Rapid communication

Contrast integration across space

Yoram Bonneh, Dov Sagi *

Department of Neurobiology, *Brain Research*, *The Weizmann Institute of Science*, *Rehovot 76100*, *Israel*

Abstract

Contrast integration across space was studied in respect to stimulus extent and the spatial layout, using high-contrast stimuli. Contrast discrimination thresholds were measured (2AFC) by either increasing the size of a peripheral (2.4°) Gabor signal (GS: $\lambda = 0.08°$) or by increasing the number of GS elements in a circular arrangement. The supra-threshold mask (pedestal) was either increased with the target or fixed at maximal size and had 30% contrast. For stimuli with an increasing size of both the pedestal and the increment target, we find approximately constant discrimination thresholds. Contrast discrimination improved linearly on a log–log scale with slopes average of $-1/4$ (fourth-root summation) when the size of the Gabor target was increased but the mask was kept at maximal size, indicating contrast integration across space. Taken together, these results indicate balanced spatial integration of both contrast increment and pedestal, resulting object-size invariant contrast discrimination. Contrast discrimination was found to improve as well when the number of aligned Gabor elements was increased (both pedestal and increment), pointing to independent contrast normalization for disconnected (sparsely positioned) stimuli. The results indicate a complex pattern of spatial integration involved in contrast discrimination, possibly depending on image segmentation. © 1999 Elsevier Science Ltd. All rights reserved.

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1. Introduction

One way in which visual integration can be addressed psychophysically is by studying summation of low level properties such as contrast and speed. In these studies, observer's performance on detection or discrimination tasks is measured as a function of stimulus extent and the performance for a compound stimulus is compared to the performance for its components. Studies of contrast summation-at-threshold show linear summation within a channel (Kulikowski, Abadi & King-Smith, 1973) but sub-linear summation between different detection channels (even when linear summation of independent noise, $1/\sqrt{n}$, is taken into account), which typically obeys a power-law function $n^{-1/q}$ with q values around 4. This sub-linear summation was found across space (Sachs, Nachmias & Robson, 1971; How-

ell & Hess, 1978; Legge, 1978; Robson & Graham, 1981), spatial frequency (Graham, Robson & Nachmias, 1978; Quick, Mullins & Riechert, 1978; Graham & Robson, 1987) orientation (Phillips & Wilson, 1984) and time (Watson, 1978) and explained by detection based on maximal activation among channels (probability summation) (Sachs et al., 1971; Quick, 1974; Robson & Graham, 1981; Pelli, 1985).

We have recently studied the dependency of contrast detection on the spatial configuration using multi-element Gabor displays (Bonneh & Sagi, 1998). We found that detection is constrained by spatial proximity and collinearity. For proximal and collinear elements, summation obeys a power-law $S \propto n^{1/q}$ with S the sensitivity, n the number of stimulus patches and q an exponent with values around 4. This has been termed fourth-root summation which was found to be insensitive to contrast polarity. In absence of a good configuration (e.g. non-colinear or non-proximal elements) the improvement in threshold is weak. This suggests that

* Corresponding author. Tel.: +972-8-9343747; fax: +972-8-9344131.

contrast summation is not based on probability summation between independent channels, but on local mechanisms that integrate across channels. Furthermore, since the summation spans a large part of a curved contour, but is constrained by proximity relations, it is likely to be mediated by activity propagation via lateral interactions between detectors. We have implemented this idea, recently, in a computational model (Usher, Bonneh, Sagi & Hermann, 1999). According to this model, each visual element provides direct input to a local detector (a cell-population, presumably in V1) that is activated in proportion to the contrast of the element. The detectors interact by excitatory collinear connections, and detection results from the most active response. Noise is assumed to be global or correlated between the detectors, so that no probability summation occurs.

The idea of lateral summation is supported by psychophysical evidence for range-dependent excitatory and inhibitory interactions (Polat & Sagi, 1993; Zenger & Sagi, 1996; Adini, Sagi & Tsodyks, 1997) and by physiological and neuroanatomical studies of the primary visual cortex which reveals extensive range of horizontal projections that connect cortical cells with similar response properties (Gilbert, 1992; Knierim & Essen, 1992; Lund, Yohioka & Levitt, 1993; Malach, Amir, Bartfeld & Grinvald, 1993) and involve both iso-orientation inhibition (Gilbert, 1992; Grinvald, Lieke, Frostig & Hildesheim, 1994) and collinear facilitation (Kapadia, Ito, Gilbert & Westheimer, 1995; Polat & Norcia, 1996).

Studies with suprathreshold stimuli do not support spatial integration of contrast. Increasing the size of a grating stimulus do not improve contrast discrimination (Legge & Foley, 1980). It is possible that this size constancy is a result of balanced excitation (spatial summation) and inhibition (contrast gain control), where increasing both pedestal and target size increases both summation within target (contrast increment) and contrast normalization due to increase in pedestal size. Here we manipulated target size independently from pedestal size to test for spatial summation above threshold.

2. Methods

2.1. Apparatus

Stimuli were displayed as gray-level modulations on Sony GDM2000-TC color monitor, using a Silicon Graphics Crimson/Reality Engine system. The video format was 60 Hz non-interlaced with 1280×1024 pixels that occupied a $13 \times 10.4°$ area. An 8-bit RGB mode was used, and Gamma correction was applied to produce linear behavior of the displayed luminance.

The thresholds for small Gabor signals, that were used here, are high enough (5–40%) to be effectively measured with 8-bit grey-level resolution. The mean display luminance was 40 cd/m² in an otherwise dark environment.

2.2. Stimuli

Stimuli consisted of displays comprised of multiple Gabor elements. The luminance profile of a single vertical Gabor patch is given by

$$G(x, y) = \cos\left(\frac{2\pi}{\lambda}x + \phi\right) \exp\left(-\frac{x^2 + y^2}{\sigma^2}\right)$$

The Gabor wave length was $\lambda = 0.08°$ of visual angle, which is equivalent to a spatial frequency of 12.5 c/deg and the phase ϕ was 0. Four basic stimulus conditions were used to measure the effect of stimulus extent on contrast discrimination (Fig. 1). Stimuli were either increased in size (size conditions) or in number (number conditions) and the pedestal for discrimination (which appeared in both the 2AFC displays, one of which with the target added to it) was either fixed at maximal size/number (fixed-pedestal, Fig. 1a, c) or increased with the target, being identical to it except for the contrast (increasing-pedestal, Fig. 1b, d). For the size conditions, two peripheral (2.4°) Gabor patches were used, with envelope range of $\sigma = 0.08–0.48°$. For the number conditions, where discrimination was measured as a function of target element number, small Gabor patches ($\lambda = \sigma = 0.08°$) were arranged in a circle of diameter 4.8° (30λ) radius). A fixed-pedestal consisted of 60 elements with 3λ spacing, where the target consisted of two fragments of this configuration from the two sides of the horizontal meridian (Fig. 1c). An increasing-pedestal was a circular arrangement with equally spaced patches so that spacing was decreased with increasing number of patches (Fig. 1d). Pedestal contrast was 30% in all experiments (about three times higher than the threshold for a full circle).

2.3. Experimental procedures

A two-alternative forced-choice (2AFC) paradigm was used in all the experiments. Each trial consisted of two stimuli that were being presented sequentially, both had a pedestal, but only one of which had a target. Before each trial, a small fixation circle was presented at the center of the screen. When ready, the observer pressed a key that activated the trial sequence: a no-stimulus interval (0.3 s), a first stimulus presentation, a no-stimulus interval with fixation (1.1 s total, 0.5 s with fixation), and a second stimulus presentation. The duration of stimulus presentation was 117 ms. The observer was asked to perform a discrimination task, that is, to determine which of the stimuli had a higher contrast.

Each block consisted of 50 trials (on average), across which the Gabor signal configuration was kept constant. Each session consisted of several blocks from the same stimulus condition, (size/number, fixed/variable pedestal) with varied stimulus extent. Block order was randomized within a session. Screen luminance was kept constant during the trials. The stimuli were viewed binocularly from a distance of 150 cm in a dark environment. Auditory feedback was given by a keyboard bell immediately after an erroneous response.

Target threshold contrast (which ranged from 5 to 40%) was determined by a staircase method, which was shown to converge to 79% correct (Levitt, 1971). With this method, the target contrast is increased by 0.1 log units ($\sim 26\%$) after an erroneous response, and is decreased by the same amount after three consecutive correct responses. The number of contrast reversals (from increased to decreased or vice versa) within each block was recorded, and the block was terminated after
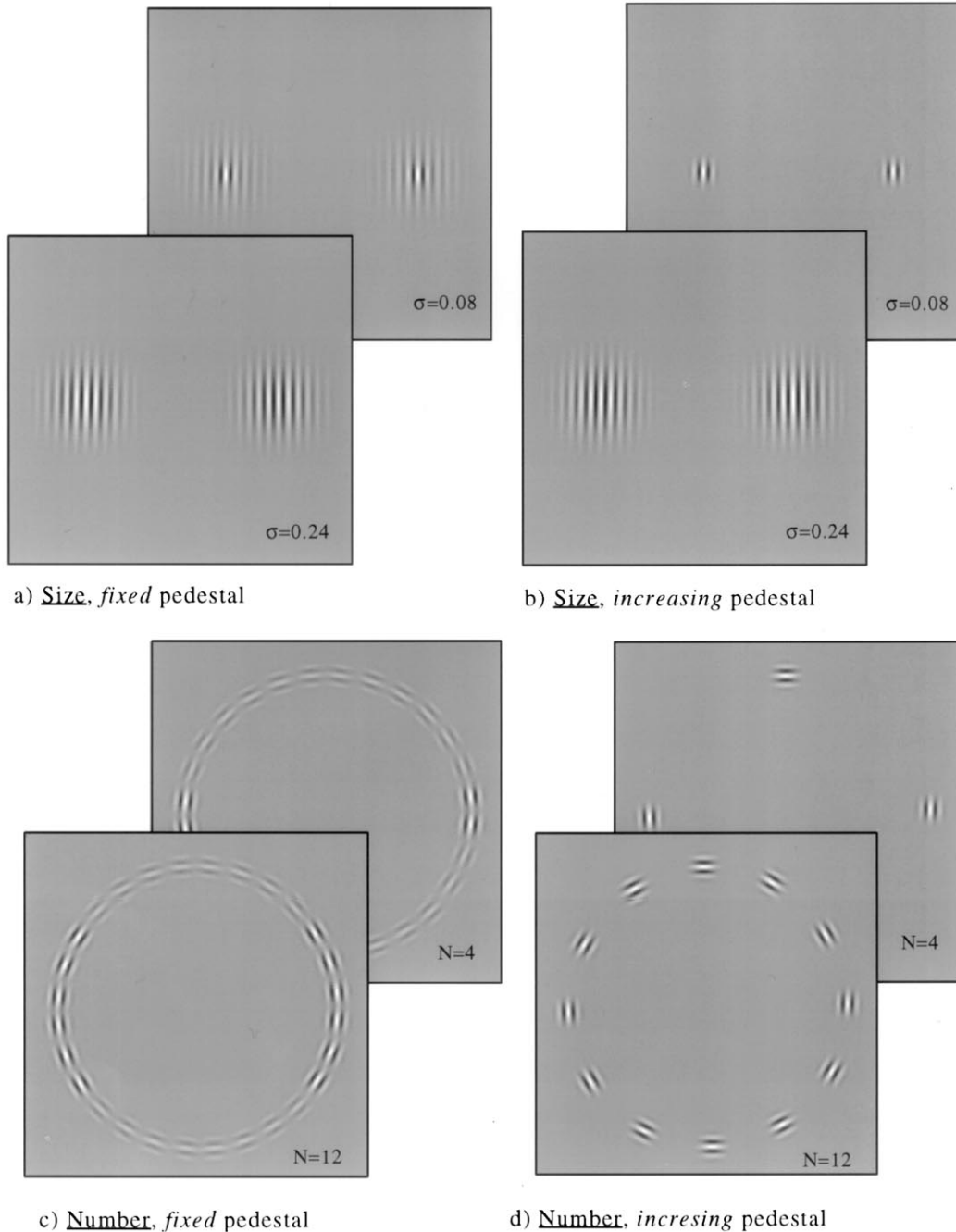

Fig. 1. Examples of stimuli used. The effect of size, fixed maximal-size pedestal (a) and increasing pedestal (b). The effect of the number of elements in fixed maximal-number pedestal (c) and increasing pedestal on an equally spaced circle (d). Stimuli are shown with reduced circle radius and pedestal size (50%) for clarity (see text for the actual sizes).
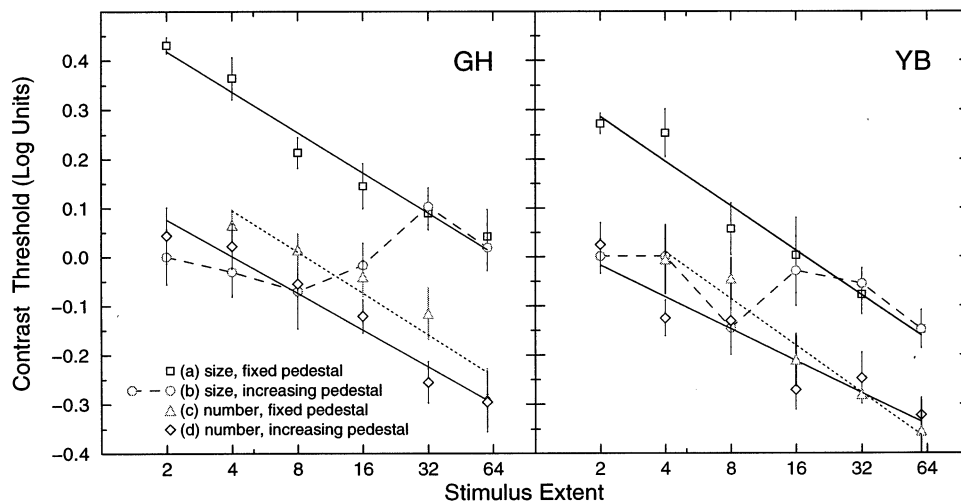
Fig. 2. The effect of stimulus extent on contrast discrimination (summation curves) for the different ways in which stimulus extent was manipulated (stimulus conditions). Discrimination threshold (relative to the discrimination threshold for two peripheral small patches with identical pedestal) is plotted as a function of the number of target patches, or its equivalent target size on a log–log scale for four conditions: size (increasing area) with fixed maximal size pedestal (a), size with increasing-pedestal (b), number with fixed maximal number pedestal (c) and number with increasing-pedestal (d). The solid and the dotted lines denote a linear least-squares fit to the corresponding data points. Each datum point is based on four to seven measurements. Error bars indicate ± 1 S.E. Observers are GH (left) and YB (right).

eight such reversals. The threshold contrast of a block was the geometric average of the last six reversals; the first two were ignored. The threshold results of four to eight blocks were averaged to compute the mean threshold and standard error of the mean (S.E.), which were plotted in the figures. In all experiments, observers were instructed to maintain their fixation at the center of the screen and not to move their eyes.

2.4. Observers

Two observers GH and YB (one of the authors) participated in the experiments. GH was naive as to the purpose of the experiments but was experienced with similar tasks, and was paid in return. Both observers had normal or corrected-to-normal vision.

3. Results

Contrast discrimination thresholds (relative to the discrimination threshold for two peripheral small patches with identical pedestal) were plotted as a function of the number of target patches, or its equivalent target size ($\sigma \propto \sqrt{n}$) on a log–log scale (Fig. 2). The data were fitted with a linear least-squares fit (solid and dotted lines). The results could be summarized as follows (conditions match the alphabetic order in Fig. 2):
1. For the size condition (increasing target area), a fixed maximal size pedestal produced a log–log linear summation with fit slopes of $-1/3.7$ for GH and $-1/3.4$ for YB.

2. For the size condition with increasing-pedestal, no summation was observed. For both observers, discrimination as a function of stimulus size improved slightly in the beginning and then deteriorated.
3. For the number condition, a fixed full circle pedestal produced a log–log linear summation, with fit slopes of $-1/3.3$ for YB and $-1/3.6$ for GH.
4. For the number condition with increasing-pedestal, a similar log–log linear summation was obtained with fit slopes of $-1/4$ for GH and $-1/4.6$ for YB.

All conditions above produced a roughly fourth-root summation, except from the size condition with a fixed maximal size pedestal, which showed no summation in agreement with Legge and Foley (1980).

In summary, summation obeyed a fourth-root power-law for a single patch (fixed pedestal) as well as for increased number of patches. Summation between far-apart patches was not restricted by proximity limitations as found previously for summation-at-threshold (Bonneh & Sagi, 1998) although it was slightly reduced relative to summation between proximal elements (compare slopes for conditions (d) and (c)).

4. Discussion

Contrast discrimination was found to improve with increasing target size and with increasing number of targets presented, pointing to spatial integration of contrast increments. Contrast discrimination was found to be independent of stimulus size when both increment and pedestal were continuously increased, pointing to range limited inhibitory effects. To account for the

data, we consider a summation model in which contrast discrimination is performed by monitoring a set of relevant detectors and looking for a fixed threshold contrast increment in any of them. In addition to the direct input, surround inhibition and long range excitation (Zenger & Sagi, 1996) modify detectors activity and thus alter discrimination. Both of these effects depend on the contrast, on the spatial configuration and on the spatial extent of the stimulus (Bonneh & Sagi, 1998, 1999). Thus, summation may depend on the net activity (as a result of lateral interactions), on the independent noise at the detector level (which may enable statistical summation) and on the integration done by single detectors (which may possibly be higher order complex cells).

4.1. The effect of inhibition

The difference between summation found for the two size conditions may be explained by inhibition which acts as a configuration dependent gain-control. Iso-orientation surround inhibition was found both physiologically (Blakemore & Tobin, 1972; Gilbert, 1992; Grinvald et al., 1994) and psychophysically (Andriessen & Bouma, 1976; Bonneh & Sagi, 1999), with increasing strength at high contrasts (Sagi & Hochstein, 1985; Grinvald et al., 1994; Stemmler, Usher & Niebur, 1995; Polat, Mizobe Pettet, Kasamutsu & Norcia, 1998; Bonneh & Sagi, 1999). We suggest that the summation in the case of target size increments with a fixed pedestal size as well the summation for number increments is not affected by inhibition which is constant for all stimulus sizes. However, when the mask is continuously increased with the target, the inhibition increases and cancels summation. Of particular interest is the comparison between results of increasing pedestal size (Results; b) and of increasing number of separated pedestal patches (Results; d), both involve increase of total activation, however only the continuous increase in size (b) points to inhibitory effects. It is possible that inhibitory interactions are short relative to element spacing in the increasing number condition (d), and relative to the spread of the excitatory interactions (inhibition along a contour is small relative to the excitation (Bonneh & Sagi, 1999)). Considering a neural network with excitatory and inhibitory connections (Adini et al., 1997), a specific detector receives inhibition from its immediate surround as well as self-inhibition. Thus the total inhibition is a result of both detector activation and surround activity. In the case of spaced stimuli, surround inhibition is not effective and self inhibition, determined by the local detector activity and a gain control factor, is only little affected by the increased excitation due to remote excitatory effects.

4.2. Fourth-root summation

Summation with a log–log linear slope in the range of $-1/3.5$ to $-1/4.5$ has been previously reported for contrast detection (Robson & Graham, 1981; Bonneh & Sagi, 1998) and for speed discrimination (Verghese & Stone, 1997) and could be termed fourth-root summation.

This type of summation was modeled as vector summation (Quick, 1974), or as probability summation between independent detectors (Robson & Graham, 1981; Pelli, 1985). We have recently modeled summation-at-threshold as based on lateral excitatory interactions between collinear and proximal detectors (Usher et al., 1999). The model was motivated by the finding of proximity and smoothness limitations on summation-at-threshold (Bonneh & Sagi, 1998), where very little summation is found between far-apart (more than five times the wave-length) Gabor patches, or between patches that make a jagged contour. This model produces the fourth-root summation by propagating local activity via local orientation specific interactions with exponential decay, and accounts for the proximity and smoothness constraints found (Bonneh & Sagi, 1998). The general effect of the interactions is the amplification of the activity of all the relevant detectors by the fourth-root of the number of inputs. Assuming the noise at the detectors is correlated or negligible, any detector can be monitored and there is no probability summation. This results in a summation pattern which well explains the summation-at-threshold data, as well as the similar summation found for detection in presence of noise (Bonneh & Sagi, 1998). The model could in principal be adapted to contrast discrimination by adding short-range inhibition and assuming longer range excitatory interactions. Alternatively, independent noise can be considered to enable statistical summation between far-apart patches and physiological summation for proximal elements.

4.3. Comparison to summation-at-threshold

Proximity limitations on summation were not found in the current study as were previously found in similar conditions for summation-at-threshold (Bonneh & Sagi, 1998). It is possible that lateral interactions at high contrasts are longer in range and that larger (nonoptimal) detectors are also involved. The long range summation could be the result of activity propagation being more effective with high contrast stimulation. According to this, summation is based on interactions with contrast dependent range. Alternatively, one may consider higher level complex cells integrating across multiple detectors (Wilson, Wilkinson & Asaad, 1997), e.g. curve or circle detectors, or a statistical integration between far-apart elements which operates at high contrast. It is possible that contrast discrimination is limited by uncorrelated noise at the detector level, allowing for probability summation, while detection thresholds are limited by noise at the higher level of integration (i.e. low detector noise at threshold) which is correlated across space.

4.4. Comparison to speed summation

Studies of speed summation found that increasing the size of a single patch did not improve performance but adding more patches produced a roughly fourth-root summation (Verghese & Stone, 1995, 1996, 1997). These results are consistent with the corresponding contrast discrimination results presented here. However, our additional results with fixed pedestal size show summation even within a single stimulus patch, indicating that contrast discrimination does not obey the rule of between-but-not-within objects spatial summation. Verghese and Stone (1997) attributed speed summation effect to two mechanisms: correlation and inhibition. A significant role of inhibition in speed summation would be consistent with the current findings, although the different tasks may involve different mechanisms.

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