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Non-linear global pooling in the discrimination of circular and non-circular shapes

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ABSTRACT

The ability to discriminate minute deviations from circularity is dependent upon global summation mechanisms integrating information along entire contours. The aim of this study was to determine how the strength of global summation depends on various stimulus features. To determine if the strength of global summation differs between shapes, contour discrimination for various contour shapes, generated by applying a sinusoidal modulation to the radius of a circle (radial frequency – RF – patterns), was measured. Shapes differed in frequency (number of lobes RF3, RF5 and RF20) and amplitude ('sharpness' of the lobes ranged between 0 and 20× thresholds for detecting deviation from a circle). Low amplitudes test discrimination against a circle while high amplitudes measure sensitivity for highly non-circular shapes (e.g. five-pointed star-shapes). The ability to integrate information along contours was assessed by comparing the effect of applying radial deformations to the entire contour or to only fractions (various number of cycles). Results show that discrimination thresholds remain in the hyperacuity range for low amplitudes, but increase for higher amplitudes. Concerning signal integration, discrimination, expressed as a function of the amount of contour deformed, exhibits a shallow and a steep regime. Discrimination improves only slowly as more contour cycles are deformed until the point when the entire pattern is modulated, when sensitivity increases substantially. The initial shallow regime is well captured by probability summation. The increase in sensitivity when the entire pattern is modulated compared to a single cycle provides evidence for global pooling. The pattern of integration and the existence of global pooling is dependent on shape frequency. The two-part behavior is independent of shape amplitude but is only seen for low RFs (3 and 5). Data for RF20 follow the prediction of probability summation.

We next investigated various stimulus characteristics and their effect on integration strength. Global pooling exceeding probability summation is evident for different pattern sizes, presentation times and for high as well as low absolute contrasts. Only if the contrasts of different fractions of a contour shape are individually scaled to match their respective visibilities is integration strength below the level of probability summation. This explains the lack of apparent global pooling in previous studies employing mixed contrasts.

The marked increase in performance for discriminating completely modulated RF patterns argues in favor of highly specialized, global shape mechanisms that are seen over a wide range of stimulus configurations. The results indicate global, non-linear mechanisms, which respond most strongly when stimulated by the entire pattern and comparatively weakly when only stimulated by parts of it.

1. Introduction

The visual scene is composed of a vast variety of shapes and objects. Their retinal image is processed via a hierarchy of cortical areas starting with the primary visual cortex (V1), which contains simple line and edge detectors sensitive to orientation, spatial frequency, polarity and contrast (Hubel & Wiesel, 1962, 1968). At subsequent cortical stages (V2 and V4) along the ventral visual processing stream (Goodale & Milner, 1992; Ungerleider & Mishkin, 1982) detectors are selective for more complex stimulus features such as angles, arcs and circles (Anzai et al., 2007; Connor, Brincat, & Pasupathy, 2007; Dobbins, Zucker, & Cynader, 1987; Hegde & Van Essen, 2000; Pasupathy & Connor, 1999, 2001, 2002), as well as for hyperbolic and polar stimuli (Gallant, Braun, & Van Essen, 1993; Gallant et al., 1996). Finally, at higher cortical areas including IT and LOC, neurons have been shown to be selective for complex stimuli such as faces and whole objects (Goodale & Milner, 1992; Gross, 2008; Ito et al., 1994; Missal et al., 1999; Murray et al., 2002; Tanaka, 1996).

Object and shape perception inevitably requires the integration of local orientation information from early processing stages. How

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this integration is achieved is as yet not completely understood (see Loffler, 2008 for a recent review).

Wilkinson, Wilson, and Habak (1998) investigated the properties of shape processing psychophysically using a class of closed contours known as radial frequency (RF) patterns. RF patterns are defined by sinusoidal modulations of a radius, where the frequency of the modulation determines the number of lobes (e.g. 5 vs. 8 sided shape) and the amplitude describes the sharpness of each lobe. Studies using fMRI (Dumoulin & Hess, 2007; Wilkinson et al., 2000) and ERP (Ohla et al., 2005) indicate that these kind of patterns are processed in human V4.

In their initial study, Wilkinson, Wilson, and Habak (1998) measured performance for discriminating RF patterns from circles. Thresholds were found to be in the 'hyperacuity' (Westheimer, 1979) range for patterns above RF2, as subjects were able to detect minute deviations (less than 10–15 arcsec) from circularity.

Theoretically, the discrimination between RF patterns and circular shapes could be realized by either local filters matched to parts of the pattern (e.g. points where the tangent or curvature of an RF pattern deviates the most from a circle) or by a global mechanism, using large filters and operating on the scale of the entire pattern, with access to information from the entire circumference of the shape. Wilkinson, Wilson, and Habak (1998) argued that subjects' remarkable sensitivity in RF discrimination tasks could neither be explained by local orientation deviation nor by local curvature analysis, but instead indicated global pooling of contour information. Further support for global strategies comes from a range of subsequent psychophysical studies (Bell & Badcock, 2008, 2009; Bell et al., 2007; Hess, Achtman, & Wang, 2001; Hess, Wang, & Dakin, 1999; Jeffrey, Wang, & Birch, 2002; Loffler, Wilson, & Wilkinson, 2003).

To describe the magnitude of global pooling, Loffler, Wilson, and Wilkinson (2003) measured the amount of pooling in a task of discriminating between various RF patterns and circles. Pooling was assessed by comparing sensitivity for variable amounts of contour deformation (number of modulated cycles). For some patterns, performance increased with the number of modulated cycles at a rate that exceeded the prediction of probability summation over multiple local independent detectors. This result supports the earlier proposal that a global mechanism underlies the high sensitivity seen in RF detection and allowed the global integration strength to be determined. However, global pooling was not found for all shapes tested. Global pooling was evident for low radial frequencies (RF3, RF5 and partially for RF10) but not for higher frequencies (RF24). It was suggested that the progressive change in the amount of summation is evidence that multiple shape mechanisms are responsible for processing these shapes (Loffler, Wilson, & Wilkinson, 2003). Studies using either adaptation (Anderson et al., 2007; Bell, Dickinson, & Badcock, 2008; Bell et al., 2009), sub-threshold summation (Bell & Badcock, 2009) or masking paradigms (Habak, Wilkinson, & Wilson, 2006; Habak et al., 2004) support the existence of multiple narrowly-tuned RF channels.

The main purpose of the current study was to examine the existence and strength of global pooling and to compare it across a range of factors including contour shape. The majority of previous studies have concentrated on discrimination between circular shapes and RF patterns (Bell & Badcock, 2008, 2009; Habak, Wilkinson, & Wilson, 2006; Hess, Wang, & Dakin, 1999; Jeffrey, Wang, & Birch, 2002; Loffler, Wilson, & Wilkinson, 2003; Wilkinson, Wilson, & Habak, 1998). Shapes tested in these studies only sampled quasi-circular shapes, which represent a restricted range of the multitude of possible closed contour shapes. Non-closed, sinusoidal contours have also been tested (Gheorghiu & Kingdom, 2009) as have non-circular RF patterns (Bell et al., 2009, 2010). For the latter case, supra-threshold (i.e. non-circular) RF patterns have been employed in adaptation (Bell et al., 2010) and masking experiments (Bell et al., 2009), with evidence in favor of global processing of these shapes. What has not been done is to measure the integration strength for supra-threshold RFs and to compare this strength for circular and non-circular shapes. Note that in this paper the term *circular* describes RF contours close to discrimination thresholds against a circle (near-threshold) and *non-circular* refers to RF contours with high modulation amplitudes (supra-threshold).

As will be shown, a range of non-circular shapes are processed globally, similar to circular contours, but the integration process is highly non-linear and more complex than previously thought. Global integration is only evident when entire contours are modulated. When only a fraction of a shape is deformed, local processes are sufficient to explain experimental results.

The existence of global pooling underlying RF shape discrimination has recently been questioned for stimuli at low contrasts (Mullen, Beaudot, & Ivanov, 2011). In that study, sensitivity to a single, isolated cycle was found equal to that for the entire RF. The issue of global pooling has significant implications for the cortical mechanisms involved in contour shape processing as well as for models aimed at capturing their behavior. We therefore investigated the reasons for the differences between Mullen, Beaudot, and Ivanov's (2011) study and a range of other investigations (Bell & Badcock, 2008, 2009; Habak, Wilkinson, & Wilson, 2006; Hess, Wang, & Dakin, 1999; Jeffrey, Wang, & Birch, 2002; Loffler, Wilson, & Wilkinson, 2003; Wilkinson, Wilson, & Habak, 1998) by determining the circumstances under which global pooling is present.

2. Material and methods

2.1. Participants

Three of the authors, all experienced psychophysical observers, participated in all experiments. A further naïve subject completed a range of conditions to confirm the main results. All subjects had normal or corrected-to-normal visual acuity. The observations were made under binocular viewing conditions. No feedback was given either during practice or the experiments.

2.2. Apparatus

Stimuli were generated using Matlab 7.7 (Mathworks). The shapes were presented on a gamma-corrected LaCie "electron22blueII" monitor (1024×768) with a frame rate of 85 Hz under the control of a Macintosh G4 computer. The pattern luminance was on average 65 cd/m^2. Observers viewed the stimuli using a chin and forehead rest to guarantee a constant viewing distance of 120 cm. At this distance the size of 1 pixel was 0.018 deg. To avoid reference cues, a white cardboard mask with a circular aperture of 12 deg was placed in front of the monitor. Experiments were carried out under dim room illumination. Routines from the Psychophysics Toolbox were used to present the stimuli (Brainard, 1997; Pelli, 1997).

2.3. Stimuli

The radial frequency patterns used in the experiments are characterized by sinusoidal modulations of the radius of a circle according to the following equation (Wilkinson, Wilson, & Habak, 1998):

$$r(\theta) = r_{mean}[1 + A(\theta) \cdot \sin(\omega\theta + \varphi)] \quad (1)$$

where r (radius) and θ (polar angle) are the polar coordinates of the contour and r_{mean} is the radius of the modulated circle (corresponding