
LAST BUT NOT LEAST

Perceptual stability—going with the flow

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Abstract. Historically, inflow and outflow hypotheses have been formulated as the primary explanations for perceptual stability. Central to these hypotheses is the postulation that, following an intended eye movement, knowledge of eye position cancels the consequences of the retinal image motion. Here, we reconsider the evidence for the extra-retinal signal and discuss whether this cancellation approach is compatible with the available empirical evidence. In particular, we propose that visual-oculomotor processing is a distributed process and that population-coding models of sensorimotor transformations are critical elements that need to be incorporated in any comprehensive explanation of spatial constancy.

When we make voluntary eye movements to view a scene, images traverse our retinæ. Yet, surprisingly, in spite of the image motion, we do not experience a moving world but one that appears stable. For nearly 200 years the possible mechanisms underpinning perceptual stability have been the subject of much heated debate. The issue is how the brain differentiates image movement produced by an eye movement from those temporal events which occur within a scene.

On the one hand, it has been postulated that, by monitoring an internal copy, or corollary discharge, of the motor commands (outflow), the visual system is able to cancel the visual consequences of an eye movement (Helmholtz 1867/1962; Hering 1868; von Holst and Mittelstaedt 1950; Sperry 1950). In support, Sommer and Wurtz (2002, 2004a, 2004b, 2006) recently identified a neural pathway (superior colliculus to the frontal eye fields via the mediodorsal thalamus) in primates which is capable of monitoring these motor commands. However, other researchers have proposed that proprioceptors in extra-ocular muscles could inform the brain about any change in eye position (inflow) (Sherrington 1918; Donaldson 2000).

To re-cap the evidence briefly: many experiments have been carried out with the non-paralysed eye using active and passive eye movements, whilst subjects view either non-stabilised or stabilised targets. Subjective responses strongly favour a dominant outflow signal determining the perceived sensations. Yet there remains uncertainty about the specific roles of inflow and outflow and whether extra-retinal signals *per se* are sufficient to account for the full behavioural operating range.

Whereas after complete muscle paralysis in humans no illusory motion was reported following intended saccadic movements by the monocularly viewing paralysed eye (Siebeck 1954; Brindley et al 1976; Kulikowski and Leighton 1976), under partial muscle paralysis an illusory movement of the world did occur (Brindley et al 1976; Kulikowski and Leighton 1976; Stevens et al 1976). In addition, Kulikowski and his colleagues found that, during the early period of recovery from complete paralysis, two of the three subjects reported that, after an attempted eye movement, afterimages moved in unison with the visual background. This coupling was interpreted as a change in the relative contribution of the outflow and inflow signals. As the level of paresis decayed, the afterimages and background began to move at different rates and by the time of full recovery, when the outflow and inflow signals had returned to their

normal steady-state levels, only the afterimages moved whilst the background remained perceptually stationary.

Finally, there is supporting evidence that afferent and efferent contributions operate over limited spatiotemporal ranges (Matin 1976; Bridgeman 2007; Wurtz, personal communication), since spatial constancy breaks down in cases of voluntary nystagmus and involuntary congenital nystagmus (Abadi et al 1999).

Underpinning explanations of these observations is that knowledge of gaze direction is driven by classical feedforward/feedback control mechanisms and that straight algebraic cancellation is the goal. However, this framework requires a linear response system, the incorporation of eye, head, and world reference representations, and does not embrace the broad coding behaviour of individual neurons. With these concerns in mind, we propose that consideration should be given to computational models of sensorimotor transformations where the concept of neural networks operating over several regions of the brain can augment the classical downstream outflow/inflow dichotomy (Georgopoloulos et al 1986; Seung and Sompolinsky 1993; Pouget and Snyder 2000; Snyder 2000; Jermakowicz and Casagrande 2007). Building upon previous neurophysiological studies (Galleti et al 1993; Martinez-Trujillo et al 2004; Duhamel et al 1997; Park et al 2005), White and Snyder (2007) have recently proposed that a three-layer recurrent neural network model, which combines both retinal and extra-retinal signals, is capable of storing and updating spatial localisation from gaze-shift signals (via neuronal gain changes) and contextual cues (Anderson et al 1990). Their neural network consisted of an input layer with activating nodes, corresponding to the retinal input, gaze position, gaze velocity, and a frame of reference (world or gaze-fixed). In their middle layer, hidden unit activity was based on the neural activity found in the receptive fields (Colby et al 1995) whilst the output nodes determined the saccadic goal location in gaze-centred coordinates. This model was successfully shown to mimic the neural activity in the lateral parietal area in monkeys that were trained to perform memory-guided saccades. Such population-coding schemes not only provide new perspectives to our understanding how motor commands affect sensory signals, but also allow additional new predictions to test spatial updating.

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