Dispatches

Vision: A Brake on the Speed of Sight

We move our eyes more often than our heart beats. Our brain seems to cope effortlessly with the consequences of these rapid visual alterations, but a new study shows that similar scene changes in the absence of eye movements delay the speed of information processing. So are there costs in constantly shifting our focus of gaze?

Alexander Thiele

When you watch a music video you are inundated with a seemingly incoherent and rapid stream of visual scenes, changing on average every 2.3 seconds. Such a rate of change may appear fast to an old fashioned television consumer, but it is still about seven times slower than the rate of scene change imposed by rapid eye movements on the visual system. While the former may be tiring, the latter goes seemingly unnoticed. How does our brain cope with this huge turnover of information and does it pay a price? Answers to these questions require experiments investigating neuronal processing under natural viewing conditions. Over the last few years a growing interest in such studies is re-emerging.

While early studies of the visual system emphasized the necessity of understanding the processing of visual stimuli in light of a subject's natural 'visual diet' [1], much of vision research over the last 40 years has focused on the analysis of neuronal responses to simple stimuli presented in isolation, assuming that responses to natural stimuli can be deduced from the response characteristics to these artificial laboratory stimuli [2]. Nonlinearities in the cortical network make it likely that such an oversimplified account has a lot of explaining to do, as a variety of studies investigating cortical processing of natural images have demonstrated [3–5]. Reassuringly, there were nevertheless large similarities between selectivity for artificial laboratory stimuli and the selectivity for natural images [4,6].

Most of these studies focused on scenarios that mimicked static viewing conditions, where stimuli were flashed inside a neuron's window to the world (the receptive field). Such viewing conditions do not reflect the primate's visual world. Normally the sudden appearance of an object is rare. When the visual world representation changes on the retina it is mostly due to rapid eye movements called saccades. Saccades ensure that an attended object is foveated for high acuity processing. Neuronal processing under these natural viewing conditions is still poorly understood. So what happens if the artificial laboratory condition of isolated simple stimulus presentation is compared to conditions that are more reminiscent of visual processing during free viewing?

Huang and Paradiso [7] have investigated some aspects of this question (Figure 1). They reasoned that, under natural visual conditions, saccadic eye movements bring stimuli to a specific retinal location. As a consequence there will also be a change of the visual background that falls onto surrounding parts of the retina. To mimic these more

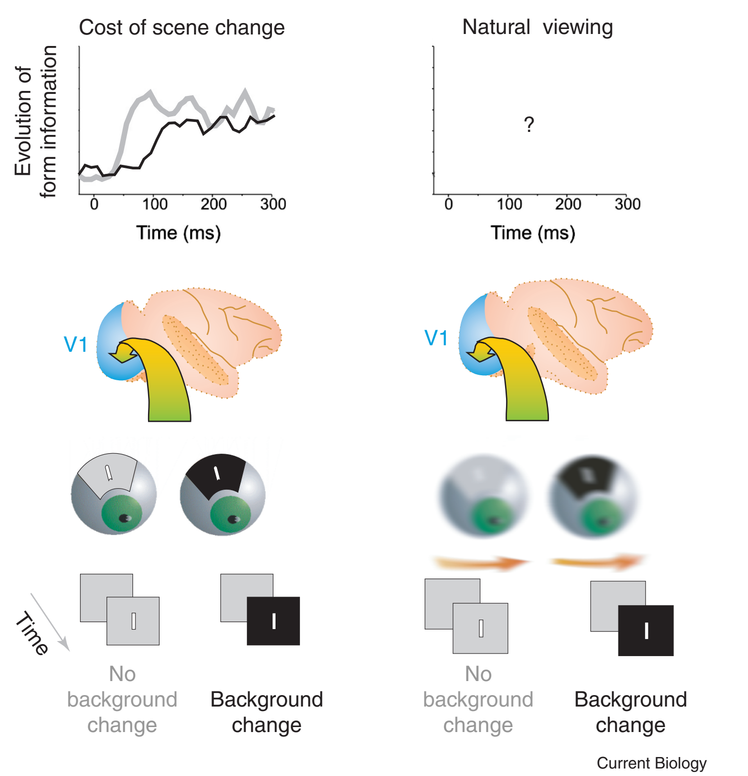

Figure 1. How scene changes affect visual processing of form information.

Huang and Paradiso [7] presented oriented bars inside the receptive field of V1 neurons either in isolation, or simultaneously with a change of the background. They found that form information is significantly delayed when stimulus appearance was coupled to a background change. Such changes are the norm during normal viewing, where eye movements cause regular retinal scene shifts. Do eye movements delay the speed of information processing, or are there mechanisms to overcome such costs? (Curves in the upper left graft reproduced with permission from [7].)

natural conditions, the authors [7] measured neuronal response functions in primary visual cortex of the macaque monkey when stimuli were presented inside a receptive field in isolation, and when such presentation occurred simultaneous with background changes. To keep precise control over visual stimulation the authors still used simple artificial stimuli, where oriented bars or gratings were presented in isolation or when their presentation was accompanied by a background (luminance or structure) change.

Surprisingly, Huang and Paradiso [7] found marked differences in the response properties under these two conditions. Detailed form information was available almost immediately after response onset in V1 neurons when stimuli were presented in isolation, but it was much delayed when a background change occurred simultaneously with the presentation of the stimulus. This delay depended on stimulus contrast, but it could easily reach 60 ms, a substantial time period in light of an average fixation duration of 300 ms between saccades. These neuronal findings suggest that discrimination abilities for simple forms should be reduced during the time period immediately following a scene change. Using carefully designed psychophysical tests the authors demonstrated that human form (orientation) perception was indeed temporarily disturbed if the appearance of a target stimulus in the centre of gaze was accompanied by simultaneous changes in the background [8].

This is another nice and important illustration that single unit activity recorded from awake macaque monkeys makes powerful and reliable predictions about information processing in the human brain. Huang and Paradiso [7] argue that ‘the changing background paradigm is more similar to natural vision in which saccades bring new stimuli and backgrounds into the field of view’. If true, their findings would show that saccades come with a hefty cost, particularly in situations where fast speed of sight could make the difference between preying or being prey.

Before such conclusions can be drawn, two potentially important differences to vision under natural conditions need to be considered. In order to retain tight control over the stimulus parameters the authors still used artificial laboratory stimuli and the subjects did not make eye movements. Artificial laboratory stimuli and natural stimuli may be processed differently by the visual system. Psychophysical studies have shown that human perceptual abilities are exquisite and extraordinarily fast when extracting information during rapid serial visual presentation of natural scenes, for example photographs of animals in their natural environment [9]. Even more surprisingly, during similar experiments, the detection and classification of objects in novel natural images is possible even in the near absence of attention, while the ability to detect simple forms (such as L versus T) is severely reduced [10]. This suggests that the human visual system has evolved to rapidly extract information from highly variable natural scenes, not to extract information from artificial laboratory stimuli.

The second difference between the work of Huang and colleagues [7,8] and natural vision regards the nature of scene changes. Scene changes brought about by saccades are predictable. We plan to move our eyes, and various mechanisms have evolved to suppress the percept of the world moving as it slips across the retina (saccadic suppression), and guarantee perceptual stability between gaze shifts. It is generally thought that saccadic suppression and perceptual stability are mediated by a recurrent signal (corollary discharge) that reflects the eye movement plan and allows adequate adjustment of sensory processing [11]. Experiments have demonstrated that identical retinal stimulation in the presence and absence of saccades results in substantially different neuronal activity in motion processing areas [12], and saccadic suppression is evident in visual processing stages as early as the lateral geniculate nucleus [13]. This indicates that modulatory signals are available to potentially overcome the upsetting effects of scene change during saccades.

Of particular importance for such adjustments may be neurons in the lateral intraparietal, frontal, and even early visual areas which shift their receptive fields shortly before the occurrence of a saccadic eye movement, causing an internal re-mapping of visual space [14–16]. These neurons signal that a saccade will bring an object into their field of view, even if that object has been removed from sight just before or during the saccade. Such a re-mapping could result in predictive adjustments in early cortical areas that prepare for scene changes, thereby minimizing their negative impact, and maximizing rapid information processing following a saccade. This requires a substantial amount of trans-saccadic integration. Supporters of trans-saccadic integration argue that information from successive fixations is stored in memory by taking shifts in eye position, represented in the corollary discharge, into account [17]. Others have argued that there is no need for trans-saccadic information transfer, as the brain has the capacity to rapidly process the whole visual scene anew at each successive fixation [18].

If trans-saccadic integration were substantial, a retinal scene change under natural viewing conditions would very likely have different consequences from those described by Huang and colleagues [7,8]. Evidence for trans-saccadic integration as early as V1 comes from elegant experiments by Khayat and colleagues [19,20]. They showed that responses to attended objects are enhanced in monkey area V1 and that retinotopic coordinates of attended objects are updated across saccades, thereby reducing the negative impact of saccades on perception and cognition. The experiments of Khayat *et al*. [19] were performed while objects were presented on a homogenous background, a potentially important difference to the study by Huang and colleagues [7,8]. Would the results reported by Khayat and colleagues [19,20] hold if more natural visual scenes had been used? Or would they find results more similar to those described by Huang and Paradiso [7]? Additional experiments are necessary to reveal the effects of saccadic eye movements under natural viewing conditions. Huang *et al*. [7] say they are currently performing such experiments and it will be exciting to learn what their outcome is.

References

1. Lettvin, J., Maturana, H., McCulloch, W., and Pitts, W. (1959). What the frog's eye tells the frog's brain. Proc IRE *47*, 1940–1950.
2. Robson, J. (1980). Neural images: the physiological basis of spatial vision. pp. 177–214. In *Visual Coding and Adaptability.* C. Harris, ed. Lawrence Erlbaum Associates: Hillsdale, NJ.
3. Ringach, D.L., Hawken, M.J., and Shapley, R. (2002). Receptive field structure of neurons in monkey primary visual cortex revealed by stimulation with natural image sequences. J. Vis. *2*, 12–24.
4. Smyth, D., Willmore, B., Baker, G.E., Thompson, I.D., and Tolhurst, D.J. (2003). The receptive-field organization of simple cells in primary visual cortex of ferrets under natural scene stimulation. J. Neurosci. *23*, 4746–4759.
5. David, S.V., Vinje, W.E., and Gallant, J.L. (2004). Natural stimulus statistics alter the receptive field structure of V1 neurons. J. Neurosci. *24*, 6991–7006.
6. Vinje, W.E., and Gallant, J.L. (2000). Sparse coding and decorrelation in primary visual cortex during natural vision. Science *287*, 1273–1276.
7. Huang, X., and Paradiso, M.A. (2005). Background changes delay information represented in macaque V1 neurons*.* J. Neurophysiol. doi:10.1152/jn.01309.2004.
8. Huang, X., Blau, S., and Paradiso, M.A. (2005). Background changes delay the perceptual availability of form information*.* J. Neurophysiol. doi:10.1152/jn.01312.2004.
9. Thorpe, S., Fize, D., and Marlot, C. (1996). Speed of processing in the human visual system. Nature *381*, 520–522.
10. Li, F.F., VanRullen, R., Koch, C., and Perona, P. (2002). Rapid natural scene categorization in the near absence of attention. Proc. Natl. Acad. Sci. USA *99*, 9596–9601.
11. Sperry, R.W. (1950). Neural basis of the spontaneous optokinetic response produced by visual inversion. J. Comp. Physiol. Psychol. *43*, 482–489.
12. Thiele, A., Henning, P., Kubischik, M., and Hoffmann, K.P. (2002). Neural mechanisms of saccadic suppression. Science *295*, 2460–2462.
13. Sylvester, R., Haynes, J.D., and Rees, G. (2005). Saccades differentially modulate human LGN and V1 responses in the presence and absence of visual stimulation. Curr. Biol. *15*, 37–41.
14. Duhamel, J.-R., Colby, C.L., and Goldberg, M.E. (1992). The updating of the representation of visual space in parietal cortex by intended eye movements. Science *255*, 90–92.
15. Tian, J., Schlag, J., and Schlag-Rey, M. (2000). Testing quasi-visual neurons in the monkey's frontal eye field with the triple-step paradigm. Exp. Brain Res. *130*, 433–440.
16. Nakamura, K., and Colby, C.L. (2002). Updating of the visual representation in monkey striate and extrastriate cortex during saccades. Proc. Natl. Acad. Sci. USA *99*, 4026–4031.
17. Jonides, J., Irwin, D.E., and Yantis, S. (1982). Integrating visual information from successive fixations. Science *215*, 192–194.
18. Bridgeman, B., Van der Hejiden, A.H.C., and Velichkovsky, B.M. (1994). A theory of perceptual stability across saccadic eye movements. Behav. Brain Sci. *17*, 247–292.
19. Khayat, P.S., Spekreijse, H., and Roelfsema, P.R. (2004). Correlates of transsaccadic integration in the primary visual cortex of the monkey. Proc. Natl. Acad. Sci. USA *101*, 12712–12717.
20. Khayat, P.S., Spekreijse, H., and Roelfsema, P.R. (2004). Visual information transfer across eye movements in the monkey. Vision Res. *44*, 2901–2917.

Henry Wellcome Building, University of Newcastle upon Tyne, NE2 4HH, UK.
E-mail: alex.thiele@ncl.ac.uk

DOI: 10.1016/j.cub.2005.10.057

Evolution: Natural Selection in the Evolution of Humans and Chimps

We now have more or less full sequences of both human and chimp genomes, allowing comparison that sheds light on their evolution. A few hundred genes show significant evidence for adaptive evolution in the two lineages, but the actual number might be much higher. Natural selection has eliminated about 75% of amino acid changes in coding sequence since the split of the human and chimpanzee genomes.

Hans Ellegren

The field of molecular evolution was born in the 1950s when it became possible to determine the amino acid sequence of proteins, and to compare these sequences among related species. Subsequent advances in DNA sequencing technology allowed homologous genes to be analyzed at the nucleotide level and, from this, we could start to infer how mutation and selection had contributed to molecular evolution. Today, the availability of full genome sequences and computational methods for comparing them means that the full spectrum of evolutionarily accumulated mutations distinguishing two species can be studied. As reported in a recent paper ([1], see also [2–4]), the human genome has now been lined up against that of our closest living relative, the chimpanzee. A comparison of the two genomes reveals a number of important features, summarized in Table 1.

In addition to the biological and medical interest in the human and chimpanzee genomes, their sequences are important to molecular evolution for several reasons. First, with two species as closely related as these two hominids, their sequences will almost always be sufficiently similar to make alignment of homologous regions unambiguous. Notably, this is true not only for conserved regions, like genes, but also for neutral sequences, as in the intergenic landscape. Second, over such a short evolutionary distance, the incidence of multiple mutational hits at individual sites is negligible, so it is usually straightforward to infer which evolutionary changes have been made since the two genomes split.

What does the chimpanzee genome sequence tell us about the role of natural selection in human evolution? Purifying selection is clearly evidenced by the fact that mutations that alter the amino acid sequence, which in many cases presumably have a deleterious effect, have gone to fixation at a much lower rate than those that do not. Traditionally,