perception, cognitive processes

Received 6/29/12; Revision accepted 5/14/13

Adaptation refers to the phenomenon whereby exposure to stimuli influences subsequent perception. In the visual domain, adaptation to color can be readily seen; exposure to red stimuli, for example, causes a short-lived aftereffect resulting in subsequent stimuli appearing greener (green is the opposite of red in color space). In recent years, there has been much interest in face adaptation as an example of higher-order adaptation (for a review, see Webster & MacLeod, 2011). Many studies have demonstrated that exposure to faces biases subsequent perceptions of novel faces by causing those that are similar to the initially viewed faces to appear more prototypical than they would otherwise be perceived (Leopold, O'Toole, Vetter, & Blanz, 2001; Leopold, Rhodes, Muller, & Jeffery, 2005; Little, DeBruine, & Jones, 2005; Little, DeBruine, Jones, & Waitt, 2008; Rhodes et al., 2004; Webster, Kaping, Mizokami, & Duhamel, 2004). Adaptation studies have also indicated that mental representations of some categories of faces can be manipulated independently. For example, opposite aftereffects can be induced for male and female faces (Bestelmeyer et al., 2008; Jaquet & Rhodes, 2008; Little et al., 2005), such that the perception of female faces and the perception of male faces are simultaneously moved in opposite directions (e.g., adaptation to male faces with wide eye spacing and female faces with narrow eye spacing causes subsequently seen male faces to appear as more normal if they have widely spaced eyes and female faces to

Corresponding Author:
Anthony C. Little, Division of Psychology, School of Natural Sciences, University of Stirling, Stirling, FK9 4LA, United Kingdom
E-mail: anthony.little@stir.ac.uk

appear as more normal if they have narrowly spaced eyes; Little et al., 2005).

Like vision, audition is susceptible to adaptation effects: Experience alters the perception of subsequently heard stimuli. Adaptation occurs for aspects of sound such as pitch and loudness (D'Alessandro & Norwich, 2009; Phillips, Scovil, Carmichael, & Hall, 2007), as well as for human voice identity (Belin & Zatorre, 2003). In studies similar to those investigating visual adaptation, exposure to voices of one gender causes subsequent probe voices to be perceived as being of the opposite gender (Schweinberger et al., 2008) in the same way that exposure to female faces, for example, causes ambiguous faces to appear more male (Webster et al., 2004). Other studies have demonstrated that emotional voices also cause adaptation effects, with exposure to angry vocalizations causing subsequent voices to be perceived as less angry than they would be otherwise (Bestelmeyer, Rouger, DeBruine, & Belin, 2010). Again, these effects are analogous to the effects of adaptation to emotional faces (Webster et al., 2004).

Although most studies of adaptation have been focused on a single modality, there is potential for cross-modal effects. Indeed, there is evidence that auditory and visual information interact to influence perception (Shams, Kamitani, & Shimojo, 2000, 2002; Shimojo & Shams, 2001; Stein, London, Wilkinson, & Price, 1996). The McGurk effect is a famous example of cross-modal effects: When people view lips making speech movements while they listen to ambiguous sounds, the patterns of the lip movement can influence what they hear (McGurk & Macdonald, 1976). Indeed, perceiving such lip movement is correlated with activity in the auditory cortex (Calvert et al., 1997). Cross-modal effects are not limited to speech perception, however. For example, presenting auditory (van der Zwan et al., 2009) or odor (Kovacs et al., 2004) cues to sex simultaneously with visual stimuli modulates classification judgments of the sex of the visual stimuli. In a variety of areas, including emotion and identity, there is much evidence for cross talk between sound and vision (see Campanella & Belin, 2007).

Currently, however, the evidence for cross-modal adaptation is mixed. In cross-modal studies, auditory or verbal representations of emotion did not influence subsequent face perception (Fox & Barton, 2007), and exposure to male or female faces did not subsequently influence the perception of sex in voices (Schweinberger et al., 2008). In contrast, cross-modal adaptation was demonstrated in a study in which adaptation to the voices of specific identities influenced subsequent perception of facial identity (Hills, Elward, & Lewis, 2010). Even within modality, there is mixed evidence that adaptation crosses stimulus types. For example, visual aftereffects for the perception of male and female hands and faces were not seen when the adaptor and test stimuli belonged to different categories (i.e., adaptation to hands did not affect the perception of faces and vice versa; Kovacs et al., 2006). In contrast, adaptation to body shape has been shown to influence subsequent perception of faces (Ghuman, McDaniel, & Martin, 2010).

Given the mixed evidence for cross-modal adaptation, in the current series of experiments we examined the extent to which adaptation effects cross modalities. In addition, as previous studies have shown that adaptation effects are weakened when the adaptor and test stimuli are of different sexes (faces: Bestelmeyer et al., 2008; Little et al., 2005; voices: Zaeske & Schweinberger, 2011), we examined whether both facial and vocal adaptation cross gender categories.

We adopted a blocked adaptation paradigm with a pretest and a posttest. In this paradigm, baseline perception is established, a block of adaptor stimuli is presented, and a postadaptation test is administered to assess whether there has been any change from baseline. This method has been used in many previous studies (Hills et al., 2010; Little et al., 2005; Little et al., 2008; Rhodes et al., 2004; Zaeske & Schweinberger, 2011). We used this method for two reasons. First, the only study to have demonstrated cross-modal adaptation used this same methodology, with a 60-s voice clip acting as an adaptor stimulus (Hills et al., 2010). Second, alternative paradigms in which perception of a target stimulus is measured immediately after presentation of an adaptor stimulus may be problematic in examining cross-modal effects because there is evidence that simultaneous presentation leads to positive (additive) effects rather than the negative aftereffects seen in such adaptation studies. For example, in a task in which participants are asked to state the number of flashes on a computer screen, presentation of more than one accompanying beep when a visual flash is presented causes participants to perceive multiple flashes, such that the number of visual stimuli is seen as more congruent with the number of auditory stimuli (Shams et al., 2000). Similarly, simultaneous presentation of emotional body expression biases recognition of the emotional tone of voices to be in line with, not opposite to, the body expression (Van den Stock, Righart, & de Gelder, 2007).

General Method

Our four experiments involved female and male faces and voices. Both faces and voices were manipulated to be either more sex typical or more sex atypical. Participants were allocated to one of two adaptation conditions, in which they were adapted to either sex-typical (feminized) female stimuli or sex-atypical (masculinized) female stimuli (see Fig. 1 for examples of the face stimuli and an illustration of the experimental paradigm).

The procedure began with a pretest in which participants' perception of the normality of feminine and masculine stimuli was assessed. In this test, pairs of female stimuli and pairs of male stimuli were presented. Half the individual stimuli in the female pairs were also used in the adaptation phase (*adapted* stimuli), and half were not (*unadapted* stimuli). No male stimuli were used in the adaptation phase, so all male stimuli were unadapted. Using adapted and unadapted stimuli allowed us to (a) determine the effects of adaptation on perception of the adapted stimuli and (b) examine how well adaptation effects generalize to new stimuli. In each test pair, one stimulus was masculinized, and one was feminized. Participants were asked to indicate which stimulus was "more normal looking" or "more normal sounding." In the subsequent adaptation phase, participants were exposed to either a set of feminized female stimuli (*feminine* condition) or a set of masculinized female stimuli (*masculine* condition). Finally, after the adaptation phase, participants completed the normality test again (posttest).

In all four experiments, participants were volunteers and completed the study under laboratory conditions.

Experiment 1

In Experiment 1, we investigated visual adaptation, examining how exposure to sex-typical or sex-atypical versions of female faces influenced the subsequent perception of female faces that had been seen in the adaptation phase, female faces that had not been seen in the adaptation phase, and male faces.

Method

Participants. There were 68 participants in Experiment 1 (50 women, 18 men; mean age = 20.6 years, *SD* = 4.0).

Stimuli. We constructed all stimuli using established (Little et al., 2005; Perrett et al., 1998) techniques for manipulating the appearance of images in an objective, systematic manner (for technical details, including mathematical algorithms, see Rowland & Perrett, 1995; Tiddeman, Burt, & Perrett, 2001). The original images were 50 photographs of young adult Caucasian men and 50 photographs of young adult Caucasian women, taken under standard lighting conditions and with the models posing a neutral expression. From these stimuli, we created 10 composite female face images and 5 composite

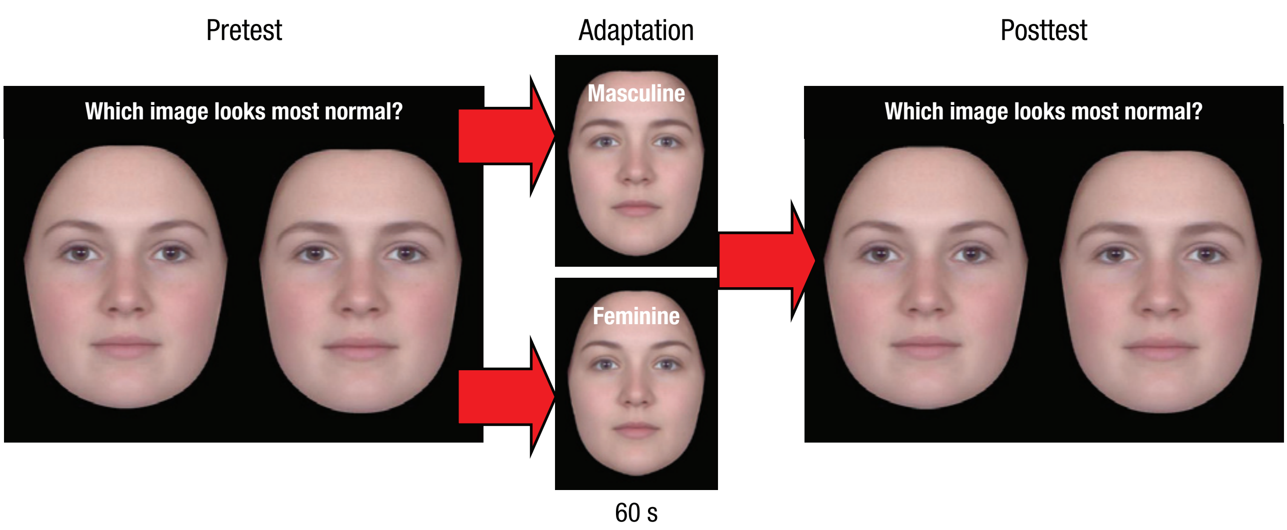

Fig. 1. Illustration of the structure of Experiment 1. In the pretest, participants viewed 15 face pairs, each consisting of a feminized and a masculinized version of the same face; the task was to indicate which face looked more "normal." In the subsequent adaptation phase, participants viewed either 10 feminized or 10 masculinized female face images, each presented for 6 s. Finally, in the posttest, participants viewed the same pairs of faces as in the pretest and again indicated which face in each pair looked more normal. The procedure was identical for Experiment 2 except that voices were used in all three phases, and participants indicated which voice in each test pair sounded more normal. In Experiment 3, the adaptors used in Experiment 1 were replaced by voices, and faces were again used in the pretest and posttest. In Experiment 4, the pretest and posttest stimuli used in Experiment 1 were replaced by voices, and participants indicated which voice in each pair sounded more normal; the adaptors were again faces. In the example pretest and posttest images in this illustration, feminized faces are on the left, and masculinized faces are on the right.

male face images. Each composite image was created by averaging 5 randomly assigned individual images. The composite images were made perfectly symmetric.

To manipulate sex typicality, for each composite we created a pair of images composed of one masculinized and one feminized version of that face (for examples, see Fig. 1). Faces were transformed on a masculine-feminine dimension using the linear difference between a composite of all 50 male images and a composite of all 50 female images (following Perrett et al., 1998). The masculinized faces were transformed 50% toward the male composite, and the feminized faces were transformed 50% toward the female composite. Masculinized versions, for example, had larger jaws and squarer faces, whereas feminized versions had smaller jaws and rounder faces.

Procedure. Participants indicated their sex and age on a short questionnaire and were then assigned to one of the two adaptation conditions. There were 36 participants in the masculine condition and 32 participants in the feminine condition. Prior to the adaptation phase (for more details, see General Method), participants took the pretest, which consisted of 5 pairs of male faces (all unadapted stimuli) and 10 pairs of female faces (half adapted and half unadapted stimuli); one image in each pair was masculinized, and one was feminized. Participants were asked to indicate which image in each pair was "more normal looking." The next trial began after an image was selected, and participants responded in their own time.

Following the pretest, participants were exposed to a set of five feminized female faces (feminine condition) or a set of five masculinized female faces. Each image was presented twice. Images were presented as a slide show, for 6 s each and a total time of 60 s. Participants were instructed to "try and look at these images carefully." After the adaptation phase, participants were given the normality test again (posttest). In both the pretest and the posttest, all images were presented in a random order, and masculinized and feminized images were randomly presented on the left or right side of the screen. This procedure and design are similar to those used in previous studies (Jaquet & Rhodes, 2008; Little et al., 2005; Little et al., 2008).

Results

We calculated *difference scores* by subtracting the percentage of trials on which the masculinized version of a face was perceived as more normal than the feminized version in the pretest from this same percentage in the posttest. Thus, a positive difference score indicates that exposure to the adaptor stimuli increased the perceived normality of masculine stimuli, and a negative score indicates that exposure to the adaptor stimuli decreased the perceived normality of masculine stimuli.

We performed a 3 (face type: adapted female, unadapted female, unadapted male; within participants) × 2 (adaptation condition: masculine, feminine; between participants) mixed-model analysis of variance (ANOVA) on the difference scores. This analysis revealed a significant interaction between face type and adaptation condition, $F(2, 132) = 4.67$, $p = .011$, $\eta_p^2 = .066$ (see Fig. 2a). There was no overall effect of face type, $F(2, 132) = 0.62$, $p = .540$, $\eta_p^2 = .009$, but a significant overall effect of adaptation condition, $F(1, 66) = 7.60$, $p = .008$, $\eta_p^2 = .103$, though this was superseded by the interaction. To parse the interaction, we ran a separate one-way ANOVA for each type of test face. These analyses revealed significant effects of adaptation condition for adapted female faces, $F(1, 66) = 11.81$, $p = .001$, $\eta_p^2 = .152$, and unadapted female faces, $F(1, 66) = 6.31$, $p = .014$, $\eta_p^2 = .087$, but no effect of adaptation condition for male faces, $F(1, 66) = 0.13$, $p = .719$, $\eta_p^2 = .002$.

Experiment 1 demonstrated that for both adapted and unadapted female face images, a masculinized version was perceived as more normal after exposure to masculinized female faces than after exposure to feminized female faces. The perception of the normality of masculinity in male faces did not change after adaptation to female faces.

Experiment 2

In Experiment 2, we investigated voice adaptation, examining how exposure to masculinized or feminized versions of female voices influenced the subsequent perception of female voices that had been heard in the adaptation phase, female voices that had not been heard in the adaptation phase, and male voices. The procedure was identical to that used in Experiment 1, except that we substituted masculinized and feminized voices for faces.

Method

Participants. There were 73 participants in Experiment 2 (49 women, 24 men; mean age = 20.6 years, $SD = 4.0$).

Stimuli. We recorded voice clips of individuals speaking common English vowel sounds (International Phonetic Alphabet: /ɑ/, /ɛ/, /i/, /o/, /u/). To manipulate the masculinity of voices, we decreased (masculinized) and increased (feminized) the pitch of 10 women's and 5 men's voices by 20 Hz, using methods identical to those of a previous study (Feinberg, Jones, Little, Burt, & Perrett, 2005). Briefly, Praat's (Boersma & Weenink, 2010) pitch-synchronous overlap add algorithm was applied to the signal to manipulate the fundamental frequency and

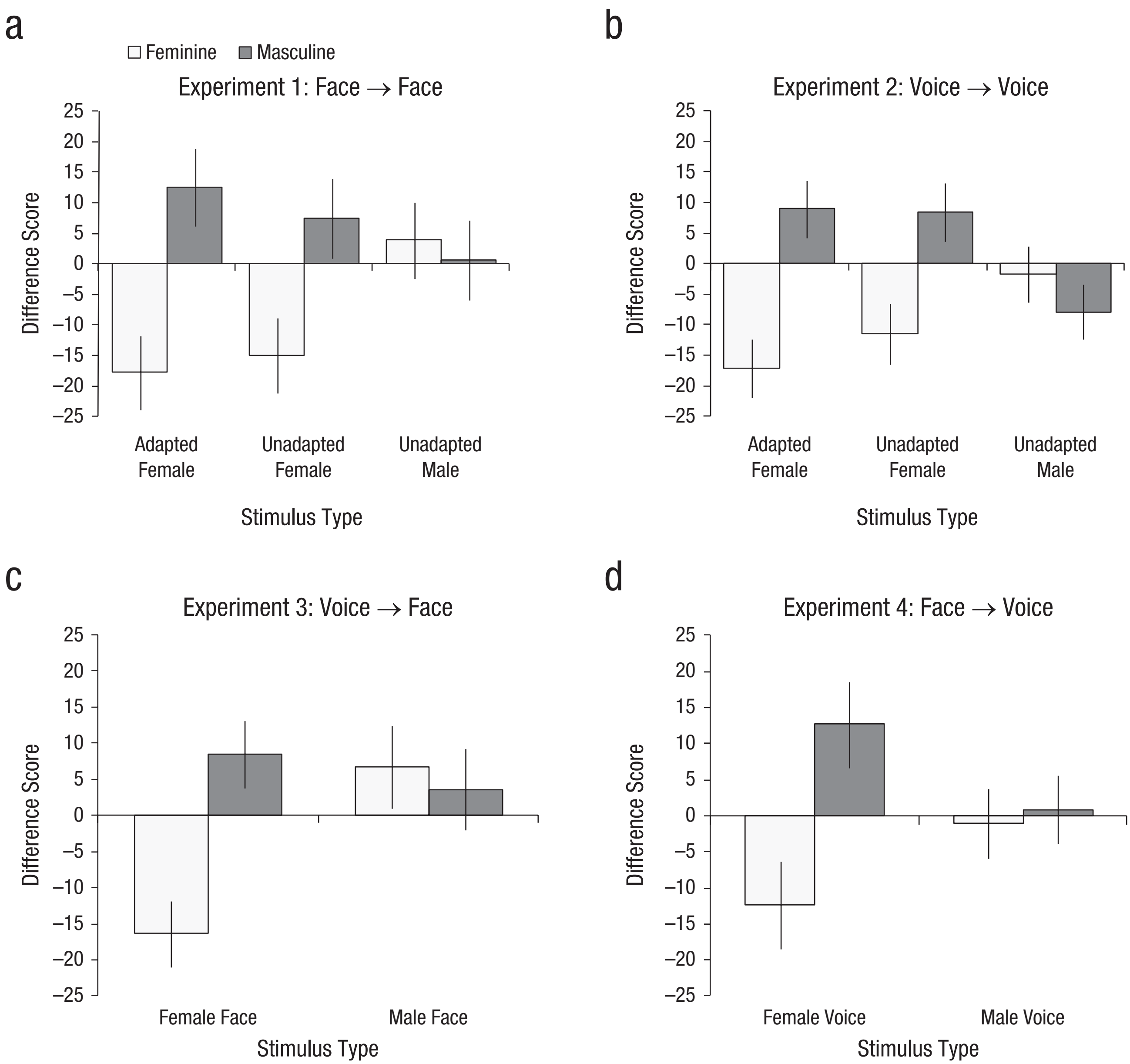

Fig. 2. Category-contingent visual and auditory adaptation following exposure to stimuli manipulated in masculinity. Adaptation was indexed by difference scores, calculated by subtracting the percentage of trials on which the masculinized version of a stimulus was perceived as more normal than the feminized version in the pretest from this same percentage in the posttest; positive scores indicate that exposure to the adaptors increased the perceived normality of masculine stimuli, whereas negative scores indicate that exposure to the adaptors decreased the perceived normality of masculine stimuli. The graphs show mean difference scores (±1 *SEM*) as a function of stimulus type and adaptation condition (see the text) in (a) Experiment 1 (unimodal face adaptation), (b) Experiment 2 (unimodal voice adaptation), (c) Experiment 3 (cross-modal adaptation: effects of exposure to voices on perception of faces), and (d) Experiment 4 (cross-modal adaptation: effects of exposure to faces on perception of voices).

corresponding harmonics independently of the formant frequencies associated with perceived masculinity (Feinberg et al., 2005). Duration was unaltered by our manipulations. The mean duration of the voice stimuli was 6 s.

Procedure. The procedure was identical to that used in Experiment 1, but the stimuli were voices instead of faces. In the adaptation phase, participants (35 in the feminine condition and 38 in the masculine condition) heard five female voices repeated twice; given the average stimulus duration of 6 s, the total exposure time was around 60 s, matching the exposure to faces in Experiment 1. In the adaptation phase, participants were instructed to "try and listen to these voices carefully." In the pretest and posttest, participants were asked to indicate which voice in each pair was more "normal sounding."

Results

A 3 (voice type: adapted female, unadapted female, unadapted male; within participants) × 2 (adaptation condition: masculine, feminine; between participants) mixed-model ANOVA on difference scores (calculated as in Experiment 1) revealed a significant interaction between voice type and adaptation condition, $F(2, 142) = 7.11$, $p = .001$, $\eta_p^2 = .091$ (see Fig. 2b). There was no overall effect of voice type, $F(2, 142) = 0.29$, $p = .746$, $\eta_p^2 = .004$, but a significant overall effect of adaptation condition, $F(1, 71) = 10.10$, $p = .002$, $\eta_p^2 = .125$, though this was superseded by the interaction. To parse the interaction, we ran a one-way ANOVA separately for each type of test voice. These analyses revealed significant effects of adaptation condition for adapted female voices, $F(1, 66) = 15.11$, $p < .001$, $\eta_p^2 = .175$, and unadapted female voices, $F(1, 66) = 8.18$, $p = .006$, $\eta_p^2 = .103$, but no effect of adaptation condition for male voices, $F(1, 66) = 0.92$, $p = .340$, $\eta_p^2 = .031$.

Experiment 2 demonstrated that for both adapted and unadapted female voices, a masculinized version was perceived as more normal after exposure to masculinized female voices than after exposure to feminized female voices. The perception of the normality of masculinity in male voices did not change after adaptation to female voices.

Experiment 3

In Experiment 3, we investigated cross-modal adaptation, examining how exposure to masculinized or feminized versions of female voices influenced the subsequent perception of female and male faces. The procedure combined elements of Experiments 1 and 2, using faces in the pre- and posttests and voices as adaptor stimuli.

Method

There were 66 participants in Experiment 3 (48 women, 18 men; mean age = 20.7 years, *SD* = 4.1). The same stimuli used in Experiments 1 and 2 were used in Experiment 3. The procedure was identical to that in Experiment 1 except that the adaptor stimuli were voices instead of faces (as in Experiment 2). There were 33 participants in the feminine condition and 33 participants in the masculine condition. Because the stimuli in the test phases differed from the stimuli in the adaptation phase, there were no adapted images; consequently, the pretest and posttest included only five pairs of female face images and five pairs of male face images.

Results

A 2 (face type: female, male; within participants) × 2 (adaptation condition: masculine, feminine; between participants) mixed-model ANOVA on the difference scores (calculated as in Experiment 1) revealed a significant interaction between face type and adaptation condition, $F(1, 64) = 7.68$, $p = .007$, $\eta_p^2 = .107$ (see Fig. 2c). There was no overall effect of face type, $F(1, 64) = 3.27$, $p = .075$, $\eta_p^2 = .049$, but an overall effect of adaptation condition, $F(1, 64) = 4.23$, $p = .044$, $\eta_p^2 = .062$, though this was superseded by the interaction. To parse the interaction, we ran a separate one-way ANOVA for each type of test face. These analyses revealed a significant effect of adaptation condition for female faces, $F(1, 64) = 14.68$, $p < .001$, $\eta_p^2 = .187$, but no effect of adaptation condition for male faces, $F(1, 64) = 0.14$, $p = .708$, $\eta_p^2 = .002$.

Experiment 3 demonstrated that for female face images, a masculinized version was perceived as more normal after exposure to masculinized female voices than after exposure to feminized female voices. The perception of the normality of masculinity in male faces did not change after adaptation to female voices.

Experiment 4

In Experiment 4, as in Experiment 3, we investigated cross-modal adaptation, this time examining how exposure to masculinized or feminized versions of female faces influenced the subsequent perception of female and male voices. The procedure combined elements of Experiments 1 and 2, using voices in the pre- and posttests and faces as adaptor stimuli.

Method

There were 43 participants in Experiment 4 (29 women, 14 men; mean age = 20.3 years, *SD* = 3.0). The same stimuli used in Experiments 1 and 2 were used in Experiment 4. The procedure was identical to that in Experiment 2 except that the adaptor stimuli were faces (as in Experiment 1). There were 21 participants in the feminine condition and 22 participants in the masculine condition. Because the stimuli in the test phases differed from the stimuli in the adaptation phase, there were no adapted voices; consequently, the pretest and posttest included only five pairs of female voices and five pairs of male voices.

Results

A 2 (voice type: female, male; within participants) × 2 (adaptation condition: masculine, feminine; between participants) mixed-model ANOVA on the difference scores (calculated as in Experiment 1) revealed a significant interaction between voice type and adaptation condition, $F(1, 41) = 4.43$, $p = .042$, $\eta_p^2 = .097$ (see Fig. 2d). There was no overall effect of voice type, $F(1, 41) < 0.01$, $p = .972$, $\eta_p^2 < .001$, but an overall effect of adaptation condition, $F(1, 41) = 6.39$, $p = .015$, $\eta_p^2 = .135$, though this was qualified by the interaction. To parse the interaction, we ran a separate one-way ANOVA for each type of test voice. These analyses revealed a significant effect of adaptation condition for female voices, $F(1, 41) = 8.67$, $p = .005$, $\eta_p^2 = .175$, but no effect of adaptation condition for male voices, $F(1, 41) = 0.08$, $p = .784$, $\eta_p^2 = .002$.

Experiment 4 demonstrated that for female voices, a masculinized version was perceived as more normal after exposure to masculinized female faces than after exposure to feminized female faces. The perception of the normality of masculinity in male voices did not change after adaptation to female faces.

General Discussion

All four of our experiments highlight the power of adaptation; in all the experiments, exposure to female stimuli influenced the subsequent perception of female stimuli, whether or not they had been seen or heard during adaptation. Very similar effects were seen for visual and auditory stimuli. In contrast, exposure to female stimuli had no influence on the subsequent perception of male stimuli. These results imply that mental representations of male and female faces are, to some extent, separable—a finding in line with previous studies of face perception (Bestelmeyer et al., 2008; Jaquet & Rhodes, 2008; Little et al., 2005)—and also suggest that representations of male and female voices are similarly separable (Zaeske & Schweinberger, 2011). Although relatively sex-specific effects could potentially be accounted for by a generally decreasing adaptation effect as similarity between adaptor and target decreases, we found that such similarity, in terms of rated masculinity, had little effect on adaptation effects (see the Supplemental Material available online). Thus, the category boundary (male vs. female) appears to be important.

The notion of *face space*, a multidimensional representational space (Valentine, 1991), has received much attention. Our data suggest a *voice space* in which voices are represented and in which male and female voices can have partially, or even fully, independent subspaces with their own prototypes (norms) or distributions. Of course, there are likely to be commonalities in processing male and female faces and voices because they have much in common as stimuli, so it is likely that there are both shared and sex-selective mechanisms that code male and female faces and voices (see, e.g., Jaquet & Rhodes, 2008). Note that effects of adaptation to simple properties of the stimuli cannot account for the effects we observed because adaptation effects were seen for female faces and voices but not for male faces and voices (see also Bestelmeyer et al., 2008; Little et al., 2005; Schweinberger et al., 2008; Zaeske & Schweinberger, 2011).

In Experiments 3 and 4, exposure to voices had a subsequent impact on the perception of faces and vice versa, which is consistent with evidence that auditory and visual information interact (Shams et al., 2000, 2002; Shimojo & Shams, 2001; Stein et al., 1996). Although a previous study of sex perception found that adaptation effects did not transfer from faces to voices (Schweinberger et al., 2008), another study showed that adaptation to voices did influence subsequent perception of face identity (Hills et al., 2010). One factor that may account for the difference in results is the paradigm used. The nearly simultaneous presentation of face and voice stimuli in Schweinberger et al. (2008) could have led to integrated perception (i.e., the perception of both stimuli as a whole), in which two presented stimuli have additive effects on perception (Shams et al., 2000; Van den Stock et al., 2007). Such additive effects could have counteracted any negative aftereffects due to adaptation.

Although nearly simultaneous presentation reliably produces negative aftereffects when stimuli of the same modality are used, the blocked design we adopted, as did Hills et al. (2010), may be better suited to demonstrate cross-modal adaptation because this prevents visual and auditory stimuli from being integrated. Indeed, cross-modal adaptation seems likely given that a wealth of studies demonstrate cross talk between sound and vision (Shimojo & Shams, 2001), and that such interaction is likely due to integration of modalities in specialized brain regions (Meredith & Stein, 1986; Wallace, Meredith, & Stein, 1992). Our data extend these previous studies of cross-modal interaction by demonstrating cross talk between higher-order representations of voices and faces that results in adaptation in both directions. Although aftereffects can disappear within seconds when nearly simultaneous presentations are used (Leopold et al., 2005), effects can last for 24 hr (Carbon et al., 2007) and up to 1 week (Carbon & Ditye, 2011) when participants are adapted to stimuli for a length of time before adaptation is tested. This difference in the duration of effects suggests that different phenomena may occur when different methods are used to study adaptation, and that long-term adaptation effects may be better addressed with block designs, as in our experiments.

In summary, our data suggest that within the broad class of faces or voices, the human brain appears to possess separable representations of male and female stimuli. Our data also demonstrate cross-modal adaptation between voices and faces, suggesting that there are shared representations independent of modality. Overall, our experiments highlight that facial and vocal characteristics related to sex and sex typicality may be processed in a similar way (i.e., effects of exposure were similar both within modality and across modalities, and effects of sex specificity were similar in the two modalities). Our results also suggest that visual information can influence auditory perceptual norms and vice versa.

Author Contributions

A. C. Little designed and conducted Experiments 1 through 4, analyzed data, and wrote the first draft of the manuscript. B. C. Jones, L. M. DeBruine, and D. R. Feinberg all contributed to the design of the experiments and the plan for analysis. A. C. Little created transformed face stimuli, and D. R. Feinberg created transformed voice stimuli. All authors commented on the analyses and contributed to writing the final draft of the manuscript.

Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

Funding

A. C. Little is supported by a Royal Society University Research Fellowship.

Supplemental Material

Additional supporting information may be found at http://pss.sagepub.com/content/by/supplemental-data

References

Belin, P., & Zatorre, R. J. (2003). Adaptation to speaker's voice in right anterior temporal lobe. *NeuroReport*, *14*, 2105–2109.

Bestelmeyer, P. E. G., Jones, B. C., DeBruine, L. M., Little, A. C., Perrett, D. I., Schneider, A., . . . Conway, C. A. (2008). Sex-contingent face aftereffects depend on perceptual category rather than structural encoding. *Cognition*, *107*, 353–365.

Bestelmeyer, P. E. G., Rouger, J., DeBruine, L. M., & Belin, P. (2010). Auditory adaptation in vocal affect perception. *Cognition*, *117*, 217–223.

Boersma, P., & Weenink, D. (2010). *Praat: Doing phonetics by computer*. Retrieved from http://www.praat.org

Calvert, G. A., Bullmore, E. T., Brammer, M. J., Campbell, R., Williams, S. C. R., McGuire, P. K., . . . David, A. S. (1997). Activation of auditory cortex during silent lipreading. *Science*, *276*, 593–596.

Campanella, S., & Belin, P. (2007). Integrating face and voice in person perception. *Trends in Cognitive Sciences*, *11*, 535–543.

Carbon, C. C., & Ditye, T. (2011). Sustained effects of adaptation on the perception of familiar faces. *Journal of Experimental Psychology: Human Perception and Performance*, *37*, 615–625.

Carbon, C. C., Strobach, T., Langton, S. R. H., Harsanyi, G., Leder, H., & Kovacs, G. (2007). Adaptation effects of highly familiar faces: Immediate and long lasting. *Memory & Cognition*, *35*, 1966–1976.

D'Alessandro, L. M., & Norwich, K. H. (2009). Loudness adaptation measured by the simultaneous dichotic loudness balance technique differs between genders. *Hearing Research*, *247*, 122–127.

Feinberg, D. R., Jones, B. C., Little, A. C., Burt, D. M., & Perrett, D. I. (2005). Manipulations of fundamental and formant frequencies influence the attractiveness of human male voices. *Animal Behaviour*, *69*, 561–568.

Fox, C. J., & Barton, J. J. S. (2007). What is adapted in face adaptation? The neural representations of expression in the human visual system. *Brain Research*, *1127*, 80–89.

Ghuman, A. S., McDaniel, J. R., & Martin, A. (2010). Face adaptation without a face. *Current Biology*, *20*, 32–36.

Hills, P. J., Elward, R. L., & Lewis, M. B. (2010). Cross-modal face identity aftereffects and their relation to priming. *Journal of Experimental Psychology: Human Perception and Performance*, *36*, 876–891. doi:10.1037/a0018731

Jaquet, E., & Rhodes, G. (2008). Face aftereffects indicate dissociable, but not distinct, coding of male and female faces. *Journal of Experimental Psychology: Human Perception and Performance*, *34*, 101–112.

Kovacs, G., Gulyas, B., Savic, I., Perrett, D. I., Cornwell, R. E., Little, A. C., . . . Vidnyanszky, Z. (2004). Smelling human sex hormone-like compounds affects face gender judgment of men. *NeuroReport*, *15*, 1275–1277.

Kovacs, G., Zimmer, M., Banko, E., Harza, I., Antal, A., & Vidnyanszky, Z. (2006). Electrophysiological correlates of visual adaptation to faces and body parts in humans. *Cerebral Cortex*, *16*, 742–753.

Leopold, D. A., O'Toole, A. J., Vetter, T., & Blanz, V. (2001). Prototype-referenced shape encoding revealed by high-level aftereffects. *Nature Neuroscience*, *4*, 89–94.

Leopold, D. A., Rhodes, G., Muller, K. M., & Jeffery, L. (2005). The dynamics of visual adaptation to faces. *Proceedings of the Royal Society B: Biological Sciences*, *272*, 897–904.

Little, A. C., DeBruine, L. M., & Jones, B. C. (2005). Sex-contingent face after-effects suggest distinct neural populations code male and female faces. *Proceedings of the Royal Society B: Biological Sciences*, *272*, 2283–2287.

Little, A. C., DeBruine, L. M., Jones, B. C., & Waitt, C. (2008). Category contingent aftereffects for faces of different races, ages and species. *Cognition*, *106*, 1537–1547.

McGurk, H., & Macdonald, J. (1976). Hearing lips and seeing voices. *Nature*, *264*, 746–748.

Meredith, M. A., & Stein, B. E. (1986). Visual, auditory, and somatosensory convergence on cells in superior colliculus results in multisensory integration. *Journal of Neurophysiology*, *56*, 640–662.

Perrett, D. I., Lee, K. J., Penton-Voak, I. S., Rowland, D. R., Yoshikawa, S., Burt, D. M., . . . Akamatsu, S. (1998). Effects of sexual dimorphism on facial attractiveness. *Nature*, *394*, 884–887.

Phillips, D. P., Scovil, S. J., Carmichael, M. E., & Hall, S. E. (2007). Adaptation of central pitch-specific mechanisms. *Perception*, *36*, 918–930.

Rhodes, G., Jeffery, L., Watson, T. L., Jaquet, E., Winkler, C., & Clifford, C. W. G. (2004). Orientation-contingent face aftereffects and implications for face-coding mechanisms. *Current Biology*, *14*, 2119–2123.

Rowland, D. A., & Perrett, D. I. (1995). Manipulating facial appearance through shape and color. *IEEE Computer Graphics and Applications*, *15*, 70–76.

Schweinberger, S. R., Casper, C., Hauthal, N., Kaufmann, J. M., Kawahara, H., Kloth, N., . . . Zaske, R. (2008). Auditory adaptation in voice perception. *Current Biology*, *18*, 684–688.

Shams, L., Kamitani, Y., & Shimojo, S. (2000). Illusions: What you see is what you hear. *Nature*, *408*, 788.

Shams, L., Kamitani, Y., & Shimojo, S. (2002). Visual illusion induced by sound. *Cognitive Brain Research*, *14*, 147–152.

Shimojo, S., & Shams, L. (2001). Sensory modalities are not separate modalities: Plasticity and interactions. *Current Opinion in Neurobiology*, *11*, 505–509.

Stein, B. E., London, N., Wilkinson, L. K., & Price, D. D. (1996). Enhancement of perceived visual intensity by auditory stimuli: A psychophysical analysis. *Journal of Cognitive Neuroscience*, *8*, 497–506.

Tiddeman, B. P., Burt, D. M., & Perrett, D. I. (2001). Prototyping and transforming facial texture for perception research. *IEEE Computer Graphics and Applications*, *21*, 42–50.

Valentine, T. (1991). A unified account of the effects of distinctiveness, inversion, and race in face recognition. *The Quarterly Journal of Experimental Psychology*, *43*, 161–204.

Van den Stock, J., Righart, R., & de Gelder, B. (2007). Body expressions influence recognition of emotions in the face and voice. *Emotion*, *7*, 487–494. doi:10.1037/1528-3542.7.3.487

van der Zwan, R., MacHatch, C., Kozlowski, D., Troje, N. F., Blanke, O., & Brooks, A. (2009). Gender bending: Auditory cues affect visual judgements of gender in biological motion displays. *Experimental Brain Research*, *198*, 373–382.

Wallace, M. T., Meredith, M. A., & Stein, B. E. (1992). Integration of multiple sensory modalities in cat cortex. *Experimental Brain Research*, *91*, 484–488.

Webster, M. A., Kaping, D., Mizokami, Y., & Duhamel, P. (2004). Adaptation to natural facial categories. *Nature*, *428*, 557–561.

Webster, M. A., & MacLeod, D. I. A. (2011). Visual adaptation and face perception. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*, 1702–1725. doi:10.1098/rstb.2010.0360

Zaeske, R., & Schweinberger, S. R. (2011). You are only as old as you sound: Auditory aftereffects in vocal age perception. *Hearing Research*, *282*, 283–288. doi:10.1016/j.heares.2011.06.008