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## 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

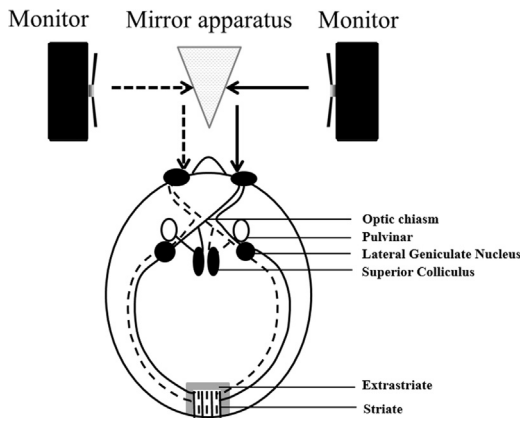
as the amygdala with the nodes of the cortical network alluded to above (Mende-Siedlecki, Verosky, Turk-Browne, & Todorov, 2013; but also see Stein, Seymour, Hebart, & Sterzer, 2013).

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 Ansong (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 extra-striate 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 extra-striate 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.cnb.cmu.edu/Face\\_Place](http://wiki.cnb.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.

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