

- Vecera, S. P., Flevaris, A. V., & Filapek, J. C. (2004). Exogenous spatial attention influences figure-ground assignment. *Psychological Science, 15*, 20–26.
- Vecera, S. P., & O'Reilly, R. C. (1998). Figure-ground organization and object recognition processes: An interactive account. *Journal of Experimental Psychology: Human Perception and Performance, 24*, 441–462.

Controlling stimulus variability reveals stronger face-selective responses near the average face

Nicolas Davidenko and Kalanit Grill-Spector

Department of Psychology, Stanford University, Stanford, CA, USA

The past decade of fMRI research has identified face-selective regions in the human ventral stream that respond more strongly when people observe faces than other objects and are thought to be critically involved in face perception and recognition (Grill-Spector, Knouf, & Kanwisher, 2004; Kanwisher, McDermott, & Chun, 1997). However, the underlying neural representations that subserve humans' remarkable ability to recognize thousands of individual faces are not well understood. A basic question is whether responses in face-selective regions increase or decrease as faces deviate from the average face. In one view, face-selective neural responses are anchored on the average (or mean) face, suggesting responses should increase as faces deviate from the mean face in particular directions (or angles) away from the mean (Leopold, Bondar, & Giese, 2006; Loffler, Yourganov, Wilkinson, & Wilson, 2005). An alternative view posits that neurons are tuned to particular stored exemplar faces, and responses decrease as faces deviate from the preferred face exemplar. Because the distribution of faces is thought to be centrally dense, the latter view predicts higher responses near the mean face. Electrophysiological and fMRI research shows that responses are reduced, or adapted (Grill-Spector et al., 1999; Li, Miller, & Desimone, 1993) to repetitions of similar faces, and thus assessing the strength of responses to faces blocked by their distance from the mean requires the control of stimulus variability within each block. Here, we use a parameterized space of face silhouettes (Davidenko, 2007) and high-resolution fMRI (HR-fMRI) to measure responses in face- and object-selective regions as we manipulate distance from the mean face and control in two ways the variability of stimuli at each distance from the mean.

Please address all correspondence to Nicolas Davidenko, Department of Psychology, 450 Serra Mall, Building 420, Stanford, CA 94107, USA. E-mail: ndaviden@stanford.edu

METHODS AND RESULTS

Stimuli

We defined blocks of parameterized face silhouettes at five different distances from the mean face in silhouette face space (Davidenko, 2007). In the “matched angular variability” (MAV) condition, we matched the number of sampled directions (or angles) sampled in each block of faces (Figure 1a). In the “matched physical variability” (MPV) condition, we matched the physical similarity of faces in each block (Figure 1b).

Downloaded By: [Davidenko, Nicolas] At: 20:18 5 May 2010

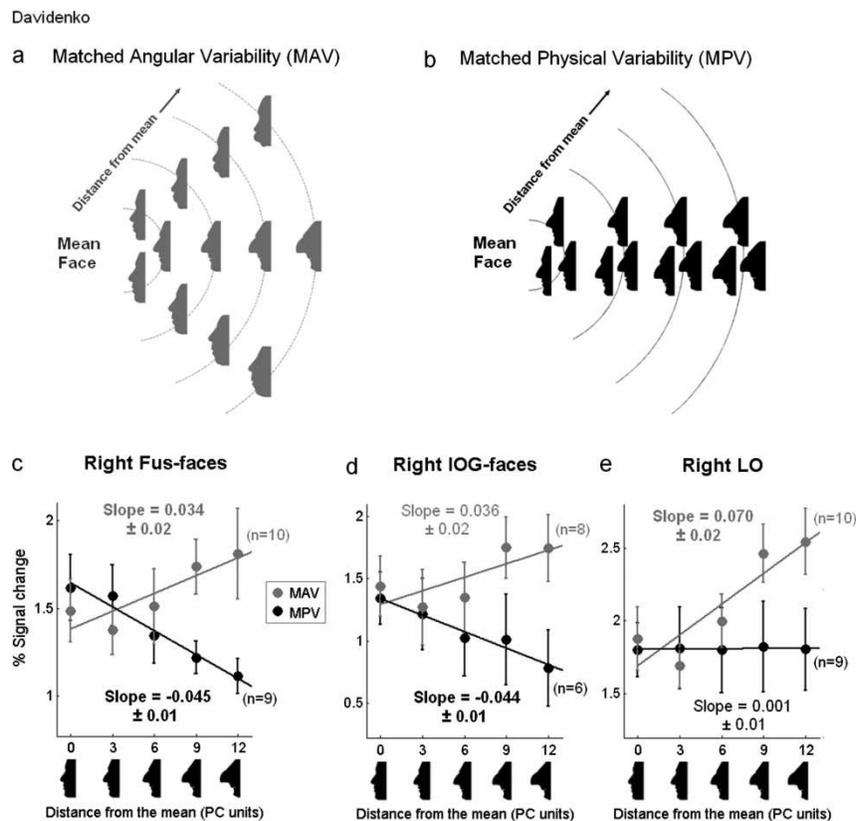


Figure 1. (a–b) Stimulus design for the MAV and MPV conditions. Arcs represent fixed distances from the mean. (c–e) Responses in face- (c–d) and object-selective (e) regions to blocks of face silhouettes in the MAV (grey) and MPV (black) conditions. Percentage signal change is versus fixation+SEM across subjects.

Behavioural measures

We assessed two behavioural measures to determine whether matching angular or physical variability resulted in matched perceptual variability among the stimuli in each block. First, we measured perceptual discrimination (d') from performance on a one-back task where subjects responded to infrequently repeating face stimuli. By examining performance across all blocks, we found d' was correlated more with physical variability ($r = .94$) than with angular variability ($r = .66$). Second, we obtained subjects' judgements of dissimilarity (on a 1–7 scale, with 1 = “identical” and 7 = “maximally dissimilar”) between pairs of face silhouettes sampled from within each block. We found that dissimilarity judgements were also more closely coupled to physical ($r = .96$) than angular ($r = .69$) variability. These results support the use of physical variability as a proxy for perceptual variability.

fMRI measures

We scanned 12 subjects at high resolution (1.5 mm isotropic voxels) as they observed blocks of face silhouettes in the MAV (10 subjects) and MPV (9 subjects, 7 overlapping) conditions. We measured responses in two independently localized face-selective regions (Fus-faces and IOG-faces) and one object-selective region (LO) as we manipulated distance from the mean face in the MAV and MPV conditions.

We found that responses as a function of distance from the mean face differed drastically across the two conditions (Figure 1c–e; significant two-way ANOVA interaction between distance from the mean and condition, all $F_s > 5.0$, $p < .01$). In the MAV condition (where angular variability was matched but physical variability increased with distance from the mean), responses in face-selective regions increased (mean slopes = 0.034 and 0.036, in Fus-faces and IOG-faces, respectively; Figure 1c–d, grey). In the MPV condition (where physical variability was matched but angular variability decreased with distance from the mean), responses in Fus-faces and IOG-faces decreased with distance from the mean (mean slopes = -0.045 and -0.044 , respectively; Figure 1c–d, black). In contrast, responses in LO increased in the MAV condition but were constant in the MPV condition across distances from the mean face (Figure 1e).

To determine how the three factors—distance from the mean, physical variability, and angular variability—contributed to responses across all conditions, we conducted a step-wise multiple regression analysis on mean responses across subjects in each block of faces. For responses in face-selective regions, physical variability was a significant positive factor

(associated with increased responses) and distance from the mean was a significant negative factor (associated with decreasing responses), together explaining 85% and 93% of the variance in Fus-faces and IOG-faces responses, respectively. Angular variability did not explain any additional variance. LO responses were highly correlated with physical variability, which explained 89% of their variance, whereas other factors were not significant.

DISCUSSION

Our data provide evidence that (1) physical variability drives responses across face- and object-selective regions, and (2) when this factor is controlled, responses in face-selective regions are strongest near the mean face. In contrast, responses in object-selective LO are not modulated by distance from the mean face when physical variability is controlled, suggesting that this is a face-specific effect. We suggest that previous studies that found increasing responses in face-selective regions as a function of distance from the mean (Leopold et al., 2006; Loffler et al., 2005) likely confounded physical variability with distance from the mean.

Stronger responses to faces near the mean face may reflect sensitivity to the distribution of experienced faces. After years perceiving and encoding faces likely drawn from a centrally dense distribution (Valentine, 1991), face-selective neurons may become tuned to best represent this distribution. As a result, faces near the mean may activate more face-selective neurons, and in turn elicit a larger BOLD response, than faces far from the mean. This interpretation is consistent with an exemplar-based neural face space (see Jiang et al., 2006) where responses are strongest to the frequently experienced faces near the mean face.

REFERENCES

- Davidenko, N. (2007). Silhouetted face profiles: A new methodology for face perception research. *Journal of Vision*, 7(4), 1–17.
- Grill-Spector, K., Knouf, N., & Kanwisher, N. (2004). The fusiform face area subserves face perception, not generic within-category identification. *Nature Neuroscience*, 7(5), 555–562.
- Grill-Spector, K., Kushnir, T., Edelman, S., Avidan, G., Itzhak, Y., & Malach, R. (1999). Differential processing of objects under various viewing conditions in the human lateral occipital complex. *Neuron*, 24, 187–203.
- Jiang, X., Rosen, E., Zeffiro, T., VanMeter, J., Blanz, V., & Riesenhuber, M. (2006). Evaluation of a shape-based model of human face discrimination using fMRI and behavioral techniques. *Neuron*, 50, 159–172.
- Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience*, 17(11), 4302–4311.

- Leopold, D. A., Bondar, I. V., & Giese, M. A. (2006). Norm-based face encoding by single neurons in the monkey inferotemporal cortex. *Nature*, *442*(7102), 572–575.
- Li, L., Miller, E. K., & Desimone, R. (1993). The representation of stimulus familiarity in anterior inferior temporal cortex. *Journal of Neurophysiology*, *69*(6), 1918–1929.
- Loffler, G., Yourganov, G., Wilkinson, F., & Wilson, H. R. (2005). fMRI evidence for the neural representation of faces. *Nature Neuroscience*, *8*(10), 1386–1390.
- Valentine, T. (1991). A unified account of the effects of distinctiveness, inversion, and race in face recognition. *Quarterly Journal of Experimental Psychology: Human Experimental Psychology*, *43A*(2), 161–204.

Target enhancement and distractor suppression in multiple object tracking

Matthew M. Doran and James E. Hoffman

University of Delaware, Newark, DE, USA

In multiple object tracking (MOT), observers keep track of target objects that move haphazardly around a display in the presence of identical distractors. The typical result from this paradigm is that observers can accurately track up to about four objects, with performance declining precipitously beyond this number. However, recent evidence indicates that the number of objects that can be effectively tracked is not fixed but depends on factors such as speed and interobject distance (Shim, Alvarez, & Jiang, 2008).

Decreasing interobject distance reduces tracking performance, which is compatible with the idea that visual attention may be particularly important in MOT in order to maintain individuation of target objects in the face of nearby distractors. Previous research has shown that one source of errors during MOT arises when observers mistakenly begin tracking distractors that pass close to targets (O’Hearn, Landau, & Hoffman, 2005; Pylyshyn, 2004). Therefore, a sensible strategy might be to suppress or inhibit distractors that pass close to and are confusable with targets. Consistent with this idea, Pylyshyn, Haladjian, King, and Reilly (2008) reported that probes appearing on distractors that were located in a different depth plane than the tracked objects were detected more frequently than same-depth plane distractor probes. According to them, objects in different depth planes are preattentively segregated, allowing observers to easily ignore different-depth plane distractors without the need to actively suppress them. This is consistent with

Please address all correspondence to Matthew M. Doran, Department of Psychology, University of Delaware, Newark, Delaware 19716, USA. E-mail: mdoran@psych.udel.edu