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JN 95:591-592, 2006. doi:10.1152/jn.01039.2005

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Textures of Natural Images in the Human Brain. Focus on “Orientation-Selective Adaptation to First- and Second-Order Patterns in Human Visual Cortex”

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Texture patterns—homogeneous regions of repeated structures—are the predominant feature of natural visual scenes. The zebra, a 1938 optical art painting by Victor Vasarely, illustrates how different textures segregate and define figures from their background. Despite the ease with which we perceive the two zebras in a background of black and white stripes this is a challenging operation for the visual system. The edges that separate the two zebras from each other and their background divide the image in homogeneous regions that differ in the orientation or the size of the black and white stripes but have similar average luminance (Fig. 1). Thus, a system based on linear filters that detect these first-order luminance changes, similar to neurons in the retina and the primary visual cortex cannot solve the figure-ground segmentation problem in this image. But how does the brain detect figures in cluttered backgrounds when their borders are defined by differences in the contrast, orientation or spatial frequency of their constituent elements rather than simply their average luminance? Larsson et al. (2006) in this issue of *Journal of Neurophysiology* (p. 862–881) provide novel evidence that the perception of these second-order texture patterns entails additional processing in ventral and dorsal extrastriate areas beyond the first stages of visual analysis in the primary visual cortex (V1).

Recent psychophysical studies (Landy and Graham 2004 for a review) have proposed different processing mechanisms for patterns that differ in their luminance intensity (first-order patterns) and texture patterns that cannot be detected by linear filters based on average luminance changes (second-order patterns). In particular, second-order processing mechanisms are tuned for orientation, similar to first-order mechanisms but have greater bandwidth, and there are weak or incomplete interactions between first- and second-order patterns. Based on these findings, Larsson et al. sought to identify brain regions with differential orientation selectivity for second-order (orientation- or contrast-defined patterns) rather than first-order patterns (luminance-defined patterns) that may support selective processing for second-order textures.

Using an elegant orientation-selective adaptation paradigm in psychophysical and fMRI (functional magnetic resonance imaging) measurements, Larsson et al. tested for 1) sensitivity to orientation differences (vertical vs. horizontal) between an adapting and test stimulus and 2) cross-modal adaptation when the adapting stimulus was a first-order pattern and the test stimulus a second-order pattern. Adaptation to first- or second-order stimuli increased the observers' sensitivity in detecting a target pattern with different orientation than the adapted stim-

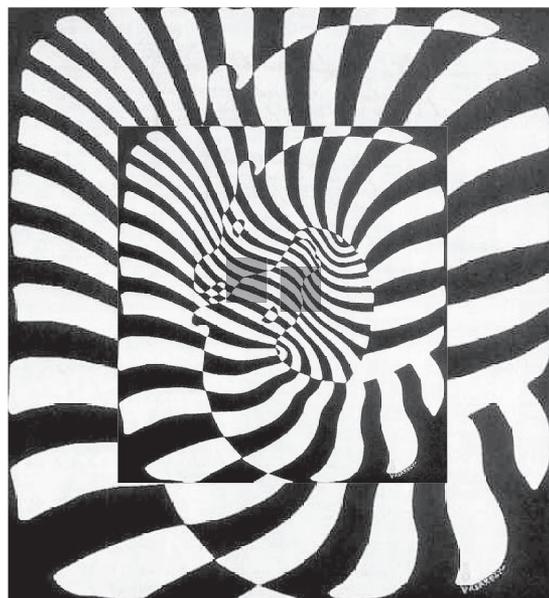


FIG. 1. The zebra (1938), an optical art painting by Victor Vasarely. The marked regions show texture boundaries that separate the two zebras from each other or their background.

ulus, consistent with classic behavioral adaptation effects. Similarly, fMRI responses in primary and extrastriate visual areas increased for test stimuli that differed in their orientation from the adapting stimulus. Interestingly, these adaptation effects were of comparable magnitude across visual occipitotemporal areas for first-order patterns, whereas orientation-selective adaptation for second-order patterns was larger in several higher extrastriate areas than in V1. What are the implications of these fMRI adaptation effects for understanding the neural mechanisms that mediate selective processing of second-order stimuli in the human brain?

fMRI adaptation capitalizes on neural adaptation after prolonged or repeated exposure to a stimulus and has been used extensively as a sensitive tool for discerning neuronal subpopulations selective for different stimulus attributes but intermingled within the measured voxels (e.g., Grill-Spector and Malach 2001). This method extends beyond the limited spatial resolution of the conventional fMRI paradigms that average across such populations. However, recent studies call for cautious interpretation of fMRI adaptation effects and their implications for neural processing across visual areas (Boynton and Finney 2003; Tolia et al. 2005). Larsson et al. demonstrate that fMRI adaptation is a powerful tool for investigating selectivity to a visual attribute (i.e., orientation) across visual areas when the stimuli used elicit strong fMRI responses but

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prevent neural saturation in these areas, and the observers' attention is controlled across stimulus conditions. Consistent with previous physiological studies, their findings show orientation selective adaptation for both first-order and second-order stimuli in primary and extrastriate areas, suggesting that the processing of second-order textures is distributed across visual areas rather than specialized within a single cortical region. The similarity in the magnitude of fMRI adaptation across visual areas for first-order stimuli suggests that these effects could be accounted for by orientation selective adaptation in V1 neurons that is propagated to downstream extrastriate areas. In contrast, the stronger orientation selective adaptation in extrastriate areas than V1, for second order stimuli, suggest a second stage of processing beyond the linear filter analysis in the primary visual cortex. Furthermore, the lack of consistent adaptation effects for the cross-modal condition support the hypothesis that different mechanisms are involved in the processing of first-order and second-order textures.

Based on these findings, Larsson et al. propose that the role of higher extrastriate areas in texture perception is to perform additional analysis (second stage filter) by pooling the output of the first-stage filters in primary visual cortex after rectification by the spiking threshold of V1 neurons, consistent with recent computational models for texture perception (Landy and Graham 2004 for a review). An alternative interpretation suggests that extrastriate areas contribute to texture perception by extracting salient surface regions (Stanley and Rubin 2003); that is, homogeneous regions of repeated structures in the case of texture patterns. This analysis is then evaluated by neurons in the primary visual cortex that may enhance texture boundaries (first- or second-order) defining a figure that pops-out from the background (i.e., the zebras in Vasarely's painting) compared with texture patterns that belong to the background (Fitzpatrick 2000; Lamme et al. 1998). This interpretation is consistent with the role of middle-level surface representations in the perception of textured figures and their surrounds (He and Nakayama 1994).

In sum, Larsson et al. provide novel insights in understanding the neural mechanisms that mediate the analysis of texture patterns in natural images. This work provides the foundations for investigating the mechanisms that underlie the analysis of "the stuff (e.g., wood, metal, plastic) that objects are made of" (Bergen and Adelson 1988; Fleming et al. 2003; Heeger and Bergen 1995; Portilla and Simoncelli 2000) and our perception

of 3D objects defined by texture (Li and Zaidi 2000; Todd 2004) in combination with other depth cues (Knill 2003). Finally, recent work on multimodal object perception (Amedi et al. 2001) raises novel questions in understanding the role of texture in our unified visual and haptic experiences of objects that is critical for successful actions and interactions in our complex environments.

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