- Friday, March 15, 1996
  Stereovision and Binocular Coordination

1.0 There was an extraordinary meeting of the YORKVIS discussion group on Friday 15th March 1996 given by Doug Tweed. The topic was "Stereovision and binocular coordination". Here is my summary. As usual, I take all the blame for any errors.

1.1 Do you think there would be any point in setting up a web page with all these minutes? Comments please. Web instead of email? Email instead of web? Both? Neither?

1.2 Reminder of the following upcoming seminars:

March 26. Joshua Solomon. (Letter identification) 2pm. room 291 BSB

March 29. Gregg Recanzone. (Cortical plasticity) 10am. room 291 BSB

March 29. Tom Heckmann. 2pm. room 061 BSB

2.0 The question that was addressed was: Do we move our eyes to optimize visual input? There are many aspects to this question embracing the role of micro eye movements and all sorts of things. More specifically the question of this meeting was: Might the constraints on eye movements that can be expressed as Listing's Law, result in a visual advantage? I guess the implication of an affirmative answer would be to assign an evolutionary pressure for the emergence of Listing's Law.

2.1 Listing's Law states: "the eye can only achieve positions that can be reached from primary position by rotation around an axis that lies in a fixed plane". (I outlined this in more detail when I was summarizing Doug Crawford's talk, there I defined primary position: copies available on request - see above suggestion about a web page).

2.2 Herman von Helmholtz and Hering thought there might be visual advantages in the constraint that result from Listing's Law. They thought (separately and differently) that it might optimize retinal image flow during eye movements.

2.3 Both Helmholtz and Hering had to be wrong, however, since Listing's plane is fixed with respect to the HEAD rather than to SPACE. Since visual movement is due to movement of the eye-relative-to-space, something that was fixed with respect to the head cannot be useful. Hering and Helmholtz's theories fit head-fixed, conjugate eye movements, but make wrong predictions when the head moves or when the eyes converge (see below).

2.4 Fick and Wundt put the emphasis on motor advantages resulting from the constraints of Listing's Law. They suggested that Listing's law minimized "3D eccentricity". 3D eccentricity is the angle through which the eye is rotated away from primary position. For any given visual target spot, there are infinitely many different 3D eye orientations compatible with foveating that target, and one of these eye orientations is the closest to primary position, ie has the smallest eccentricity.

3.0 Recent data show that Listing's plane does not in fact stay still in the head OR in space! It varies systematically in the head with vergence angle. To explore this, surfaces can be constructed which require constant vergence angles to fixate objects on them. For 0 degs of vergence the Listing's planes of the two eyes are approximately flat in the head and parallel to each other and to the coronal plane. As vergence angle increases, Listing's plane in both eyes tilts out, that is the temporal edges move backwards and the nasal edges move forwards.

3.1 The amount of the tilt depends on vergence. The exact value of the tilt is controversial, but probably it is about 1/4 of the vergence angle. An important point is that it is symmetrical: that is the orientation of the plane in one eye depends on the position of the other eye! At least the relative position. Doug calls this variation of Listing's plane with vergence, the 'VERGENCE LAW' although without a certain fraction to put in to describe the relationship, I feel it may be a little premature to call it a law.

3.2 Thus since the plane is not fixed in head or space coordinates, it seems unlikely that it can have a purely MOTOR or a VISUAL explanation. Perhaps there are elements of both.

4.0 Van den Berg and Van Rijn came up with a theory that a consequence of Listing's Law might be that lines orthogonal to the visual plane (the plane that goes through both eyes and the intersection of the two lines of sight) are seen singly (fall on corresponding retinal points) but lines tilted away will be seen as double (or at least will not fall on corresponding retinal points). This would be a predominantly visual advantage arising from the law. Alas this cannot be, however, because of cyclotorsion of the eyes with eccentric eye fixation. These eye movements shift the orientation of the retina in opposite directions in the two eyes and therefore alter the orientation of a line in the outside world that would fall on corresponding retinal points: they tilt the vertical horopter.

4.1 But a simpler visual consequence could be that at least the visual planes of the two eyes line up. Doug Tweed comments: "The asymmetry between vertical and horizontal comes about because the geometrically vertical meridians through the foveas on the two retinas are not corresponding lines, ie a line casting its images on these two meridians will be seen double; but the geometrically horizontal meridians on the two retinas ARE corresponding lines, so a line that casts its images on these two meridians will be seen singly. The visual plane casts its images on these horizontal meridians when the subject looks at the horizon, and is therefore seen singly. When the subject converges, obeying the vergence law, the two images of the visual plane rotate torsionally through the same small angle, and so they continue to lie on meridians that are corresponding lines (or are at least very close to corresponding, because they are close to horizontal)." This is a visual advantage, but there are multiple solutions that would allow this. Thus this cannot be the only drive to Listing's law if Listing's law has evolved to allow this alignment.

5.0 So how about if Listing's Law arises as a result of trying to align the visual planes in the two eyes (a sort of minimal Van Rijn and Van den Berg idea) AND maximizing efficiency in motor terms (the Wundt and Fick idea)? By varying the weighting between these two goals, good prediction of the orientation of Listing's plane and its variation with vergence can be made.

6.0 One possible visual advantage of Listing's Law, that turns out not to happen, is that the constraint on eye positions might simplify the correspondence problem: the search for corresponding images when matching the components of the left and right eye's images. The set of possible places on say the left retina where all possible points corresponding to the right eye's view, is called the epipolar line. Wouldn't it be nice if Listing's law ensured that this line always fell on the same part of the retina? Well it doesn't! It seems to work for points in the visual plane but not elsewhere.

7.0 The conclusion is that Listing's Law probably has originated to satisfy both motor and visual demands and that neither one of those demands can explain the pattern of eye movements observed. However a weighted sum appears to do a good job.

Below are some comments from Doug which expand on the points made in his talk. I am not sending them around with the YorkVis minutes.

QUESTION 2.3: Hering and Helmholtz's theories fit head-fixed, conjugate eye movements, but make wrong predictions when the head moves or when the eyes converge. One can plead that these theories only "apply" to head-fixed, conjugate movements, and that the eye movement patterns in other situations require a separate theory, but obviously it would be better to have one theory that handles all cases. I grant you, it's likely that many factors shape our motor programs, and perhaps the head-fixed, conjugate benefits of Listing's law (e.g. benefits like retinal self-congruence for lines through primary gaze direction) were part of the reason that natural selection favoured this law, but certainly other factors are needed to explain gaze control in a wider setting. Put another way, given Hering's or Helmholtz's theories we still need the visual-motor theory or something like it to explain eye-head coordination and vergence, but given the visual-motor theory we have no need for Hering's or Helmholtz's theories in any situation.

To be more specific, Hering's theory held that the purpose of Listing's law is to maintain retinal self-congruence; ie when you scan along a line, its image continues to fall on the same line of retinal receptors. If we still wanted to maintain self-congruence during head movements, we would move our eyes and head so as to preserve Listing's law of the eye in space, but in fact this doesn't happen. To maintain self-congruence during vergence, our Listing's planes would have to rotate nasally, which is the opposite of what actually happens. So the Heringite has to claim that in these situations, some new factors arise which override retinal self-congruence, and these new factors must be identified by some other theory. Similar remarks apply to Helmholtz's idea.

Another problem with Hering's theory is that self-congruence only works for lines through the primary gaze direction. Therefore, if you were scanning a pattern containing many lines, you would usually have to move your head when you switched fixation between lines, so as to keep the primary gaze direction pointed at the line of current interest. In short, Hering's theory doesn't even apply to head-fixed scanning.

It's true that Listing's law and the vergence law fail transiently during eye-head saccades (although this is not directly due to the VOR, which is turned down or off during these movements). But the laws hold between saccades, which is what matters most for perception and for muscle effort. These laws also fail during eye-head pursuit, but here you are presumably compromising between optimal pursuit (which is compatible with Listing's law) and optimal VOR (which isn't).

QUESTION 2.4 No, minimizing 3D eccentricity is not the same as optimizing flight paths. 3D eccentricity is just the angle through which the eye is rotated away from primary position. For any given visual target spot, there are infinitely many different 3D eye orientations compatible with foveating that target, and one of these eye orientations is the closest to primary position, ie has the smallest eccentricity. One can show that moving the eye so as to keep eye eccentricity as small as possible is not compatible with taking the optimal (ie shortest) paths between different gaze directions.

QUESTION 4.0 I'm not sure whether I made it clear that the reason the vertical horopter tilts is not that the eyes cyclorotate, but that the "corresponding""vertical" meridians on the two retinas are not aligned, even when ocular torsion is "zero", ie when you look straight ahead at the horizon. In other words, for a line in the sagittal plane to be seen singly when your eyes are in this position, it must cast its image onto the retinal meridian tilted about 1 deg CW (from the subject's viewpoint) away from vertical in the right eye, and onto the retinal meridian tilted about 1 deg CCW in the left retina. Of course when your eyes twist about their own lines of sight to different degrees, as during vergence, these retinal meridians also rotate differently, and this changes the orientation of the vertical horopter. One of my slides showed how the vertical horopter would tilt, assuming that the eyes cyclorotate in accordance with the vergence law. So this pattern of cyclorotation was incompatible with Listing's law, but predicted by the vergence law.

QUESTION 4.1 Yes, cyclorotation will affect vertical and horizontal images the same way. The asymmetry between vertical and horizontal comes about because the geometrically vertical meridians through the foveas on the two retinas are not corresponding lines, ie a line casting its images on these two meridians will be seen double; but the geometrically horizontal meridians on the two retinas ARE corresponding lines, so a line that casts its images on these two meridians will be seen singly. The visual plane casts its images on these horizontal meridians when the subject looks at the horizon, and is therefore seen singly. When the subject converges, obeying the vergence law, the two images of the visual plane rotate torsionally through the same small angle, and so they continue to lie on meridians that are corresponding lines (or are at least very close to corresponding, because they are close to horizontal).

Thanks for all your effort. I hope my replies haven't made things more confusing. Please contact me if you want more details.

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