

Opposite effects of visual versus imagined presentation of faces on subsequent sex perception

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Viewing faces of one sex changes the perception of subsequently seen ambiguous faces. Here we investigate if the mechanisms responsible for this sex aftereffect are also activated during mental imagery of faces. Participants categorized the sex of ambiguous faces after either viewing images of male or female actors' faces or imagining these same faces. As in previous studies, the ambiguous images were categorized as female more often after viewing male faces than after viewing female faces. The opposite effect was found for imagined faces, however; the ambiguous images were categorized as female more often after imagining female faces than after imagining male faces. Although our results are inconsistent with findings that imagined faces cause either no aftereffects or similar aftereffects to visually presented faces, our results are consistent with recent evidence that visual and imagined presentation of faces cause opposite adaptation effects on an early electrophysiological response associated with face processing.

Keywords: Adaptation; Aftereffects; Categorical perception; Faces; Imagery.

Debate is ongoing as to the extent to which the neural correlates of visual perception and imagery overlap (Bartolomeo, 2008; Farah, 1988; Kosslyn, Thompson, & Ganis, 2006). Mental imagery has been shown to activate many of the same neural areas as visual presentation (Kreiman, Koch, & Fried, 2000). For example, the face-responsive region of the fusiform area is more active when viewing faces than scenes, and is also more active when imagining faces than scenes (O'Craven & Kanwisher, 2000). Indeed, in O'Craven and Kanwisher's (2000) study, whether a participant was imagining a face or a

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<http://www.psypress.com/viscog> DOI: 10.1080/13506281003691357

place could be identified from inspection of the fMRI data alone on 85% of trials. Stimulus-specific activation was also found to be stronger for visual perception than for imagery, suggesting that the two processes may differ quantitatively, but not qualitatively (O'Craven & Kanwisher, 2000). In contrast to studies demonstrating similar data resulting from perception and imagery, Cabeza, Burton, Kelly, and Akamatsu (1997) dissociated visual perception and imagery of faces in a priming paradigm where participants were asked to view or imagine celebrity faces and then perform either a speeded visual recognition task or a speeded imagery task. Visual presentation primed the visual task and imagery primed the imagery task, but visual presentation did not prime the imagery task and imagery did not prime the visual task. In light of these findings, Cabeza et al. concluded that visual perception and imagery of faces are qualitatively different. With these conflicting findings, the question of how well visual imagery equates to actual perception remains open.

Visual aftereffects, the "psychologist's microelectrode" (Frisby, 1980), have been widely used to investigate face processing (e.g., Leopold, O'Toole, Vetter, & Blanz, 2001; Little, DeBruine & Jones, 2005; Rhodes et al., 2004; Welling et al., 2009). Visual exposure to faces of one type (e.g., faces with compressed features) alters subsequent perception of faces in the opposite direction (e.g., unaltered faces appear to have expanded features; Webster & MacLin, 1999). For example, exposure to angry faces causes subsequent faces expressing a mixture of anger and fear to appear more fearful (Webster, Kaping, Mizokami, & Duhamel, 2004). Such "face aftereffects" are not solely retinotopic and reflect the adaptation of neural mechanisms for coding faces (Afraz & Cavanagh, 2006; Bestelmeyer, Jones, DeBruine, Little, & Welling, 2010; Rhodes, Jeffery, Clifford, & Leopold, 2007). Thus, if mental imagery of faces activates the same neural mechanisms responsible for visual adaptation to faces (O'Craven & Kanwisher, 2000), we would expect visual presentation and mental imagery of faces to have similar effects on subsequent face perception. Investigations using adaptation to answer the question of equivalence of imagery and perception have again yielded inconsistent results. 471-68ent d Kdoch, and Shimojo (2005) found that visual presentation of an antiface (a face perceptually opposite from a target) decreased that threshold for identifying the corresponding target face, whereas mental imagery of an antiface had no effect on identity perception.

Induced in the same direction as the aftereffects by visually presented stimuli and by mental imagery were smaller in magnitude than those induced by visual presentation of faces (Ryu, Borrmann, & Chaudhuri, 2008). In contrast, Ganis and Schendan (2008) demonstrated opposite adaptation effects of visual presentation and

the amplitude of the N170 response, imagined faces enhanced the N170 (Ganis & Schendan, 2008). In other words, visual presentation of faces caused an electrophysiological aftereffect (decreased response to subsequent presentation) that is analogous to previously reported perceptual after-effects, whereas imagined presentation caused the opposite effect. Although findings for neural adaptation may not necessarily translate to equivalent findings for perceptual adaptation, Kovács et al. (2006) demonstrated a perceptual face aftereffect (decreased categorization of ambiguous faces as female after exposure to female faces) that was also evident as a reduction in the amplitude of the N170.

Given these inconsistent results for the effects of adaptation on visually presented and imagined stimuli, further exploration of imagery and after-effects is warranted. Here, we use a face aftereffects paradigm to test if visual presentation and imagery of familiar male or female actors' faces cause similar adaptation effects. Because viewing faces of one sex has been shown to shift the category boundary for sex, biasing the categorization of ambiguous faces towards the opposite sex to that previously seen (Webster et al., 2004), we had participants view or imagine the faces of well-known male or female actors and tested their subsequent categorization of faces with ambiguous sex. Following previous research (Webster et al., 2004), ambiguous faces should be categorized as male more often after visual presentation of female faces than after visual presentation of male faces. If visual presentation and imagery both activate the neural mechanisms responsible for face aftereffects in a similar way (e.g., Ryu et al., 2008), then imagined faces will cause the same aftereffect as visually presented faces. However, if visual presentation and imagery have different and opposite effects on neural mechanisms responsible for face aftereffects, as was found for an electrophysiological marker of early face processing (Ganis & Schendan, 2008), then imagined faces will cause an opposite aftereffect to visually presented faces.

METHODS

Stimuli

For the adaptation phase, face images of eight male and eight female actors were taken from public websites. The faces were cropped to show only the head and resized to 300×400 pixels (see Figure 1).

For the test phase, faces with ambiguous sex were manufactured by averaging 60 white male faces and 60 white female faces to make male and female composite (i.e., average) faces. These composite faces were averaged together in varying percentages from 0% male / 100% female to 100% male / 0% female in 5% steps. To determine the most ambiguous faces, 882

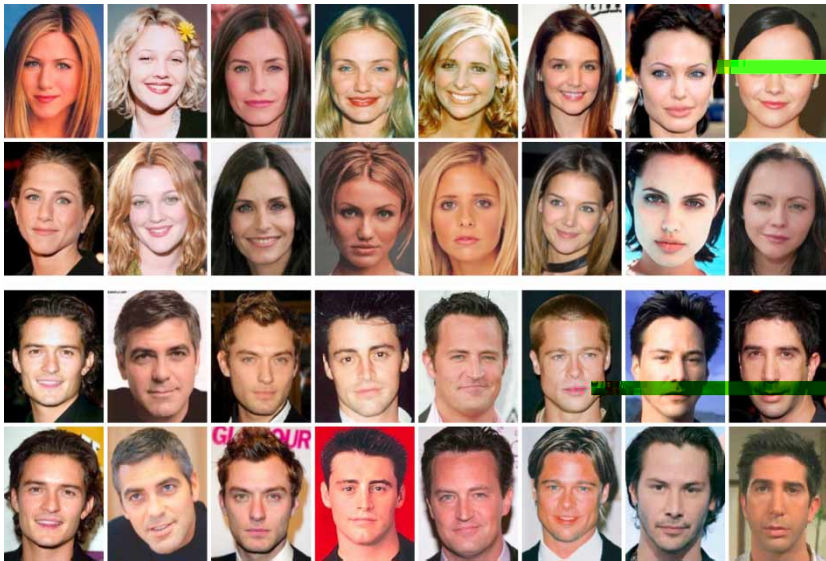


Figure 1. Images of the eight female and eight male actors used in the adaptation phase. Two images per actor were presented for 4 s each. To view this figure in colour, please see the online issue of the Journal.

participants were asked to classify the sex of all ambiguous faces. This pilot test indicated that the eight faces ranging from 20% male / 80% female to 55% male / 45% female (see Figure 2) were the most ambiguous faces (sex categorization was near ceiling for all other faces; see Figure 3).

Participants and procedure

Participants completed the experiment online and were sequentially allocated to one of four conditions: (1) Visual presentation of female faces, (2) visual presentation of male faces, (3) imagined presentation of female faces, or (4) imagined presentation of male faces. Previous studies have demonstrated that face aftereffects in online studies are equivalent to those in laboratory studies (Bestelmeyer et al., 2010; DeBruine, Jones, Unger, Little, & Feinberg, 2007; Jones, DeBruine, & Little, 2008). Data from



Figure 2. The eight ambiguous face stimuli. The images range from 20% male / 80% female to 55% male / 45% female in 5% steps. To view this figure in colour, please see the online issue of the Journal.

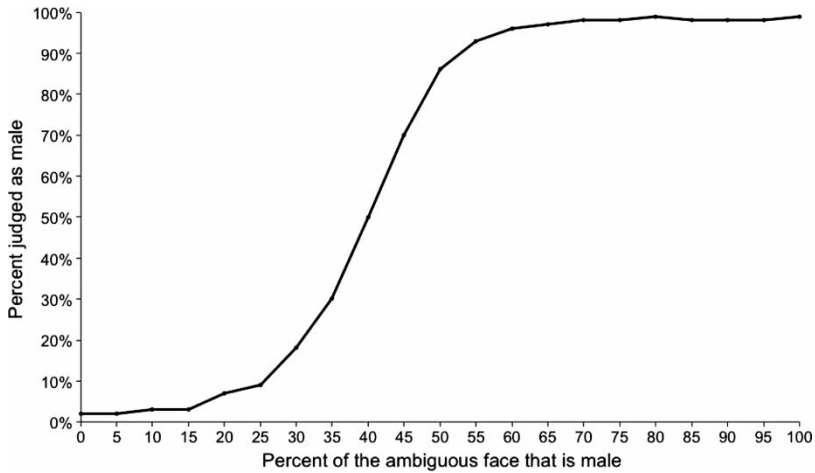


Figure 3. Percentage of 882 participants who classified each level of ambiguous face as male in the pilot test.

duplicate IP addresses were not recorded in order to ensure independent responses. Data were collected until 100 men and 100 women who could correctly identify all of the actors in the adaptation phase completed each of the four conditions. Results are presented for these 400 men and 400 women (mean age = 25.4 years, $SD = 7.7$ years).

Participants first completed an adaptation phase where they either viewed images of male or female actors' faces or were given the name and a prominent role of these same actors and asked to imagine each face (see Table 1). For both visual and imagined presentation, eight male or female actors were presented twice each in a random order for 4 s each time, totalling 64 s of exposure in the adaptation phase.

Immediately after the adaptation phase, participants were shown the eight ambiguous-sex faces and were asked to categorize each face as male or female. These faces were presented in a random order. Responses were self-paced and the image remained on the screen until a response was made. Average response time was 3.2 s ($SD = 2.7$ s).

After this sex-judgement task, participants were asked to match the eight actors' face images with their names and prominent roles. Only participants who correctly identified all eight actors were included in analyses.

RESULTS

Univariate ANOVA [dv: The percentage of ambiguous faces categorized as male; between-subjects factors: adaptation type (visual, imagined),

TABLE 1
The actors from the adaptation conditions

Sex	Name	Role
female	Jennifer Aniston	Rachel from <i>Friends</i>
female	Drew Barrymore	Dylan from <i>Charlie's Angels</i>
female	Courtney Cox	Monica from <i>Friends</i>
female	Cameron Diaz	Mary from <i>There's Something About Mary</i>
female	Sarah Michelle Gellar	Buffy from <i>Buffy the Vampire Slayer (TV)</i>
female	Katie Holmes	Joey from <i>Dawson's Creek</i>
female	Angelina Jolie	Mrs. Smith from <i>Mr. and Mrs. Smith</i>
female	Christina Ricci	Katrina Van Tassel from <i>Sleepy Hollow</i>
male	Orlando Bloom	Will Turner from <i>Pirates of the Caribbean</i>
male	George Clooney	Danny Ocean from <i>Ocean's Eleven</i>
male	Jude Law	Alfie from <i>Alfie (2004)</i>
male	Matt LeBlanc	Joey from <i>Friends</i>
male	Matthew Perry	Chandler from <i>Friends</i>
male	Brad Pitt	Mr. Smith from <i>Mr. and Mrs. Smith</i>
male	Keanu Reeves	Neo from <i>The Matrix</i>
male	David Schwimmer	Ross from <i>Friends</i>

Participants in the imagined presentation conditions saw the name of each actor and their role and were asked to imagine the face of that actor.

adaptation sex (male, female), participant sex (male, female)] revealed an interaction between adaptation sex and adaptation type, $F(1, 792) = 28.1$, $p < .001$, $\eta_p^2 = .034$. No other main effects or interactions were significant, all $F(1, 792) \leq 1.97$, $p \geq .16$, $\eta_p^2 \leq .002$. Of note is a failure to replicate the effect of participant sex found by Webster et al. (2004); women were not more likely than men were to categorize the ambiguous faces as male, $F(1, 791) = 0.04$, $p = .85$, $\eta_p^2 < .001$. See Figure 4 for a graph of the results broken down individually for the eight stimuli in the sex continuum.

Planned comparisons determined that the ambiguous images were categorized as male *more* often after visual presentation of female faces than after visual presentation of male faces, $t(398) = 4.73$, $p < .001$, $d = 0.47$, but that the ambiguous images were categorized as male *less* often after imagining female faces than after imagining male faces, $t(398) = -2.78$, $p = .006$, $d = 0.28$ (see Figure 5).

Additionally, the ambiguous images were categorized as male more often after imagining male faces than after viewing male faces, $t(398) = 3.51$, $p = .001$, $d = 0.35$, whereas the ambiguous images were categorized as male *less* often after imagining female faces than after viewing female faces, $t(398) = -3.99$, $p < .001$, $d = 0.40$. The ambiguous faces were categorized as male equally often after viewing female faces and imagining male faces, $t(398) = 1.42$, $p = .157$, $d = 0.14$, and also after viewing male faces and imagining female faces, $t(398) = 0.57$, $p = .566$, $d = 0.06$.

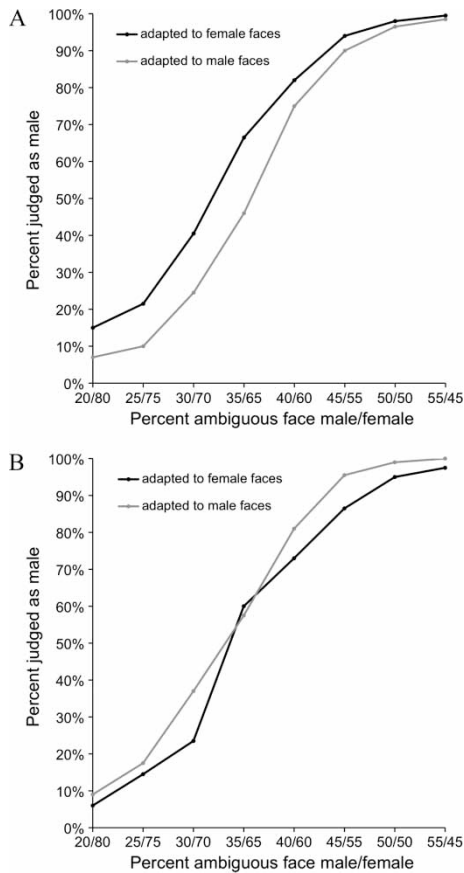


Figure 4. Percentage of participants who classified each level of ambiguous face as male after visual (a) or imagined (b) presentation of male or female actors' faces.

Reaction time analyses

Alternately analysing the data including mean response time as a covariate [dv: The percentage of ambiguous faces categorized as male; between-subjects factors: Adaptation type (visual, imagined), adaptation sex (male, female); covariate: Mean response time] did not change the significance of any effects. The interaction between adaptation type and adaptation sex remained significant, $F(1, 792) = 24.0$, $p < .001$, $\eta_p^2 = .029$.

Additionally, there was a significant three-way interaction among adaptation type, adaptation sex, and response time, $F(1, 792) = 5.38$, $p = .021$, $\eta_p^2 = .007$. This reflected small, nonsignificant correlations between response time and the percentage of ambiguous faces categorized as male

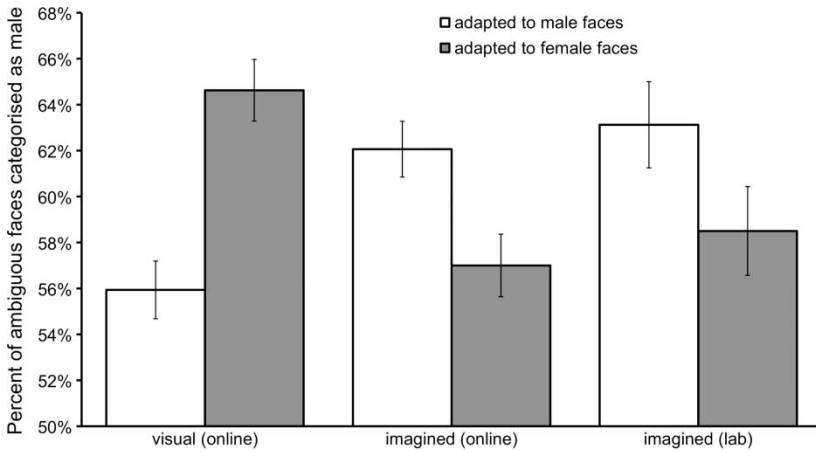


Figure 5. Mean percentage of ambiguous faces classified as male after visual (online), imagined (online), or imagined (lab) presentation of male or female actors' faces. Error bars represent SEM.

that were positive for male visual adaptation, $r = .091$, $p = .20$, and female imagery, $r = .036$, $p = .61$, but negative for female visual adaptation, $r = -.069$, $p = .33$, and male imagery, $r = -.125$, $p = .08$.

Laboratory replication

Because the imagery component of the study has not previously been tested in a laboratory setting, we replicated this component in the laboratory with 155 participants (119 female, mean age = 20.5 years, $SD = 4.11$ years) who each correctly identified all of the actors in the adaptation phase. As in the online test, ambiguous images were categorized as male more often after imagining male faces than after imagining female faces, $t(153) = 1.72$, $p = .044$ (one-tailed), $d = 0.28$. The effect size is identical to the effect size seen in the online sample (Figure 2).

DISCUSSION

Here we tested if visual presentation of male or female actors' faces and imagery of these same faces cause similar face aftereffects on subsequently viewed faces. We found the expected adaptation effect (Webster et al., 2004) when faces were presented visually; ambiguous faces were categorized as female more often after viewing male actors than after viewing female actors. However, we found the opposite pattern of results for imagined faces;

ambiguous faces were categorized as female more often after imagining female actors than after imagining male actors.

Our findings suggest that visual presentation of faces and imagining faces have opposite effects on subsequent sex-categorization, but the finding for imagined faces is inconsistent with some previous studies (Moradi et al., 2005; Ryu et al., 2008) and consistent with others (Ganis & Schendan, 2008). Findings reported by Ryu et al. (2008) suggest that perception and imagery share the same neural substrates governing adaptation and that imagining faces produces an aftereffect in the same direction as visual presentation (albeit reduced in magnitude). The data presented by Moradi et al. (2005) suggest that perception and imagery do not share such neural substrates and that imagining faces produces no aftereffect. However, the results of the EEG study by Ganis and Schendan (2008) show that visually presented and imagined faces have opposite effects on the early electrophysiological response of the N170, suggesting that visually presented and imagined faces may lead to opposite effects in term of the direction in which perception is shifted by adaptation.

Also consistent with our finding that sex categorization is affected differently by visual perception versus imagery of faces are other studies that have shown differences in the effects of top-down activation by mental imagery versus bottom-up activation by visual perception on subsequent perception of faces. Cabeza et al. (1997) found that visual and imagined presentation of faces primed tasks involving vision and imagery, respectively, but not vice versa. Additionally, top-down activation of faces by imagery facilitates featural representations of faces more than configural representations of faces, while bottom-up activation of faces by visual presentation facilitates configural representations of faces more than featural representations (Lobmaier & Mast, 2008). Their conclusion that top-down and bottom-up activation of faces rely on partially dissociable pathways is consistent with reports that face imagery is spared in some prosopagnosics (see Bartolomeo, 2008, for a review).

Our results are unlikely to be explained by demand characteristics having different effects for imagined and visual presentation. Demand characteristics have been shown to bias aftereffects for visual and imagined stimuli in identical ways (Singer & Sheehan, 1965); however, our data demonstrate opposite effects under the two conditions. Moreover, the strength of the face aftereffects observed following visual presentation of faces and imagined faces decreased as average response time in the test phase increased. This pattern is consistent with previous findings that the magnitude of adaptation effects decreases as time between the adaptation and test increases (Leopold, Rhodes, Muller, & Jeffery, 2005; Rhodes et al., 2007) and suggests that the opposite aftereffect for imagined faces does not solely reflect a demand

characteristic, since demand characteristics are unlikely to decrease with the time between adaptation and test phases.

Our findings for opposite effects of adaptation to visual and imagined stimuli are also unlikely to be a result of interference with imagery, inaccurate imagery, or online methods. Ryu et al. (2008) suggested that the difference between their study, which found significant identity aftereffects for imagined faces, and the study by Moradi et al. (2005), which found no identity aftereffect for imagined faces, is that the presence of the imagined face's name during adaptation interferes with imagery. Although the name was visible throughout the adaptation period in our study as well, this hypothesis would not lead to the prediction of a significant effect in the opposite direction of the visual aftereffect, which is what our study found. Additionally, although we ensured that our participants could correctly identify the famous faces, any inaccuracy in imagining these faces could not explain the significant effect we found for imagined stimuli. The nature of the sex aftereffect that we investigated does not require that participants be able to imagine a particular identity with great accuracy. Simply imagining any face of the correct sex should be sufficient to alter perceptions of the sex of ambiguous faces, as sex and not identity is the important variable for adaptation here. Moreover, our finding for imagined faces was replicated in a laboratory setting with identical results. In a laboratory study, Webster et al. (2004) have previously demonstrated an effect of visual presentation of male and female faces on sex categorization that is identical to that in our own online study. Consequently, it is also unlikely that the different effects observed for imagined and visually presented faces are an artifact of our online methods.

Why our study conflicts with some previous findings remains unclear. First, we note that this area has already produced conflicting results (Moradi et al., 2005; Ryu et al., 2008) and that our results are consistent with other data (e.g., Ganis & Schendan, 2008). Intriguingly, a study of the orientation-contingent colour aftereffect (i.e., McCulloch effect) showed similar results for visually perceived and imagined stimuli when participants were instructed to imagine horizontal or vertical bars while viewing red or green fields, but opposite results for visually perceived and imagined stimuli when participants were instructed to imagine red or green while viewing achromatic horizontal or vertical bars (Finke & Schmidt, 1977). The opposite effects of imagery of orientation and colour suggest that not all low-level perceptual mechanisms respond to imagery in the same way. Similarly, it is possible that not all high-level face-perception mechanisms respond to imagined faces in the same way. We compared the effects of imagery and visual adaptation on sex categorization; other studies have compared the effects of imagery and visual adaptation on identity perception (Moradi et al., 2005; Ryu et al., 2008). Thus, imagery may affect

sex categorization and identity perception in different ways, much as Finke and Schmidt's (1977) findings suggest that imagery can have different effects on orientation and colour perception. Additionally, numerous methodological differences among studies that have investigated the effects of visual adaptation and imagery on subsequent face perception, such as the use of famous rather than recently learned faces, may explain differences among findings in face perception studies. Carefully controlled investigation of the effects of different methodologies on face aftereffects would be a fruitful avenue for future study that may reconcile these findings.

Taken together, the data accumulated so far suggest that face sex and face identity may be affected in the same way by visual presentation of faces, but differently by face imagery. In turn, this would suggest that dissociable mechanisms underpin some aspects of the processing of face identity and sex. This is consistent with the finding that sex classification is spared in some prosopagnosics, while identity processing is poor (Kress & Daum, 2003). Although dissociations between processing of changeable and invariant aspects of faces have been extensively studied in recent years (e.g., Ganel, Goshen-Gottstein, & Goodale, 2005; Haxby, Hoffman, & Gobbini, 2000; Winston, Henson, Fine-Goulden, & Dolan, 2004), there has been very little research into possible dissociations in the processing of different invariant facial cues (e.g., sex, identity). However, the possibility remains that imagined faces influence responses in ways that may be susceptible to differences in study methodologies as yet unidentified and that such differences may explain the inconsistencies in findings in this area so far (e.g., Ganis & Schendan, 2008; Moradi et al., 2005; Ryu et al., 2008).

REFERENCES

- Afraz, S., & Cavanagh, P. (2006). Is the "face aftereffect" retinotopic or spatiotopic? *Journal of Vision, 6*, 882a.
- Bartolomeo, P. (2008). The neural correlates of visual mental imagery: An ongoing debate. *Cortex, 44*, 107–108.
- Bestelmeyer, P. E. G., Jones, B. C., DeBruine, L. M., Little, A. C., & Welling, L. L. M. (2010). Face aftereffects demonstrate interdependent processing of expressions and the invariant characteristics of sex and race. *Visual Cognition, 18*, 255–274.
- Cabeza, R., Burton, A. M., Kelly, S. W., & Akamatsu, S. (1997). Investigating the relation between imagery and perception: Evidence from face priming. *Quarterly Journal of Experimental Psychology, 50A*, 274–289.
- DeBruine, L. M., Jones, B. C., Unger, L., Little, A. C., & Feinberg, D. R. (2007). Dissociating averageness and attractiveness: Attractive faces are not always average. *Journal of Experimental Psychology: Human Perception and Performance, 33*(6), 1420–1430.

- Farah, M. J. (1988). Is visual imagery really visual? Overlooked evidence from neuropsychology. *Psychological Review*, *95*, 307–317.
- Finke, R. A., & Schmidt, M. J. (1977). Orientation-specific color aftereffects following imagination. *Journal of Experimental Psychology: Human Perception and Performance*, *3*, 599–606.
- Frisby, J. P. (1980). *Seeing: Illusion, brain and mind*. Oxford, UK: Oxford Press.
- Ganel, T., Goshen-Gottstein, Y., & Goodale, M. A. (2005). Interactions between the processing of gaze direction and facial expression. *Vision Research*, *45*, 1191–1200.
- Ganis, G., & Schendan, H. E. (2008). Visual mental imagery and perception produce opposite adaptation effects on early brain potentials. *NeuroImage*, *42*, 1714–1727.
- Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences*, *4*, 223–233.
- Jones, B. C., DeBruine, L. M., & Little, A. C. (2008). Adaptation reinforces preferences for correlates of attractive facial cues. *Visual Cognition*, *16*(7), 849–858.
- Kosslyn, S. M., Thompson, W. L., & Ganis, G. (2006). *The case for mental imagery*. New York: Oxford University Press.
- Kovács, G., Zimmer, M., Bankó, E., Harza, I., Antal, A., & Vidnyánszky, Z. (2006). Electrophysiological correlates of visual adaptation to faces and body parts in humans. *Cerebral Cortex*, *16*, 742–753.
- Kreiman, G., Koch, C., & Fried, I. (2000). Imagery neurons in the human brain. *Nature*, *408*, 357–361.
- Kress, T., & Daum, I. (2003). Developmental prosopagnosia: A review. *Behavioural Neurology*, *14*, 109–121.
- 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., & Jeffery, L. (2005). The dynamics of visual adaptation to faces. *Proceedings of the Royal Society of London*, *272B*, 897–904.
- Little, A. C., DeBruine, L. M., & Jones, B. C. (2005). Sex-contingent face aftereffects suggest distinct neural populations code male and female faces. *Proceedings of the Royal Society of London*, *272B*, 2283–2287.
- Lobmaier, J. S., & Mast, F. W. (2008). Face imagery is based on featural representations. *Experimental Psychology*, *55*, 47–53.
- Moradi, F., Koch, C., & Shimojo, S. (2005). Face adaptation depends on seeing the face. *Neuron*, *45*, 169–175.
- O'Craven, K., & Kanwisher, N. (2000). Mental imagery of faces and places activates corresponding stimulus-specific brain regions. *Journal of Cognitive Neuroscience*, *12*, 1013–1023.
- Rhodes, G., Jeffery, L., Clifford, C. W. G., & Leopold, D. A. (2007). The timecourse of higher-level face aftereffects. *Vision Research*, *47*, 2291–2296.
- 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.
- Ryu, J.-J., Borrmann, K., & Chaudhuri, A. (2008, May). Imagine Jane and identify John: Face identity aftereffects induced by imagined faces. *PLoS ONE*, *3*, e2195.
- Singer, G., & Sheehan, P. W. (1965). The effect of demand characteristics on the figural after-effect with real and imaged inducing figures. *American Journal of Psychology*, *78*, 96–101.
- Webster, M. A., Kaping, D., Mizokami, Y., & Duhamel, P. (2004). Adaptation to natural facial categories. *Nature*, *428*, 557–561.
- Webster, M. A., & MacLin, O. H. (1999). Figural after-effects in the perception of faces. *Psychonomic Bulletin and Review*, *6*, 647–653.

- Welling, L. L. M., Jones, B. C., Bestelmeyer, P. E. G., DeBruine, L. M., Little, A. C., & Conway, C. A. (2009). View-contingent aftereffects suggest joint coding of face shape and view. *Perception, 38*, 133–141.
- Winston, J. S., Henson, R., Fine-Goulden, M. R., & Dolan, R. J. (2004). fMRI-adaptation reveals dissociable neural representations of identity and expression in face perception. *Journal of Neurophysiology, 92*, 1830–1839.

Manuscript received February 2009

Manuscript accepted February 2010