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The company they keep: Background similarity influences transfer of aftereffects from second- to first-order stimuli

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ABSTRACT

A wealth of studies has found that adapting to second-order visual stimuli has little effect on the perception of first-order stimuli. This is physiologically and psychologically troubling, since many cells show similar tuning to both classes of stimuli, and since adapting to first-order stimuli leads to aftereffects that do generalize to second-order stimuli. Focusing on high-level visual stimuli, we recently proposed the novel explanation that the lack of transfer arises partially from the characteristically different backgrounds of the two stimulus classes. Here, we consider the effect of stimulus backgrounds in the far more prevalent, lower-level, case of the orientation tilt aftereffect. Using a variety of first- and second-order oriented stimuli, we show that we could increase or decrease both within- and cross-class adaptation aftereffects by increasing or decreasing the similarity of the otherwise apparently uninteresting or irrelevant backgrounds of adapting and test patterns. Our results suggest that similarity between background statistics of the adapting and test stimuli contributes to low-level visual adaptation, and that these backgrounds are thus not discarded by visual processing but provide contextual modulation of adaptation. Null cross-adaptation aftereffects must also be interpreted cautiously. These findings reduce the apparent inconsistency between psychophysical and neurophysiological data about first- and second-order stimuli.

1. Introduction

The ubiquity of adaptation makes it a major experimental paradigm both in its own right and as a methodological tool for investigating other questions. Psychophysically, adaptation is measured by means of aftereffects, and a central issue is how the strength of such aftereffects depends on the relationship between adapting and test stimuli. It is well known that to produce strong aftereffects, adapting and test stimuli should have similar features. For example, to maximize the tilt aftereffect, the adapting and test orientations should have matched retinal location (Gibson & Radner, 1937) and spatial frequency (Ware & Mitchell, 1974). We will refer to this as the foreground similarity effect because the matched feature (e.g., spatial frequency) is a property of the foreground feature (e.g., orientation) whose adaptation is measured. The effect is easy to understand because many visual cells are jointly tuned to multiple features (e.g., orientation *and* spatial frequency), and by matching them, the adapting and test stimuli will engage maximally overlapping cell groups to produce a strong aftereffect. Indeed, the contingency of adaptation of one feature (e.g., color) on matching another feature (e.g., orientation) is viewed as evidence of joint tuning to those features (McCollough, 1965).

Using high level visual stimuli, we recently found a new form of contingent adaptation which we call the background similarity effect (Wu et al., 2009). This involves the relationship between the backgrounds rather than the foregrounds of adapting and test stimuli. For instance, adaptation to a real-face image produced a larger facial-expression aftereffect on test cartoon faces after noise with the same correlation statistics as real faces or natural images was added to the cartoon faces. This is surprising because joint tuning to facial expression and background noise is unlikely (and certainly unreported). Moreover, the background noise alone carried no facial expression and was not an integral part of, or an associated property of, the foreground faces. Thus, according to most accounts of face processing, would have been squelched or eliminated as early as possible so as not to interfere with face processing.

This study raises the question as to whether the background similarity effect for faces applies to simpler stimuli to which neurons in lower-level areas such as V1 are tuned. This is important because a great number of adaptation studies has used simple

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stimuli instead of faces, leading to the overwhelming consensus that second-order adaptation does not transfer to first-order stimuli (Ashida et al., 2007; Larsson, Landy, & Heeger, 2006; Nishida, Ledgeway, & Edwards, 1997; Paradiso, Shimojo, & Nakayama, 1989; Schofield, Ledgeway, & Hutchinson, 2007). The background similarity finding challenges this consensus since, by construction, first- and second-order stimuli typically have different background statistics. To our knowledge, previous studies using simple stimuli never systematically investigated the impact of this difference on the transfer of aftereffects. We therefore tested the background similarity hypothesis with the low-level, orientation tilt aftereffect. Specifically, we examined the transfer of the tilt-aftereffect from second- to first-order orientations, and also between orientations of the same type, under various manipulations of background similarity. Preliminary results were reported in an abstract (Qian and Dayan, Society for Neuroscience Abstract, 2010).

Our results demand a reevaluation of the large body of literature on cross-order adaptation, help reduce the apparent contradiction between these psychophysical studies and physiological findings on cue-invariant cells that show similar tuning to first- and second-order stimuli (Albright, 1992; Sheth et al., 1996; von der Heydt, Peterhans, & Baumgartner, 1984), and offer insights into the role of seemingly uninteresting or irrelevant backgrounds in visual processing.

2. Methods

2.1. Subjects

A total of 12 subjects consented to participate in the experiments of this study. All subjects had normal or corrected to normal vision. Experiment 1 had four subjects, Experiments 2, 3 and 4 had six subjects each. For each experiment, one subject was an author (NQ), and the rest were naive to the purpose of the study. The study was approved by the Institutional Review Board of the New York State Psychiatric Institute.

2.2. Apparatus

The visual stimuli were presented on a 21 in. ViewSonic (Walnut, CA) P225f monitor controlled by a Macintosh G4 computer. The vertical refresh rate was 100 Hz, and the spatial resolution was 1024 × 768 pixels. The monitor was calibrated for linearity with a Minolta LS-110 photometer. In a dimly lit room, subjects viewed the monitor from a distance of 75 cm through a black, cylindrical viewing tube (10-cm inner diameter) to exclude potential influence from external orientations. Each pixel subtended 0.029° at this distance. A chin rest was used to stabilize the head position. All experiments were run in Matlab with Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997).

2.3. Visual stimuli

A round, black (0.47 cd/m^2) fixation dot, 0.23° in diameter, was always shown at the center of the white (50.6 cd/m^2) screen. All stimuli were grayscale in a 2.9° × 2.9° area. They included second-order, illusory lines and first-order, luminance-defined bars. We used an anti-aliasing method (Matthews et al., 2003) to ensure that the stimuli appeared smooth under the viewing condition of our experiments. In all subsequent descriptions, we define vertical orientation as 0° and orientations clockwise (CW) and counter-clockwise (CCW) from vertical as positive and negative angles, respectively. The orientation of the adapting stimuli was always $-15°$, and the orientations of the test stimuli were within a few degrees around the vertical.

2.3.1. Second-order illusory lines

We created second-order, illusory lines by offsetting black inducing lines. In Experiment 1, a $-15°$ illusory line was used as an adaptor (Fig. 1a); it was induced by offsetting eight evenly-spaced horizontal lines. The width of the inducing lines was 0.058° and the center-to-center vertical distance between the adjacent lines was 0.29°. In Experiment 2, illusory lines of various orientations were created by placing +45° and $-45°$ diagonal lines on the opposite sides of the stimuli (Fig. 3). When the +45° and $-45°$ diagonals were on the right and left sides, respectively, the resulting illusory orientations had a V-shaped background (Fig. 3, panels a and c). Conversely, when the +45° and $-45°$ diagonals were on the left and right sides, respectively, the resulting illusory orientations had a Λ-shaped background (Fig. 3, panels b and d). The inducing lines had a width of 0.029° and the center-to-center distance in the perpendicular dimension was randomly drawn from a uniform distribution of 1–5 pixels (or 0.029° to 0.15°). A center-to-center spacing of 1 pixel means that the two adjacent lines merged into a thicker line. A $-15°$ illusory orientation of either the V or Λ background was used as an adaptor, and a set of near-vertical illusory orientations of either the V or Λ background were used as test stimuli.

2.3.2. Luminance bars

We generated first-order, luminance-defined bars of various orientations. All bars had a length of 2.6° and width of 0.087°. In Experiment 1, black, near-vertical test bars were placed on four kinds of backgrounds. The first was uniform gray (Fig. 1c) that matched the mean luminance (42.6 cd/m^2) of the illusory adaptor (Fig. 1a). The second background was made of long horizontal lines that matched those of the inducing lines of the illusory adaptor but without the offset (Fig. 1d) and had vertical positions midway between the inducing lines of the illusory adaptor. The third background was made of short horizontal lines that did not intersect the bars (Fig. 1e). This was done by excluding the background lines from a central rectangular region of 0.46° in width. Additionally, each end of a horizontal line was reduced randomly by up to 10 pixels (0.29°) to avoid a specific illusory orientation. The fourth background was made of short vertical lines (Fig. 1f) whose lengths on average match the lengths of the short horizontal lines in the third background. These vertical background lines were also excluded from a central rectangular region of 0.46° in width but otherwise had horizontal positions that were randomized over 10 pixels (0.29°) on each side. Therefore, the distances between the test bars and the background lines did not provide reliable cues to the test bars' orientation. For Experiment 1, we also created a $-15°$ luminance bar on the uniform background (Fig. 1b) as an adaptor.

In Experiment 3, the black bars were placed on two kinds of background. The first was $1/f$ noise (Fig. 5, panels a and c) produced online in each trial without repetition of samples. The second was uniform gray (Fig. 5, panels b and d) that matched the mean luminance of the $1/f$ noise (25.3 cd/m^2). The stimuli for Experiment 4 were identical to those for Experiment 3 except that the bars were gray (17.1 cd/m^2) in order to reduce their contrast (Fig. 7). The Weber contrasts were 0.98 and 0.32 for Experiments 3 and 4, respectively.

2.4. Procedures

We used the method of constant stimuli for Experiment 1 and a more efficient, one-up-one-down double staircase procedure for Experiments 2–4. Subjects received no feedback on their performance at any time.