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Rejecting probability summation for radial frequency patterns, not so Quick!

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ABSTRACT

Radial frequency (RF) patterns are used to assess how the visual system processes shape. They are thought to be detected globally. This is supported by studies that have found summation for RF patterns to be greater than what is possible if the parts were being independently detected and performance only then improved with an increasing number of cycles by probability summation between them. However, the model of probability summation employed in these previous studies was based on High Threshold Theory (HTT), rather than Signal Detection Theory (SDT). We conducted rating scale experiments to investigate the receiver operating characteristics. We find these are of the curved form predicted by SDT, rather than the straight lines predicted by HTT. This means that to test probability summation we must use a model based on SDT. We conducted a set of summation experiments finding that thresholds decrease as the number of modulated cycles increases at approximately the same rate as previously found. As this could be consistent with either additive or probability summation, we performed maximum-likelihood fitting of a set of summation models (Matlab code provided in our Supplementary material) and assessed the fits using cross validation. We find we are not able to distinguish whether the responses to the parts of an RF pattern are combined by additive or probability summation, because the predictions are too similar. We present similar results for summation between separate RF patterns, suggesting that the summation process there may be the same as that within a single RF.

1. Introduction

To a first approximation the visual system can be considered a series of feedforward stages, where the neurones at each stage exhibit tuning to progressively more complex stimulus features. In primary visual cortex (V1) for example, we find cells tuned to orientation and spatial frequency (Hubel & Wiesel, 1962, 1968). Beyond V1 the system diverges into the dorsal stream, handling motion information, and the ventral stream where shape information is processed (Goodale & Milner, 1992; Ungerleider & Mishkin, 1982). As we move along the ventral stream the neurones exhibit tuning to more complex shape information (see Kravitz, Saleem, Baker, Ungerleider, & Mishkin, 2013 for recent review); these properties have inspired many models of shape and object processing (Cadieu et al., 2007; DiCarlo, Zoccolan, & Rust, 2012; Riesenhuber & Poggio, 2000; Serre, Oliva, & Poggio, 2007; Van Essen, Anderson, & Felleman, 1992). Neurones in primate V2 and V4 selectively respond to stimuli that combine multiple orientations such as angles, arcs, circles, hyperbolic gratings, and polar gratings (Anzai, Peng, & Van Essen, 2007; Gallant, Connor, Rakshit, Lewis, & Van Essen, 1996; Hegdé & Van Essen, 2007). Shape representation is believed to be mediated by a population code of cells in primate V4, which have been shown to exhibit tuning to specific contour features, e.g. convex and concave curvature maxima relative to the centre of a shape (Carlson, Rasquinha, Zhang, & Connor, 2011; Pasupathy & Connor, 1999, 2002; Yau, Pasupathy, Brincat, & Connor, 2013). Further along the ventral stream in inferotemporal cortex we find neurones selective for complex shapes and objects such as faces (Albright, Desimone, & Gross, 1984; Tanaka, 1996; Tsao & Livingstone, 2008).

As evidence continues to grow for this hierarchy, where progressively more complex stimulus features are represented along the ventral stream, the question of how this is achieved arises (Loffler, 2008; Wilson & Wilkinson, 2015). Radial frequency (RF) patterns were introduced by Wilkinson, Wilson, and Habak (1998) to address this question. An RF pattern is defined as a circular contour with a sinusoidally-modulated radius. Each cycle of the sinusoid gives a bulge at its peak and an indent at its trough. The frequency of the modulation determines the number of cycles in

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the pattern (e.g. an RF4 has four peak-and-trough cycles) and the amplitude describes the magnitude of the distortion from a circle. Discriminating RF patterns from circles could be accomplished either by comparing the outputs of local filters matched to parts of the pattern, or by a global mechanism operating at the scale of the entire shape (taking those local filters as its input). Wilkinson et al. (1998) argued that the high sensitivity for the detection of RF modulations could not be achieved simply by local orientation or curvature analysis, but requires pooling of local contour information into a global representation of the RF shape. Further support for the global integration of RF shapes at threshold amplitude comes from a range of subsequent psychophysical studies (e.g. Bell & Badcock, 2008, 2009; Bell, Badcock, Wilson, & Wilkinson, 2007; Bell, Gheorghiu, Hess, & Kingdom, 2011; Hess, Achtman, & Wang, 2001; Hess, Wang, & Dakin, 1999; Jeffrey, Wang, & Birch, 2002; Loffler, Wilson, & Wilkinson, 2003; Schmidtmann, Kennedy, Orbach, & Loffler, 2012; Wang & Hess, 2005). For amplitudes above threshold, global integration receives support from studies of RF shape aftereffects (Bell, Hancock, Kingdom, & Peirce, 2010; Bell et al., 2011).

A subset of these studies used a summation paradigm in which the number of modulated cycles n in the pattern was varied and the effect on threshold measured (Bell & Badcock, 2008; Dickinson, Han, Bell, & Badcock, 2010; Dickinson, McGinty, Webster, & Badcock, 2012; Hess et al., 1999; Loffler et al., 2003; Schmidtmann et al., 2012; Tan, Dickinson, & Badcock, 2013). In a linear system that performs global pooling one expects to see an inversely proportional relationship between the threshold and the number of modulated cycles (i.e. doubling the number of modulated cycles should halve the threshold). This gives a summation slope of -1 when threshold is plotted against n on log–log axes. This prediction can be contrasted against that from a system where there is no global pooling and each cycle of the RF pattern is detected independently. In that case the improvement in performance due to the increasing number of modulated cycles would be due to probability summation between the mechanisms responsible for detecting each individual cycle (Sachs, Nachmias, & Robson, 1971). Probability summation is typically modelled under the assumptions of High Threshold Theory (HTT; see Green & Swets, 1966). Under HTT the predicted summation slope is $-1/\beta$, where β is the parameter controlling the slope of the psychometric function obtained from a Weibull fit to the data (Quick, 1974). The summation slopes and HTT probability summation predictions from several previous experiments are shown in Table A1. As summation slopes are typically steeper than that predicted by probability summation under HTT, the authors of these studies have rejected this model. Although the empirical summation slopes do not reach the -1 predicted by the linear summation model (which under HTT means that the fixed high threshold occurs *after* the global pooling, as opposed to *before* the global pooling for the probability summation model), an additive global pooling model can still account for their data if there is a nonlinearity in the response to the individual cycles before the global pooling occurs. For example, a nonlinear transducer where the local response $r_{\text{local}} = A^{\tau}$, would give a predicted summation slope of $-1/\tau$.

Although these previous studies have focused on rejecting the HTT probability summation model, it is now widely accepted that Signal Detection Theory (SDT) provides the more appropriate framework to characterise decision processes in psychophysical experiments (Green & Swets, 1966; Meese & Summers, 2012; Nachmias, 1981; Tyler & Chen, 2000). This raises the question of whether probability summation modelled under the assumptions of SDT can so easily be rejected (Kingdom, Baldwin, & Schmidtmann, 2015; Tyler & Chen, 2000). Note that under SDT detection is also affected by uncertainty (Pelli, 1985), which introduces other model forms such as those featuring template-matching. If the noise affecting the inputs is uncorrelated and the observer is able to ignore noise from irrelevant inputs (i.e. those not being stimulated) this will also reduce the measured summation. In the ideal case where each input is weighted by the expected magnitude of its stimulation the slope will be $-1/2$ (Tanner, 1956). In the case where there is both a nonlinear transducer and an adjustable template their effects on the summation slope will multiply together to give even shallower summation slopes, on par with those predicted by HTT probability summation (Wilson, 1980). It is important to note that the derivation provided in Wilson (1980) does not describe a probability summation model; this detail is sometimes overlooked (e.g. Dickinson, Cribb, Riddell, & Badcock, 2015). Recent studies in the summation of contrast over area have rejected previous probability summation accounts and concluded that a “noisy energy” model of this form (where $\tau = 2$) provides the best explanation of the results (Baldwin & Meese, 2015; Meese, 2010; Meese & Summers, 2012).

In this study we first collect receiver operating characteristic (ROC) data to demonstrate that SDT, rather than HTT, is the correct theory in the context of RF pattern discrimination. This is simple to demonstrate as under HTT the ROC should be straight whereas under SDT it should be curved (Green & Swets, 1966). This finding makes the predictions of the HTT-based probability summation model irrelevant to the study of the detection of RF pattern modulation. In the second part we perform additional experiments and modelling (Matlab code is provided as a Supplementary material) to investigate whether this rejection of HTT changes our conclusions about how summation occurs within RF patterns. We also compare summation within an RF pattern against summation between RF patterns in order to see whether summation within an RF pattern has any special properties. We find that we are unable to reject a probability summation model formulated under SDT. When comparing summation within an RF pattern to summation between RF patterns we find little difference.

2. Methods

2.1. Equipment

The stimuli were generated in Matlab (Matlab R2013a, MathWorks) and presented on a gamma-corrected Iiyama Vision Master Pro 513 CRT monitor with a resolution of 1024 × 768 pixels and a frame rate of 85 Hz (mean luminance 38 cd/m^2) using an Apple Mac Pro (3.33 GHz). Observers viewed the stimuli at a distance of 1.2 m. At this distance one pixel on the monitor subtended 0.018 degrees of visual angle (deg). Experiments were carried out under dim room illumination. Routines from the PsychToolbox were used to present the stimuli (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007).

2.2. Observers

Three observers participated in the complete set of experiments. Two were authors (ASB and GS), and the third was a psychophysically-experienced observer who was naive to the purposes of the experiment (AR). Two more naive observers were brought in to collect additional data (YG and TT). All observers wore their appropriate optical correction for the viewing distance. Experiments were carried out with the participants’ informed consent in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki) and were approved by the Biomedical B Research Ethics Board of the McGill University Health Centre.