Center–surround organization of face-space: evidence from contrast-based face-priming

Shabnam Rostamirad[a,b], Jason J.S. Barton[a,b,c] and İpek Oruç[a,b]

'Face-space' is an abstract concept of the multidimensional representation of faces. Faces of similar appearance are closer in face-space than dissimilar faces; however, it is not clear how representations interact. Examining contrast thresholds for facial recognition, we show that a 200 ms preview of a face facilitates recognition of the same face, but inhibits recognition of other faces, more so for the same ethnic group than for a different ethnic group. This suggests a center–surround organization in which facial representations close to the priming stimulus are more suppressed than those that are distant. *NeuroReport* 20:1177–1182 © 2009 Wolters Kluwer Health | Lippincott Williams & Wilkins.

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Departments of [a]Ophthalmology and Visual Science, [b]Medicine (Neurology) and [c]Psychology, University of British Columbia, Vancouver, British Columbia, Canada

Correspondence to İpek Oruç, Neuro-ophthalmology Section K, VGH Eye Care Centre, 2550 Willow Street, Vancouver, BC V5Z 3N9, Canada
Tel: + 1 604 875 4111 x67672; fax: + 1 604 875 4302; e-mail: ipek@psych.ubc.ca

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Introduction

Many visual cortical areas display an orderly organization in stimulus representations, one of the best examples being the orientation columns found in striate cortex. Responses of neurons in these areas often show interactions between representations, in that the activity evoked by one stimulus is modulated by other stimuli. Thus, in V1 orientation, responses are inhibited by bars of different orientations in the same receptive field ('cross-orientation suppression' [1]) and by bars of similar orientation in regions outside the classical receptive field ('center–surround inhibition' [2]).

How representations of more complex stimuli, such as faces, are organized and interact is not known. Face-space is an abstract concept in which facial representations are situated in a multidimensional space [3,4]. Computational estimates suggest that 15–22 dimensions may suffice to encode all the human faces encountered in an average lifetime [3]. What is represented along these axes is unclear, however, with suggestions ranging from features and their spatial configuration [5,6] to eigenfaces from a principle component analysis [7]. Regardless, a general principle is that faces that are similar to each other are closer in face-space than faces that are dissimilar. In particular, faces from the same ethnic group will often be more similar and closer in face-space than faces from different ethnic groups [8].

Adaptation has emerged recently as a tool for exploring face-space [9]. A common technique is to show that perception of a morphed face that is ambiguous regarding a specific attribute (e.g. identity, expression, viewpoint) is altered by prior exposure to other faces. These face aftereffects are observed even when the adapting and test stimuli differ in size by a factor of four [10], and when their corresponding retinal images are separated by as much as 6° [9], suggesting that high-level face-specific processes are the basis of this effect, rather than simple retinotopic contrast or orientation aftereffects. Face aftereffects have been used to infer the organization of face-space, for example, to suggest that there may be a prototypical 'average face' at an origin in face-space [9].

As this adaptation technique relies on a relative shift in perception along a morph continuum, it cannot show absolute effects of adaptation – that is, whether the shift stems from a change in activity for the adapting-face, a change in activity for nonadapted faces, or both. To address this, we used a technique based on contrast adaptation and a forced-choice discrimination paradigm [11], (also see Ref. [12], for use of this methodology in lower-level visual adaptation to, for example, spatial frequency). This method determines the luminance contrast required to recognize a face after preview of another high-contrast face. With brief preview, contrast thresholds are reduced when the previewed face is the same as the test-face [11], indicating a facilitating repetition-priming effect. This effect seems to have a higher-level locus of origin than conventional retinotopic aftereffects, as significant facilitation is obtained even when the adapting-face and test-face are mismatched in size and retinal location (adapting-face was 50% larger, and presented 1° left or right of test; for further details, see Ref. [11]). In this report, we used this technique to explore interactions between facial representations. We

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examined whether brief preview of a face also alters contrast thresholds for recognizing other faces, and if so, whether such effects vary with similarity to the adapting-face.

We used ethnicity to vary face similarity. We obtained two Chinese and two Caucasian faces with neutral expressions. To begin, we used two techniques to confirm that, in our stimulus set, faces were more similar to those of the same ethnic group than to those of the other ethnic group. First, we showed that psychophysical contrast thresholds in two human observers were higher for discriminating between two Caucasian or two Chinese faces than for discriminating between a Chinese and a Caucasian face [$F(1,46) = 4.34$, $P < 0.05$]. Second, we used an ideal observer method to show that contrast thresholds for discriminating between two faces of the same ethnic group were higher than those for discriminating between two faces differing in ethnicity [$F(1,4) = 9.72$, $P < 0.05$] (Table 1).

In our first adaptation experiment, each trial consisted of a 200 ms adapting stimulus, followed by a 50 ms white-noise mask, a 150 ms fixation, a 150 ms blank, and a 150 ms low-contrast test version of one of the four faces (Fig. 1). An answer display then showed all four faces of the stimulus set and the participant indicated which one the test-face resembled, followed by auditory feedback.

There were five different adapting stimuli: high-contrast versions of one of the four faces in the stimulus set, and a ‘blank’ gray mask to generate a baseline threshold. Four different test-face identities and five different adapting stimuli gave 20 adapting/test-face combinations. Discrimination contrast thresholds for each test–adaptor pair were individually measured by means of 20 randomly interleaved staircases, each controlling the contrast of the test stimulus in a single condition.

Table 1 Discrimination contrast thresholds for within-race and across-race face stimuli

	Within-race		Across-race	
	Mean	Standard error	Mean	Standard error
Experiment 1				
Physical thresholds				
Ideal observer	18.50	0.92	15.50	0.49
Psychophysical thresholds				
Participant S	20.60	1.30	17.80	0.74
Participant I	14.40	0.38	12.00	0.60
Experiment 2				
Physical thresholds				
Ideal observer	16.80	0.76	14.50	0.43
contrast = values $\times 10^{-3}$				

Pair-wise discrimination contrast thresholds were measured in a two-alternative forced-choice paradigm for all faces in the stimulus set (four faces resulting in six pairs in Experiment 1, and six faces resulting in 15 pairs in Experiment 2). For Experiment 1, thresholds averaged over pairs of faces chosen form the same ethnic group (within-race, two pairs), and those chosen from different ethnic groups (across-race, four pairs) are shown for two human observers and the ideal observer simulation. Thresholds were lower for across-race pairs than within-race pairs for both the human and the ideal observers, indicating that faces of the same race are more similar to one another than to faces from a different race. We confirmed this for the stimulus set of Experiment 2 using the ideal observer thresholds. Experiment 2 stimulus set included six faces: two new faces (one Asian and one Caucasian) in addition to the original stimulus set of Experiment 1. Ideal observer thresholds averaged over across-race faces (nine pairs) was lower than that for within-race faces (six pairs).

We calculated the threshold change induced by adaptation by dividing the threshold of each of the face adaptation conditions by the blank adaptation threshold (baseline), yielding a threshold elevation ratio. Threshold changes from combinations with the same face as adapting and test stimulus were classified as the ‘same-face’ condition (pooled across four same-face staircases). Those from combinations in which the adaptor was the other face of the same ethnic group were classified as the ‘same-race’ condition (pooled across four same-race staircases). Finally, threshold changes from combinations where the adapting-face was from the other ethnic group were classified as the ‘different-race’ condition (pooled across eight different-race staircases). Threshold elevation ratios were analyzed by a Kruskal–Wallis one-way analysis of variance with condition (same-face, same-race, different-race) as a within-subjects factor, followed by one-tailed Wilcoxon signed-rank tests for pair-wise and single sample comparisons.

Methods

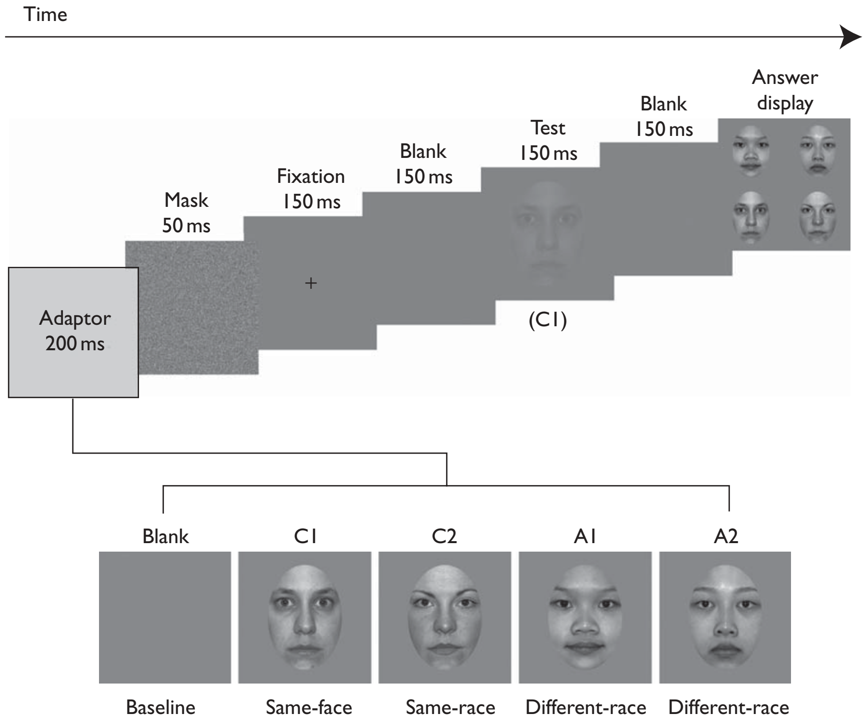
Observers and apparatus

Seven observers (three female, two Asian and five Caucasian, aged 19–45 years) participated in Experiment 1, and seven observers (four female, three Asian and four Caucasian, aged 19–33 years) participated in Experiment 2. All our observers in Experiment 1 were born and brought up in their respective ethnic societies (e.g. Asian participants in an Asian country). In Experiment 2, two of the Asian participants were born and brought up in an Asian society, the rest of the participants were brought up in a Caucasian society. Participants viewed stimuli displayed on a SONY Trinitron 17 (SONY, Tokyo, Japan) GDM-G500 monitor at 1024 × 768 resolution at a distance of 99 cm in a dark room. Stimuli were generated by a PC equipped with Cambridge Research Systems VSG 2/3 (Cambridge Research Systems, Rochester, Kent, England). Display was gamma-corrected and average luminance was 40 cd/m^2. CRS VSG Toolbox for Matlab (Cambridge Research Systems) was used to present the stimuli.

Stimuli

We obtained our face stimuli from the NimStim Set of Facial Expressions (*http://macbrain.org/resources.htm*), and Hong Kong University database of Chinese faces (*http://viscog.hku.hk/facedatabase.htm*). Color images were first gray-scaled using Adobe Photoshop (*www.adobe.com*). Faces were seen through an oval aperture with a minor axis of 282 pixels and the major axis of 400 pixels corresponding to a face-width of 5.1° and face-height of

Fig. 1



Trial design. An adapting-face is shown for 200 ms. A blank adaptor is used to estimate baseline thresholds. Adapting-faces are a high contrast version of any one of the four different faces. Following a 50 ms mask, a 150 ms fixation, and a 150 ms blank, the test-face is shown for 150 ms: this is a low-contrast version of one of the four faces (in this example, C1). An answer screen then appears after another 150 ms blank and the participant indicates which of the four faces they thought was present in the test. Trials are classified at bottom by the relationship between the adapting-face and the test-face. A1 and A2, Asian; C1 and C2, Caucasian.

7.2° of visual angle. The display outside the oval aperture was set to average luminance. Faces were aligned vertically for pupil position and horizontally with the nasal tip at screen center. To avoid discrimination based on trivial differences, we made sure that all faces had same eye color (brown), same pose and tilt (frontal and vertical), and were devoid of obvious facial marks such as moles, hair, etc. Luminance values inside the oval frame were normalized so that all face images had a mean of half the maximum luminance and root-mean-square contrast of one (before adjustment of contrast for the psychophysical measurement).

Procedure

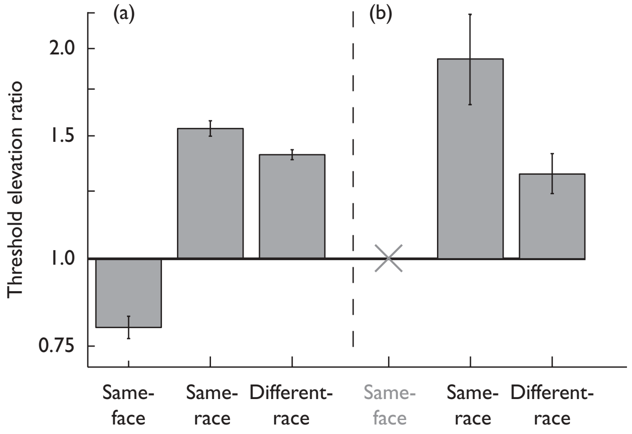
In Experiment 1 the psychophysical task was four-alternative forced-choice discrimination. Following the 200 ms preview of the adapting-face, the observers viewed one of four faces (test-face) for 150 ms and responded by indicating which one of the four faces they saw. The contrast of test-face for each adapting–test combination was controlled by an independent staircase (resulting in 20 staircases) to estimate 82% accuracy thresholds using the Quest [13] procedure in Psychophysics Toolbox [14] for Matlab 7.0. The 20 staircases were randomly interleaved in a single block, with 40 trials/staircase. Experiment 2 was similar, except that the same-face condition was removed from the design: participants were informed that the test-face would never be the same as the adapting-face. This manipulation on its own results in unequal task difficulty between the same-race and different-race conditions; in the same-race condition, simply recognizing the race of the test-face would suffice to pick the correct answer, as there is only one choice available to the participant. To prevent this, two more faces were added to the stimulus set, one Asian and one Caucasian, to be used as test stimuli. Data from trials with the two additional faces as test stimuli were not included in the analysis, therefore the results of Experiment 2 are directly comparable with those of Experiment 1, for the same test and adapting stimuli.

Discrimination thresholds and ideal observer analysis

To confirm that faces within one ethnicity are more similar (i.e. closer in face-space) to one another than to faces of a different ethnicity we performed a control experiment (to estimate perceptual distance) and an ideal observer simulation (to estimate physical distance). We determined two-alternative forced-choice discrimination contrast thresholds for all pairs of faces in our stimulus set (six pairs) as a measure of similarity/distance. For the human observers, at each trial one of two possible faces was shown for 150 ms. A choice screen followed this where the two alternative faces were displayed until the observer indicated which one of the two faces the stimulus resembled. The control experiment consisted of six blocks. Within each block the face pair was fixed and the contrast of the stimulus was controlled by two interleaved staircases that lasted for 40 trials each. Two six-block sessions were completed by each observer, resulting in 160 trials per threshold estimate.

Discrimination thresholds were also computed based on an ideal observer method [15]. The ideal observer was given a test stimulus in Gaussian white noise with zero-mean and unit variance. (Note that the value of noise variance is chosen arbitrarily as our analysis involves comparison of thresholds at the same noise level. The accuracy of the ideal depends on the signal-to-noise ratio.) The ideal observer's response was based on a Bayesian maximum a posteriori rule. This, in our case, is equivalent to choosing the face with maximum cross-correlation with the noisy stimulus because both alternative faces in the discrimination tasks were chosen with equal probability as test stimuli and all face templates in our stimulus set had the same signal energy by design (for further details on the ideal observer simulation, see Ref. [16]).

Fig. 2



Threshold changes induced by previewing faces for the three different conditions. (a) Experiment 1: 200 ms adaptation to a face reduces contrast threshold for recognizing the same face, but elevates thresholds for recognizing other faces. Adaptation increases thresholds for recognizing other faces of the same-race more than those for recognizing other faces of a different-race. (b) Experiment 2: similar effects were found when the same-face condition was eliminated showing that larger impairment in the same-race condition was not caused by confusion with the adapting-face. These results show that inhibition of other face representations is greater for faces that are more similar to the adapting-face. Error bars indicate 68% bootstrap confidence intervals.

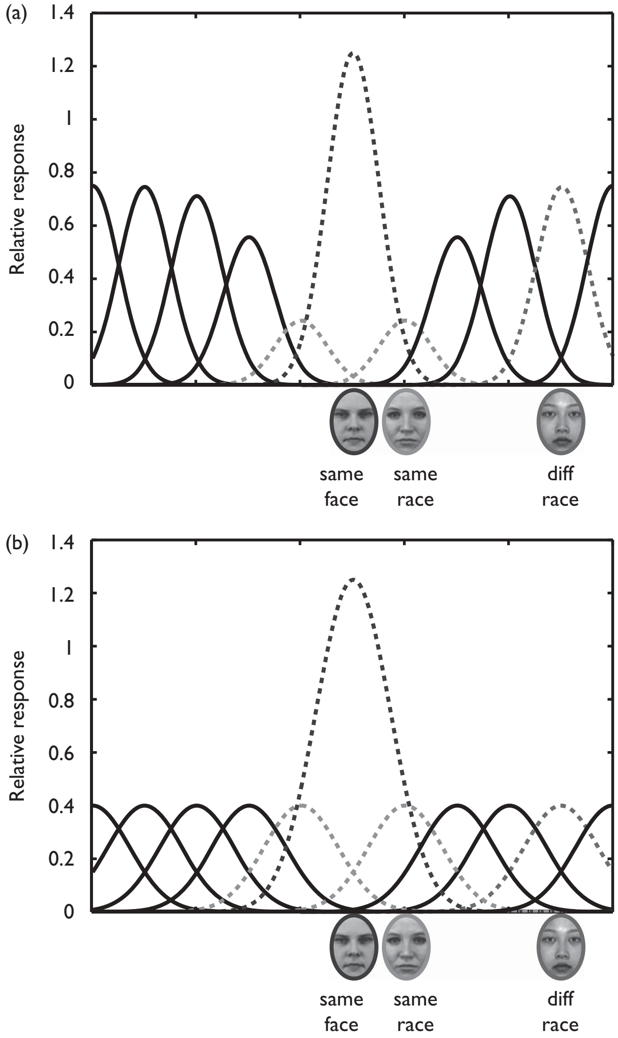
Results

The effect of adapting condition on the threshold elevation ratios was significant ($H = 15.90$, d.f. $= 2$, $P < 0.001$). Preview of the 'same-face' decreased contrast thresholds for face identification, indicating a priming effect ($W = 28$, $P < 0.01$) (Fig. 2a). Conversely, contrast thresholds were elevated for test-faces different from the adapting-face (same-race and different-race conditions) (both $W = 28$, $P < 0.01$). Threshold elevation ratios in the same-face condition were lower than both the same-race and the different-race conditions (both $W = 28$, $P < 0.01$). More importantly, adaptation effects on threshold also differed significantly between same-race and different-race conditions ($W = 28$, $P < 0.01$): threshold elevation ratios were larger when the adapting-face and test-face were of the 'same-race' than when they were of 'different-races'.

Thus, these findings show that while a short preview facilitates identification of the previewed face, it inhibits recognition of other faces, more so for faces of the same-race than for faces of a different-race. In the abstract geography of face-space, one possible explanation of the last finding is a zone of more pronounced inhibition surrounding the primed face, with inhibition declining with increasing distance from the prime (Fig. 3a). A second possible explanation is that priming causes test-faces similar to the primed face to be mistaken for the latter. It may be that the heightened responsivity of a primed unit will also give large responses when a sufficiently similar face is seen, perhaps more so than units specifically tuned to that similar face. If so, the participant would respond that the similar face is actually the primed face. Thus, priming may create a transient 'attractor basin' in the vicinity of the primed face (Fig. 3b) [17]. Analysis of the error data was suggestive of this possibility as same-race faces were (incorrectly) chosen slightly more frequently (38% of errors) than the two different-race faces (28 and 33% of errors), however, this difference was not significant [$F(2,12) = 2.23$, $P > 0.1$].

Nevertheless, to distinguish between these two explanations, we performed a second adaptation experiment, similar to the first one in every way, except that the adapting-face and test-face were never identical, and the response options did not include the same face as the adapting-face. If the 'transient attractor basin' explanation is correct, removal of the option of responding 'same-face' would eliminate the difference in effects on recognition thresholds between the same-race and different-race conditions. If the center–surround inhibition explanation is correct, then the difference would remain, despite the change in experimental design. We found that adaptation again significantly elevated

Fig. 3



Two alternative explanations of the results of Experiment 1. Adaptation (priming) occurs for the unit represented with the dashed-black curve in the center. (a) Center–surround inhibition: face priming enhances the response of the unit tuned to it (dashed-black curve – same-face). This inhibits units tuned to other faces, more so for similar faces (dashed-light grey curves, e.g. same-race) than dissimilar ones (dashed-dark grey curves, e.g. different-race), consistent with a center–surround organization. Thus, more contrast is required to perceive similar same-race faces than dissimilar different-race ones. (b) Transient attractor basin: in this model, all units other than the primed one are inhibited equally. The response profile of the primed unit (dashed-black) is so enhanced that its response to a similar face is larger than the peak response of the unit tuned for that similar face (dashed-light grey). Thus, a similar same-race face is confused with the primed face, in effect because of a 'transient attractor basin' around the adapting-face, but a dissimilar different-race face is not.

thresholds for both conditions (both $W = 28$, $P < 0.01$) (Fig. 2b), and that threshold elevation ratios were still significantly larger in the same-race condition than in the different-race condition ($W = 26$, $P < 0.03$). This result is thus more consistent with center–surround inhibition than a transient attractor basin.

Discussion

These results in part replicate the findings of our earlier study showing that a repetition-priming that facilitates recognition of the same face as the adapting-face is simultaneously accompanied by inhibition of recognition of other faces [11], a study that excluded low-level retinotopic contributions to these aftereffects by showing that they persist despite variations in image size and position. Short-term repetition-priming has been shown previously for word [18] and face recognition accuracy [19], but without a baseline condition these latter studies could not confirm the second phenomenon we observed, inhibition of stimuli differing from the prime. Nevertheless, inhibition for dissimilar items has been proposed in models of repetition-priming [20]. Inhibition between facial representations is also incorporated in computational models of face processing [21]: our studies provide the first direct psychophysical evidence for such inhibition in face perception. Such interactions may also be supported by electrophysiological studies showing reduction in N170 amplitude to one face when a second face is present [22]. The current findings advance on those in our prior report by showing that suppression or inhibition is greater for faces of the same ethnic group, and therefore closer to the primed face than those of the other ethnic group. This pattern of greater inhibition for 'nearer' or more similar representations is indicative of a center–surround pattern of organization.

Conclusion

The suggestion of a center–surround pattern of inhibition is reminiscent of inhibitory interactions at many other levels of the visual system, ranging from the retina to striate and intermediate levels of visual cortex such as V5, interactions that are reflected in psychophysical data on surround effects in contrast and orientation judgments, for example see Ref. [23]. Inhibitory interactions in the retina and V1 contribute to perception by sharpening neural tuning and enhancing segmentation [24]. Although our study cannot directly address the neurophysiological mechanisms underlying our results, it may suggest that there is an analogous suppression of competing representations in close vicinity or alternatively across nearby axes of face-space [25], and that this serves to help segment individual faces and facilitate recognition of a specific face from the many others seen in a lifetime. Our results suggest that center–surround relationships are ubiquitous mechanisms, enhancing perception from the retina to the most complex levels of visual cortex.

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