The physiological and clinical significance of this peptide will now be established in consequence of what has been expected of GRF in the many years of the search for it. Beyond that, and in keeping with other past experience, probably the most interesting role, effect, or use of GRF or of some of its future structural analogs is currently totally unsuspected.

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## A New Perceptual Context-Superiority Effect: Line Segments Are More Visible Against a Figure than Against a Ground

Abstract. Context, specifically the perceived figure or ground of an ambiguous form that surrounds a diagonal line segment, can influence the discrimination of that line segment even though the physical attributes of the context remain the same during figure-ground reversals. When the line segment was flashed on a region of the form seen as figure, discrimination was twice as accurate as when the line segment was flashed in isolation, and it was at least three times as accurate as when the line segment was flashed on that same region seen as ground.

A barely visible, briefly flashed line segment is discriminated with greater accuracy when it is part of a pattern that looks like an object than when it is flashed alone or when it is part of a pattern that appears to be a random collection of lines (I). A letter is typically identified better when it is presented as part of a pronounceable word than when it is flashed among an unpronounceable string of letters or alone (2). And an object is better recognized when it is part of a coherent scene than when it is flashed in a scene whose parts have been jumbled (3). These object, word, and scene superiority effects can all be classified more generally as "context effects" in perception. Such context effects show that perceptual variables influence task performance quite apart from the physical aspects of the stimuli.

We now report effects of context that are entirely perceptual. Visual discrimi-



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nation is dramatically enhanced when line segments are flashed in a region that is perceived as figure. Discrimination is substantially degraded when the same region is seen as ground even though the physical stimulus remains identical throughout figure-ground reversals.

In our experiment, we chose Rubin's face-vase reversible figure as the context stimulus (Fig. 1) (4). If one fixates at A, the perception of two identical faces, one on each side of the central region, alternates with the perception of a vase in the middle of the figure. When the central region is perceived as a vase (or figure) the surrounding regions become a background (ground) with no definite shape. Conversely, when the surrounding regions are seen as two faces, the central region loses its figural identity and assumes the characteristic of a formless background. The common boundary contour shared by the central and flanking regions seems to belong to the region seen as figure (4). In this stimulus, local and global environments, spatial frequency and phase, in fact, all the physical aspects of the stimulus are identical whether a region is seen as figure or as ground. Only the perception varies.

Our experiment compared observers' ability to identify the direction of tilt of a test line that was flashed within a given region of Fig. 1 when that region was perceived as figure or when seen as ground. The context pattern occupied a region 3.2° by 3.2° with a dim fixation point located at the center. The target was a line 0.9° long and 0.06° wide. On a

Table 1. Mean d' (± standard deviations) across all conditions. A three-way repeated-measures analysis of variance: differences among observation conditions [F(2, 8) = 13.86, P < .01]; difference between viewing at fixation and viewing 1° left or right of fixation [F(1, 4) = 8.64, P < .05]; no interactions were significant.

Obser- vation condition of target	Viewing at fixation		Viewing 1° left or right of fixation	
	At luminance threshold, above tilt threshold	At tilt threshold, above luminance threshold	At luminance threshold, above tilt threshold	At tilt threshold, above luminance threshold
On figure Alone On ground	$\begin{array}{c} 1.73  \pm  0.25 \\ 0.82  \pm  0.20 \\ 0.59  \pm  0.19 \end{array}$	$\begin{array}{c} 1.55 \pm 0.21 \\ 0.69 \pm 0.15 \\ 0.55 \pm 0.12 \end{array}$	$\begin{array}{c} 1.10 \pm 0.35 \\ 0.42 \pm 0.18 \\ 0.26 \pm 0.15 \end{array}$	$\begin{array}{c} 0.96  \pm  0.15 \\ 0.41  \pm  0.15 \\ 0.18  \pm  0.11 \end{array}$

given trial, this line segment, tilted left or right, was flashed for 20 msec at one of three positions (A, B, or C in Fig. 1). The target line was always  $0.5^{\circ}$  from the contours making up the context pattern.

A computer (PDP-11) with a graphics display processor (GT-40) generated the stimuli, controlled the experiment, and collected and analyzed the data. Observers viewed the display monocularly and were instructed to fixate the dim fixation point during each trial. Since observers tend to fixate a figure, they might direct their gaze to the flanking regions when faces are perceived. If the target appeared in the central region (or ground) while observers were fixating the faces, this would confound the perceptual factors of figure-ground with fixation patterns. Therefore we included the following task to aid subjects in maintaining their fixation. A square containing an X was positioned at the blind spot so that accurate fixation would render it invisible (5). A trial was initiated only if the blind-spot stimulus was not visible. This precaution eliminated as far as possible the effects of eye movements and fixation location on the performance of the perceptual task (6).

On each trial, the observer fixated the point in the center of the display, noted that the blind-spot stimulus was invisible, and pressed a key to present the target line. On one block of trials, the observers initiated the trial only when they perceived the central region as the vase and on another block of trials only when they saw the flanking regions as two faces. Because the target appeared randomly within the central and flanking regions from trial to trial, the contextual effect of each region as figure or as ground could be evaluated. We also included a block of trials in which the target line was presented alone in a homogeneous dark field. A two-alternative forced-choice method was used, and the data were analyzed according to signal detection theory (7).

In condition 1, the luminance of the display was set at threshold (75 percent correct), while the tilt angle of the target was set above its discrimination threshold (80 percent correct) (8). A tilt angle of  $1.6^{\circ}$  gave this desired accuracy. In



Fig. 2. (A) Display luminance was set at threshold while the tilt angle of the target was set above its discrimination threshold. (B) Tilt angle of the target was set above discrimination threshold while the luminance of the display was set at its discrimination threshold.

condition 2, the target's tilt angle was set at discrimination threshold ( $0.8^{\circ}$  tilt from the vertical), while the display luminance was set above threshold (9).

The results are shown in Fig. 2. Table 1 shows the mean d' (discrimination index) across five observers from the two conditions. Observers performed significantly better when the region surrounding the target was perceived as figure than when it was perceived as ground even though the physical stimulus remained unchanged. The d' for the target presented against the ground was actually lower than that for targets presented alone in the visual field. Thus, the better discrimination of the target within the figure cannot be due to luminance summation of target and context (10).

Discrimination for targets flashed at fixation was somewhat better than for targets flashed in locations 1° left or right of fixation. This result is consistent with data showing that visual resolution decreases with distance from the fovea (11). However, this decrease of accuracy was constant across all stimulus conditions and did not interactively affect a particular condition (Table 1) (12).

Our findings reveal that discrimination can be affected by whether a context is perceived as figure or as ground as well as by the more elementary factors such as luminance and receptive field characteristics. Our findings also add to the growing class of context effects showing that perceptual variables, specifically figure, improve orientation discrimination of a line segment (13). Our results demonstrate that such perceptual context effects can influence orientation discrimination accuracy even when a physical stimulus stays the same.

Perception of figure and ground has been suggested to involve two systems with different information processing characteristics (14). Figure perception is characterized by detail analysis and high resolution, while ground perception is characterized by low resolution and insensitivity to phase information. Our findings support this dichotomy of figure- versus ground-analysis as basic descriptors of visual processing in addition to the more established dichotomies of sustained versus transient channels and central versus peripheral vision.

Note added in proof: It has been brought to our attention that an earlier experiment (15) apparently found the opposite effect on figure-ground thresholds using different stimuli and procedures.

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- Two preliminary experiments were run to estimate the luminance and the minimum tilt of the target required for 75 percent correct in dis-criminating whether the target was tilted left or right. The resulting display luminance ranged from  $3.1 \text{ cd/m}^2$  to  $3.9 \text{ cd/m}^2$  across five observers; for all observers, a tilt of 0.8° placed tilt discrimination at 70 percent correct. The param-eter estimation by sequential testing (PEST) procedure [M. M. Taylor and C. D. Creelman, *J. Acoust. Soc. Am.* **41**, 782 (1977)] was used to determine the tilt threshold. Luminance thresh olds were obtained for two tilt angles-0.8° and 1.6° from the vertical--by adjusting the lumi nance of the display until the accuracy was 75 percent correct
- Since the luminance threshold was more vari able between individual observers than the tilt threshold, the luminance of the display was adjusted according to each observer's threshold n both conditions.
- 10. The randomizing of target location is perhaps the best argument against an eye movement explanation of our results. According to an eye movement account, observers would tend to movement account, observers would tend to move their eyes towards the flanking areas when these were perceived as faces. For example, if observers perceived faces, they might move their eyes to the left. Fixating the middle of the left foce would immoust discrimination if the left face would improve discrimination if the target appeared there. But the target appeared there randomly only one-third of the time. The rest of the time it appeared at the center or at the right. In this case, looking at the left face would decrease discrimination because the target would be viewed off fixation. Overall performance would suffer if fixation were directed at any location other than the center. Hence, if observ-

ers moved their eyes to the flanking regions when these were perceived as figure, they should be less accurate than if they maintained fixation. But observers were more accurate when the flanking regions were perceived as figure than when they were perceived as ground. Therefore eye movements cannot explain these increases in accuracy

- Increases in accuracy.
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## **Tetrodotoxin Blocks the Formation of Ocular Dominance Columns in Goldfish**

Abstract. Optic fibers from both eyes were made to regenerate simultaneously into one tectum in goldfish. Autoradiography at various times later revealed that regenerating left and right fibers overlapped extensively for up to 4 weeks and subsequently segregated into eye dominance columns by 8 weeks. Continuous tetrodotoxin treatment of both eyes prevented the formation of columns for up to 13 weeks and was equally effective if begun at 6 weeks. When tetrodotoxin treatment was stopped after 11 weeks, columns subsequently formed in the next 3 weeks. Blockade of only one eye did not prevent column formation at 8 weeks.

Neurons are linked by highly ordered axonal connections that, in vertebrates, are typically topographical. This topography can be complex and discontinuous as in the alternating ocular dominance columns of visual cortex (1, 2). The formation of such diverse connections may be mainly attributed to a single mechanism such as chemoaffinity, spatiotemporal chronology, fiber guidance, or self-organization of fibers (3). Alternatively, there may be a number of different mechanisms, each with a specific and limited role. Impulse activity, for example, has been implicated in a number of developing systems, particularly the mammalian visual cortex (1, 4-6). Interpretation has been complicated by the multiplicity and sensitivity of developmental events. Because regeneration offers some simplification and a number of technical advantages, a model regenerating central nervous projection formally similar to the mammalian visual cortex was used to examine the effects of eliminating impulse activity.

In goldfish, optic fibers from both eyes can be surgically induced to regenerate into one tectum and eventually form eyespecific patches of innervation similar to cortical ocular dominance columns in mammals (7, 8). Tectal columns have also been demonstrated in developing three-eyed frogs (9). We studied goldfish, 5 to 7 cm in body length, because they are advantageous for a surgical technique by which the number, position, and time of ingrowth of optic fibers can be controlled (7). Specifically, optic

fibers running near the medial edge of right dorsal "donor tectum" and innervating much of its dorsal posterior quadrant (10 to 15 percent of the tectum) were cut from the surrounding tectum by a three-sided incision that preserved the proximal segment of the fibers. The posterior end of this strip was lifted across the midline and inserted into a large mediolateral incision extending across the anterior end of the left ("host") dorsal tectum. The latter incision severed the optic fibers innervating this tectum and ensured that "donor" (ipsilaterally deflected) and host fibers regenerated from the same point.

Regeneration was studied autoradiographically from 13 to 90 days later by injecting 25 to 50 µCi of tritiated proline into one eye, donor or host, and fixing after 12 to 24 hours. Frontal paraffin serial sections at 20 to 30 µm were exposed to NTB-2 emulsion (Kodak) for 1 week. The normal chronology will be described first. At 13 to 14 days (four fish) regenerating host and donor (deflected) fibers coextended throughout the anterior half of dorsal host tectum and were largely absent from the posterior half. At the site of the insertion and incision, many fibers had been forced into the nonoptic laminae of the deep tectum. This depth error was quickly corrected by radially oriented growth toward the superficial main optic layer (stratum opticum and stratum fibrosum et griseum superficiale), and within 200 to 300 µm, label was largely normal in lamination. At 27 to 33 days (five fish)