

15. Yamamoto, H., Fukui, K., Takahashi, H., Kitamura, S., Shiota, T., Terao, K., Uchida, M., Esaki, M., Nishikawa, S., Yoshihisa, T., *et al.* (2009). Roles of Tom70 in import of presequence-containing mitochondrial proteins. *J. Biol. Chem.* 284, 31635–31646.
16. Kohler, R., Boehringer, D., Greber, B., Bingel-Erlenmeyer, R., Collinson, I., Schaffitzel, C., and Ban, N. (2009). YidC and Oxa1 form dimeric insertion pores on the translating ribosome. *Mol. Cell* 34, 344–353.
17. Bonnefoy, N., Fiumera, H.L., Dujardin, G., and Fox, T.D. (2009). Roles of Oxa1-related inner-membrane translocases in assembly of respiratory chain complexes. *Biochim. Biophys. Acta.* 1793, 60–70.
18. Kol, S., Nouwen, N., and Driessen, A.J.M. (2008). Mechanisms of YidC-mediated insertion and assembly of multimeric membrane protein complexes. *J. Biol. Chem.* 283, 31269–31273.
19. Clements, A., Bursac, D., Gatsos, X., Perry, A., Civciristov, S., Celik, N., Likić, V., Poggio, S., Jacobs-Wagner, C., Strugnell, R., and Lithgow, T. (2009). The reducible complexity of a mitochondrial molecular machine. *Proc. Natl. Acad. Sci. USA* 106, 15791–15795.
20. Dawson, R.J., and Locher, K.P. (2007). Structure of the multidrug ABC transporter Sav1866 from *Staphylococcus aureus* in complex with AMP-PNP. *FEBS Lett.* 581, 935–938.

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Stereo-Vision: Head-Centric Coding of Retinal Signals

Stereo-vision is generally considered to provide information about depth in a visual scene derived from disparities in the positions of an image on the two eyes; a new study has found evidence that retinal-image coding relative to the head is also important.

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There is a consensus in the vision literature that stereo-depth is inferred from position differences (disparities) between the two retinal projections of an object, and does not incorporate eye posture — in other words, that stereo-vision involves retinal coding. There is in principle an alternative, which is to use differences between an object's directions relative to the head as they are measured in either eye separately — head-centric coding. Head-centric coding was suggested a decade ago in a mathematically straightforward theory [1] that capitalized on the geometry of horizontally separated eyes (Figure 1). It has been difficult empirically to distinguish retinal from head-centric disparity coding, although a few adaptation experiments have attempted to do so [2,3]. As they report in this issue of *Current Biology*, Zhang *et al.* [4] have now obtained convincing evidence for head-centric coding in stereo-vision, using a novel viewing situation. They exploited the phenomenon in which visual targets flashed just before the onset of a (saccadic) eye movement undergo a shift in perceived head-centric direction [5]. This shift depends on the time between flash and saccade [6], enabling Zhang *et al.* [4] to demonstrate that observers perceived non-zero stereo-depth from zero retinal

disparity, and zero stereo-depth from non-zero retinal disparity. This is of general interest to researchers working on sensory coding as it may reshape how scientists think about coding of our three-dimensional environment.

Influential early computational theories showed how a binocular system can in principle compute depth from disparity without using extra-retinal information [7–10]; for more recent theoretical accounts of stereo-vision based on retinal disparities, see Noest *et al.* [3] and Read *et al.* [11]. Relevant to our present discussion is that integrating horizontal and vertical components of retinal disparity makes a non-trivial computational complication [11]. Another issue for retinal disparity coding is explaining the robustness and stability of stereo-depth vision given the continual occurrence of eye movements [12]. As a possible solution to this problem, we hypothesized [12] that the (whole-field) disparities caused by our own eye movements are selectively filtered out during retinal disparity processing. Calculations showed that our own eye-movement-induced disparities influence absolute distance and slant perception, but not shape-in-depth perception [12].

Observers have detectors to measure absolute distance and slant [13,14], but binocular disparity can be regarded as one of many cues to three-dimensional vision, with

whole-field disparities having in most observers a small weight relative to monocular cues [15]. Such a low relative weight would indeed make stereo-depth stable in the presence of eye movements without compromising shape-in-depth perception [12]. A further discussion of the contribution of stereo-disparities relative to other monocular cues goes, for now, beyond the scope of this dispatch but we come back to the issue as it might inspire neurophysiologists.

The stability of stereo-depth under eye movements is not an issue for head-centric disparity coding, because it naturally incorporates eye movements. The reason is that head-centric disparity is in principle one-dimensional, because the object's head-centric disparity is zero perpendicular to the plane through the object and the centers of the eye (the epi-polar plane; Figure 1A). The one-dimensionality reduces the number of potential corresponding points in binocular matching. Furthermore, if there is a non-zero disparity perpendicular to the epi-polar plane, the brain knows that those disparities ought to have been caused by imperfections in eye posture. This feature provides a unique tool for detecting errors in oculomotor signals. Head-centric disparity processing also provides an explanation for the problem of why vertical retinal disparity is processed in a global, but not local manner (reviewed in [16]): in head-centric disparity coding, 'vertical' disparities are essentially global [1].

The experience of Zhang *et al.* [4] with strabismic patients helped to inspire their head-centric disparity experiments. Strabismic patients lack bifoveal fixation and therefore have to rely on a coarse stereo-depth mechanism using (low-resolution)

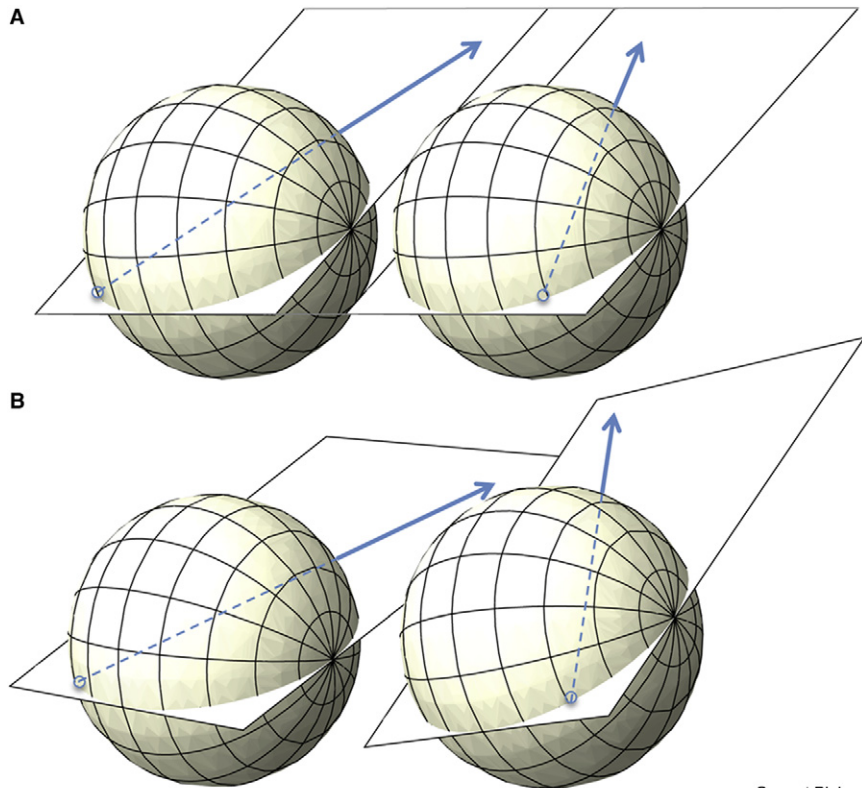


Figure 1. Epi-polar geometry.

In binocular vision there are geometric constraints between the three-dimensional points and their projections onto the retinae. This epi-polar geometry is simplified if the coordinate systems are fixed to the head (A). For each point in one image, its corresponding point in the other image can be found along a horizontal great circle. The difference between the horizontal coordinates of the projections is defined as head-centric disparity. If the coordinate systems are attached to the eyes (B), each eye movement requires a new search for correspondence along other great circles.

peripheral retinal information. In their experiments, Zhang *et al.* [4] demonstrated that normal observers are also able to use head-centric disparity coding. To what extent head-centric disparity coding is used in normal vision is not clear at this point. The authors suggest this coding is a system for qualitative (coarse) stereo-depth vision, but not necessarily for quantitative (fine) stereo-depth — “an additional mechanism” that complements the more quantitative retinal disparity coding. We would go a step further and suggest that head-centric disparity coding also underlies quantitative fine stereo-depth. Why would the visual system bother to calculate an additional retinal-coded disparity of an object if it has already calculated the head-centric coded disparity?

Two adaptation studies [17,18] support the view that eye-position signals are used early in disparity

coding by normal observers. The first of these [17] showed that adaptation to stereo-depth does not depend on eye posture, implying that adaptation to disparity occurs after eye position has been incorporated in the disparity calculations. The second [18] showed that this disparity adaptation must have occurred before the various other cues to three-dimensional vision, such as monocular perspective cues, are integrated into the final depth percept, because the individual cues to three-dimensional vision adapt individually. It is probably here, by putting into conflict the three-dimensional depth generated by the various other cues [19] with eye-posture manipulations [13,14,17] that there may be an opening for neurophysiologists to find support for a neural correlate of head-centric disparity processing.

In sum, the work of Zhang *et al.* [4] questions a centuries-old consensus

on disparity processing. So far there is no convincing neurophysiological evidence for (or against) head-centric disparity processing (for review see [20]). The new results, however, challenge neurophysiologists to search for a neural substrate.

References

1. Erkelens, C.J., and van Ee, R. (1998). A computational model of depth perception based on headcentric disparity. *Vis. Res.* 38, 2999–3018.
2. Berends, E.M., and Erkelens, C.J. (2001). Adaptation to disparity but not to perceived depth. *Vis. Res.* 41, 883–892.
3. Noest, A.J., van Ee, R., and van den Berg, A.V. (2006). Direct extraction of curvature-based metric shape from stereo by view-modulated receptive fields. *Biol. Cybernet.* 95, 455–486.
4. Zhang, Z.-L., Cantor, C.R.L., and Schor, C.M. (2010). Perisaccadic stereo depth with zero retinal disparity. *Curr. Biol.* 20, 1176–1181.
5. Morrone, M.C., Ross, J., and Burr, D.C. (1997). Apparent position of visual targets during real and simulated saccadic eye movements. *J. Neurosci.* 17, 7941–7953.
6. Zhang, Z.-L., Cantor, C.R.L., and Schor, C.M. (2008). Effects of luminance and saccadic suppression on perisaccadic spatial distortions. *J. Vis.* 8, 1–18.
7. Koenderink, J.J., and van Doorn, A.J. (1976). Geometry of binocular vision and a model for stereopsis. *Biol. Cybern.* 21, 29–35.
8. Longuet-Higgins, H.C. (1982). The role of the vertical dimension in stereoscopic vision. *Perception* 11, 377–386.
9. Mayhew, J. (1982). The interpretation of stereo-disparity information: the computation of surface orientation and depth. *Perception* 11, 387–403.
10. Gärding, J., Porrill, J., Mayhew, J.E., and Frisby, J.P. (1995). Stereopsis, vertical disparity and relief transformations. *Vis. Res.* 35, 703–722.
11. Read, J.C.A., Phillipson, G.P., and Glennerster, A. (2009). Latitude and longitude vertical disparities. *J. Vis.* 9, 11.1–37.
12. van Ee, R., and Erkelens, C.J. (1996). Stability of binocular depth perception with moving head and eyes. *Vis. Res.* 36, 3827–3842.
13. Rogers, B.J., and Bradshaw, M.F. (1993). Vertical disparities, differential perspective and binocular stereopsis. *Nature* 361, 253–255.
14. Backus, B.T., Banks, M.S., van Ee, R., and Crowell, J.A. (1999). Horizontal and vertical disparity, eye position, and stereoscopic slant perception. *Vis. Res.* 39, 1143–1170.
15. Gillam, B.J., and Lawergren, B. (1983). The induced effect, vertical disparity, and stereoscopic theory. *Percept. Psychophys.* 34, 121–130.
16. Howard, I.P., and Rogers, B.J. (2002). *Seeing in Depth; vol 2, Depth Perception* (Toronto: Porteous).
17. Berends, E.M., Liu, B., and Schor, C.M. (2005). Stereo-slant adaptation is high level and does not involve disparity coding. *J. Vis.* 5, 71–80.
18. Knapen, T.H.J., and van Ee, R. (2006). Slant perception, and its voluntary control, do not govern the slant aftereffect: Multiple slant signals adapt independently. *Vis. Res.* 46, 3381–3392.
19. Brouwer, G.J., van Ee, R., and Schwarzbach, J. (2005). Activation in visual cortex correlates with the awareness of stereoscopic depth. *J. Neurosci.* 25, 10403–10420.
20. Parker, A.J. (2007). Binocular depth perception and the cerebral cortex. *Nat. Rev. Neurosci.* 8, 379–391.

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