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Vision: Neuronal mechanisms enabling stable perception

David Burr[1] and Maria Concetta Morrone[2]
[1]Department of Neuroscience, Psychology, Pharmacology and Child Health, University of Florence, Firenze, Italy
[2]Department of Translational Research on New Technologies in Medicine and Surgery, University of Pisa, Pisa, Italy
Correspondence: davidcharles.burr@unifi.it (D.B.), concetta.morrone@unipi.it (M.C.M.)
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Eye movements cause rapid motion of the retinal image, potentially confusable with external motion. A recent study shows that neurons in mouse primary visual cortex distinguish self-generated from external motion by combining sensory input with saccade-related signals from the thalamic pulvinar nucleus.

Vision is an active process: animals continuously seek information by purposeful scanning of the environment with eye, head and body movements. The average human typically makes two or three rapid saccadic eye movements per second, but we are mostly unaware of them. Eye movements probably evolved to keep images stable on the retina in the face of head, body and external motion[1], but in humans and other mammals with retinal foveae they are also essential for directing the high-resolution fovea to objects of interest. However, constant repositioning of gaze presents serious challenges to mammalian visual systems, not least the rapid motion of the retinal image as the eyes sweep over the scene, potentially confoundable with real motion of the world. While saccades can be fast (up to 900° per second), the image motion they create is well within the resolution limits of human vision[2]: the same motion dynamics delivered to the stationary eye, during a simulated saccade, elicits a startling and disconcerting sense of movement[3]. To explain why we are not startled and confused by saccade-induced motion, it has long been supposed that the system actively inhibits vision during saccades[4,5] and there is now good evidence in humans and other animals that motion systems, particularly those driven by the magnocellular system, are selectively damped during saccades[3,6–10].

The mechanisms behind these processes has been far from clear. A recent study by Miura and Scanziani[11] sheds new light on the issue by demonstrating that the selectivity of cortical visual neurons depends on whether the motion was caused by saccades or external motion. The authors recorded responses from primary visual cortex (V1) of unrestrained mice moving freely within an arena. The mice made frequent saccades, about 1 per second, with an average peak speed of 700° per second. About half of the recorded neurons responded to the saccades, but some were excited while others were inhibited. More importantly, individual neurons responded selectively to the direction of the saccades (Figure 1C). In separate experiments with immobilised mice, the authors measured responses of the same cells and showed that their direction preference to comparable external visual input, during a simulated saccade, was totally uncorrelated with that produced by saccades (Figure 1B).

The difference in response to real and simulated saccades was governed primarily from non-visual input from the pulvinar. When this non-visual input was silenced, the response to saccades over a patterned surface was very similar to the response to simulated saccades. The modelling by Miura and Scanziani[11] suggested that, during saccades, the responses corresponded to the sum of the retinal visual motion response and the non-visual saccadic-related signal mediated by the pulvinar (Figure 1D). The overall gain controlling the visual component of the response was around 0.6, consistent with a saccade-induced change in response gain as observed in humans[12].

That visual neurons can be either excited or inhibited during saccades is a well accepted finding in primates. Enhancement and suppression have been demonstrated psychophysically[3,6], as well as in neurons in LGN[13], V1[14] and MT[8,15]. The new work of Miura and Scanziani[11], however, shows that both the excitation and inhibition are selective to the direction of the saccade, and that the origin is not only visual, but probably associated with the motor signal planning the saccade. Indeed, both excitation and inhibition start before the onset of the saccade in many neurons.

This new study by Miura and Scanziani[11] in freely moving mice reinforces a fascinating 20-year-old study of Thiele and colleagues[16] on early motion-specific areas MT and MST in monkey (areas that probably subserve similar functions to motion-selective neurons of primary cortex of rodent). They found that 38% of cells inverted their direction selectivity when image motion was produced by real, rather than simulated, saccades. Although their paradigm did not measure correlations between saccade-induced and external-motion direction preferences, the collective direction selectivity of their neuronal population was constant across directions, so the population coding during saccades approximated no net motion, potentially the signal for a stable world. But the finding of Miura and Scanziani[11] of selectivity of visual neurons to saccade direction, uncorrelated to the selectivity to motion direction, could in principle provide a richer source of information to distinguish real from saccade-induced motion in the population code, more robust than simply annulling the retinal motion, as has been suggested[4,16]. It would be interesting to unravel the details of this mechanism, and see if the effect also emerges early in primates (possibly in V1), as human studies suggest[6,17].

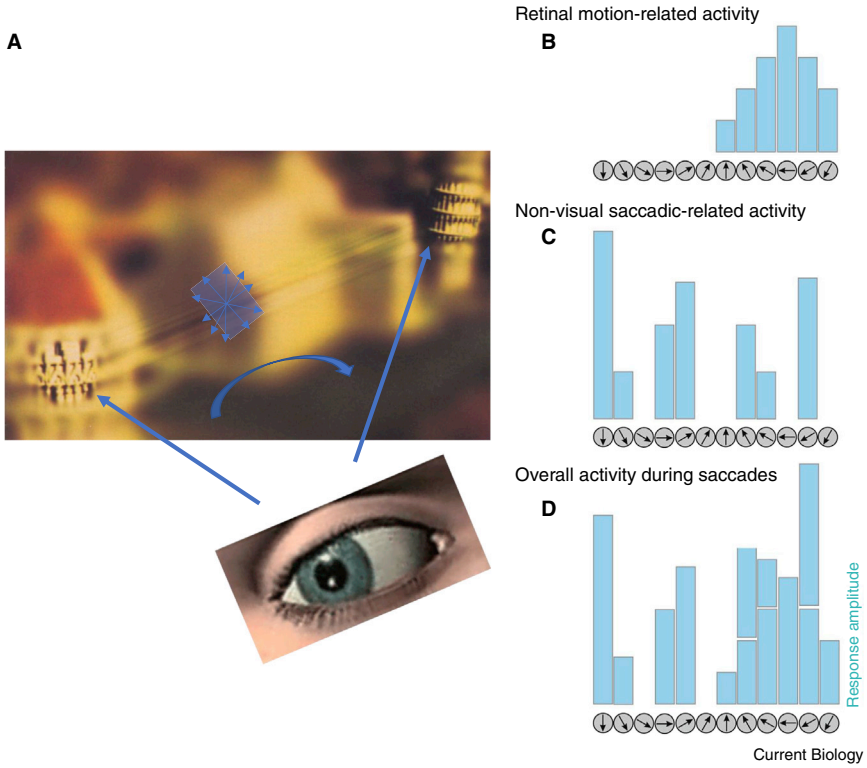

Figure 1. Integration of visual and non-visual inputs during saccades alters direction preferences of neurons in mouse visual cortex (V1).
(A) A saccade across a visual scene causes rapid image motion which will excite neurons whose receptive fields have appropriate direction selectivity. (B) The response of a sample of 12 V1 mouse neurons to leftward external motion (nasal pseudo-saccade). The response is best for the neuron tuned to leftward horizontal motion (indicated by the arrows under each response bar), and tapers off as the preferred direction moves away from horizontal. The population coding of the direction of this response is clearly 'leftward'. (C) Response of the same neurons to a real nasal saccade over an untextured background. Neurons respond selectively to the direction of the saccade, but the selectivity is completely different from that to the external motion of the pseudo-saccade. (D) Theoretical response of the same 12 neurons to a real saccade over a grating background, generating both a visual and a non-visual response (illustrated as their sum). The population code is now clearly distinguishable from that representing pure leftward motion. Other measurements showed that this predicted response is in fact very close to the measured response to saccades over a textured background. Image used with permission from Miura and Scanziani[11] (CC BY 4.0).

The dynamics of the saccade-induced responses of free-moving mice observed by Miura and Scanziani[11] was interesting. Responses started early, often preceding the saccade, and continued strongly for 200 ms or so (compared with less than 100 ms for visually driven responses). Why should the response be so prolonged? The early response is clearly desirable, so the visually driven motion response does not dominate to give an erroneous motion signal. But the extended response, past 200 ms? This may serve a different function, sensitizing neurons once the saccade has finished and the new fixation begun. Post-saccadic enhancement has been observed in humans[6,18], as well as along all the visual pathways in non-human primates[8,9,14]. This effect may be functionally important in allowing a quick recovery from suppression, as has been reported for human perception[7,8] .

The brain must distinguish real motion not only from saccade-induced motion, but also from motion induced by head and body movements. One of the major innovations of Miura and Scanziani[11] was to measure neural responses in free-moving mice, free to run and to rotate their heads through three degrees of freedom. All these movements will cause image motion on the retinae which, in principle, can be confounded with external image motion. The measurements distinguishing external from saccade-induced motion were all made with the head fixed, however, so it is unclear whether image motion induced by head and body motions is also discounted. That selectivity to saccade direction did not change between the free-moving and head-fixed conditions suggests that head and body movements did not significantly impact cell selectivity; but it would be nice to confirm this directly. Old evidence in humans shows that image motion resulting from self-motion does not create a strong motion aftereffect[19], suggesting that self-generated image motion is distinguishable from external motion to the nervous system. Perhaps technological advances will permit future studies to test how all self-motion signals are analysed in freely moving animals.

The new work of Miura and Scanziani[11] goes a long way towards providing a neural mechanism for how external motion (and motion created by body and head movements) can be distinguished from saccade-induced motion. They also give us a new hypothesis to be tested on the mechanisms that stabilize vision: net neuronal activity signalling balanced motion in all directions, controlled by the action of pre-motor signals mediated by the pulvinar. All these interesting facts and ideas need to be corroborated by studies in primates, keeping in mind that this is only one of the challenges introduced by saccades. Saccades are an intrinsic part of the perceptual process, serving to actively explore the environment for objects of interest and survival importance. The hard-wired mapping from retina to early visual cortex ensures an accurate cortical representation of the retinal image; but as that retinotopic image changes with each saccade, it is a long road from this early retinotopic cortical map to a stable and veridical representation of the external world.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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Phylogenomics: Is less more when using large-scale datasets?

Davide Pisani[1,2,*], Maria Eleonora Rossi[2], Ferdinand Marlétaz[3], and Roberto Feuda[4]
[1]Palaeobiology Research Group, School of Biological Sciences, University of Bristol, Bristol, UK
[2]Palaeobiology Research Group, School of Earth Sciences, University of Bristol, Bristol, UK
[3]Centre for Life's Origin & Evolution, Department of Genetics, Evolution & Environment, University College London, London, UK
[4]Department of Genetics and Genome Biology, University of Leicester, Leicester, UK
*Correspondence: Davide.pisani@bristol.ac.uk
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Phylogenetic studies have traditionally placed the simple Xenoacoelomorph worms as the sister group of all other animals with bilateral body symmetry. A new study shows that misidentification of orthologous genes might have been the source of at least some support for this placement.

Resolving evolutionary (i.e. phylogenetic) relationships among species or more inclusive taxa such as families and phyla is notoriously difficult. It has thus become common for phylogenetic studies to use datasets consisting of hundreds, sometimes thousands, of genes sampled from complete genomes[1–4]. This approach is rooted in a series of seminal papers that first attempted to "concatenate" (join) individual gene alignments, which are usually not very informative because they include few sites, into a single "supermatrix" to increase signal and reduce the effect of stochastic errors[5,6]. Early supermatrices including tens of genes[7] were considered large, but the datasets available to modern phylogenetic studies have swollen enormously[4]. In the early days of molecular phylogenetics, scientists struggled to sequence the genes to include in their datasets. Today, the trend is for genomic data to be generated by large scale initiatives such as the Darwin Tree of Life[8], and phylogeneticists mostly engage instead in the development of computational pipelines to subsample the data and identify the genes that are most appropriate to attempt to accurately resolve specific phylogenetic problems. While it would be tempting to assume that the rule of thumb should be that supermatrices should include as many genes as possible, maybe even all the genes in the genomes of the species under study, this is both unrealistic and problematic. It is unrealistic because the analysis of massive datasets continues to be extremely time consuming[4] and has a large, associated carbon footprint. It is problematic because, when assembling increasingly large datasets, more genes with complex evolutionary histories (i.e. genes that underwent many duplications and deletions) will tend to be included in the supermatrix. For such genes, it can be impossible to distinguish orthologs (genes separated by speciation) from paralogs (genes separated by duplication), and this can potentially lead to the inference of incorrect phylogenies (Figure 1). In a recent paper in *Current Biology*, Mulhair, McCarthy and colleagues[9] address the problem of filtering collections of single gene alignments to reduce the potential negative effect of 'hidden paralogy', that is