

# Reaction Times to Predictable Visual Patterns Reflect Neural Responses in Early Visual Cortex

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## Abstract

It has long been speculated that the visual system should use a coding strategy that takes advantage of statistical redundancies in images. But how such a coding strategy should manifest in neural responses has been less clear. Low-level image structure related to the power spectrum of natural images appears to be captured by a hard-wired efficient code in the retina of the fly and precortical structures like the LGN of cats that maximizes information content through the limited capacity channel of the optic nerve. But visual images are typically filled with higher-order structure beyond that captured by the power spectrum and visual cortex is not constrained by the same capacity limits as the optic nerve. Whether and how visual cortex can flexibly code for higher order redundancies is unknown. Here we show using psychophysical techniques that the neural response in early human visual cortex may be modulated by orientation redundancies in images such that a visual feature that is contained within a predictive pattern results in slower reaction times than a feature that deviates from a pattern, suggesting lower neural responses to predictable stimuli in the visual cortex. Our results point to a neural response in early visual cortex that is sensitive to global patterns and redundancies in visual images and is in marked contrast to standard models of cortical visual processing.

**Key words:** Predictive Coding, Reaction Time, Redundancy Reduction, Visual Pattern

## 1. INTRODUCTION

The standard model of information processing in early visual cortex is that neurons behave like localized, linear, band-pass filters that are optimized to detect specific features in restricted regions of an image (Adelson & Bergen, 1985; Carandini et al., 2005; Jones & Palmer, 1987; Lennie & Movshon, 2005; Ringach, 2002; Rust & Movshon, 2005). However, inconsistent with the standard model, it is well known that responses of V1 neurons to a stimulus inside the classical receptive field (CRF) can be modulated by stimuli presented outside the CRF (Albright & Stoner, 2002; Allman et al., 1985; Fitzpatrick,

2000). These findings have led to revisions of the standard model that include various forms of divisive normalization from neighboring neurons (Carandini et al., 1997; Heeger, 1992; Schwartz & Simoncelli, 2001) and, to a first approximation, these revised models can account for a wide variety of contextual, surround effects (Cavanaugh et al., 2002a, 2002b; Shapley, 2004). Importantly, normalization models still act like localized feature detectors but offer a mechanism for nonlinear gain control.

But the view that neurons in early visual cortex are localized feature detectors has been challenged in recent years (Lee & Mumford, 2003; Olshausen & Field, 2005) and recent studies have pointed to a potential role of

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early visual areas in processing high-level, “global” attributes of an image. What constitutes a global attribute is open to interpretation but, at a minimum, it would involve identifying how multiple and potentially far-removed features in an image relate to each other. For example, global-based explanations for contextual modulation have included perceptual pop-out (Kastner et al., 1997; Knierim & van Essen, 1992; Nothdurft et al., 1999; Sillito et al., 1995), figure-ground segmentation (Lamme, 1995; Zipser et al., 1996) and contour integration (Field et al., 1993; Kapadia et al., 1995, 2000; Polat et al., 1998). However, it has been shown that many of the apparently complex contextual effects that might appear to be related to global attributes of an image can be accounted for through simple, local spatial summation and normalization processes (Cavanaugh et al., 2002a). In addition, many of the studies that have examined global, perceptually-based explanations for surround effects have confounded changes in local stimulation in V1 and perception. For example, studies that have examined perceptual pop-out (Kastner et al., 1997; Knierim & van Essen, 1992; Nothdurft et al., 1999; Sillito et al., 1995) have changed the orientation relationship between a target and immediately adjacent flankers. Similarly, contour integration has been investigated by varying the distance between a target and collinear flankers (Kapadia et al., 1995, 2000). In both instances, it is not possible to determine whether modulations of neural activity are due to changes in the stimulus configuration affecting low-level summation and normalization processes (Cavanaugh et al., 2002a, 2002b) or are due to changes in global attributes of the image, or both. For example, the modulation of neural activity to the vertical grating surrounded by the horizontal orientation could be due to the simple presence of the horizontal surrounds or due to perceptual pop-out.

To overcome this limitation in the previous literature, we devised a stimulus that eliminates the confound between the local stimulus arrangement and global attributes of an image. Specifically, we varied whether a central target was part of a predictable sequence by changing the orientation of distant gratings while maintaining the same local stimulus arrangement (where “local” re-

fers to a central target and its immediate surrounding flankers). For example, a vertically oriented target grating that is flanked locally with horizontal flankers (HVH), can be made to be part of a predictable sequence by adding vertical distant flankers (VHVHV).

We conducted a reaction time experiment, in which we measured a simple reflex towards an oriented target. Specifically, we adopted a widely used Posner task paradigm (Posner et al., 1980) to show a reaction time effect on a visual stimulus. Previously, it has been shown that the very first sensory event-related potential (ERP) component was smaller for the predictable target compared to other patterns (Joo et al., 2012, 2014). Thus, we hypothesized that reaction times would be slower when the neural response to a target is weak and conversely, the reaction times would be faster when the neural response to a target is strong. We found that even when the local configuration (e.g. HVH) around the target was kept the same, thus eliminating any effects of simple spatial summation (Cavanaugh et al., 2002a, 2002b; Shapley, 2004), there was slower reaction times when the target was part of a predictable sequence (VHVHV). These results are consistent with an efficient coding strategy that is sensitive to the predictability of image features and are not easily explained by standard models of visual processing (Adelson & Bergen, 1985; Carandini et al., 2005; Jones & Palmer, 1987; Lennie & Movshon, 2005; Ringach, 2002; Rust & Movshon, 2005).

## 2. METHOD

### 2.1. Subjects

Twenty observers participated in the main experiment. All observers had normal or corrected-to-normal vision, and all gave informed written consent in accordance with the University of Washington Institutional Review Board (#35433).

### 2.2. Stimuli

The experiments were conducted in a dark room and

head position was stabilized using a chin rest. Stimuli were presented on a 19" linearized CRT monitor with vertical refresh rate of 60 Hz. The distance between observers and the monitor was 50 cm. We used a video attenuator device (Video Switcher, Xiangrui Li, Los Angeles, CA) to generate 10-bit gray-scale luminance values (Li et al., 2003). We used the MATLAB Psychtoolbox (Brainard, 1997; Pelli, 1997) on a PC to create stimuli, to control stimulus presentation, and to record responses.

Stimuli consisted of Gabor patches ( $\sigma = 0.72^\circ$ , spatial frequency = 2 cycles per degree (cpd), sinusoidal counterphase-flickering at 2 Hz). A fixation point ( $0.48^\circ$  in diameter) was displayed at the center of the display. The distance between the fixation point and the center of the target location was  $6^\circ$ , and the distance between each stimulus was  $3^\circ$ . The flanker contrast was 25% and the target contrast was 6.25%.

### 2.3. Design

There are two target orientations—either vertical or horizontal. The target could be surrounded by (1) No flanker condition in which the target was displayed alone, (2) V-V condition where V is the vertically oriented flanker and ‘-’ stands for the target, (3) H-H condition where H is the horizontally oriented flanker, (4) VV-VV condition, (5) HH-HH condition, and (6) VH-HV condition. Thus, there were 12 conditions (2 target orientations x 6 flanker conditions). These 12 conditions constituted an experimental block and there were 30 repetition of each block, which made the total number of trials 360. The order of presentation was counter-balanced such that 12 conditions were randomly presented within the block before the next block was presented.

### 2.4. Procedure

Fig. 1 shows the procedure of the main experiment. Each trial was initiated by observers. Observers were told to fixate at the fixation cross to start the trial. The

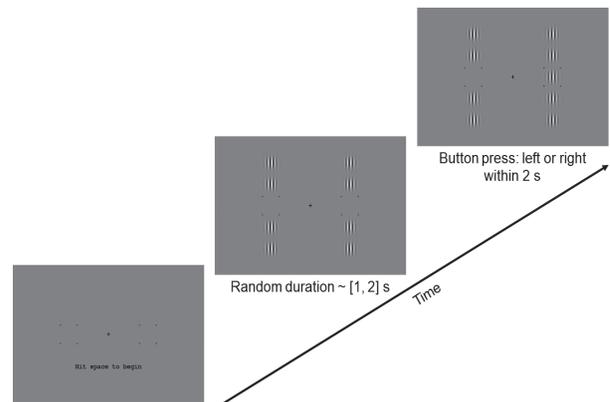


Fig. 1. The procedure of the experiment

contextual stimuli were displayed first and after a random duration selected from a uniform distribution of [1, 2] s, the target appeared either the left or right target location randomly. We used this random duration to (1) make sure the context is shown before the target appeared and (2) discourage observers to expect when the target appeared. By doing so, we could measure any effect due to the predictability of the target and uncontaminated reaction times of the detection of the target by removing the temporal expectation of the stimulus. All stimuli remained in the display until response or for the response window of 2 s. The target location was visible throughout the trial. Observers were told to press the ‘1’ key when the target orientation was vertical and ‘2’ key when the target orientation was horizontal as quickly and accurately as possible regardless of target location. The target location was randomly chosen for each trial. Observers were given auditory feedback for incorrect responses only.

In a control experiment, in which we asked the observers ( $n = 12$ ) to make a decision about the predictability of the central target. Specifically, Observers were presented with two configurations for 2 seconds and were asked to decide which center element is most ‘predictable’ or ‘least deviant’ based on the orientations of the other elements. There were four possible paired comparisons (only comparisons between configuration types—alternating versus symmetric—were made): HVHVH versus HVVVH, VHVHV versus VHHHV, HVHVH versus VHHHV, and VHVHV versus HVVVH. There were six trials per possible comparison.

### 3. RESULTS

Observers' performance to decide whether the central target is vertically or horizontally oriented was accurate ( $92.9 \pm 1.2\%$ ). Neither target orientation or context condition affected observers' performance (all  $p$ s > 0.05), and there was no interaction between target orientation and context condition ( $F(5,95) = 0.09$ ,  $p = 0.99$ ). So, any effect on reaction times (RTs) cannot be attributed to speed-accuracy trade-offs.

Next, we analyzed the RT data (Fig. 2). There was no main effect of target orientation and context condition (all  $p$ s > 0.05). However, the interaction between target orientation and context condition was significant ( $F(5,95) = 11.1$ ,  $p < 0.000001$ ) suggesting that the context affected target processing differently. To further assess how the context affected target processing, we tested whether RTs for each target orientation differed within each context condition.

The results show that RTs are slower when the central target is embedded in a predictable pattern. RTs for the vertically oriented target (V) was slower than the horizontally oriented target (H) in V-V and VV-VV ( $p = 0.0033$  and  $p = 0.0004$ , respectively), in which VVV and VVVVV make more predictable patterns compared to VHV and VVHV. Similarly, RTs for the horizontally oriented target was slower than the vertically oriented target in H-H and HH-HH ( $p = 0.08$ , marginally significant and  $p = 0.004$ , respectively). RTs for each target orientation

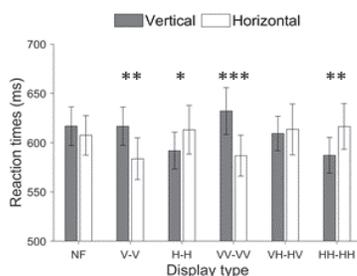


Fig. 2. The context affected target processing. X-axis is the context condition. NF is the no flanker condition. V and H stand for the vertical and horizontal orientation, respectively. Y-axis is the reaction times in each condition. The gray and white bars represent the vertical and horizontal orientation of the target, respectively. \*  $p = 0.08$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ . The error bar is the standard error of the mean across observers

were not different in the no flanker (NF) condition ( $p = 0.25$ ). Interestingly, RTs for each target orientation were not different in the VH-HV condition ( $p = 0.75$ ), suggesting that both the vertical and horizontal orientations are equally predictable within the VH-HV pattern.

To better characterize how RTs for the central target were affected by the context, we defined the context effect by subtracting RTs for no flanker (NF) condition from each context condition. Fig. 3 shows the flanker effect across the context condition. Compared to RTs for the isolated target, detecting predictable target was slower within the context. Detecting the vertical target (V) was slower compared to the horizontal target (H) when the target was embedded in V-V ( $p = 0.04$ ) and VV-VV ( $p = 0.003$ ). Likewise, detecting the horizontal target (H) was slower than the vertical target (V) when the target was embedded in H-H ( $p = 0.01$ ) and HH-HH ( $p = 0.0003$ ). Detecting the vertical and horizontal target in VH-HV was not modulated by the context ( $p = 0.29$ ).

Importantly, adding the far removed vertically-oriented flankers around H-H changes the predictability of the vertically-oriented target. That is, in the visual pattern HVH, the central target V is not predictable based on other orientations (deviant from the pattern) whereas in the alternating pattern VHVHV, the central V is now predictable. This was confirmed by the difference in the context effect for the vertical target between the H-H and VH-HV condition. The context effect was reduced in the VH-HV condition compared to the H-H condition

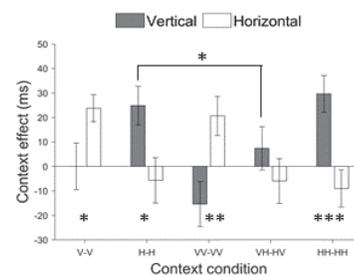


Fig. 3. The predictable target shows smaller context effect. X-axis is the context condition. Y-axis is the context effect ( $RT_{context} - RT_{NoFlanker}$ ). Smaller context effect occurs when RTs in the context condition was slower compared to the No flanker condition. . \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ .

The error bar is the standard error of the mean across observers

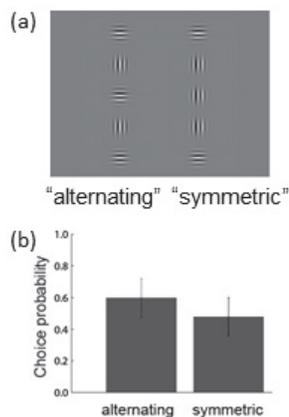


Fig. 4. Behavioral experiment to estimate the “predictability” of the central target. (a) An example of one comparison between one (of two) possible alternating conditions and one (of two) possible symmetric conditions. Observers were presented with two configurations for 2 seconds and were asked to “decide which center element is most ‘predictable’ or ‘least deviant’ based on the orientations of the other elements.” For each subject, we calculated the probability of responding “alternating” and the probability of responding “symmetric.” Perfectly reliable responses would yield values of 1.0 for one configuration type and 0.0 for the other configuration type for each subject. However, subjects sometimes changed their decision about a particular comparison over trials yielding intermediate probability values. (b) Average probability values across observers. Comparing the choice probability values between the alternating and symmetric conditions revealed no significant difference ( $p = 0.75$ ). The error bars are the standard error of the mean across observers

( $p = 0.04$ ). Note that the “local” configuration (HVH) is the same between the two patterns.

There was no difference in RT between the vertical and horizontal target in the VH-HV condition, suggesting that the vertical and horizontal target is similarly predictable in the context. To test whether both the vertical and horizontal targets are predictable in the VH-HV condition, we directly asked observers to decide the predictability of the central target embedded in VH-HV and HV-VH conditions. Both conditions made the “alternating” condition, VHVHV and HVHVH, and the “symmetric” condition, VHHHV and HVVVH (Fig. 4a). Observers were presented with two configurations for 2 seconds and were asked to “decide which center element is most ‘predictable’ or ‘least deviant’ based on the orientations of the other elements.” Fig. 4b shows the result. For each observer, we calculated the probability of responding “alternating” and the probability of responding

“symmetric”. Observers’ choice probability between “alternating” and “symmetric” was not different ( $p = 0.75$ ), confirming that both the vertical and horizontal targets are similarly predictable in the VH-HV condition. Because our sample size for this control experiment is relatively small ( $n = 12$ ), the null result might have been caused by the small power. Thus, we conducted a Bayes Factor analysis, in which the relative likelihood of the null hypothesis over the alternative hypothesis (Rouder et al., 2009), to confirm the null effect and to show how much evidence indicates effects favorable to null hypothesis. The Bayes Factor indicated “strong evidence for the null hypothesis” ( $BF_{10} = 0.37$ ) confirming our null effect in the control experiment.

## 4. DISCUSSION

A key advance of the experiments presented here is the addition of the second flankers that allowed us to maintain the same local stimulus arrangement (target plus immediately adjacent flankers) while changing whether the target was part of a predictable sequence. We have used reaction times as proxy to infer neural response to a stimulus embedded in various visual pattern. If neural activity is modulated by local, low-level summation processes, reaction times to the vertical target (or horizontal target) would not be different between H-H (V-V) and VH-HV (HV-VH). Alternatively, neural activity is modulated by global attributes of the vertical target (or horizontal target), there would reaction time difference between H-H (V-V) and VH-HV (VH-VH). We found that reaction times are slower for VHVHV and HVHVH compared to HVH and VHV, respectively. Thus, our results clearly show that the neural response to the target is affected by global attributes of the image—when the target is part of a predictable sequence neural responses were smaller compared to when it deviated from a predictable sequence. We consider this to be a global process because to recognize whether the central target belongs to or deviates from a pattern necessarily means that its orientation relationship to all other features in the image is analyzed. This is a novel finding that ap-

pears to contradict standard models of visual processing that emphasize the role of early visual areas in localized feature detection (Adelson & Bergen, 1985; Carandini et al., 2005; Jones & Palmer, 1987; Lennie & Movshon, 2005; Ringach, 2002; Rust & Movshon, 2005).

Revisions of the standard model designed to account for nonlinear neural activity in V1 can explain some types of contextual effects such as surround suppression. While many of these models are not orientation-specific, there do exist versions of the standard model that have been proposed to account for orientation-specific surround effects between a target and immediately adjacent flankers (Cavanaugh et al., 2002a, 2002b). Our results are inconsistent with these models. Suppose a model is constructed—based purely on local mechanisms between the receptive field and immediately adjacent surround—that predicts larger responses when flankers are orthogonal (i.e., larger response to the target in a VHV configuration than a HHH configuration). This model would necessarily predict a further enhancement of the central target when distant flankers are added that are orthogonal to the first flankers (HVHVH) because the second distant flankers would enhance the response to the first flankers (since they are orthogonal) which would in turn further enhance the response to the target. Instead we show that the response to the target is reduced in a HVHVH configuration. Our results show that, in addition to the known local, normalization processes in early visual cortex, there is also an additional global, pattern-based process that is sensitive to the predictability of image features.

How could orientation-specific predictions be generated by the visual system in our experiments? A key design feature of our experiments was the relative timing between the presentation of the contextual flanking stimuli and the presentation of the target. In all of our experiments the flanking stimuli were continuously present for relatively long periods of time (e.g., up to 2 seconds before the target appeared). The visual system's knowledge of the context—specifically, the orientation configuration of the flanking stimuli—in advance of the target presentation may have encouraged predictive, feedback

processes (Rao & Ballard, 1999). The likelihood of a significant feedback contribution is consistent with recent findings on the timing of contextual influences (Bair et al., 2003) and the anatomical architecture of feedback connections (Angelucci & Bressloff, 2006). Whether our results generalize to other timing relationships between the target and flankers, such as their simultaneous onset, remains an open question.

By identifying a neural response in early visual areas that is global and pattern-specific, our results suggest a new interpretation of surround influences. It has long been speculated that the visual system might use a coding strategy that takes advantage of statistical redundancies in images (Attneave, 1954; Barlow, 1961). As Attneave (1954) recognized over 50 years ago, “*It appears likely that a major function of the perceptual machinery is to strip away some of the redundancy of stimulation, to describe or encode incoming information in a form more economical than that in which it impinges on the receptors.*” We suspect that the pattern-dependent increases and decreases of neural activity to the target may reflect a code that is sensitive to redundancies. Specifically, a target with low redundancy (e.g., is orthogonal to its flankers) carries relatively high information and this is reflected in a larger neural response resulting in faster reaction times. This modulation of reaction times might affect visually driven fast reflexes to threatening stimuli in environment (Kim et al., 2020). Similarly, as originally recognized by Attneave (1954), image elements that vary according to a predictable pattern (e.g., the alternating sequence in our experiment such as HVHVH) have high redundancy. Accordingly, we observed a slower reaction times to targets embedded in alternating, predictable patterns, suggesting that smaller neural responses to predictable stimuli. Furthermore, our results can be applied to research in which predicting emotional responses to visual patterns by developing computational models using responses to various visual patterns in early visual cortex (Kragel et al., 2019). Overall, our results suggest that modulations of the neural response in early visual cortex may serve to emphasize the locations of an image with high information content.

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