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  NRTP and 3D Saccadic Control

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1.1 Intro: An eye position can be described in 'virtual terms' as a vector that describes the eye rotation that would be required to get to that position from a standard, reference, primary position. Listing's Law states that one particular dimension (call it Rx) out of the three dimensions of that vector is always 0. In practice Rx is not zero but within +/- 0.3 degs. This vectorial definition of eye position can be described as 'virtual' because the rotation from primary position is never actually performed. In reality you want to move from one position (ie. vector) to another, neither of which is the primary position. Such a real movement has a desired rotation axis and a desired eye displacement. If each eye position can be expressed as a vector, then clearly eye movements can be described by simple vector arithmetic. Doing the maths (or math) as a vector subtraction shows that the rotation axis to go between two non-primary points does not have Rx=0 and is therefore not in Listing's plane. So here's a nice paradox: to maintain Listing's plane, you must always leave the plane during a real eye movement!

So why is Listing's plane found? It is certainly not an oculomotor constraint as the eye is free to leave the plane during VOR etc.. Helmholtz thought it might help binocular vision. Is it a nervous system strategy to optimize performance? John gave us nice demonstration of the sort of mess you can get into if you DON'T have a Listing's-type constraint by waving his arms around. An accumulation of torsion can be quite painful!!

1.2 Model 1 (Raphan/Miller/Zee/Straumann): Saccades are worked out in 2D somewhere and Listing's Law is added at the level of the plant. (The 'plant' is shorthand to describe the last stage of the brainstem's output relevant to eye movement production. It includes the oculomotor nuclei, their interconnections, the oculomotor nerves and the eye muscles themselves.)

Model 2 (Tweed/Vilis/Crawford/Hepp/Van Opstal): Saccades are converted into 3D form higher up in their generation (eg. in the superior colliculus) and the plant is presented with what it has to do.

How can we distinguish between these two models? In some ways, it seems to me, model 1 is a bit of a straw person because we already know that some eye movements are not restricted to obey Listing's Law and they all pass through the plant. Anyway we need a pile of different torsions and to find which cells are correlated with the torsional values.

1.3 How to get torsion:

1.3.1 It turns out that in monkeys, sometimes spontaneous eye movements occur that violate Listing's Law. The eye just ends up after a saccade with a bit of torsion (Rx not = 0). The aberrant torsion is maintained, as if the monkey did not realize its mistake, until the next saccade which zeroes it. I am not sure how often you find these weirdos or whether there is anything you can do to encourage them (Peter Hallett, do you know?), but I bet they occur more often in monkeys with their heads held. Anyway, they are jolly useful for testing models about where torsion is generated.

1.3.2 All saccades are associated with some transient torsion (remember?).

1.4 Activity in the superior colliculus is related to the generation of saccadic eye movements. But only to do with amplitude and direction. That is, a given cell will fire in connection with a saccade of a given amplitude and direction, IRRESPECTIVE OF THE EYE MOVEMENT'S STARTING POSITION. But the TORSION (Rx) associated with the eye movement, needed to maintain Listing's Law, DOES depend on starting position. For example, it will be zero if the saccade starts at the primary position and other, predictable, systematically-calculable values for other starting positions. Close inspection of the firing pattern of superior collicular cells shows no systematic correlation with the torsional component. Listing's Law must be being handled downstream. Ooops, not the plant, surely!

1.5 Electrical stimulation of the colliculus generates eye movements that maintain Listing's plane. This also suggests that Listing's law is implemented downstream of the colliculus. Ooops! More support for that straw model...But there are other candidates before you get to the plant. And all sorts of loops the colliculus is involved in. One such involves the NRTP (see 1.0) which passes collicular signals to the cerebellar vermis.

1.6 Looking at activity of cells in the NRTP, which also fire related to saccades, shows that, in contrast to the superior colliculus, these cells ARE modulated by the concurrent torsional component of the saccades that they are associated with. That is, they can be said to have 3D movement fields.

1.7 Electrical stimulation of the NRTP evokes saccades with torsional components that takes eye position out of Listing's plane where it stays until the next, natural saccade counteracts the violation. This torsional component is constant for any one stimulation site and does NOT depend on eye position. The NRTP on each side of the brain has cells and electrical stimulation sites associated with both clockwise and counterclockwise torsion.

1.8 Muscimol is a GABA-ergic agonist: that is it stimulates cells which use GABA as their transmitter. It turns out these are usually inhibitory and so the effect of muscimol is to simulate the natural inhibitory cells in an area and shut down the local system. Normally, spontaneous torsional errors are corrected by the next saccade (see 1.3.1). The effect of muscimol injections to the NRTP is to stop this correction. The plant cannot do this job on its own.

1.9 All these observations argue strongly for the involvement of the NRTP in the implementation of Listing's Law, perhaps as a part of an error correction loop.

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