



## Relating spatial and temporal orientation pooling to population decoding solutions in human vision

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### ABSTRACT

Spatial pooling is often considered synonymous with averaging (or other statistical combinations) of local information contained within a complex visual image. We have recently shown, however, that spatial pooling of motion signals is better characterized in terms of optimal decoding of neuronal populations rather than image statistics (Webb et al., 2007). Here we ask which computations guide the spatial and temporal pooling of local orientation signals in human vision. The observers' task was to discriminate which of two texture patterns had a more clockwise global orientation. *Standard* textures had a common orientation; *comparison* textures were chosen independently from a skewed (asymmetrical) probability distribution with distinct spatial or temporal statistics. We simulated observers' performance using different estimators (vector average, winner-takes-all and maximum likelihood) to decode the orientation-tuned activity of a population of model neurons. Our results revealed that the perceived global orientation of texture patterns coincided with the mean (or vector average read-out) of orientation signals accumulated over both space and time. To reconcile these results with our previous work on direction pooling, we varied stimulus duration. Perceived global orientation was accurately predicted by a vector average read-out of orientation signals at relatively short stimulus durations and maximum likelihood read-out at longer durations. Moreover, decreasing the luminance contrast of texture patterns increased the duration of the transition from a vector average to maximum likelihood read-out. Our results suggest that direction and orientation pooling use similar probabilistic read-out strategies when sufficient time is available.

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### 1. Introduction

The cortex accumulates sensory evidence from early visual areas in order to form purposeful decisions and initiate motor commands. To overcome the ambiguity inherent within early, noisy neural representations, cortical pathways combine ('pool') incoming visual signals. The visual system has to strike a delicate balance between combining signals from a common surface and segregating signals from the other surfaces and objects. Yet there still remains little consensus on the precise nature of the computations which govern how local visual signals are pooled across space and time.

One simple solution with substantial empirical support is that the visual system averages incoming signals in order to guide perception. (Ariely, 2001; Chong & Treisman, 2003; Cohen, Singh, & Maloney, 2008; Dakin, 1999; Dakin & Watt, 1997; Morgan, Chubb, & Solomon, 2008; Morgan, Ward, & Castet, 1998; Motoyoshi, Nishida, Sharan, & Adelson, 2007; Parkes, Lund, Angelucci, Solomon, &

Morgan, 2001; Pavlovskaya, Vol, & Blum, 1992; Sharan, Li, Motoyoshi, Nishida, & Adelson, 2008; Watamaniuk & Duchon, 1992; Watt, Morgan, & Ward, 1983; Whitaker, McGraw, Pacey, & Barrett, 1996; Williams & Sekuler, 1984; Wilson, Ferrera, & Yo, 1992; Zohary, Scase, & Braddick, 1996). For example, perception of a moving surface, such as a field of dots where local motion is pooled across space or a plaid pattern where the components are pooled across orientation, frequently coincides with the vector average direction or velocity of the local samples (Kim & Wilson, 1993; Mingolla, Todd, & Norman, 1992; Watamaniuk & Duchon, 1992; Williams & Sekuler, 1984; Wilson & Kim, 1994; Wilson et al., 1992; Zohary et al., 1996). Following earlier pioneering work on reaching direction (Georgopoulos, Kettner, & Schwartz, 1988; Georgopoulos, Schwartz, & Kettner, 1986), many physiological studies have demonstrated that neurons in the motion pathway compute a vector average of velocity signals in order to guide ocular following and smooth pursuit eye movements. (Ferrera, 2000; Groh, Born, & Newsome, 1997; Huang & Lisberger, 2009; Lisberger & Ferrera, 1997; Masson, 2004; Recanzone & Wurtz, 1999; Wallace, Stone, & Masson, 2005; Yang & Lisberger, 2009). In the spatial domain, texture perception also frequently coincides with spatial summary

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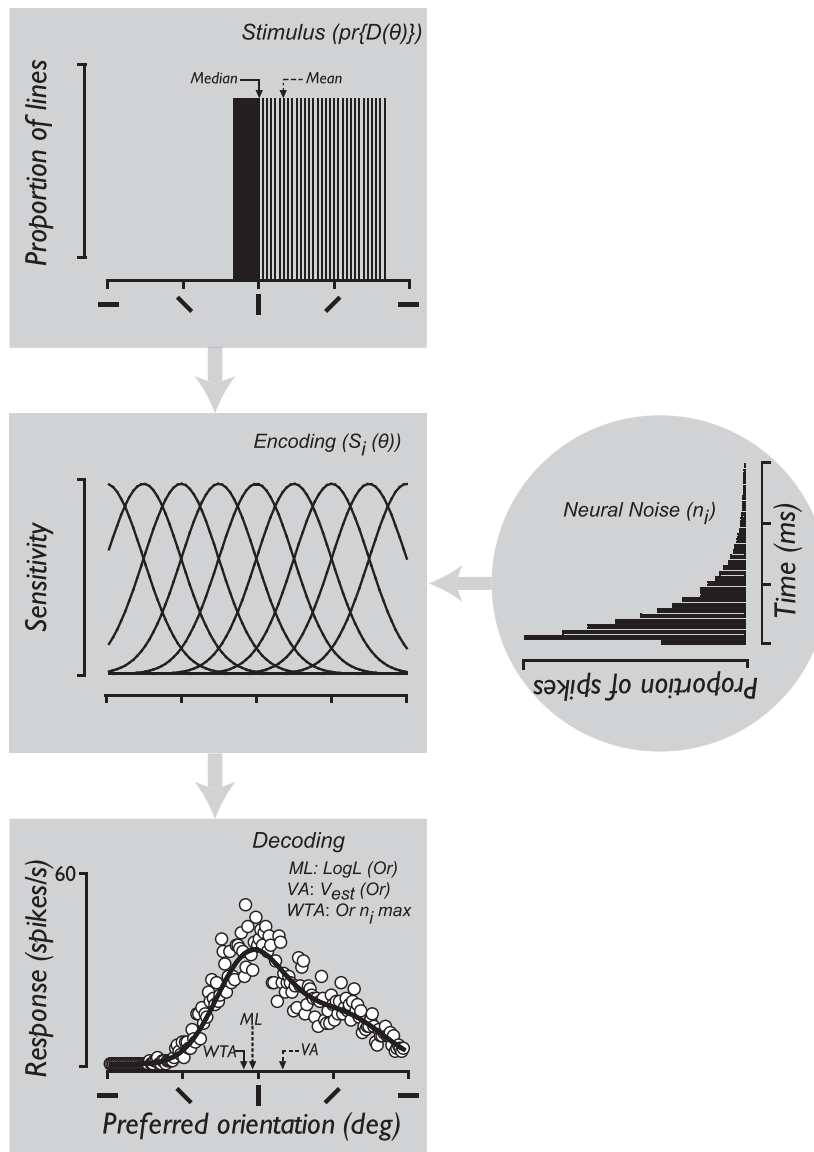
E-mail address: [bsw@psychology.nottingham.ac.uk](mailto:bsw@psychology.nottingham.ac.uk) (B.S. Webb).

statistics (Balas, 2006; Balas, Nakano, & Rosenholtz, 2009; Beck, 1983; Dakin, 1999; Dakin & Watt, 1997; Julesz, 1981; Keeble, Kingdom, Moulden, & Morgan, 1995; Kingdom, Hayes, & Field, 2001; Morgan et al., 1998, 2008; Parkes et al., 2001; Voorhees & Poggio, 1988). Analogous statistical processes have been invoked to explain other visual decisions, including the precision with which humans judge relative position (Watt et al., 1983; Whitaker et al., 1996), tilt (Morgan et al., 1998; Parkes et al., 2001), size (Ariely, 2001; Chong & Treisman, 2003) and surface reflectance (Motoyoshi et al., 2007; Sharan et al., 2008).

Although appealing because of its simplicity (Salinas & Abbott, 1994), linear operations like vector averaging can be biased estimators if the underlying detectors are irregularly spaced or narrowly tuned (Seung & Sompolinsky, 1993; Snippe, 1996) or the local samples are distributed asymmetrically (Webb, Ledgeway, & McGraw, 2007). For local orientation pooling with some types of moving plaid stimuli, the computations may be better characterized by the intersection of constraints (IOC) rule (Adelson &

Movshon, 1982; Albright, 1984; Fennema & Thompson, 1979; Movshon, Adelson, Gizzi, & Newsome, 1986; Weiss, Simoncelli, & Adelson, 2002). The IOC is an accurate mathematical description of rigid motion, but is limited by its inability to explain non-rigid forms of motion.

An alternative to averaging and IOC is a “winner-takes-all” (WTA) or “max” rule which selects the preferred stimulus of a neuron or detector with the strongest response. This form of non-linear pooling has been successfully applied to many domains, including both spatial and motion processing (Anstis, 2009; Baldassi & Burr, 2004; Baldassi, Megna, & Burr, 2006; Baldassi & Verghese, 2002; Gheri & Baldassi, 2008; Palmer, 1994; Palmer, Ames, & Lindsey, 1993; Palmer, Verghese, & Pavel, 2000; Salzman & Newsome, 1994; Shaw, 1980, 1982; Shiu & Pashler, 1995; Solomon, Lavie, & Morgan, 1997; Verghese & Stone, 1995; Webb et al., 2007). Unlike averaging, the fidelity of a WTA estimate is much less susceptible to changes in the spacing and number of detectors (Shamir, 2006). Moreover, it is simple to implement (Baldassi &



**Fig. 1.** Simulation of global orientation discrimination. We simulated trial-by-trial performance on a global orientation discrimination task. A bank of orientation tuned neurons responds to an asymmetrical distribution of orientations with a Gaussian sensitivity profile corrupted by Poisson noise. From the population response, we derive the maximum likelihood, winner-take-all and vector average read-out of orientation signals accumulated over space and time.

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