Title: A simple receptive field model for the multiplexing of shape and intensity in the early visual system

Authors: Xoana G. Troncoso, Stephen L. Macknik, Susana Martinez-Conde

1000-word Summary

What physical computations occur within our brains in order to recognize an object? This complex task is complicated further by the fact that each optic nerve contains only about 1,000,000 axons, giving it about the same resolution as a typical video monitor. So how do we see such a rich visual scene with seemingly infinite resolution and colors? In part, the visual system accomplishes this task by multiplexing information at the level of the optic nerve: each receptive field conveys information about shape, intensity, and color. Therefore, information about shape and intensity is confounded during, at least, the first stages of visual processing. The result of this confound should be that optimizing the shape of a stimulus to a receptive field will be indistinguishable to increasing the stimulus's contrast. If this is true, we should be able to determine the most optimal shapes for visual processing by changing the shape of objects while keeping their luminance stable: the elements of the visual scene that are most optimally shaped should also appear to be more salient perceptually, and their neural correlate should be greater responses in neurons.

Because receptive fields of the early visual system are often referred to as "edge-detectors", we compared neuronal responses to edges to other types of shapes in the visual scene. Neurons in the lateral geniculate nucleus (LGN) and primary visual cortex (area V1) of the awake monkey responded more strongly to junctions than to edges. This suggests that junction processing may not be a subsequent stage to edge processing, but that junctions may rather be a more optimal stimulus than edges for early visual receptive fields. To test this theory we convolved simple, linear computational models of receptive fields in the retina/LGN and area V1 with visual scenes (both illusory and non-illusory) containing edges, bars and junctions. This is the first time that the salience of junctions has been quantified against the salience of edges and bars by computational and physiological methods. To model the neurons of the retina and the visual thalamus (lateral geniculate nucleus, LGN), we used two-dimensional Difference of Gaussians filters (DOG) (Rodiek, 1965; Enroth-Cugell and Robson, 1966). To model the receptive fields of simple neurons in area V1 we used two-dimensional Gabor filters (Jones and Palmer, 1987). The models predicted maximal neuronal responses to junctions of sharp angles and high contrasts, rather than to edges or bars. For both DOG and Gabor filters, there was a subspace of angles and contrasts in which junctions were stronger stimuli than any possible edge. These computational and

physiological results match our qualitative perception of visual illusions in which junctions are more salient than edges.

Furthermore, responses to bars and spots are dependent on the specific receptive field sizes of the neurons processing them. Therefore, if the perception of shape was fundamentally rooted in the detection and processing of bars and spots, the perceived shape of an object would vary between foveal vision (where receptive fields are small) and peripheral vision (where receptive fields are bigger). Exploratory eye movements would produce dramatic distortions in the perceived shape of an object. Junctions and edges, on the contrary, evoke the same responses from neurons irrespective of their receptive field size. This may provide a mechanism for shape constancy in foveal and peripheral vision: if the visual system is primarily encoded to sample junctions and edges from the visual scene, then the shape of objects should not vary between the fovea and the periphery (matching our perception). Moreover, edges are not more optimal than junctions in causing responses in early visual neurons, and in fact, edges are generally worse than junctions. These results together suggest that junctions may be the most fundamental feature sampled by the visual system, rather than edges, bars or spots. Finally, direct inspection of visual stimuli, which allows one to compare perceptually the effects of junctions versus edges, shows that junctions appear more salient than edges in a approximately the same proportion that neural responses to junctions are stronger than neural responses to edges.

These results are compatible with the idea that junctions begin to be processed subcortically in the visual system (i.e starting in the retina, with antagonistic center-surround receptive fields), without the need for feedback loops or intracortical circuits. This idea contradicts current prevalent models of junction processing: most prevalent models require that two or more oriented cortical neurons (sensitive to edges of different orientations) converge onto a single neuron that prefers a junction made up of those orientations. These circuits may yet exist in the primary visual cortex, or they may be necessary to determine the orientation of a junction. However, we suggest that junction processing is a fundamental feature of subcortical neurons and that the increased responsivity of neurons to junctions is not necessarily due to cortical circuits.

Finally, why should we expect the early visual system to sample primarily junctions rather than spots, bars, and edges? Previous studies (Attneave, 1953) have shown that junctions and "points of maximum curvature" in a visual scene are the points of least redundancy, and they provide maximum information content. Furthermore, we propose that the junction-principle is more intuitive than the spots, bars, and edges idea: while the visual scene does not appear at first glance to made up out of spots, bars and edges, it does indeed appear to be made out of the junctions between curved and folded surfaces.

REFERENCES

Attneave, F. (1954) Informational aspects of visual perception. *Psychological Review,* **61** 183-193.

Enroth-Cugell C and Robson JG (1966). "The contrast sensitivity of retinal ganglion cells of the cat." *J. Physiol.* **198**: 517-552.

Jones JP and Palmer LA (1987). "An evaluation of the two-dimensional Gabor filter model of simple receptive fields in cat striate cortex." *J Neurophysiol* **5**(6): 1233-1258.

Martinez-Conde S and Macknik SL (2001). *Junctions are the most salient visual features in the early visual system.* Society for Neuroscience Meeting (Abstract), San Diego, USA.

Rodieck RW (1965). "Quantitative analysis of cat retinal ganglion cell response to visual stimuli." *Vision Research* **5**: 583-601.

ACKNOWLEDGEMENTS: We thank Fight for Sight and the Medical Research Council (UK) for funding these experiments. X.G. Troncoso is a Fundación Barrié de la Maza/The British Council Fellow.