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Active Vision: Dynamic Reformatting of Visual Information by the Saccade-Drift Cycle

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Visual processing depends on rapid parsing of global features followed by analysis of fine detail. A new study suggests that this transformation is enabled by a cycle of saccades and fixational drifts, which reformat visual input to match the spatiotemporal sensitivity of fast and slow neuronal pathways.

The first neuronal recordings in awake behaving monkeys performing eye movements were conducted more than 50 years ago, but most of what is known about the neural encoding in the early visual system in primates comes from experiments in anaesthetized or steadily fixating monkeys. However, it has been extensively documented that eye movements exert a strong influence on perception in humans [1]. Recently, the work of Rucci, Victor and colleagues [2,3] has demonstrated that smaller and slower eye movements occurring during fixation also affect visual processing, facilitating the perception of fine spatial features. Now a new study from the Rucci group reported in this issue of *Current Biology* [4] shows that both saccades and slower fixational drifts reshape the spectral content of natural visual input to match the spatiotemporal profiles of fast magnocellular and slow parvocellular pathways. This dynamic reformatting could underlie a system of coarse-to-fine analysis of visual scenes, which has been proposed as an efficient means of image coding, often ascribed to the dynamic tuning properties of thalamic and cortical neurons in the magnocellular and parvocellular channels [5,6].

The notion that vision performs a progressive coarse-to-fine scene analysis — analysing progressively low to high spatial frequencies — goes back to the work of David Marr, and has been frequently revived, with empirical support [7,8]. The study of Boi *et al.* [4] gives a new perspective on these theories, providing a plausible mechanism whereby normal oculomotor behaviour could underlie the cause of the temporal ordering of the analysis by fast magnocellular and slow parvocellular neurons, which respond preferentially to post-saccadic transients or in a sustained manner during drifts [9].

In contrast to previous work on coarse-to-fine perception of abruptly presented images during fixation, Boi *et al.* [4] recorded the eye movements of subjects freely exploring natural scenes in unconstrained conditions, and showed how these should, in theory, affect visual processing. They reported, as many others have noted, that the eyes are never still, but follow the well-known pattern of fast, ballistic

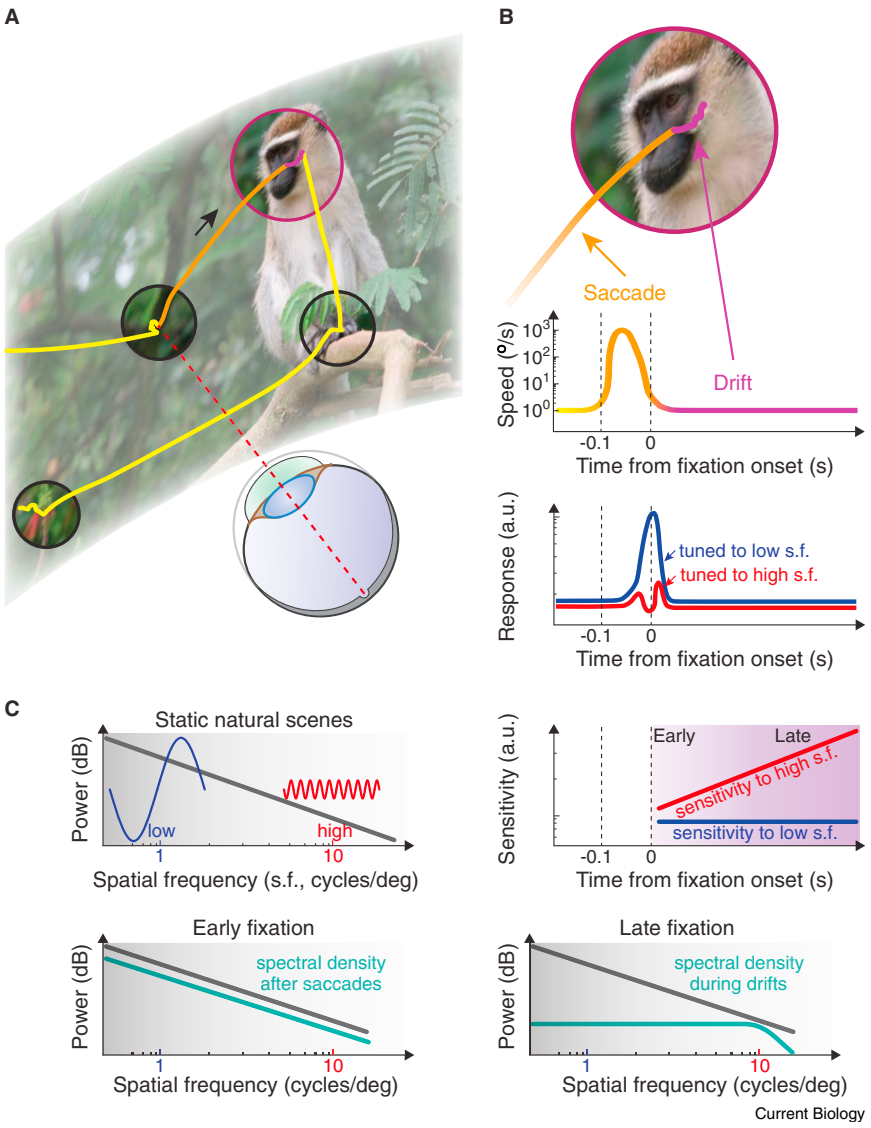

Figure 1. Saccades and slow fixational drifts enable coarse-to-fine analysis of visual scenes.
(A) Eye position trace during fast saccades and slower drifts in periods of fixation (circles) during free viewing. (B) A one saccade (orange)–fixational drift (magenta) sequence. Top plot: retinal image speed as function of time; bottom plot: simulated firing rate of neurons tuned to low (blue curve) and high (red curve) spatial frequency in response to spatiotemporal luminance modulations imposed by eye movements. (C) Top left: ideal $1/f^2$ (f – spatial frequency) power spectrum of static natural scenes, dominated by low frequencies. Top right: dynamics of post-saccadic contrast sensitivity to low (blue curve) and high (red curve) spatial frequency gratings embedded in noise. This pattern of contrast sensitivity results from a domination of the spectral power by low spatial frequencies immediately after saccades, across all non-zero temporal frequencies (early fixation, bottom left), and a subsequent redistribution of power across a broad range of spatial frequencies by ensuing drifts, which counterbalance the $1/f^2$ spectrum of natural scenes, enhancing high spatial frequencies (late fixation, bottom right).

saccades at very fast speeds, interspersed with slow, seemingly random drifts of about 1°/s. Using the same time-varying inputs as experienced by free-viewing subjects, they simulated the response of two realistic classes of cortical simple cells, one tuned to low spatial frequencies (1 cycle/°), the other to high spatial frequencies (10 cycles/°), both temporally selective to frequencies around 10 Hz. Given the temporal tuning, neither population responded well to stationary stimuli; however, both saccades and slow drifts generate a temporal modulation of the images, which increases the simulated responses (Figure 1). The saccades modulate the image rapidly, and this favours the response to low spatial frequencies: as the temporal frequency of modulation is the product of speed and spatial frequency, the temporal modulation caused by saccades is preferred by cells with lower spatial tuning.

Thus, saccades cause a stronger response in the population selective for low spatial frequencies, with a peak towards the end of the saccade, at the onset of the fixation period. During the period of drift, however, the simulated responses of both cell classes were lower but similar, even though the presented images had 100 times more power in the low than in the high spatial frequencies, following the typical natural scenes spectral power distribution. This spatial frequency content is redistributed by temporal modulations due to the two types of eye movements in a distinct manner: saccades preserve the prevalence of low spatial frequencies, while drifts counterbalance this prevalence, thereby enhancing high spatial frequencies. The pattern of preferred sensitivities — to low spatial frequencies immediately after the saccade followed by a relative boost of high spatial frequencies — is consistent with the notion of coarse-to-fine analysis. Indeed, the simulations of post-saccadic time course of contrast sensitivity during 'detection' of noisy stimuli predicted that the detection of low spatial frequency is facilitated only immediately after the saccade, while that of high spatial frequency improves gradually during fixation.

Boi *et al.* [4] next tested the idea psychophysically, and found empirical validation for the major predictions: similar to the model, sensitivity to low spatial frequencies did not improve throughout fixation, while that to high spatial frequencies did, resulting in a relative shift in the weighting of sensitivity to the two frequencies. It has long been known that high frequency stationary stimuli benefit more from temporal summation than do low frequencies [10], but the present study provides the mechanism for the enhanced summation. Indeed, when Boi *et al.* [4]. eliminated the slow drifts by retinal image

stabilization, the benefit of prolonged summation during fixation was far less. Conversely, the removal of post-saccadic transients decreased sensitivity to low but not to high spatial frequencies, demonstrating the importance of saccades for the perception of coarse features.

Most research into vision at the time of eye movements regards saccades as a difficult problem for visual system to solve [1]. But Rucci's approach has been to ask how vision can benefit from these movements. He and his team have previously shown how slow drifts can benefit sensitivity to high spatial frequencies [2,3,11], and now suggest that the saccades themselves can also be advantageous, by structuring the temporal ordering of analysis, so coarse information is analysed first, providing a 'scaffolding' for subsequent filling in with finer details.

Perhaps the most exciting suggestion of this new paper [4] is that eye movements — both fast and slow — serve to actively *reformat* the visual image, converting spatial information to temporal modulations on the retina. This concept of encoding space through time has been around for a long time [12], and re-emerges periodically [13–16]. Several demonstrations show that when objects are in motion, temporal signals can be used to provide information about space [13,15]: in effect, motion converts time to space. Some forty years ago, Horace Barlow wrote a provocative opinion piece suggesting that spatiotemporal interpolation could be fundamental for increasing spatial resolution past the photoreceptor sampling limit (see discussion in [13]). Rucci's group takes this idea a step further in showing that the image motion does not need to be caused by an external object — instead the eyes themselves may generate the motion necessary to convert space to time. And having two types of motion allows this to occur selectively for coarse and fine scales, implementing a hierarchical scheme of visual analysis. These results also suggest that distinct spatiotemporal characteristics of magno- and parvocellular neurons and the oculomotor behaviour evolved together to match the spectral content of the visual flow to the retina during natural viewing.

The study by Boi *et al.* [4] raises several intriguing questions. The first obvious question is how this study can be reconciled with evidence showing that saccades cause strong suppression of visual signals, particularly of low spatial frequencies ostensibly selective for the magnocellular system [1,17]. Although seemingly contradictory, there are several important differences between the two studies. Firstly, saccadic suppression is maximal at the beginning of the saccade, and an enhancement has often been reported after the saccade is concluded [1,9,17,18], in agreement with Boi *et al.*'s [4] findings showing maximal visual enhancement at fixation onset. Secondly, maximum suppression was observed at very low spatial frequencies, lower than 0.1 cycle/°, with little suppression at the moderate frequency of 1 cycle/° [1]. Thirdly, most work on saccadic suppression has been done with very large saccades (over 20°, whereas this study used small 7° saccades). And finally, there is evidence suggesting that it is specifically the motion signals that are suppressed during saccades [17], rather than the spatial information *per se*.

It is reasonable to suppose that saccades generate many processes, including both an enhancement of mid-range spatial frequencies and a suppression of motion driven by the very low spatial frequencies. Nevertheless, to distinguish between the physical, visual consequences of eye movements and centrally driven suppression due to extraretinal/efference copy signals [9], Rucci and colleagues should conduct similar measurements with 'simulated saccades', where the image is moved artificially at comparable speeds and durations [18]. Any differences observed between the real and simulated saccades could be put down to active suppression mechanisms. Similarly, it would be interesting to relate Boi *et al.*'s [4] novel take on the role of eye movements to the more classic work showing active processes accompanying saccades, such as compression and remapping [1].

Finally, it is important to ask to what extent is the reformatting of visual input goal-directed, and how adaptive is oculomotor behaviour for the purposes of task requirements or image statistics of a scene? Is any of the process under voluntary control? It has been shown, also by Rucci and colleagues, that even the smallest fixational microsaccades can be accurately directed to the most sensitive part of the fovea to view the minute detail of interest [19]. Can slow drifts be also controlled precisely and adapted to the current requirements? There is considerable evidence for control of drifts [20], but the neural mechanisms for such control are still unknown.

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Plant Defense: Timing Is Everything

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How do plants use scent to attract pollinators while preventing herbivory? New research reveals the genetic basis by which tobacco plants control the temporal emission of volatile attractants from flowers and leaves, enabling attraction of the predators of pests during the day and pollinators at night.

Flowering plants are under incredible selective pressure from a variety of biological sources; they must maximize their reproductive fitness while often encountering intense selective pressure through herbivory. Charles Darwin famously referred to the origin of flowering plants as an 'abominable mystery' in his correspondence with Joseph Hooker in 1879 [1]. Although often credited with this idea, Darwin built upon ideas of Gaston de Saporta, a paleobotanist, who believed that the diversification and species richness of flowering plants was due to their relationship with insects [2]. Today, we have increased understanding of how pollinating insects shape the evolution of flower and plant traits [3,4], but how response to herbivory shapes these traits remains comparatively understudied. A fascinating new study on how herbivory modifies emission of leaf and flower volatiles in *Nicotiana attenuata*, published in this issue of *Current Biology* [5], demonstrates that plants have a remarkable ability to reduce potential conflict between plant defense and pollination, and suggests that Darwin's abominable mystery may also reflect the interplay between these two processes.

Plants have evolved a suite of traits in their secondary defenses to modify insect pest behavior, as well as to attract predators of the pests. One of those traits is herbivory-induced volatile production, where damage from pests induces changes in the plant's volatile emissions that causes effects across trophic levels, including signaling from the damaged plant to its neighbors, attraction of predatory insects that feed on the pests, and reduction in the behavioral attraction to the plant by the pests themselves [6,7]. Nonetheless, the induced volatiles may have a direct impact on plant fitness — for instance, in the case where the predator presence might not only mean a threat for herbivores but also for pollinators, or where the induced volatiles are aversive to the pollinators. Plant responses might thus directly conflict with pollinator attraction.

The complex interplay of forces operating on herbivory- and pollination-related plant traits is especially apparent when an insect is not only the dominant pollinator of the plant, but also the dominant pest. Such is the case for the interaction between *Manduca* spp. moths and the tobacco plant, *Nicotiana attenuata* (Figure 1A). In the semi-arid environment of the Southwest USA, *N. attenuata* relies on adult *Manduca* moths for pollination (Figure 1B), but female moths also oviposit on the plant and, once hatched, a single *Manduca* larva has the ability to consume an entire plant (Figure 1C). Previous studies have shown that larval damage to *N. attenuata* induces emission of volatiles that attract carnivorous insects [8], but how the plant responds to the conflict between herbivory while maintaining pollination services by adult *Manduca* was unclear.

To explore the bases of this conflict, Zhou *et al.* [5] studied the temporal emission of herbivory-induced volatiles between leaves and flowers — in particular, focusing on the sesquiterpene (*E*)-α-bergamotene, an induced volatile that was previously shown to attract carnivorous insects [8]. When subject to herbivory, (*E*)-α-bergamotene is produced at much higher levels from the leaves. Remarkably, (*E*)-α-bergamotene is produced at two peaks during the day — the first in the morning and the second later in the afternoon. These two peaks match the activity levels of carnivorous insects (*Geocoris* spp.). The daytime (*E*)-α-bergamotene emissions from leaves are the opposite of those from flowers, which has a peak at night when *Manduca* adults are present, suggesting that circadian control of tissue-specific volatile pathways might be one mechanism to control pest abundances