The nature of face representations in subcortical regions

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ABSTRACT

Studies examining the neural correlates of face perception in humans have focused almost exclusively on the distributed *cortical* network of face-selective regions. Recently, however, investigations have also identified subcortical correlates of face perception and the question addressed here concerns the nature of these subcortical face representations. To explore this issue, we presented to participants pairs of images sequentially to the same or to different eyes. Superior performance in the former over latter condition implicates monocular, prestriate portions of the visual system. Over a series of five experiments, we manipulated both lower-level (size, location) as well as higher-level (identity) similarity across the pair of faces. A monocular advantage was observed even when the faces in a pair differed in location and in size, implicating some subcortical invariance across lower-level image properties. A monocular advantage was also observed when the faces in a pair were two different images of the same individual, indicating the engagement of subcortical representations in more abstract, higher-level aspects of face processing. We conclude that subcortical structures of the visual system are involved, perhaps interactively, in multiple aspects of face perception, and not simply in deriving initial coarse representations.

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1. Introduction

Face perception involves a network of cortical structures and, over the last decade, many studies have focused on uncovering the functional contribution of the different nodes of this network (for example, Avidan & Behrmann, 2009; Fairhall & Ishai, 2007; Haxby, Hoffman, & Gobbini, 2000; Nestor, Plaut, & Behrmann, 2011). Surprisingly, little attention has been paid to the contribution of lower-order structures to face processing, although there is both ontogenetic (for example, Johnson, 2005) and phylogenetic (for example, Dyer, Neumeyer, & Chittka, 2005; Sheehan & Tibbetts, 2011; Tibbetts, 2002) evidence that implicates more rudimentary neural structures in the identification of individual faces. One possible explanation for the relative neglect of studies of subcortical structures is that these structures are small in size and located deep in the nervous system, making them difficult to image because of the reduced signal-to-noise ratio (LaBar, Gitelman, Mesulam, & Parrish, 2001). Indeed, when substantial data and statistical power are available, face-selective activation of subcortical structures is observed: for example, analysis of imaging data from a large group ($N=215$) of individuals reveals robust and replicable selective activation for faces (in the absence of emotional expression) and reveals connectivity from structures such as the amygdala with the nodes of the cortical network alluded to above (Mende-Siedlecki, Verosky, Turk-Browne, & Todorov, 2013; but also see Stein, Seymour, Hebart, & Sterzer, 2013).

Concurrent with the growing attention to subcortical structures as revealed by neuroimaging, some recent studies have used targeted manipulations of behavior to characterize the subcortical representations. For example, Khalid, Finkbeiner, Konig, and Ansorge (2012) have demonstrated that low-pass (but not high-pass) filtered face primes presented peripherally produce a congruency effect in a sex discrimination task; that is performance was enhanced when the preceding prime and following probe were of the same gender compared with when they were not. The authors concluded that the retino-collicular route, targeted by the peripherally presented low-pass images, is involved in sex-specific features of face images. In a related study, Pallett and Dobkins (2013) reported a significant relationship between age-related increases in luminance contrast sensitivity and face discrimination ability and concluded that the properties of the subcortical M pathway may play a critical role in face perception. Consistent with this, in a previous study, we used a Wheatstone stereoscope and presented two successive images of either faces, cars or letter-strings to the same or different eyes and required participants to make same/different judgments (Gabay, Nestor, Dundas, & Behrmann, 2014). This technique capitalizes on the known properties of the visual system: the visual input, once received by the retina, is propagated in an eye-specific fashion through the early stages of the visual system and this monocular segregation is

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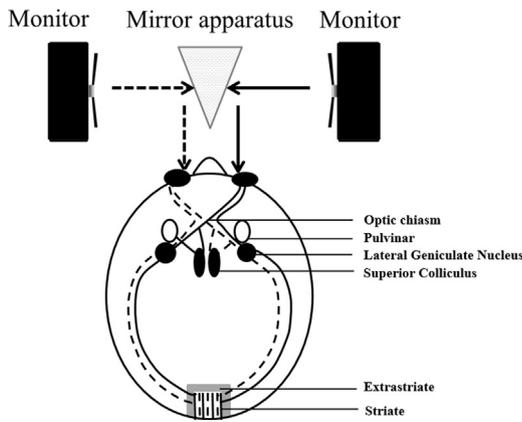
Fig. 1. A schematic depiction of the experimental apparatus and visual pathways from the eyes to the brain. Each monitor delivers visual information to a different eye. The visual information first passes through monocularly segregated subcortical regions (left eye-dashed lines right eye—solid lines), which is then projected to the pulvinar, lateral geniculate nucleus (LGN) and superior colliculus en route to the striate and then binocular extrastriate regions.

retained up to layer IV of striate cortex (Horton, Dagi, McCrane, & de Monasterio, 1990; Menon, Ogawa, Strupp, & Ugurbil, 1997). Because there are relatively few monocular neurons beyond area V1 (Bi et al., 2011), activation of extrastriate areas is not eye-dependent (see Fig. 1). Given that observers are not explicitly aware of the eye to which a visual stimulus is projected (Blake & Cormack, 1979; Schwarzkopf, Schindler, & Rees, 2010) they perceive the images from different eyes as 'fused'. This technique has been used successfully in the past to examine plasticity in transferring perceptual learning from one eye to another (Karni & Sagi, 1991), examination of spatial attention (Self & Roelfsema, 2010) and multi-sensory perception (Batson, Beer, Seitz, & Watanabe, 2011).

Gabay et al. (2014) concluded that because participants performed significantly better when the two face images were shown monocularly to the same eye compared with when they were presented interocularly to two different eyes, subcortical mechanisms are implicated in face perception. This monocular advantage was only evident on trials that required the comparison of faces (upright or inverted), but not of cars or of letter-strings. Interestingly, the monocular benefit was present for low- but not high- frequency images of faces and was also evident for face-like configurations of geometric shapes, offering further evidence for the specific involvement of subcortical, rather than cortical structures. Finally, we showed a monocular advantage for low spatial frequency face-like images made of blobs in the configural arrangement of a face and perceptual sensitivity of this sort is also considered to be compatible with subcortical computations (Johnson, 2005; Johnson, Dziurawiec, Ellis, & Morton, 1991; Johnson & Morton, 1991). Based on these findings, the authors concluded that subcortical structures afford a coarse representation of a face, comprised of primarily low spatial frequency information.

2. Current study

The findings of Gabay et al. (2014) are provocative and implicate evolutionarily older parts of the central nervous system in face perception. What remains to be revealed is a fuller understanding of the nature of these subcortical representations. One obvious prediction is that these lower order mechanisms are limited to a veridical representation of the visual input. If so, this would predict that there would be no monocular advantage (i.e. same-eye versus different-eye facilitation) when participants are

required to judge whether two faces are the same or different under conditions when the faces differed in any way such as varying in size or location. Alternatively, if these subcortical representations are abstracted away from the absolute retinal image, a monocular advantage might still be apparent even when the face images differ in some way.

Across five different experiments, our results reveal a monocular advantage independent of changes in the size or spatial location of the input faces. Critically, this benefit was observed only when two faces shared a visual field of one eye (and hence were presented to the same hemisphere), revealing the specificity of the effect. Finally, a monocular benefit was also present when participants compared two different face images of the same individual, suggesting some invariance over changes in retinal image. This benefit was observed even when controlling for image similarity, which suggests that the representations generated at lower regions of the visual system are engaged in somewhat more abstract identity processing, as well. Finally, we offer a potential explanation which might account for the constellation of findings.

2.1. Experiment 1: Location variability

In this first experiment, we examine whether a monocular advantage accrues for faces when the input images differ to some extent in their absolute retinal location. Robust visual representations should overcome small changes in the input (as is also true for those created by the rapid and continuous movements of the eyes) and the question is whether subcortical representations are also invariant to small changes in the spatial location of the image.

3. Methods

3.1. Participants

Participants (age 18–25 years; 10 females and 12 males), all of whom had normal or corrected-to-normal vision, consented to participate. Here, and in all following experiments, participants volunteered to participate in exchange for payment or course credit and the protocol was approved by the Institutional Review Board of Carnegie Mellon University.

Participants performed same/different judgments on pairs of faces, cars and letter-string stimuli. The stimuli could appear either at the same exact location or at a different location in which the images were shifted up or down from fixation.

3.2. Stimuli

Twenty-four male and 24 female face images, obtained from the Face-Place Database Project (Copyright 2008, Dr M. Tarr, http://wiki.cnbc.cmu.edu/Face_Place), were used. All images displayed front views of faces with neutral emotional expression (see example in Fig. 2). The faces were cropped to remove hair cues and were presented in grayscale against a black background. Face stimuli were 8° in height and 6° in width. Letter-string stimuli consisted of 48 four-letter strings (24 pairs), presented in white Times New Roman font against a black background, approximately 2° in height and 5.5° in width. Each pair differed in a single letter. Car stimuli consisted of 48 cars, oriented to 45° (24 pairs), approximately 8.5° in width and 6° in height.

3.2.1. Procedure

The participant's head was stabilized with the aid of a chin rest. Two mirrors, one at 45° and one at 135°, each reflecting one of two monitors (50 cm from left or right side of observer), were placed in front of the participant (see Fig. 1). Two cardboard dividers were attached to the chin rest, blocking the participant's direct view of the monitors, so that the display was only visible in the mirror. A single trial started with the appearance of a fixation cross (0.5°) for 1000 ms on both monitors (see Fig. 2A). Participants were instructed to maintain fixation throughout the experiment. The first image appeared for 150 ms followed by 1000 ms fixation and then by the second image for 150 ms. Participants were instructed to respond after the appearance of the second image. If no response (by 1500 ms) or a wrong response was delivered, three red X's appeared on the screen providing feedback for 1500 ms. If a correct response was given, a blank screen ensued for 1500 ms prior to the next trial.
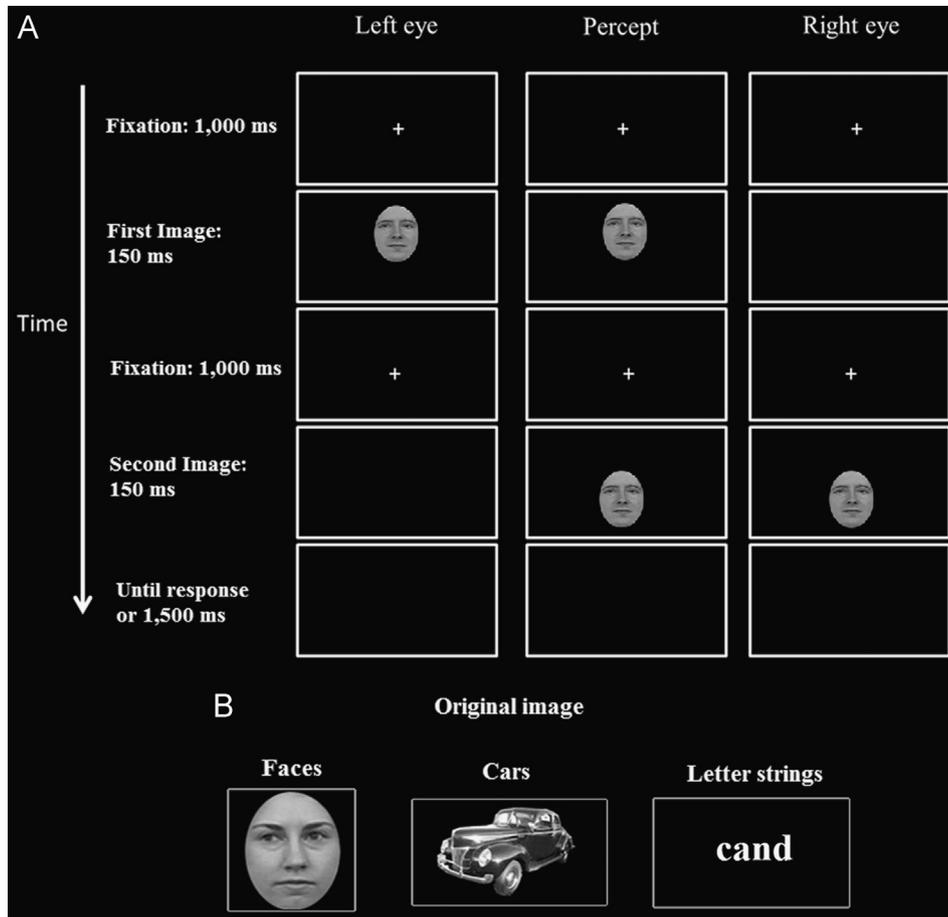
Fig. 2. (A) A typical different-eye and different location trial from Experiment 1. In this example, the first image is presented to the left eye (left column) and the left visual field and the second image is presented to the right eye (right column) and the right visual field. The middle column represents the participant's fused perception. A "same" response is required. (B) An example of each of the face, cars and letter string images used.
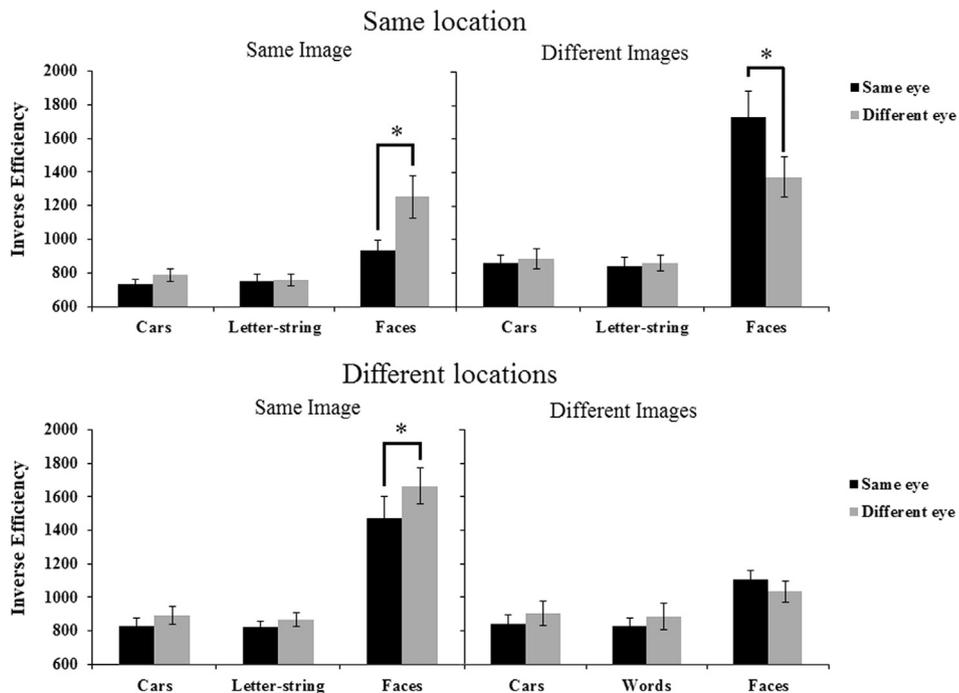
Fig. 3. Results from Experiment 1. Inverse efficiency score (RT/proportion accuracy) for same location (top panel) and different locations (bottom panel) trials as a function of stimulus type and eye plotted separately for same/different image trials. Lower values represent better performance, and the error bars represent 1SE.

A trial consisted of a pair of faces (front views, neutral expressions; see Fig. 2B), letter-strings or cars (all randomized within a block), presented sequentially. Half of the trials contained the identical image presented twice (the 'same' condition) whereas the remaining half contained two different images (the 'different' condition).

Images could appear 1.5° above or below the center of the screen. On half of the trials, both images were presented at the same visual location, and, on the other half, images were presented in two different locations. On half of the trials, both images were presented to the same eye and, on the other half, each image was presented to a different eye, and these trial types were randomized in a block. Trials were also divided between three visual categories (faces, cars, strings); participants completed 3 blocks of trials with each block comprising 192 trials (a total of 576 trials; 24 trials for same/different response × same/different eye presentation × same/different location, for every visual category separately). Responses were made via button presses, and accuracy and reaction time (RT) were measured. In all experiments, participants responded by pressing the "P" button of a keyboard using the right index finger for "same" and "Q" button of a keyboard using the left index finger for "different".

4. Results

Because the experimental manipulation can influence both RT and accuracy, in all of the experiments we used an inverse efficiency (IE) score (RT correct responses divided by the proportion of correct responses) as the dependent measure, with lower scores reflecting better performance (Townsend & Ashby, 1983).

Trials in which response time (RT) was longer than 1500 ms or shorter than 100 ms were excluded from the analyses (5%). On average, error rates constituted 20% of the trials. To explore the category effects, we conducted an analysis of variance (ANOVA) with stimulus presentation (same, different eye), image match (same, different), stimulus type (faces, letter-string, and cars) and location (same, different locations) as within-subjects factors. Fig. 3 presents the mean IE for same and different responses for trials at the same location (top panel) and at the different locations (bottom panel) as a function of stimulus type and eye. Note that the higher the IE score, the poorer performance.

As evident from Fig. 3, the four-way interaction was significant, $F(2,42)=3.3$, $MSE=41,777$, $p<.05$. Post hoc comparisons with Fisher correction revealed that this interaction was a result of a reduction in performance for same- over different-eyes viewing conditions when two different images of faces appeared at the same location, $F(1,21)=10.3$, $MSE=135,337$, $p<.01$, but not when different images of faces appeared at different locations, $F(1,21)=1.7$, NS. More importantly for the current purpose is that the interaction between stimulus type, stimulus presentation and image match was also observed,[1] $F(2,42)=30.7$, $MSE=26,317$, $p<.01$, as the advantage for the same- over different-eyes was greater when the two faces were the same than when they were different, and the different- versus same-eye advantage was greater when the two faces were different than when they were the same. This enhancement was evident only for the face trials and not for the other visual stimuli ($p<.05$ paired comparisons with Fisher correction).

The three-way interaction of stimulus type × location changes × image matching was also significant, $F(2, 42)=33.2$, $MSE=82,260$, $p<.001$, indicating that, for faces but not for other stimuli types, there was an advantage for same over different locations for same images and for different over same locations for different images. The three-way interaction of stimulus presentation × location changes × image matching was also significant, $F(1,21)=8.8$, $MSE=20,784$, $p<.01$, indicating an advantage for different over same eye presentation when images were presented at different locations and required a different response.

Unsurprisingly, in light of the higher-order interactions, there was a significant stimulus presentation × image matching

interaction, $F(1,21)=38.6$, $MSE=21,792$, $p<.001$, and a location change × image matching interaction, $F(1,21)=41.7$, $MSE=113,323$, $p<.001$. Finally, there was a main effect of stimulus type, $F(2,42)=88.6$, $MSE=156,932$, $p<.001$, with faces discriminated overall more poorly than letter-strings or cars, and no significant difference between the latter two categories ($p<.05$ paired comparisons with Fisher correction).

5. Discussion

This experiment demonstrates that small variations in the spatial location of the inputs do not eliminate the monocular benefit observed for faces: there was a monocular advantage for comparing faces both when the faces were presented in the identical and in slightly different locations. This finding suggests that the facial representations generated by lower parts of the visual system are not a function solely of the responding neurons and that there is sufficient generalizability and abstraction in the signal to overcome small spatial changes. Interestingly, a reduction in performance was observed for monocular viewing when *different* face images were presented at the same exact location. This finding might represent the additional competing demands when the same neural tissue is used to represent two different images and the decrement in the monocular advantage (or superior performance in the interocular case) reflects the greater ease in processing different images in different channels. Taken together, both the facilitation and decrement in performance under monocular conditions attest to the functional contribution of earlier parts of the visual system to the process of face perception.

5.1. Experiment 2: Visual field variability

The previous finding reveals the performance advantage when the same eye receives the same face images for comparison and we have ascribed this benefit to the shared neural signal in the monocular channel of the visual pathway. If the monocular benefit observed above is really a product of facial representations mediated by lower visual structures, presenting two face images to different visual fields (which involve different monocular channels) should abolish the monocular benefit for faces. To examine this prediction, we adopted a stronger location manipulation, in which the two consecutive images could appear in the same visual field or in different visual fields (and, obviously, hemisphere).

We also used this experiment to begin to elucidate the particular subcortical structures that might give rise to this monocular enhancement. In the superior colliculus, there is a biased representation of the visual fields, favoring the temporal over the nasal half-field (Conley, Lachica, & Casagrande, 1985; Perry & Cowey, 1985; Kaas & Lyon, 2007; Rodman, Gross, & Albright, 1990). Accordingly, images that are presented to the temporal half-field should activate the retinocollicular pathway to a greater extent than images that are presented to the nasal half-field. Manipulating the visual field and eye to which the images are presented will allow us to examine if there is a nasal-temporal asymmetry in the monocular benefit for face stimuli. If it is the case that a larger monocular benefit is observed when both face images are presented to the nasal hemi-retina compared to the temporal hemi-retina, this would suggest that the effect is modulated by the retinocollicular pathway. If the monocular benefit for faces is equivalent across hemi-retinae, this would suggest that the monocular benefit for faces involves the retinogeniculate pathway (e.g. lateral geniculate nucleus—LGN).

In this experiment, then, we manipulated the visual field to which images were presented. In the same location condition, images were presented to the same visual field, while in the different location condition, images were presented to different visual fields and, therefore, to different monocular channels.

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[1] This interaction was marginally significant even when analyzing accuracy rates separately ($p=.069$). In a separate ANOVA this effect did not interacted with general performance on the face task when participants were divided into two groups of high/low performance on faces.

6. Methods

6.1. Participants

Participants (age 20–25 years; 9 females and 10 males), all of whom had normal or corrected-to-normal vision, consented to participate.

6.2. Stimuli

Participants performed the same/different judgment task with the same stimuli as in the first experiment but only on faces and car stimuli (as car and word stimuli revealed the same pattern and, therefore, serve as an equivalent contrast with faces).

6.2.1. Procedure

This experiment was similar to the previous one except for the following differences: (i) the images could appear either 9.5° to the right or to the left of fixation (see Fig. 4 upper panel); (ii) only cars and face images were presented; and (iii) participants completed 3 blocks of trials with each block comprising 192 trials (a total of 576 trials; 36 trials for same/different response × same/different eye presentation × same/different location, for each visual category). As above, responses were made via button presses, and accuracy and reaction time (RT) were measured. As in all experiments images exposure duration was time-limited (150 ms) to preclude saccades.

7. Results

Trials in which response time (RT) was longer than 1500 ms or shorter than 100 ms were excluded from the analyses (7%). On
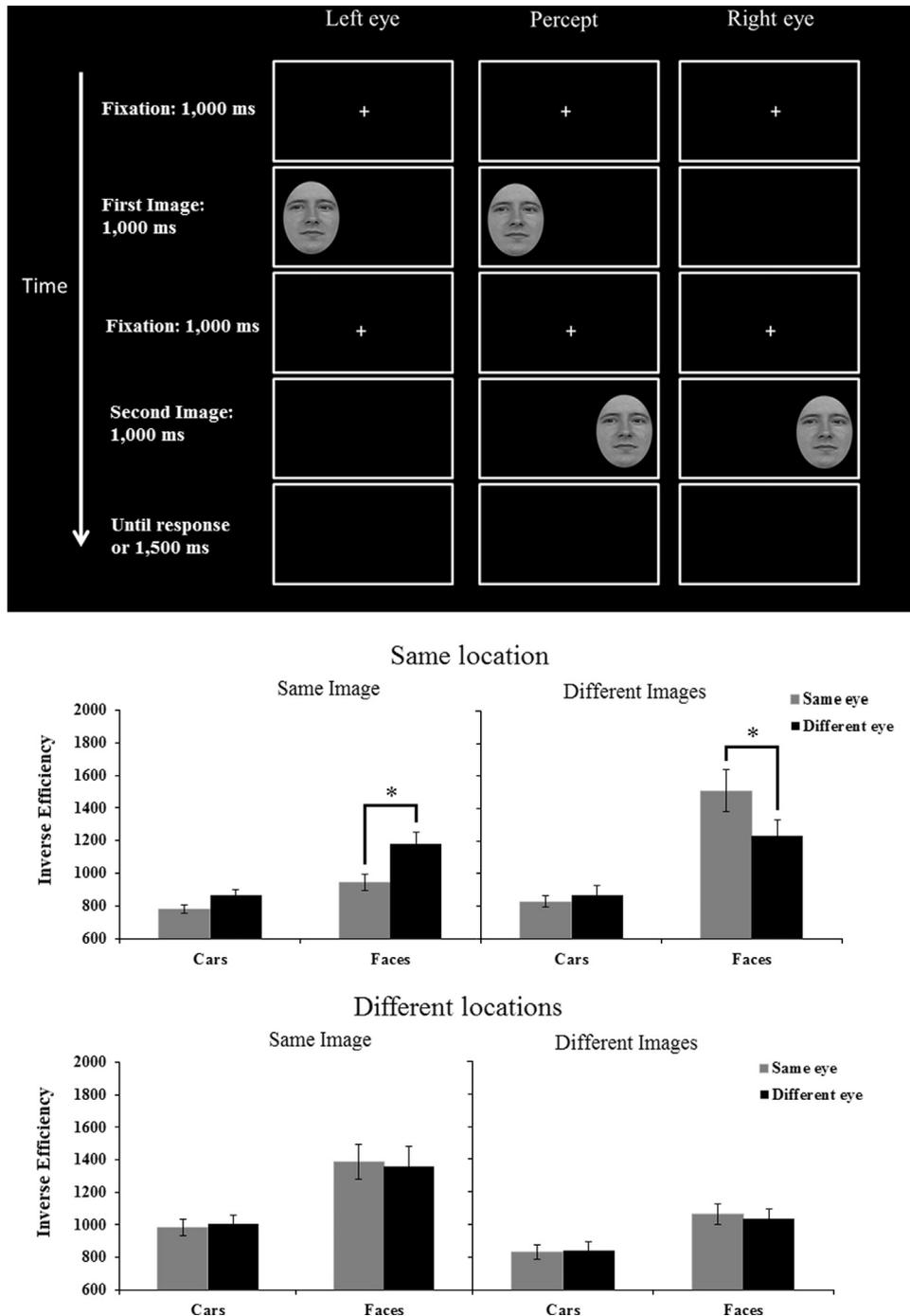
Fig. 4. Results from Experiment 2. Inverse efficiency score (RT/proportion accuracy) for same location (top panel) and different locations (bottom panel) trials as a function of stimulus type and eye plotted separately for same/different image trials. Lower values represent better performance, and the error bars represent 1SE.

average, error rates constituted 25% of the trials. To explore the category effects, we conducted an analysis of variance (ANOVA) with stimulus presentation (same, different eye), image match (same, different), stimulus type (faces and cars) and visual-field changes (same visual-field, different visual-field) as within-subjects factors. Fig. 4 (lower panel) presents the difference in mean inverse efficiency between the same versus different eyes as a function of the three other factors listed above.

Importantly, the four-way interaction between stimulus type, stimulus presentation, visual-field changes and same/different matching was significant,[2] $F(1,18)=10.6$, $MSE=26,148$, $p < .05$. This interaction demonstrated that the same- versus different-eye advantage was greater when the two faces were the same than when they were different and a different- versus same-eye advantage was greater when the two faces were different than when they were the same. Critically, this enhancement was only evident when the two faces were presented to the same visual-field but not to different visual-fields, and there was no enhancement for cars in any condition ($p < .05$ paired comparisons with Fisher correction). As in Experiment 1, performance was lower for same than different eyes presentation when different face images were presented (again implicating the same channels but in this case reflecting the competition for representation).

In order to examine whether the monocular benefit for faces is modulated by the visual field to which the image was presented, we conducted a separate analyses in which we examined only face trials in which the two images were of the same face and presented to the same eye. Specifically, we compared performance for trials in which the images were presented to the nasal hemi-retina or to the temporal hemi-retina. No difference was observed between the two conditions ($F < 1$), and this rules out any contribution from the retinocollicular pathway.

All three-way interactions were significant, stimulus type $\times$ stimulus presentation $\times$ image matching ($F(1,18)=11.6$, $MSE=20,881$, $p < .01$), stimulus type $\times$ visual-field changes $\times$ image matching ($F(1,18)=14.5$, $MSE=65,538$, $p < .01$), and stimulus presentation $\times$ visual-field changes $\times$ same/different matching ($F(1,18)=9.4$, $MSE=36,837$, $p < .01$). There was a significant stimulus presentation $\times$ image matching interaction, $F(1,18)=16.2$, $MSE=23,472$, $p < .001$. There was also significant visual-field changes $\times$ image matching interaction, $F(1,18)=39.8$, $MSE=80,445$, $p < .001$. There was also a significant main effect of stimulus type, $F(1,18)=102.1$, $MSE=85,388$, $p < .001$, with faces discriminated more poorly than cars.

8. Discussion

This experiment replicates the monocular advantage for faces but not for cars when the two images were presented to the same eye and, in complementary fashion, shows that two different images presented to the same location resulted in interference. The novel result here is that the monocular performance advantage is abolished when face images are presented to different monocular channels. This finding suggests that the facial representations generated by lower parts of the visual system are restricted to the specific monocular channel in which they were activated. In addition, the observed effect was not modulated be the hemi-retina to which the images were presented. This finding might suggest that the monocular advantage for faces is mediated by the retinogeniculate pathway.

8.1. Experiment 3: Size variability

Thus far, the findings from the first two studies show that facial representations generated by lower parts of the visual system are indifferent to small (but not large) changes in spatial location, suggesting that there is some tolerance for changes in the retinal input. We explore this tolerance further by determining whether there is also some tolerance across variability in image size (which, in the real world, could result from changes in proximity to the attended face). To the extent that the subcortical representations are not limited to the absolute retinal input, we might still expect to see a monocular advantage when the images to be compared vary in size.

9. Methods

9.1. Participants

Participants (age 18–23 years; 11 females and 9 males), all of whom had normal or corrected-to-normal vision, consented to participate.

9.2. Stimuli

This experiment was identical to the previous experiment except that, instead of manipulating the location of the images, we manipulated the size of the images. Images could either be identical, sharing one of two possible size or not (images could ether be 12° in height and 9° in width or 6° in height and 4.5° in width).

9.2.1. Procedure
Participants completed 3 blocks of trials with each block comprising 192 trials (a total of 576 trials; 24 trials for same/different response × same/different eye presentation × same/different size, for every visual category). Responses were made via button presses, and accuracy and reaction time (RT) were measured.
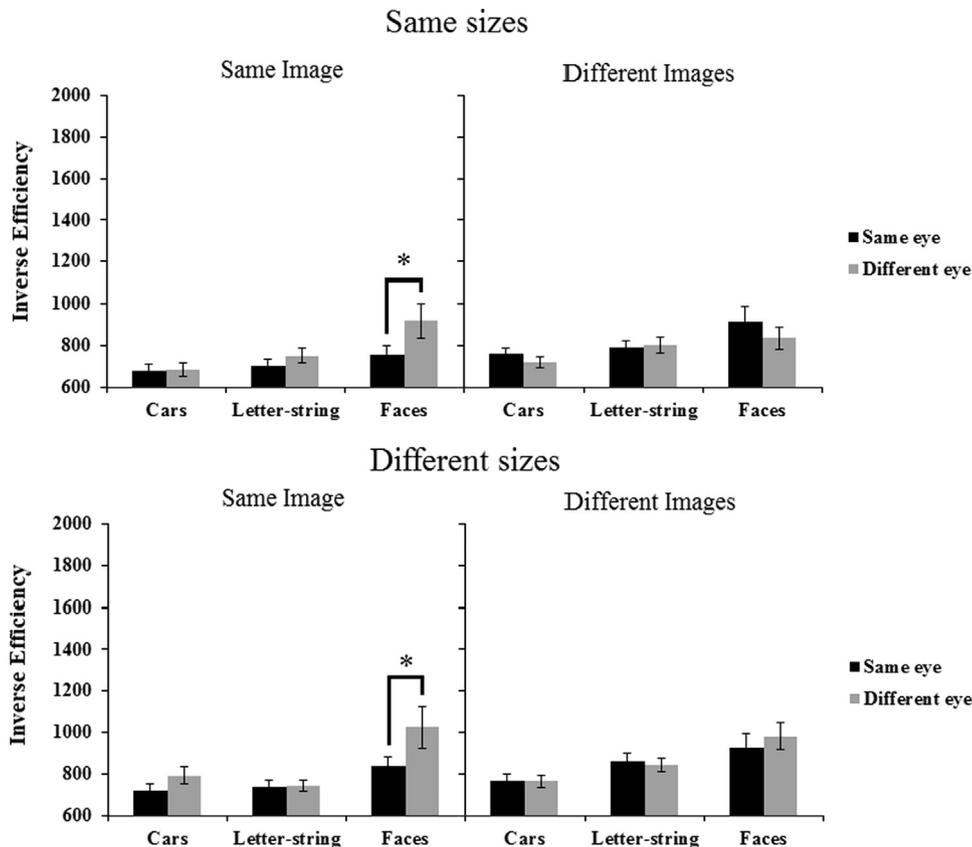
10. Results

Trials in which response time (RT) was longer than 1500 ms or shorter than 100 ms were excluded from the analyses (4%). On average, error rates constituted 11% of the trials. To explore the category effects, we conducted an analysis of variance (ANOVA) with stimulus presentation (same, different eye), image match (same, different), stimulus type (faces, letter-string, and cars) and size variability (same size, and different sizes) as within-subjects factors. Fig. 5 presents the difference in mean inverse efficiency between the same versus different eyes as a function of the three other factors listed above.

The interaction between stimulus type $\times$ stimulus presentation $\times$ same/different matching was observed,[3] $F(2,38)=5.3$, $MSE=13,621$, $p < .01$, indicating that the same- versus different-eye advantage was apparent only for faces and only when the two images were identical ($p < .05$ paired comparisons with Fisher correction). The three-way interaction of stimulus type $\times$ stimulus presentation $\times$ size variability was also significant, $F(2,38)=4.8$, $MSE=7121$, $p < .05$, indicating improved performance for same eye compared to different eyes presentation only for the same size condition ($p < .05$ paired comparisons with Fisher correction).

The two-way interaction of image matching $\times$ stimulus presentation reached significance, $F(1,19)=13.3$, $MSE=19,368$, $p < .01$ (with improved performance for same eye presentation over different presentation only for same images). The two-way interactions of stimulus type $\times$ size variability was also significant, $F(2,38)=4$, $MSE=6743$, $p < .05$ (with larger improvement for same size presentation for faces than other stimuli).

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[2] This interaction was also significant when analyzing accuracy rates separately ($p < .01$). A separate analysis demonstrated that the monocular benefit for faces for different-location conditions differed statistically between experiment 1 (in which it was observed) and the present experiment (in which it was absent).

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[3] This interaction was significant when accuracy rates separately ($p < .05$).

Fig. 5. Results from Experiment 3. Inverse efficiency score (RT/proportion accuracy) for same size (top panel) and different size (bottom panel) trials as a function of stimulus type and eye, plotted separately for same/different image trials. Lower values represent better performance, and the error bars represent 1SE.

Finally, there were significant main effects of stimulus type, $F(2,38)=20.7$, $MSE=54,898$, $p<.001$ (with faces discriminated more poorly than letter-strings or cars), stimulus presentation, $F(1,19)=9.4$, $MSE=15,461$, $p<.01$ (with same eye presentation producing better discrimination than different eyes presentation), and size variability $F(1,19)=60$, $MSE=6482$, $p<.001$ (with same size producing better performance than different sizes).

11. Discussion

This experiment demonstrates that variations in image size do not adversely influence the monocular benefit observed for faces and that the benefit is of equivalent magnitude for images of the same and different sizes. Although not quite reaching statistical significance in this case, the pattern of results again demonstrated that when two different images were presented to the same eye and had the same retinal size, performance was poorer.

11.1. Experiment 4: Identity matching

In this experiment, we shift focus somewhat and, instead of manipulating the bottom-up properties of the images (same/different spatial position in display or same/different size), we manipulate the images themselves and examine how robust the face representations are when facial geometry is altered but identity is retained. If, as we have suggested, monocular portions of the visual system are involved in generating basic facial representations, and these representations are then used for higher visual processing, we might expect to find a monocular advantage even for comparisons of faces that differ substantially in image structure but share identity. In this experiment, we

examined whether a monocular benefit would be evident when participants were presented with two different images of the same person, and not only when two identical images were presented.

12. Methods

12.1. Participants

Participants (age 18–20 years; 5 females and 14 males), all of whom had normal or corrected-to-normal vision, consented to participate.

Participants performed same/different identity judgments of faces. When identity was shared, the two images could either be a repeat of the identical image or two different images of the same person, one with a neutral facial expression and the other one with a smile.

12.2. Stimuli

In this experiment, we used a new set of face images. This set was composed of 24 males. The stimulus set was generated based on color face images extracted from four databases: FERET (Phillips, Moon, Rizvi, & Rauss, 2000; Phillips, Wechsler, Huang, & Rauss, 1998), FEI (Thomaz & Giraldi, 2010), AR (Martinez, 1998) and Radboud (Langner et al., 2010). These images displayed front-view faces of Caucasian young adult males with frontal gaze, frontal lighting and no facial hair or other accessories. All individuals had short hair that did not occlude the forehead. For each individual, we selected two expressions: neutral and happy. These images were further scaled to align the same position of the eyes, were cropped to eliminate background and hair and were normalized with the same mean and contrast values separately for each color channel (see Fig. 6A).

12.2.1. Procedure

In this experiment, only face images were presented. Same responses were given to images reflecting the same identity, either two identical images or the two different images of the same individual (one smiling and the other with neutral expression), and different responses were given to images presenting different
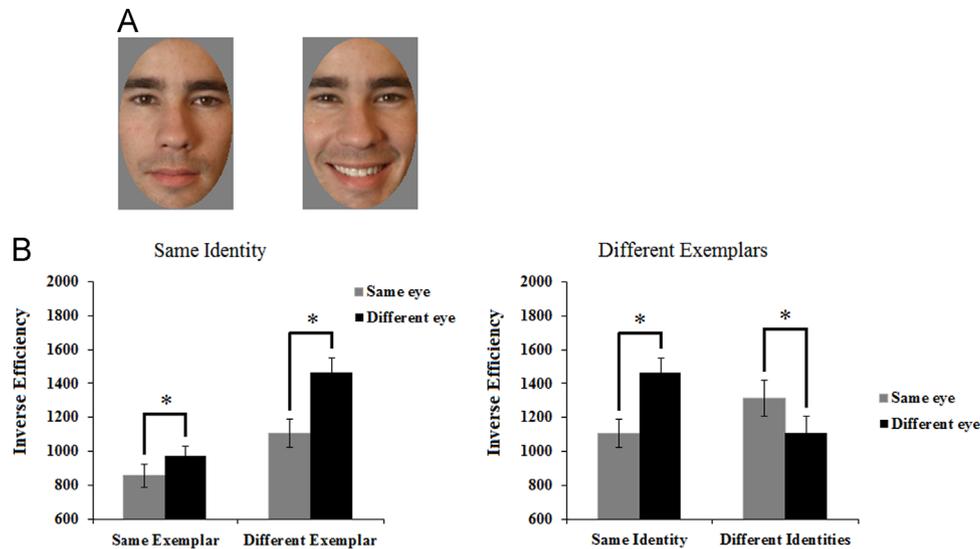
Fig. 6. (A) example of images used in Experiment 4. (B) Results from Experiment 5. Inverse efficiency score (RT/proportion accuracy) for same identities trials as a function of exemplar type and eye (left column) and different exemplar trials as a function of identity type and eye (right column). Lower values represent better performance, and the error bars represent 1SE.

identities (half presented with a similar facial expression and half with different facial expression). Participants completed 3 blocks of trials with each block comprising 128 trials (a total of 384 trials; 48 trials for same/different response × same/different eye presentation × same/different exemplar). Responses were made via button presses, and accuracy and reaction time (RT) were measured.

13. Results

Trials in which response time (RT) was longer than 1500 ms or shorter than 100 ms were excluded from the analyses (5%). On average, error rates constituted 25% of the trials. Since only the same identity condition had both same exemplars and different exemplars conditions (different identities only have different exemplars) the design was not fully factorial. Therefore, we conducted two separate ANOVAs: (1) one that focuses only on same-identity trials, and considers same versus different eye presentation as a function of exemplars (same or different), and (2) one that focuses only on different-exemplar trials, and considers same versus different eye presentation as a function or identities (same or different—across expressions).

The first ANOVA examined only same-identity trials with stimulus presentation (same, different eye) and image exemplar (same exemplar, different exemplars of same individual) as a within-subjects factors. Fig. 5B (left panel) presents the mean inverse efficiency score for same versus different eyes as a function of image exemplar.

The two-way interaction of stimulus presentation × image exemplar was significant, $F(1,18) = 11.02$, $MSE = 25,339$, $p < .01$ (with larger monocular benefit for different exemplars trials compared to same exemplars trials). The monocular benefit was significant for both image exemplar conditions ($p < .05$ paired comparisons with Fisher correction).

Finally, there were two main effects: image exemplar, $F(1,18) = 42.89$, $MSE = 60,599$, $p < .001$ (with the same exemplars producing better performance than different exemplars) and stimulus presentation, $F(1,18) = 17.35$, $MSE = 61,498$, $p < .001$ (with the same eye producing better performance than different eyes).

The second ANOVA examined only different exemplar trials with stimulus presentation (same, different eye) and image identity (same identity—which are the same trials used in the first analysis, or different identities) as a within-subjects factor. Fig. 5B (right panel) presents the mean inverse efficiency score

between the same versus different eyes as a function of image identity.

The two-way interaction of stimulus presentation × image identity was significant, $F(1,18) = 27.13$, $MSE = 55,263$, $p < .001$. Examining this interaction further demonstrates a monocular benefit for same identity trials, $F(1,18) = 16.22$, $MSE = 75,134$, $p < .001$, (for which same eye producing better performance than different eyes) and a reversed significant effect for different identity trials, $F(1,18) = 23.14$, $MSE = 17,020$, $p < .001$, (for which different eyes producing better performance than same eyes). No other effects were significant.

14. Discussion

This experiment indicates that the basic facial representations created by monocular portions of the visual system play some functional role in higher-order or more abstract visual representations, as required for identity processing. This claim is supported by the monocular advantage for two faces that share identity even though they do not share the identical image or facial expression. As in the previous experiments, we also observed a reduction in performance when two images of different identity were presented to the same eye, reflecting the difficulty in simultaneously representing two competing images. In this experiment, all images appeared at the same location and size, so the facial features of the faces were presented at the same location. This result is particularly intriguing in that it suggests that competition between different facial geometries at the same location ensues, but when these different geometries represent the same identity, the competition is eliminated and the monocular advantage is even enhanced (relative to two identical images). A possible explanation is that additional top-down support may be engaged in the two different images—same identity condition potentially in order to overcome the competitive effects that might otherwise occur.

Before we can reach the conclusion of engagement of top-down representations, we need to rule out an alternative explanation. Although an interpretation of the presented results in terms of identity processing is compelling, it is possible that bottom-up image similarities between the two images of the same person are driving the observed effect rather than a more complex, abstract representation; that is, the two images of the same individual may

still be sufficiently similar so that judgments of similarity can still be based on featural overlap between images rather than on identity per se. In order to examine the influence of facial identity without the possible influence of image similarity, a more variable set of images for every identity should be used.

14.1. Experiment 5: Identity matching with larger image variability

In this final experiment, we explore the monocular benefit for identity matching further by using a larger set of images for every identity in order to reduce featural overlap and similarity between same-identity images. We also ensured that any monocular advantage could not be explained in terms of image similarity by directly computing the similarity values across faces.

15. Methods

15.1. Participants

Participants (age 18–22 years; 12 females and 7 males), all of whom had normal or corrected-to-normal vision, consented to participate.

15.2. Stimuli

In this experiment, images of 24 individuals were used (12 male and 12 female). Each individual had 5 different image exemplars (images taken at different times in different postures/viewpoints and lighting conditions), 14° in height and 10° in width (see Fig. 7A). The images were all of unknown individuals (adopted from Avidan & Behrmann, 2009).

15.2.1. Procedure

In this experiment, only face images were presented. Same responses were given to images presenting the same identity, either two identical images or two different images of the same individual randomly chosen out of the 5 possible exemplars, and different responses were given to images presenting different identities. Participants completed 3 blocks of trials with each block comprising 128 trials (a total of 384 trials; 48 trials for same/different response × same/different eye presentation × same/different exemplar). Responses were made via button presses, and accuracy and reaction time (RT) were measured.

16. Results

Trials in which response time (RT) was longer than 1500 ms or shorter than 100 ms were excluded from the analyses (5%). On average, error rates constituted 19% of the trials. Similarly to Experiment 4, we conducted two separate ANOVAs: (1) one that focuses only on same-identity trials, and considers same versus different eye presentation as a function of exemplars, and (2) one that focuses only on different-exemplar trials, and considers same versus different eye presentation as a function of identities.

The first ANOVA examined only same-identity trials with stimulus presentation (same, different eye) and image exemplar (same exemplar, different exemplars) as a within-subjects factor. Fig. 6B (left panel) presents the mean inverse efficiency scores for the same versus different eyes as a function of image exemplar.

The two-way interaction of stimulus presentation × image exemplar was significant, $F(1,18)=33.49$, $MSE=3550$, $p < .001$ (with larger monocular benefit for different exemplars trials compared to same exemplars trials). The monocular benefit was significant for both image exemplar conditions ($p < .05$ paired comparisons with Fisher correction).

Finally, there were two main effects of image exemplar $F(1,18)=75.27$, $MSE=55,451$, $p < .001$ (with the same exemplars producing better performance than different exemplars) and stimulus presentation $F(1,18)=67.16$, $MSE=6423$, $p < .001$ (with the same eye producing better performance than different eyes).

The second ANOVA examined only different exemplars trials with stimulus presentation (same, different eye) and image identity (same identity, different identities) as a within-subjects factor. Fig. 6B (right panel) presents the mean inverse efficiency score for the same versus different eyes as a function of image identity.

The two-way interaction of stimulus presentation × image identity was significant, $F(1,18)=36.82$, $MSE=6335$, $p < .001$. Examining this interaction further demonstrates a monocular benefit for same identity trials, $F(1,18)=57.36$, $MSE=8743$, $p < .001$, but no monocular benefit for different identity trials, $F(1,18) < 1$.

Finally, there was a main effect of stimulus presentation $F(1,18)=44.25$, $MSE=6078$, $p < .001$ (with the same eye producing better performance than different eyes).

In order to exclude image similarity further as a potential influence on the monocular benefit observed for the same identity different exemplars condition, we calculated Z-scored average pixelwise Euclidean distances for every identity (between the different exemplars) and for every pair of images presented during the task. The average pixelwise similarities within identities were -0.1 while the average pixelwise similarities between identities was 0.2 (more negative values represent greater similarity between images). In order to compare the similarity between and within identities, we excluded from the analyses the 4 identities with the greatest within identity similarity. This reduced the average pixelwise similarities within identities to 0.27 (a more positive value than the average pixelwise similarities between identities). For the new analyses, the monocular benefit for same identity was still significant for different exemplars ($p < .05$ paired comparisons with Fisher correction). Of relevance too, the monocular benefit observed here applies not only to the identification of the same individual across different images, but some of the images depict the face from different viewpoints, implicating the subcortical structures in viewpoint invariance (to some extent) as well.

17. Discussion

In this experiment, we replicated the results of the previous investigation in the context of a larger and more variable set of images for every identity. We demonstrated that even when the pixel similarity was equated across pairs of images, a monocular benefit was still observed for same-identity images, and that the monocular enhancement was still evident (and relatively stronger) for different exemplars of the same identity. Interestingly, in this experiment we did not observe a reduction in performance when two images of different identity were presented to the same eye. In this experiment, images differed in viewpoint (each picture was taken from a different angle), so the facial features of the faces were presented at different retinal locations. In contrast to the previous experiment, different neural regions responded to the facial features of the first and second image and so the absence of the competitive effects observed previously is not surprising.

18. General discussion

This study examined the nature of face representations mediated by prestriate or subcortical structures of the visual system. There has been growing interest in the potential contribution from subcortical representations to visual object recognition (with special emphasis on face recognition) in adult humans (for example, Mende-Siedlecki et al., 2013). Recent studies (Gabay et al., 2014; Khalid et al., 2012) have offered behavioral evidence
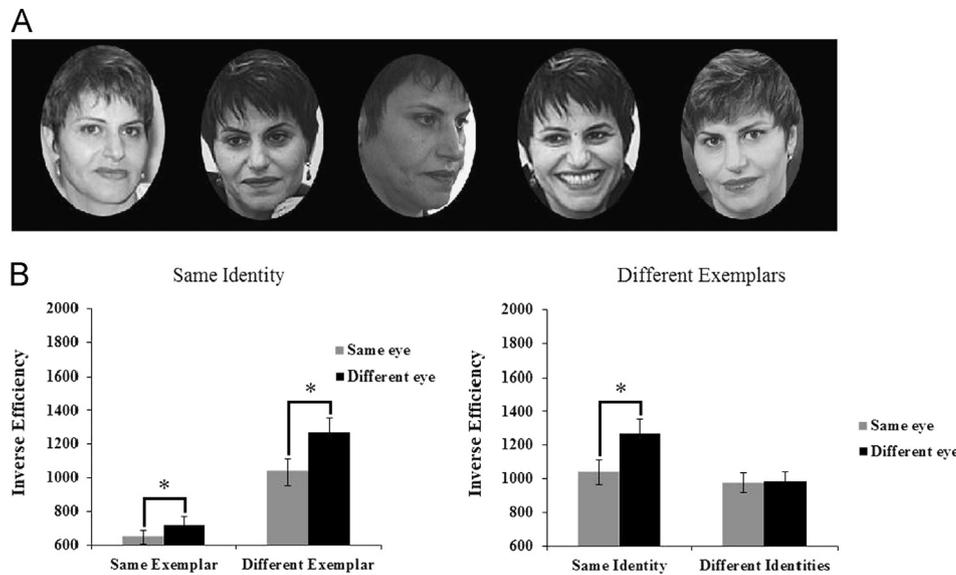
Fig. 7. (A) Example of images used in Experiment 5. (B) Results from Experiment 6. Inverse efficiency score (RT/proportion accuracy) for same identities (left column) and different identities (right column) trials as a function of exemplar type and eye. Lower values represent better performance, and the error bars represent 1SE.

consistent with the contribution of subcortical structures to the perception of faces, independent of sensitivity to facial expression (mediated by amygdala and already well-established, see Pessoa & Adolphs, 2010). For example, in our previous study, we observed that adult participants were significantly better at judging the likeness of two sequentially-presented faces than the likeness of two cars or of two letter-strings, when the stimuli were presented to the same eye compared to when they were presented to different eyes. The facilitation of performance afforded by two stimuli presented to the same eye (monocularly) versus to two different eyes (interocularly) is indicative of the involvement of the early, monocular portions of the visual pathway.

In the present study, we have elaborated on this initial finding and explored the nature of the functional contribution of rudimentary visual regions to face perception. Across five studies, we have obtained several novel findings. The first major result is that the representations derived in the monocular pathway are somewhat indifferent to changes in image size and location. This conclusion is licensed by the finding that the monocular benefit extends to pairs of faces that differ in size or in location, as long as the images are presented to the same subcortical visual pathway. We also demonstrated that there is no nasal-temporal asymmetry i.e. no difference in the magnitude of the monocular effect in the nasal versus temporal hemi-fields, which might implicate the retinogeniculate pathway in this monocular advantage.

The second major result concerns the engagement of subcortical regions in the processing of more abstract aspects of face representations: interestingly and perhaps counterinutitively, a monocular benefit is still evident even when two different images of the same person were presented to the same versus different eye and this benefit still held even when image similarity was equated within- and between-identity. Because some of the different images shown depict the face from difference viewpoints, the monocular benefit is evident across viewpoint invariant (to some extent) representations, as well.

At the same time that we observed the monocular benefit for the same images, we repeatedly noted a reduction in performance when two different face images were presented at the same retinal location and to the same eye. This finding could be interpreted as a congruency effect between stimulus presentation (same/different eyes) and the required response (same/different image); however, because this reduction in performance was only observed for faces (and not for any of the other stimulus types), we need to account

for the specificity associated with this result. We suggest that this finding might represent the flip side of the monocular enhancement coin: that is, inhibition, rather than facilitation, accrues when two different face images are being mediated by the same underlying mechanism. In this case, the same neurons that have mediated the representation of the first image are also engaged in processing the second image, resulting in competition for representation. As such, this decrement in performance under this condition provides further testament to the claim that subcortical regions are engaged (by either facilitation or inhibition) in face perception. Interestingly, when these neurons represent a different image of the same identity i.e. different exemplars but of the same person, the competition is eliminated, and the monocular advantage is still observed. We suggest that additional top-down support may be engaged in the processing of two different images of the same identity, potentially in order to overcome the competitive effects that might otherwise occur.

That the subcortical structures are able to compute size and location invariant representations (although of course we did not test all sizes nor all distances and so the limit on this remains to be determined) is interesting. Perhaps the more provocative result concerns the more abstract nature of these representations that evince some generalization over geometry, viewpoint and expression such that identity information can be derived. There are two possible explanations for mechanisms that might support this more complex representation at a subcortical level. The first possible explanation is that the subcortical structures are indeed 'smart' and can compute identity information when there is no featural overlap or other more physical or surface properties shared by two faces. Indeed it has been demonstrated that nonlinear representations, which are necessary for the representation of complex visual pattern, are evident subcortically at the LGN Y-cells (as observed in cats, Rosenberg, Husson, & Issa, 2010). This finding demonstrates that subcortical regions do have the ability to represent complex visual patterns, and that this might even extend to faces. The second possible explanation is that subcortical structures are not computing the representations in and of themselves and that the readout of identity (and perhaps other visual) information from subcortical structures is the consequence of top-down feedback from cortical regions. While there is no obvious way to adjudicate between the two possible explanations based on our findings, we outline one possible scenario that is consistent with our data and with other existing findings. There is growing evidence that information

from the magnocellular (M) pathway might be transmitted early and rapidly to orbitofrontal cortex (Chaumon, Kveraga, Barrett, & Bar, 2013; Kveraga, Boshyan, & Bar, 2007). Consequently, the signal from frontal cortex might facilitate object-recognition in a top-down fashion. Indeed, evidence to support the claim of top-down constraints on shape perception is gleaned from effective connectivity analyses of fMRI data showing a link between early visual and inferotemporal object recognition regions with the orbitofrontal cortex (Kveraga et al., 2007). Given that there are no firewalls in cortex, the feedback signal which provides top-down facilitation from frontal cortex might propagate back down the M pathway and influence face perception in the prestriate structures, as well (see Pallett & Dobkins, 2013). While this notion is speculative, there is sufficient empirical support for top-down cortical modulation of subcortical structures (O'Connor, Fukui, Pinsk, & Kastner, 2002) and there is already documentation of functional connectivity between amygdala and face-selective regions (Mende-Siedlecki et al., 2013). The speculative claim we offer, and which needs to be tested, then, is that the monocular benefit that is apparent for identify and viewpoint invariance (and perhaps for size and location invariance too) is the consequence of both a feed-forward and feed-back cascade between subcortical and cortical structures. Whether the subcortical structures serve as the primary computational system or not remains to be determined. What is clear is that these structures are engaged in a circuit that supports face perception in all of its complexity.

The finding that subcortical regions are involved in the abstract representation of faces (as suggested by the two last experiments) and are also sensitive to the image retinal location (as suggested by the reduction in performance when two different face images were presented at the same retinal location) might be perceived as conflicting—it is not clear how these two representations (abstract and retinal) might co-exist in the subcortical visual pathway. A similar dual representation was demonstrated for an attentional inhibitory tagging. Inhibition of return (IOR—the reduced performance at already attended location) has been shown to exist at both retinotopic and spatiotopic coordinates (Maylor & Hockey, 1985; Sapir, Hayes, Henik, Danziger, & Rafal, 2004). It has been demonstrated that these two manifestations of IOR differ in their time course dynamic (Pertzov, Avidan, & Zohary, 2011). IOR was recently demonstrated in a freely swimming fish (Gabay, Leibovich, Ben-Simon, Henik, & Segev, 2013) which also suggests that a spatiotopic representation of IOR can be accomplished even without a visual cortex. In a similar manner, one might hypothesize that abstract face representations and more basic retinotopic face representation might co-exist simultaneously.

The present findings implicate the involvement of lower parts of the visual system in face perception. Taken together, the five experiments provide evidence that subcortical face representations play a role in perception in adults and contribute beyond bootstrapping face recognition in infancy, or aiding automatic emotional processing (Kleinhans et al., 2011). The contribution of subcortical structures suggests that there is both conservation across phylogeny and ontogeny and that, rather than being relieved of their duties following the bootstrapping of cortical representations (Johnson, 2005, 2010), subcortical structures continue to be actively engaged in representing face images across the lifespan. Subcortical visual regions contribute by deriving a representation of a face that is indifferent to changes in size or location, identity and even viewpoint, displaying an impressive feat of representational competence.

Acknowledgments

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