How ideal do macaque monkeys integrate contours?

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Abstract

In this contribution, we present a joint study combining psychophysical investigations with macaque monkeys and probabilistic modelling of contour integration. We study the detection of S- and U-shaped contours of aligned Gabor patches among a set of unaligned distracters. This approach allows to compare quantitatively the performance of monkeys with the performance predicted by a probabilistic model. We find that the performance of the animals is very high, and we show that these experimental results can satisfactorily be explained by the structure of long-ranging horizontal interactions in V1.

Key words: gestalt perception, psychophysics, long-ranging horizontal axons, probabilistic model.

1 Introduction

Detecting the boundaries of an object is one of the fundamental steps during the process of object recognition. Although in complex real world environments the contours of an object are often partially occluded by other objects, they are easily detected by the visual system. Central to the contour-integration process is the rule of 'good continuation', i.e. line elements are perceived as a coherent contour if they are arranged colinearly (4; 5; 6).

Based on neuroanatomical and physiological properties of the mammalian primary visual cortex (V1) many authors suggested a prime importance of this area for object delineation and contour perception (4; 7; 8). In particular

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long-range connections, preferentially linking neurons with similar orientation (9; 10) and collinear aligned receptive fields (11), can contribute to contour perception. Further evidence is provided by the finding that orientation-specific neurons in V1 are markedly fascilitated by a single collinear line element placed outside the classical receptive field (12; 13; 14).

In typical modeling studies, contour integration and Gestalt perception is investigated employing a 'classical' neural architecture closely resembling the typical connection patterns found in V1. The models can quite successfully explain psychophysical phenomena (2), and can even yield a quantitative prediction of the performance of the observers (3). However, most modeling studies lack a solid mathematical description of the Gestalt criteria which is needed for developing a consistent theory.

Recent work by Williams and Thornber (1) has bridged this gap by providing a probabilistic framework for contour integration. This approach allows both to draw contour ensembles from a given probability distribution, and to define an ideal observer which uses the same probability distribution to detect contours hidden among a set of distractors.

In this contribution, we test the hypothesis if long-ranging horizontal axons, whose structure resembles the link statistics of edges in contours, can explain the performance of the monkeys in our experiments. For this purpose, we construct an artificial observer who uses the typical pattern of long-ranging axons as a probability distribution for detecting contours. The performance of this observer is then compared to the performance of two macaque monkeys.

2   Experimental Methods

Stimulation Paradigm. We trained two monkeys to perform a two-alternative forced-choice paradigm. The monkeys sat in a primate chair in front of a 21" CRT screen (1152 by 864 pixels, refresh rate 100 Hz). Each trial started with the appearance of a small fixation spot in the display center. After a fixation period of 800–1000 ms an image was presented containing either a S- or an U-shaped path of Gabor elements with random phases embedded in a random array of Gabor elements of identical contrast and spatial frequency (Fig. 1(a)). The Gabor-element stimulus was displayed for 600 ms and then followed by a gray screen of same mean luminance containing saccade targets on the left and right side. Monkeys indicated by means of a saccade the side of the display containing the contour. Only correct trials were rewarded with a drop of fruit juice.

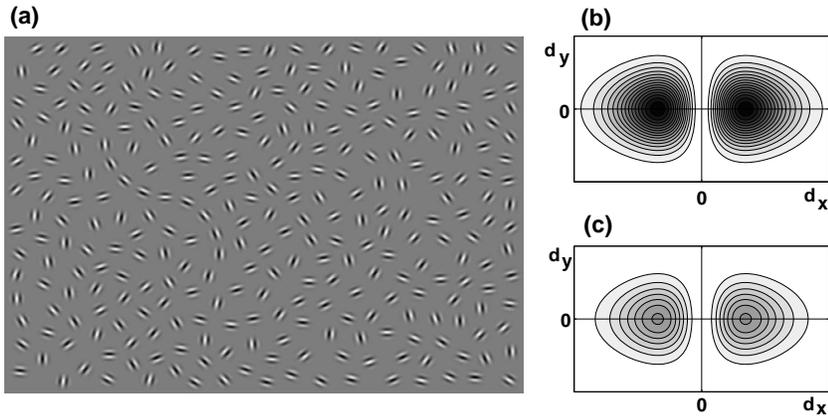**Stimulus Construction.** The path of the contour was computed using the

Fig. 1. Examples of a typical stimulus, and cross-sections from an association field. (a) Gabor-element stimulus with S-shaped contour and orientation jitter $\alpha = 0$. (b) and (c): Two-dimensional cross-sections through the AF defined by Eq.(3), with gray levels indicating the magnitude of ρ. The AFs are shown relative to an edge with an orientation 0 located in the origin. (b) shows the AF extending to horizontal edges, while (c) shows the AF extending to oblique edges with an orientation $\pi/4$. The scales of (b) and (c) are three times larger than the scale of (a).

method described in (4). In short, the path was constructed by joining together $L = 9$ line elements to form a S- or an U-shape. The length of the line was four times the period of the modulating sinusoid of the Gabor elements. A random jitter between $\pm 5\%$ was added to each line length. In addition, the shapes were distorted by adding a random jitter between $\pm 30\%$ to the angle that would lead to a regular S- or U-shape ($22.5^o \pm 6.7^o$). Then, a Gabor element was placed at the halfway of each line. The contour was turned and moved to an arbitrary position on the left or right side of the image. After the positions of the contour elements had been determined, background elements were added to the image by using a method adopted from (6). This method ensures same pair-distribution functions for contour and background elements. To investigate the influence of colinearity on contour salience, the orientation of the path elements was varied relative to the orientation of the path. The orientation of each contour element was given a random change of $\pm \alpha$, which was varied in the range of 0 to $\pi/5$.

3 Theory

For an overview and derivation of the methods used and extended in this contribution, see (1) and references herein.

Stochastic model. Contours formed by a succession of edge elements can be described as generated by a stochastic process using the transition probability distribution $\rho(\mathbf{y}, \theta | \mathbf{x}, \phi)$. Given that a contour passes through an edge

in direction ϕ located at $\mathbf{x}$, ρ quantifies the transition probabilities that the contour will next pass through an edge at $\mathbf{y}$ in direction θ. ρ is often referred to as the association field (AF). In our stimuli, N edges (Gabor patches) are specified by sets of coordinates $(\mathbf{x}_n, \phi_n)$ with $n = 1, \ldots, N$. Inserting these coordinates into ρ yields a quadratic matrix $P_{m,n} = \rho(\mathbf{x}_m, \phi_m | \mathbf{x}_n, \phi_n)$ with link probabilities. We define the 'saliency' s_n of edge n as the relative probability for this element to belong to a contour. s_n can be computed from P with

$$s_n = \sum_{l=1}^{L} \left(\sum_{n_e=1}^{N} \sum_{n_s=1}^{N} \beta_{n_e,n,n_s}^{l} \right) \Big/ \sum_{n=1}^{N} \left(\ldots \right) \tag{1}$$

$$\beta_{n_e,n,n_s}^{l} = \left(\sum_{i_{l-1}=1}^{N} \sum_{i_l=1}^{N} \cdots \sum_{i_{L-3}=1}^{N} P_{n_e,i_{L-3}} \cdots P_{i_l,i_{l-1}} P_{i_{l-1},n} \right)$$
$$\left(\sum_{i_1=1}^{N} \sum_{i_2=1}^{N} \cdots \sum_{i_{l-2}=1}^{N} P_{n,i_{l-2}} \cdots P_{i_2,i_1} P_{i_1,n_s} \right) . \tag{2}$$

Because a contour could start at any edge n_s and end at any edge n_e while running through edge n which could be at any position l within the L elements of the contour, s_n is given by a sum over all these alternatives (Eq.(1)). For fixed n_s and n_e, β_{n_e,n,n_s}^{l} denotes the relative probability that n is the l-th edge of all possible contours passing through n_s, n_e, and n. β is computed by Eq.(2), again by summing over all possibilities using the link probabilities from P. The term $\sum_n(\ldots)$ normalizes s_n.

Association Field. As mentioned before, we would like to test the hypothesis if the structure of long-ranging horizontal axons can explain the contour integration performance of macaques. Therefore we choose the AF ρ such that its geometry duplicates the anatomy of horizontal interconnections within V1. Adapting the results from Stettler et al. (10), we derived an analytical expression for ρ written as a product-sum of Gaussians

$$\rho(\mathbf{y}, \theta | \mathbf{x}, \phi) = c F_s(\mathbf{x}, \mathbf{y}, \phi) \exp\left(-|\phi - \theta|^2 / 2\sigma_a \right) \tag{3}$$

$$F_s(\mathbf{x}, \mathbf{y}, \phi) = \exp\left(-d_x^2 / 2\sigma_x^2 - d_y^2 / 2\sigma_y^2 \right) - \exp\left(-(d_x^2 + d_y^2) / 2\sigma_y^2 \right) . \tag{4}$$

With $\mathbf{R}_\phi(\mathbf{x}) = (R_{x,\phi}(\mathbf{x}), R_{y,\phi}(\mathbf{x}))$ specifying a rotation of size ϕ around the origin, d_x is given by $d_x = R_{x,\phi}(\mathbf{x} - \mathbf{y})$ and d_y by $d_y = R_{y,\phi}(\mathbf{x} - \mathbf{y})$. $|\phi - \theta|$ denotes the smallest angle difference between ϕ and θ. ρ comprises of an angular term, a spatial term F_s, and a normalisation constant c. The angular term describes the orientation-specificity of horizontal axons, which connect primarily neurons of similar orientation preference. The spatial term describes the extensions of the excitatory (positive term) and the inhibitory interactions (negative term). Inhibitory interactions are assumed to be rotational

invariant, while excitatory axons are asymmetric, covering larger distances in retinal space in the direction of aligned orientation columns (for examples, see Fig.1(b) and (c)). The length constants were choosen as $\sigma_x = 2\sigma_y = d$ and $\sigma_a = \pi/5$, where d denotes the typical mean distance between two neighboring Gabors in the stimulus (ca. 1° of the visual field).

Computation of performance. Having obtained the saliences s_n via Eq.(1), the location of the contour (left or right hemifield of the display) is estimated by the position of the edge with the highest salience. The performance is then given by the percentage of correct estimations.
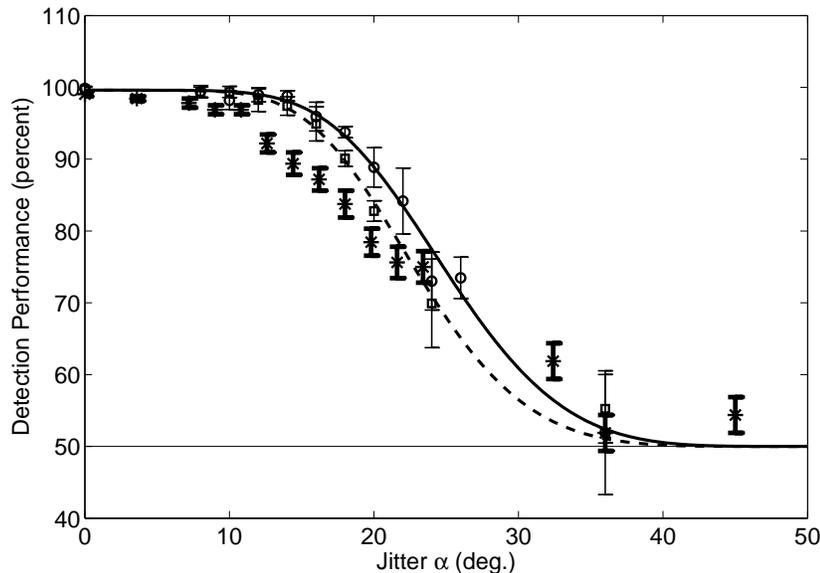

Fig. 2. Performance displayed as the percentage of correct detections, for monkey 1 (solid line, open circles) and monkey 2 (broken line, open squares), as well as for the theoretical observer (stars, with thick error bars).

4 Results

Fig. 2 shows the detection performance of both monkeys as a function of the jitter α. The performance remains above 95% up to a jitter of $\alpha = 16^o$. For larger α values, the performance drops towards chance level, which is reached approximately around $\alpha = 40^o$.

We computed the saliencies and best detection performances with the algorithm outlined in the Theory section, using the same stimulus ensembles which were shown to the monkeys. The resulting curve is drawn together with the experimental results (Fig. 2). We observed that the performance of the theoretical observer closely approaches the performance of the monkeys. This

result suggests that long-ranging axons are suitable candidates for a neuronal substrate responsible for contour integration.

In the range from 10° to 20°, however, we see a drop in the performance of the theoretical observer. An explanation for this gap between theoretical and real performance may be found in the intense training of the animals (perceptual learning), during which the neuronal structure of V1 is likely to be adapted for this special task.

5 Discussion

Our experiments show that monkeys are able to detect the contours with a similar or even better performance than human observers (4). In addition, the statistical approach outlined allows to investigate the phenomenon of contour integration on a solid mathematical background. In particular, one can compare the performance of monkeys to the performance of probabilistic observers, and test whether certain structures in the brain are likely substrates for contour integration. Our simulations indicate that long-ranging interactions could be the main substrate, and demonstrate that the monkeys are ideal observers in the sense that they approach or even exceed the theoretically predicted performance.

Currently, we optimise the detailed match between the algorithm generating the psychophysical stimuli and the statistical model underlying our theoretical studies. In future studies, we will compare the performance of monkeys and humans directly to the performance of an ideal observer. For detecting contours, this ideal observer uses the same AF from which the contour ensembles were originally drawn, thus achieving a maximal performance which no other algorithm or organism can exceed. Using this approach as a benchmark, we can identify contour integration tasks in which monkeys perform near optimal, revealing further information about the most relevant steps during the processing of visual information.

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