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Research report

Facial age after-effects show partial identity invariance and transfer from hands to faces

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ABSTRACT

Age imparts long-term dynamic changes to faces: how these are represented in the human visual system has seldom been investigated. We investigated facial age after-effects using a perceptual bias paradigm, and studied the ability of adaptation to transfer across face identity, visual stimuli and sensory modality, as has been done for the short-term dynamic changes of facial expression. Age after-effects were reduced but still significant when the identity of the face was changed between the adapting and test stimuli, as we had found for expression after-effects, suggesting identity-specific and identity-invariant components of age after-effects. Although body silhouettes and greyscale body images failed to generate age after-effects in faces, we did find cross-stimulus transfer of age adaptation from hands to faces. There was no cross-modal transfer of after-effects from voices to faces. These findings confirm that face adaptation has components that cannot be explained by low-level image-based effects but involve high-level representations that may be influenced by related visual semantic information.

Faces can convey a wide variety of information about people, including their identity, gender, emotional state, attractiveness, age and ethnic origin. The neural systems responsible for these varied representations are relevant to our understanding of high-level object recognition and its interaction with memory and social cognition. An important distinction between the representation of identity, a relatively static facial property, and that of expression, a dynamic facial property, has been proposed in both older cognitive models (Bruce and Young, 1986) and more recent neuro-anatomic models, which suggest a link between identity processing and the fusiform face area on the one hand, and between expression processing and the superior temporal sulcus on the other (Haxby et al., 2000; Gobbini and Haxby, 2007). How other types of facial information map onto these models remains to be determined: for example there is some evidence that attractiveness, also a relatively stable facial property, may rely at least in part on processing in the fusiform face area (Iaria et al., 2008).

Compared to other types of facial information, the perception of facial age has been less studied. Like expression, aging is a dynamic facial property, but one with a vastly different time course. Unlike the short-term fluctuations of expression, aging is a long-term change, imparting slowly evolving but characteristic changes to faces, including loss of facial fullness, decreased tissue elasticity, deep wrinkling and progressive bone resorption (Fedok, 1996), changes that are also captured

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incidentally by caricature algorithms (O'Toole et al., 1997). Human observers can use these changes to make reasonably accurate estimations of facial age over a wide age range (Burt and Perrett, 1995; George and Hole, 1995), and computer algorithms using craniofacial structure ratios and wrinkling indices can also successfully classify faces by age (Kwon and de Vitoria Lobo, 1999). Hence facial changes appear to be robust and reliable perceptual indices of the aging process in humans.

How facial age relates to the neuro-anatomic dichotomy between the short-term dynamic of expression and the stable facial structure of identity is uncertain. To a large degree, expression and identity can be considered as relatively orthogonal dimensions: facial identity remains consistent despite variations in expression while expression can be generalized from one face to another. This orthogonality is not necessarily true for other facial dimensions. Consider the relation between ethnicity and identity: while a common ethnic representation can be extracted and perceived across many different identities, a facial identity will always have an unchanging specific ethnicity. This is because ethnicity, like identity, is a stable facial property. Because of its long-term dynamic, though, age has a more ambiguous relationship to identity. On the one hand, individuals at a specific point in time have a stable facial age: when searching for a young adult friend in a crowd, one would not expect to find them among the pediatric or geriatric members. Hence face identity has a degree of age-specificity. On the other hand, observers can match the faces of familiar individuals in two photographs taken many years apart (Sergent and Poncet, 1990; Bahrick et al., 1975). In this sense, there is also a degree of age-invariance to identity representations.

Because of this ambiguity, it is of interest to ask what similarities exist between the representations of the long-term dynamic of facial age and those of the short-term dynamic of expression. One means of exploring these representations is the study of face adaptation. Adaptation has long been recognized as a useful probe of the neural representations of basic visual properties such as spatial frequency, colour, orientation, and motion (Anstis et al., 1998; Blakemore and Campbell, 1969; Gibson and Radner, 1937). More recent studies have established the existence of after-effects for high-level representations such as faces. Moreover, adaptation can occur for different types of facial properties, having been shown for identity (Leopold et al., 2001; Fox et al., 2008), expression, gender, and ethnicity (Fox and Barton, 2007; Webster et al., 2004), viewpoint (Fang and He, 2005), and gaze direction (Jenkins et al., 2006). These face after-effects are not due to adaptation for image-specific properties such as contrast, size, or tilt (Butler et al., 2008), as they persist despite changes in image size (Zhao and Chubb, 2001), retinal location (Fang and He, 2005; Leopold et al., 2001) and viewpoint (Jiang et al., 2007).

Studies of expression and identity after-effects have revealed an interesting asymmetry in the relationship between these two facial properties. While identity after-effects transfer completely from one expression to another (Fox et al., 2008), indicating an expression invariance that would be consistent with phenomenological orthogonality, expression after-effects only partially transfer from one identity to another (Fox and Barton, 2007; Campbell and Burke, 2009; Vida and Mondloch, 2009), a finding which can be interpreted as suggesting the existence of both identity-dependent and identity-invariant representations of expression.

In addition, our study of expression after-effects produced two other findings. First, expression adaptation was specific for sensory modality, in that voices of similar expressive intensity did not generate face expression after-effects. Second, it also had some degree of stimulus specificity, when we investigated the ability to generate face after-effects from non-face visual stimuli: emotions portrayed in depictions of dogs showed only a weak trend for generating expression after-effects in human faces (Fox and Barton, 2007). The latter point contrasts with a recent report that cross-stimulus transfer of adaptation can occur, in that after-effects for face identity and gender can be generated from images of human bodies (Ghuman et al., 2010). The mechanism for transfer of adaptation from bodies to faces remains unclear, but one possible speculated anatomic basis was the proximity of the fusiform body area to the fusiform face area, creating a substrate for potential lateral interactions.

In the current study we first aimed to verify results showing that facial age after-effects exist. Such after-effects have recently been suggested in a study that had subjects adapt to a series of faces of different identity but all at one extreme of the age spectrum, then provide an estimate of the age of a following morphed image (Schweinberger et al., 2010). Following this verification we then asked whether facial age after-effects had similar properties as expression after-effects, focusing on three key points that followed a logical gradient regarding the specificity of the adapting stimulus, similar to our previous study (Fox and Barton, 2007). In a first experiment we investigated whether facial age after-effects were specific for face identity, or if they transferred across identities. In a second experiment we asked whether facial age after-effects showed specificity for face stimuli: to do this we used protocols that examined whether bodies, body silhouettes, or hands were able to generate after-effects in the perception of facial age. In a third and final experiment we assessed whether facial age after-effects showed modality specificity, by examining whether auditory stimuli consisting of young and old voices altered the perception of facial age.

1. Methods

1.1. Subjects

Forty-eight healthy observers (26 females, 22 males) participated in the entire study. All were naïve to the purpose of the experiment and had normal or corrected-to-normal vision. The protocol was approved by the review boards of the University of British Columbia and Vancouver Hospital, and informed consent was obtained in accordance with the principles in the Declaration of Helsinki.

Twelve subjects (7 females, 5 males; age = 29.8 years, SD = 11.5 years) participated in Experiment 1, which used only faces as adapting and test stimuli. In Experiment 2, another set of 12 subjects (6 females, 6 males; age = 27.3 years, SD = 4.3) participated in the component with hands or body silhouettes as adapting stimuli, while another 12 subjects (7 females, 5 males; age = 29.9 years, SD = 9.2) participated in the follow-up experiment with body photographs as adapting stimuli. A last set of 12 subjects (6 females, 6 males; age = 29.3 years, SD = 4.7) participated in Experiment 3, using voices as adapting stimuli.

1.2. Stimuli

For the facial stimuli used in Experiment 1, we found a young image and an old image from the Internet for each of the following celebrities: Deborah Harry, Elizabeth Taylor, Henry Winkler and Don Johnson (Fig. 1). The images in each young/old pair were selected because the facial expressions and head positions were highly similar between the young and the old image, so that variations in these properties would not serve as inadvertent cues in the test stimuli generated by the morphing process applied to the images. All images were converted to greyscale and matched for contrast, brightness and sharpness using Adobe Photoshop CS 8.0 (www.adobe.com). Faces were cropped to eliminate the background but the external contour of the lower face was preserved, to ensure that effects of cardioidal strain or change in the jowls were included. These were then set against a homogenous white background. The resulting young and old images served

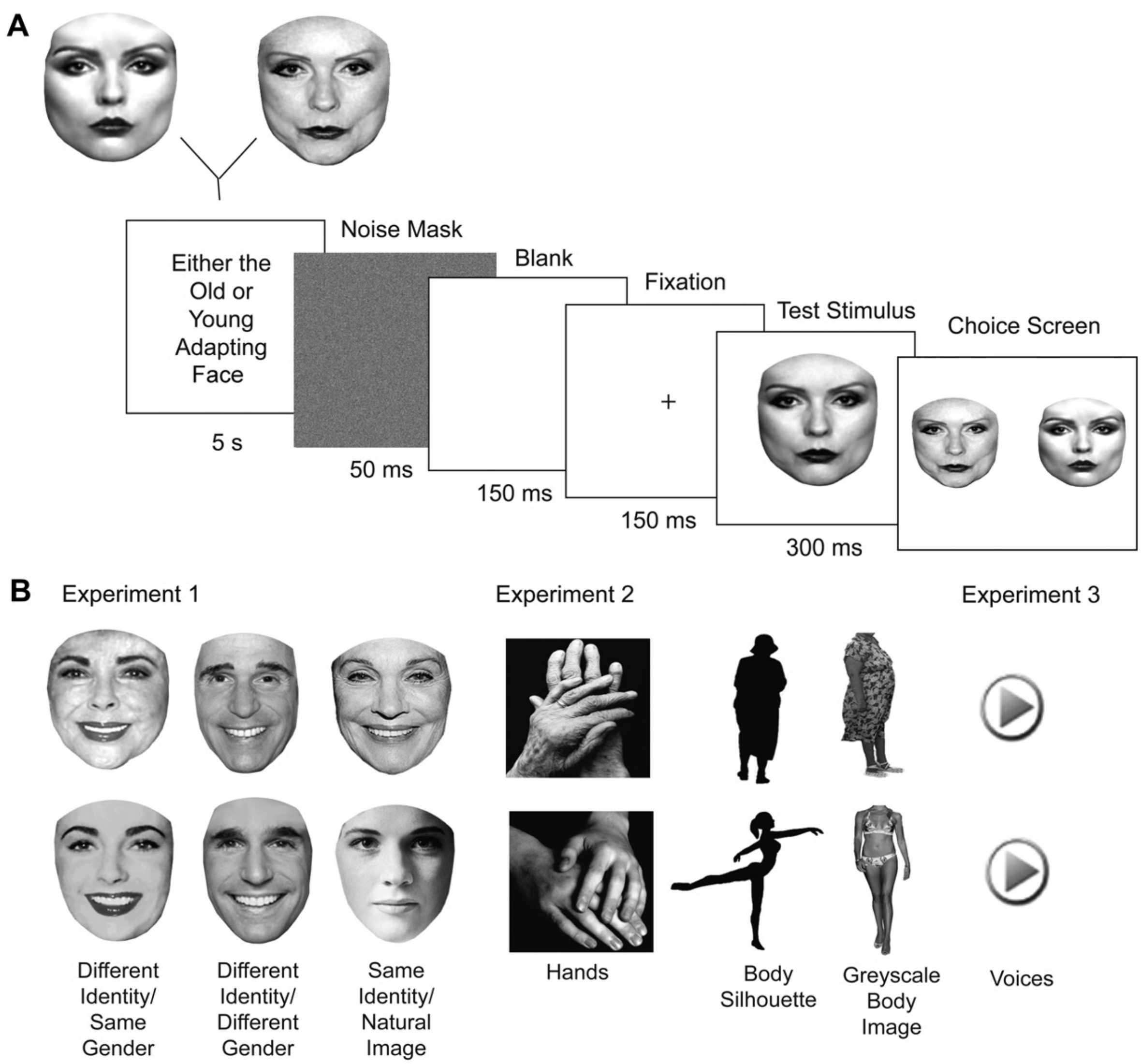

Fig. 1 – Methods. (A) Trial sequence for *same-identity* condition. Each trial began with a 5-second view of an adapting face, which was either a young or an old image of one celebrity. This was followed by a mask, a blank interval, and a fixation cross, followed by a 300 msec view of a test face, which was an ambiguous image created by morphing between the old and young image of that celebrity. A choice screen showing the old and young images then appeared, and the observer indicated which of the two the test face had most resembled. (B) Example stimuli for the different conditions – old stimuli in top row, young in the bottom. For *different identity/same gender*, the young and old adapting images were of another celebrity of the same gender as that used in the test face. Here this would be Elizabeth Taylor for the Debbie Harry test stimulus in (A), for instance. For *different identity/different gender*, the other celebrity was of the opposite gender – i.e., old and young Henry Winkler adapting faces for the Debbie Harry test stimulus. In Experiment 2, we used the same morphed faces as test stimuli, but used non-face images as adapting stimuli, which were hands, body silhouettes, or greyscale body images. In Experiment 3, we used old and young voices as adapting stimuli.

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as adapting stimuli in Experiment 1. Next, these images were also used as the starting and ending images employed by the morphing program Fantamorph 3.0 (www.fantamorph.com) to create test stimuli that were intermediate in age. From each pair of young and old faces of the same person, we created a morph continuum of 41 images, each a 2.5% increment in morphing degree from the previous image. For test stimuli we selected the 13 images ranging from 35% young/65% old to 65% young/35% old.

Given the degree of artificiality in the morphing process, we included a second component in Experiment 1. From the Internet we obtained not only young and old images of four celebrities (Julie Andrews, Meryl Streep, Paul Newman and Harrison Ford) but also 10 images of each of these same four people at intermediate ages to be used as test stimuli instead of morphed images. These have the disadvantage of unavoidable variations in viewpoint and expression, which were minimal in the first component of Experiment 1, but have the advantage of being true appearances of these people in mid-adulthood. All images were processed in the manner described above using Photoshop, and used in the *same-identity/natural-image* condition.

In Experiments 2 and 3, we continued to use as test stimuli the morphed facial images generated in the first component of Experiment 1. The adapting stimuli were changed to non-face stimuli. Experiment 2 asked whether perception of face age could be adapted by visual non-face stimuli. The three stimulus classes were body silhouettes, hands, and body images (Fig. 1B). Given that face silhouettes have many of the same perceptual effects as real facial images (Davidenko, 2007), we chose to explore the effect of black body silhouettes, which were standing positions of six young females, six young males, six old females and six old males, selected from clipart pieces found on Shutterstock (www.shutterstock.com). Six greyscale images of old hands and six images of young hands without nail polish were selected from the Internet. Hands were not categorized by gender since this proved difficult for hands lacking accessories and other size cues. Images were again cropped to remove background details and clothing cues. Because the body silhouettes proved to be ineffective adapting stimuli, we added a follow-up study to Experiment 2, using body photographs. These were greyscale images of the clothed standing bodies of six young females, six young males, six old females and six old males taken from the Internet. The heads were erased to ensure that adaptation was based solely on the body and not on the face. These images varied in dress and viewpoint, but the latter was balanced across the four stimuli, with frontal, three-quarter and side views represented.

Experiment 3 asked whether auditory stimuli could cause after-effects for facial age. For adapting stimuli we presented audio recordings of six young females, six young males, six old females and six old males. These were movie audio clips found on www.entertonement.com that were clipped to fit a duration of 5 sec. All audio stimuli were in English and were fragments of conversation taken from talk shows or interviews. While audio clips were playing, the presentation screen was a blank white background.

To determine whether the different stimuli used in the different experiments and blocks evoked a similar impression of age, in each of the three experiments, after the subjects had completed the adaptation blocks, they then provided age estimates for each of the young and old adapting stimuli they had seen. Because of the discordant results with the different stimuli in Experiment 2, these were supplemented with confidence ratings regarding their age estimation, in which subjects used a 7-point Likert scale ranging from no confidence at all (0) to completely confident (6). Estimates of age in the adapting stimuli and their confidence ratings were assessed with a repeated measures ANOVA with adapting stimulus age (young, old) and adapting stimulus types as main factors, with subjects as a random effect, and Tukey's honestly significant difference (HSD) test to examine the origins of interactions.

For the adapting stimuli of the two parts of Experiment 1, the ANOVA of age estimates with main factors of stimulus age (young, old) and experiment part (part 1, part 2) showed an interaction between stimulus age and experiment part [$F(1, 63) = 43.9$, $p < .0001$]. Tukey's HSD test showed that the younger faces of part 2 were perceived as slightly younger and the older faces perceived as slightly older than those in part 1 (Table 1). We evaluated the age estimates for Experiments 2 and 3 together, with an ANOVA with main factors of stimulus age (young, old) and adapting stimulus type (hand, silhouette, greyscale body, voice). There was an interaction between stimulus age and adapting stimulus type [$F(3, 72) = 3.95$, $p < .0115$]. Tukey's HSD test showed that the only difference was

Table 1 – Control data for age estimates of stimuli used as young and old adaptors in all experiments.

	Age estimates				Confidence ratings			
	Old		Young		Old		Young	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Face stimuli								
Part 1	60.45	3.12	26.00	2.17				
Part 2 (same identity/natural image)	65.83	4.37	23.55	2.75				
Non-face visual images								
Hands	67.33	5.84	23.33	2.00	4.33	.45	4.13	.46
Body silhouette	65.40	4.31	22.87	1.48	4.13	.27	4.11	.38
Greyscale bodies	69.07	1.91	22.65	.91	4.30	.29	4.17	.31
Auditory stimuli								
Voices	61.59	5.82	22.73	2.02				

that the old voices were not perceived to be as old as the hands and greyscale body images (Table 1). However, old voices were perceived to be at least as old as the faces used as adapting stimuli in part 1 of Experiment 1.

Because of the discrepant results in Experiment 2, we also considered whether subjects might have been less confident in their ratings for both types of body stimuli than for hand stimuli, even if the mean age estimates were similar. However, ANOVA with main factors of stimulus age (young, old) and adapting stimulus type (hand, silhouette, greyscale body, voice) showed no main effect or interaction of adapting stimulus type for confidence ratings (Table 1). Overall, these analyses suggest that we cannot attribute the finding in our results that some conditions generated after-effects while others did not to differences in the efficacy of our adapting stimuli to evoke perceptions of age.

1.3. *Procedure and apparatus*

All three experiments were created and run using SuperLab 4.0 (www.cedrus.com) on a Toshiba laptop computer with a 19″ screen. All subjects sat 33 cm away from the presentation screen and performed tasks in a dark room. Audio clips were presented on Dr. Dre Beats Solo Headphones (www.drdreheadphones.ca).

The trials in all experiments had a common design (Fig. 1A). An adapting stimulus was presented for 5 s, followed by a mask of random black and white pixels lasting 50 msec, a blank screen for 150 msec, and then a fixation cross spanning 1.4° at screen centre for 150 msec. A test stimulus then appeared for 300 msec followed by a final choice screen, which presented the two faces used to make the morphed test stimulus, the old version of the face on the left and the young version of the face on the right, which remained visible until the subject pressed a key to enter their answer. The task was to indicate which of the two choice faces the test stimulus was closer to in age. Test images were presented as 50% smaller than adapting images, to minimize any contribution from low-level retinotopic after-effects, as done in previous studies (Zhao and Chubb, 2001; Jenkins et al., 2006; Jeffery et al., 2006; Anderson and Wilson, 2005; Guo et al., 2009; Oruç and Barton, 2010). The images on the choice screen had images 75% smaller than the adapting images, and hence a size different from either adapting or test stimuli.

Experiment 1 consisted of two parts given in the same session. The first part used morphed images as test stimuli. There were three blocks. In the *same-identity* block, the adapting and test stimuli on each trial were from the same person. In the *different-identity/same-gender* block, the adapting stimulus was an image of the other celebrity of the same gender. In the *different-identity/different-gender* block, the male and female celebrities were paired so that the adapting stimulus was of a different gender than the test stimulus. Because for each of the celebrities in our set of four there were two celebrities of the other gender, this created twice as many trials as in the *same-identity* and the *different-identity/same-gender* blocks. In the latter two blocks there was one trial for each of the 13 morphed test stimuli with a young adaptor, and one trial with an old adaptor: with four different morph series, one for each of the four celebrities, this created 104 trials per block, given in random order. In the *different-identity/different-gender* block, there were 208 trials per block. Thus there were 416 trials overall for the first part of Experiment 1. The order of the three blocks was counterbalanced across the 12 subjects. After completion of this first part, the second part was given, using natural images as test stimuli. There was only one *same-identity/natural-image* block, in which the adapting and test stimuli on a trial were always of the same person. With 10 different test stimuli instead of 13, this block contained 80 trials.

Experiment 2 used as test stimuli the same morphed images that were created for the first part of Experiment 1 but the adapting images were non-facial visual stimuli. In the first component, there were two blocks, one that used young or old hands as adapting stimuli, and one that used young or old body silhouettes. As above, there were 104 trials in each of the two blocks, for a total of 208 trials in the experiment. Half of the subjects were given the hand block first, and the other half the silhouettes first. Because the latter proved ineffective at generating after-effects, we performed a follow-up study in a different group of 12 subjects, using young or old headless greyscale body images. This single-block study had 104 trials only.

Experiment 3 used the same morphed test stimuli as Experiment 1, but with adapting stimuli that were old and young voices. Gender was kept consistent between adapting and test stimuli. As above, this single-block experiment contained 104 trials.

Before each block in all experiments each subject performed 5 practice trials, using stimuli not from the actual experiment. In Experiment 1, for the *same-identity* block practice, subjects saw images of Hillary Clinton. Morphed images of Hillary Clinton were also used in the different identity blocks, but with Queen Elizabeth for the adapting stimuli in the *different-identity/same-gender* block, and Ronald Reagan for the adapting stimuli in the *different-identity/different-gender* block. For the *same-identity/natural-image* block, we used images of Barbra Streisand. In Experiments 2 and 3, the practice morphed test stimuli were always images of David Gilmour. Each of the 5 practice trials had a different adapting stimulus, again not taken from the adapting stimuli used in the experiment.

1.4. *Analysis*

For each condition in each subject we calculated an after-effect score, using the method in our prior studies (Fox and Barton, 2007; Fox et al., 2008), by subtracting the proportion of total responses that were "old" when the adapting stimulus was an old image or voice, from the proportion of total responses that were "old" when the adapting stimulus was a young image or voice.

To determine if each condition generated a significant after-effect, we used *t*-tests with Bonferroni correction for multiple comparisons, adjusted for across-item correlation (Sankoh et al., 1997). To contrast conditions within an experiment we used repeated measures ANOVA with adapting stimulus type as main factor and subjects as a random factor, using JMP 8.0.2 (www.jmpin.com). Significant results were investigated using Tukey's HSD test. *A priori* comparisons between conditions of different experiments were done with 2-way *t*-tests for 2 samples, with Bonferroni correction.

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2. Results

2.1. Experiment 1

As stated, our first task was to determine if facial age after-effects exist (Fig. 2). The *same-identity* condition showed a significant after-effect size of .23 [SD .15, $t(11) = 5.34$, $p < .0003$]. This was confirmed in the *same-identity/natural-image* condition, which also showed a significant after-effect size of .18 [SD .08, $t(11) = 7.94$, $p < .0001$].

We then asked if facial age after-effects could still be generated even if the adapting and test faces were of different people. This did show significant after-effects for both the *different-identity/same-gender* condition [.12, SD .06, $t(11) = 7.32$, $p < .0001$] and the *different-identity/different-gender* condition [.11, SD .05, $t(11) = 8.19$, $p < .0001$].

The ANOVA of after-effect size showed a significant effect of condition [$F(3, 33) = 6.43$, $p < .0015$]. Tukey's HSD test showed that the after-effect produced in the *same-identity* condition was larger than those produced in the two *different-identity* conditions, which did not differ from each other. The *same-identity/natural-image* condition did not differ from either the *same-identity* or *different-identity* conditions.

2.2. Experiments 2 and 3

In Experiment 2 we determined if non-facial visual stimuli could also generate facial age after-effects. The *hands* condition generated facial age after-effects [.07, SD .06, $t(11) = 4.10$, $p < .002$]. *A priori* comparison with the conditions of part 1 of Experiment 1, which used the same test stimuli, showed that the facial age after-effects generated by hands were less than those from the *same-identity* condition [$t(11) = 3.60$, $p < .005$], with a trend to being less than that from the *different-identity/same-gender* condition [$t(11) = 2.07$, $p = .065$], but not significantly different from the *different-identity/different-gender* condition [$t(11) = 1.82$, $p = .102$].

The *body silhouette* condition did not generate a facial age after-effect [.02, SD = .08, $t(11) = .65$, n.s.]. We considered the possibility that this was because of the impoverished nature of silhouette images, and conducted a follow-up study using *headless greyscale body images*. However, these images also failed to generate facial age after-effect [−.01, SD = .06, $t(11) = .64$, n.s.].

In Experiment 3 we asked if adaptation could transfer across sensory modalities: the *voice* condition did not produce any facial age after-effect [.001, SD = .06, $t(11) = .09$, n.s.].

3. Discussion

Our results first confirmed that adaptation for facial age does generate significant after-effects, and that this was true whether the test stimuli were artificially created morphs of intermediate age, or real images of the celebrities in mid-life. Second, after-effects could still be generated when the identity of the adapting face differed from the test face, though these were reduced in magnitude. Third, facial age after-effects could be induced by hands but not by bodies, neither when bodies were silhouettes nor when they were headless greyscale images. Finally, we did not find any cross-modal transfer of adaptation from voices to faces.

Age after-effects were recently demonstrated in another study (Schweinberger et al., 2010). This used a different adaptation technique, with a long 40 sec adaptation phase consisting of many different faces of the same age, following

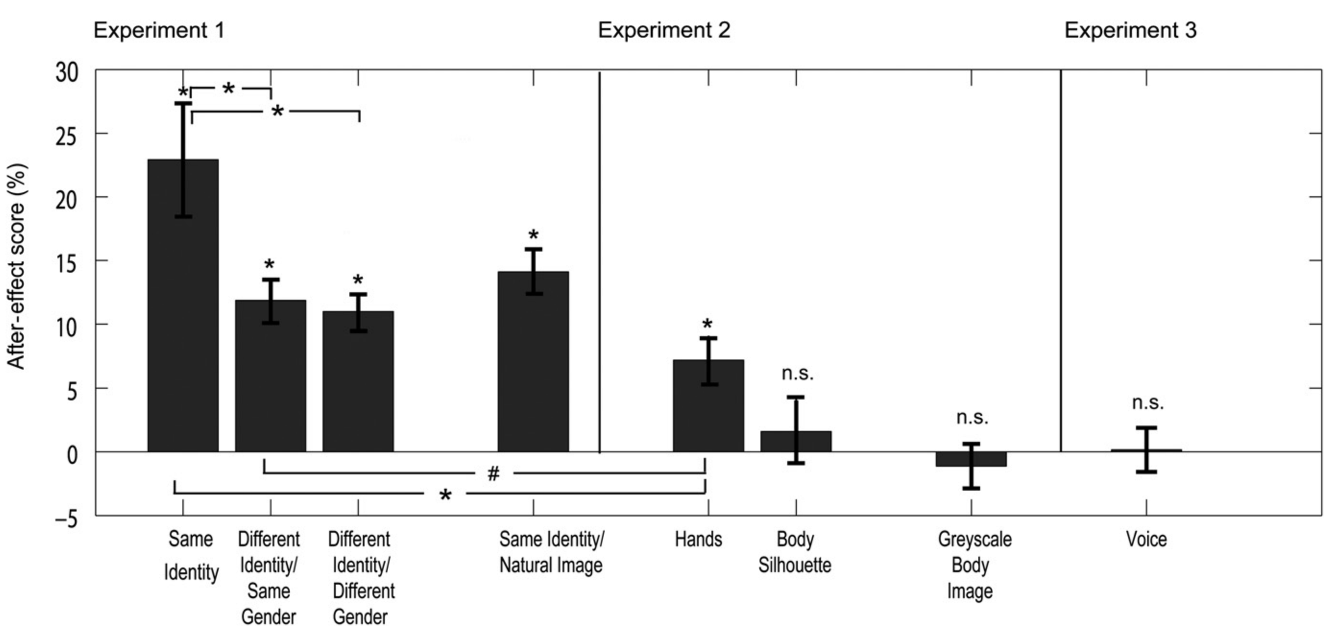

Fig. 2 – Results. The group mean after-effect score is plotted for each of the different conditions in the three experiments, with error bars indicating one standard error. An asterisk above a bar indicates a significant after-effect for that condition. Brackets with asterisks (*) indicate a significant difference between two conditions, while brackets with a number sign (#) indicate a trend to significance for such a contrast.

which subjects had to provide an age estimate of a facial image that had been morphed between one young person and another old person. As such, this technique cannot determine whether there is an identity-dependent component to age after-effects, which our results do show. Like us, this other study examined if cross-gender transfer occurred: our study goes further to investigate cross-stimulus and cross-modal transfer as well.

The finding of partial transfer of facial age adaptation across different facial identities is highly reminiscent of prior results for expression adaptation, where the after-effect is reduced by more than half when the face identity differs between adapting and test stimuli (Fox and Barton, 2007; Campbell and Burke, 2009; Vida and Mondloch, 2009). As in our prior study of expression after-effects (Fox and Barton, 2007), the difference in after-effect size between the *same-identity* condition and the two *different-identity* conditions could not be attributed to the differences in adapting and test stimuli across conditions since these were identical, with adapting and test stimuli merely paired differently to create the different conditions. The lack of effect of gender in the different-identity conditions also parallels our prior results for expression adaptation (Fox and Barton, 2007), and the findings of the other recent study of age after-effects (Schweinberger et al., 2010).

One possible explanation for reduced facial age after-effects when facial identity is changed is that there is greater image-based physical dissimilarity between the adapting and test images in the *different-identity* conditions than in the *same-identity* condition. However, adaptation to low-level retinotopic properties is unlikely because first, subjects did not have to stabilize their gaze during the adaptation period of 5 sec, and second, even if they did the test stimuli were considerably different in size from the adapting stimuli, a maneuver that we and others have used in many face adaptation studies for this reason (Zhao and Chubb, 2001; Jenkins et al., 2006; Jeffery et al., 2006; Anderson and Wilson, 2005; Guo et al., 2009; Oruç and Barton, 2010). We have shown that with these experimental conditions there is very little image-based contribution to facial after-effects (Butler et al., 2008).

Thus, as with expression after-effects, facial age after-effects are partially identity-invariant and partially identity-dependent. How could this duality arise? There are at least two potential explanations. One is to consider the effects of changing identity on putative units or neurons that encode age. If these units are also tuned to face identity, then their tuning curves for identity will show maximal responsivity to the preferred face identity, weaker responses for other faces that have some similarity to the preferred identity, and none for highly dissimilar faces. Such similarity-based tuning curves are well described for cortical neuron sensitive to orientation and motion (Maunsell and Van Essen, 1983; Anderson et al., 2000) and postulated in models of after-effects for orientation, motion and faces (Mather, 1980; Coltheart, 1971; Oruç and Barton, 2010), among others. This fact that weaker but still significant responses can be generated by non-preferred faces would explain the finding that adaptation is still significant but weaker when the identity of the face is changed, if age after-effects are generated in units that are sensitive to identity. An alternative explanation based on neural network models is that there may be separate representational levels, with identity-dependent representations of a facial property that feed forward to identity-invariant representations of that same property (Rosen, 2003). Populations with identity-dependent and identity-invariant responses to face viewpoint have been described in monkeys (Perrett et al., 1991), for example, and in the human neuroimaging literature there is some evidence that the superior temporal sulcus, hypothesized to be a key component in the representation of facial expression (Gobbini and Haxby, 2007; Fox et al., 2009), may have a posterior component that shows adaptation effects for identity and an anterior component that does not (Winston et al., 2004). Whether the representation of age may have this type of layered structure is an open question.

As with our prior study of expression after-effects (Fox and Barton, 2007), we find a significant transfer of after-effects across gender. Similarly, other studies have found cross-gender after-effects for age (Schweinberger et al., 2010) and shape distortions (Jaquet and Rhodes, 2008): in the former study they were reduced compared to same-gender after-effects, but like us, the latter study found no difference. Cross-gender transfer may appear to contradict other reports of gender-contingent after-effects, in which simultaneous adaptation with male faces possessing one property (e.g., wide eyes), and with female faces possessing its opposite (e.g., narrow eyes) leads to opposite after-effects on male versus female test stimuli (Little et al., 2005). However, the methodology in contingent adaptation designs is directed at showing whether after-effects are potentially dissociable between the two categories being tested, and cannot exclude the possibility that after-effects transfer across categories when there is only one adapting stimulus rather than two with opposing properties. This is most clearly shown in studies that report both cross-gender transfer of after-effects in one experiment and gender-contingent after-effects in a second (Schweinberger et al., 2010; Jaquet and Rhodes, 2008). The implication has to be that the genders are not completely segregated from each other in face space, since transfer can occur, but do occupy different regions in face space, which can then be differentially influenced by contingent techniques.

Possibly the most interesting result of this study was the ability of hand stimuli to cause facial age after-effects. Cross-stimulus transfer of adaptation within the visual modality has been studied at least three times before. The first study found no transfer of gender after-effects between hands and faces (Kovacs et al., 2006). Second, we found only a trend to an effect from emotions seen in canine images to facial expression (Fox and Barton, 2007). Most recently, one study found that perception of identity or gender in faces could be adapted by body images (Ghuman et al., 2010).

The mechanism of cross-stimulus transfer is still unknown. There are several possibilities. First, at a perceptual level, it may be that there are similarities in skin texture between hands and faces of a certain age, and that textural properties may contribute to face after-effects. While this is not yet known, there is evidence that the surface properties of facial complexion do contribute to age perception (Burt and Perrett, 1995). Second, hands and faces may converge at an age abstraction at a visual semantic level. After-effects may be either partially mediated by representations at this point, or modulated through top–down feedback from such visual semantic processing to the facial representations responsible for after-effects (Ghuman et al., 2010). A third possibility that has been considered for body-to-face adaptation transfer has been lateral interactions between spatially adjacent representations of bodies and faces, given the anatomic proximity between the fusiform face and body areas (Schwarzlose et al., 2005). However, our results are somewhat problematic for the latter 'interaction by neural-proximity' explanation, as we found cross-stimulus transfer for hands only, and not for bodies. Whether hand representations are physically closer to face representations than body representations is not known. A hand region near the left extra-striate body area has been described recently, but its location with respect to the occipital and fusiform face areas has not yet been clarified (Bracci et al., 2010).

One intriguing question is why we found that cross-stimulus transfer can occur for facial age after-effects from hands but not bodies, while prior studies seem to suggest that transfer for facial gender after-effects may occur from bodies (Ghuman et al., 2010) but not hands (Kovacs et al., 2006). In our study at least the difference in cross-stimulus adaptation efficacy between bodies and hands could not be attributed to differences in the perceived age of the adapting stimuli, given the equivalent age estimates and their confidence ratings. Nevertheless, it remains possible that hands with their textural cues are simply more common and potent indicators of age than bodies, to explain our results. The fact that adaptation transfer from hands to faces occurs for age but not gender may suggest that hand cues to age may be more powerful than hand cues to gender. Conversely, adaptation transfer from bodies to faces for gender but not for age may reflect a reverse difference in cue potency: clothing and body shape are strong gender cues in our society, but may not be as reliable predictors of age. Arguments based on different potency for different attributes would be particularly cogent for transfer at the level of visual semantics. Alternatively, cross-stimulus transfer from hands for facial age after-effects and from bodies for facial gender after-effects may reflect entirely different phenomena. If the effects of hands on facial age after-effects reflect a contribution of shared texture, this may be far less significant for gender after-effects, which may depend more on semantic effects.

Our final result was a negative one, that there was no cross-modal transfer of adaptation from voices to faces for age after-effects, again despite the fact that the perceived ages of the voices were similar to the perceived ages of our adapting faces. This too is consistent with our study of expression adaptation, where expressive voices failed to generate face after-effects (Fox and Barton, 2007). Another study found that evidence for transfer from voices to faces for gender after-effects was minimal, if any (Kloth et al., 2010). Thus at present there seems to be little evidence of significant transfer of adaptation from auditory-to-visual modalities for faces, at a more general semantic level. In the reverse direction, while some have also failed to find face-to-voice transfer of gender after-effects (Schweinberger et al., 2008), there has been a recent demonstration of cross-modal transfer of identity adaptation from faces to voices (Zaske et al., 2010). While this could reflect a difference between age, gender and identity representations, or the influence of greater personal familiarity with stimuli as suggested by the authors of the latter study (Zaske et al., 2010), it could also speak to an asymmetry in cross-modal influences between the auditory and visual modalities. Cross-modal transfer of motion adaptation occurs from the visual to the auditory modality, but minimally if any in the reverse direction (Kitagawa and Ichihara, 2002; Jain et al., 2008). On a similar note, visual but not auditory distractors have been shown to reduce face after-effects when they reduce awareness of the adapting face (Moradi et al., 2005). Several reasons have been proposed for an asymmetry in cross-modal auditory and visual influences (Jain et al., 2008), including differences in the robustness and ecological validity of auditory versus visual motion stimuli, and greater resistance of visual than auditory neurons to top–down influences from multimodal areas. If visual responses are more powerful and less ambiguous than auditory responses, this may parallel neurophysiological findings in structures like the superior colliculus, showing that multimodal enhancement of responses is greater for weaker unimodal stimuli (Wallace et al., 1996). Regardless, our data add to a growing body of evidence that cross-modal auditory influences on visual processing may be relatively weak, though still possible in some circumstances (Meyer and Wuerger, 2001; Maeda et al., 2004).

In summary, our data show parallels between adaptation effects for aging, a long-term dynamic in facial structure, and expression, a rapid short-term change. Both show partial but significant transfer across changes in identity, in contrast to the complete transfer of identity after-effects across changes in expression (Fox et al., 2008): whether identity after-effects also transfer completely across changes in age remains to be determined. Neither showed any evidence of cross-modal transfer from auditory stimuli that generated percepts of age or expression equivalent to those generated by the faces used in these experiments. However, while we found only a weak trend for cross-stimulus transfer of adaptation from canine images to faces for expression previously, in this report we did find a robust transfer of adaptation from hands but not bodies to faces for age after-effects. The fact that cross-stimulus transfer can occur in some circumstances underscores the fact that face adaptation is not a low-level phenomenon, but represents changes in high-level representations that can be influenced by visual semantic content in images that are highly different from faces.

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