comprehensively-sampled phylogenetic analyses will permit new insight on the evolution of major patterns of biological diversity.

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DOI: 10.1016/j.cub.2010.03.032

Vision: Keeping the World Still When the Eyes Move

A long-standing problem for visual science is how the world remains so apparently stable in the face of continual rapid eye movements. New experimental evidence, and computational models are helping to solve this mystery.

David C. Burr[1,2] and Maria Concetta Morrone[3,4]

In a recent issue of *Current Biology*, De Pisapia, Kaunitz and Melcher [1] report a new study investigating how the world remains stable in the face of the continual rapid movements of the eyes, called saccades. Visual stability is an old and venerable problem, which has fascinated many scientists, including Descartes, Helmholtz, Mach and Sherrington. Indeed it goes back to the 11th century Persian scholar Abū ibn al-Hasan ibn al-Haytham (Latinized "Alhazen"), who, like many to follow him, put the stability down to the visual system adapting itself to the situation: "sight has become accustomed to the motion of the objects' forms on its surface when the objects are stationary, and therefore does not judge the objects to be in motion" [2]. MacKay [3] took this idea a step further, proposing that saccades form an essential part of active vision, just as exploring a surface with hand-movements is for the haptic system. Saccades, he claimed, "are perceptual questions posed by the visual system", questions like "what is that red blob over there?" The saccade brings the high-resolution fovea to bear on the object of interest, to answer the question. As the system has asked this question, it will not be surprised by the answer, provided it is roughly consistent with expectations. MacKay's idea was innovative and clearly ahead of its time, viewing eye movements as an integral part of active perception rather than an awkward consequence of a motor action. But there remains the non-trivial issue of what neural mechanisms distinguish image motion caused by movement of the eye from that caused by object-motion, and how these permit the seamless transition from one fixation to the next.

Recent research has shown that saccadic eye-movements have many transient but profound perceptual and neurophysiological ramifications. Low-frequency, fast-moving stimuli are hard to see at the time of saccades [4], possibly reflecting suppression of neurons in the superior colliculus which respond well to these types of stimulus (see [5]). This suppression could subdue the sense of motion elicited by the eye sweeping rapidly over the scene. But far more bizarre things happen than a simple reduction of sensitivity. Stimuli briefly displayed just before a saccade are grossly mislocalized, by up to 10° for a 20° saccade. The mislocalization tends to be towards the saccadic target [6], resulting in a compression of space. More recent results show that stimuli are also mislocalized in time, delayed and compressed as they are in space [7,8].

The new study of De Pisapia *et al.* [1] shows that making saccadic eye movements can actually enhance (rather than degrade) the visibility of a brief peri-saccadic stimulus. They presented a brief visual target, followed at various intervals by a surrounding annulus 'mask', which impedes recognition of the test by 'backward masking'. The most interesting condition was when test and mask were separated by a brief (12 ms) interval, both presented to stationary eyes, at the same retinal position. When presented 20–30 ms before saccadic onset, visibility of the test improved considerably, particularly for trials where it was perceived as displaced. The results imply that the peri-saccadic displacement of the test shifts it away from the mask, effectively *demasking* it. In another condition, they used a long test-mask separation with the test and mask straddling the saccade, therefore stimulating distinctly different retinal positions: yet the masking was strong, suggesting that the representation had been transferred

to a spatiotopically corresponding position.

The study [1] is important in that it shows that the perceived displacements of brief peri-saccadic targets are not merely perceptual epiphenomena, but very real in that they affect visual discrimination, improving performance in the demasking condition. Masking is a well studied perceptual phenomenon, thought to result from integration of the test with the more salient mask, which modulates sensitivity to raise discrimination thresholds. So what neural mechanisms allow a test and mask that excite distant retinal locations to be integrated in one case, and to reduce the integration of test and mask in the same retinal locations in another? In a landmark paper, Duhamel *et al.* [9] reported that receptive fields of many neurons in the lateral intraparaietal area (LIP) change drastically at the time of saccades, shifting in the direction of the saccade, before the eyes have moved. If the monkey were observing Pisa's famous *Piazza dei Miracoli* (Figure 1A), fixating point F1 above the bell tower, a particular LIP neuron could have a receptive field encompassing the tower. The odd thing about these cells is that, just before the monkey makes a saccade to F2, the receptive field of the cell shifts in the direction of the saccade, falling on the baptistery. Anticipatory shifts have been observed in receptive fields of cells of many visual areas, including superior colliculus, frontal eye fields, area V3 and even, to a lesser extent, in V1 (see [5]). This behaviour seems to be driven by a *corollary discharge* signal, originating in the superior colliculus and projecting to the frontal eye fields via the dorsal nucleus of the thalamus [5].

How exactly might the behaviour of these cells explain De Pisapia *et al.*'s [1] results? And how can a shift in the *same* direction as the saccade compensate for the motion induced by the saccade, aiding stability (a compensation should be in the other direction)? To fully understand the shifting receptive fields, it is necessary to consider the temporal dynamics of the response. Figure 1B is a cartoon drawn from data of Wang *et al.* [10], showing the response of an LIP neuron to stimulation to the 'future receptive field' before, during and after the saccade. The responses are aligned to the saccade, and sorted by stimulus presentation time. The first spikes to all stimuli occur at about the same time, implying that pre- and post-saccadic stimulation to this part of space (corresponding to different retinal positions) cause spike trains that are effectively identical. A higher-order cell (or a neurophysiologist) monitoring the response has no way of distinguishing whether a particular spike results from early pre-saccadic stimulation to the future receptive field or later post-saccadic stimulation of the classic receptive field. By definition, the region in space-time that elicits identical responses defines the receptive field of the cell, in space and in time.

The receptive field at the time of the saccade of this hypothetical LIP cell is illustrated schematically in Figure 1C in retinal (not allocentric) coordinates. It is oriented in space-time, in the direction *opposite* to the saccade motion, therefore aligned to the retinal motion caused by the saccade. In effect, it is tuned to the saccade-induced motion, and therefore effectively cancels it (a similar argument has previously been developed for the mechanisms involved in the perception of spatial form of moving objects [11,12]). The purple symbols illustrate the test and mask presentations in De Pisapia *et al.*'s [1] study. When the time between presentations is long, and the stimuli have straddled the saccade, they excite different regions of retinal space. As the receptive field is oriented, however, both stimuli fall upon it and are therefore integrated, reducing detectability of the test. In the other situation, however, the slant of the receptive field means that it is less excited by the mask than it would have been if it were not oriented, so detection of the test is less impaired.

Interestingly, the spatio-temporal behaviour of the LIP neurons described by Wang *et al.* [10] closely resembles the psychophysical results for perception of transient stimuli around the time of saccades, well simulated by receptive fields similar to Figure 1C [8]. Stimuli presented just before and during the saccade are delayed relative to those presented later, similar to the neural discharges of LIP cells. The result is that stimuli presented over a wide range of times are localised in time to appear just after the saccade,

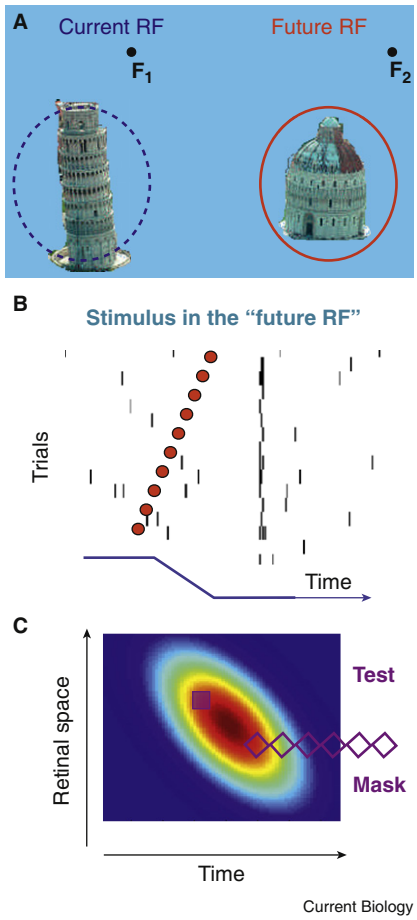

Figure 1. Shifting receptive fields in monkey lateral intraparietal cortical area.

(A) Illustration of the concept of anticipatory shifts in receptive fields. The monkey initially fixates F1 and saccades to F2. The receptive field shifts to the baptistery (future receptive field) before the eyes move. (B) Cartoon drawn from data of Wang *et al.* [10] showing responses of a typical LIP cell to stimulation in the 'future receptive field' (which becomes the classical receptive field after the eye movement). The responses are all aligned to the saccade, and sorted by stimulus presentation time. The dynamics of the response cause the responses to occur at the same time, so they are therefore indistinguishable. (C) Schematic spatiotemporal receptive field of the neuron, defining the region of confusion in space-time with the same spiking pattern. As the eye-movement changes the retinal position stimulated at the extreme position of the 'future receptive field', this spatio-temporal receptive field is oriented in space-time along the same direction as the retinal motion, and thereby annuls it. The purple rectangles depict the test and mask in De Pisapia *et al.*'s [1] study, in the condition where they straddle the saccade. Although they fall on different retinal locations, they stimulate the same receptive field, and are therefore integrated.

just as stimuli presented at different times to the 'future' receptive field of LIP cells all cause spike trains that

arrive at a similar time, after the saccade has been completed.

To conclude, we agree that eye movements should be thought of as an essential part of active vision, a form of 'interrogation' [3], not merely a nuisance by-product of motor acts. But it is also clear that there must exist neural mechanisms to amalgamate these movements with perceptual processes. Tantalizing progress of how this occurs has been made over the past few years, identifying many transient changes in spatio-temporal tuning that create a local and very rapid spatiotopicity. Exactly how this transient spatiotopicity interacts with other spatiotopic mechanisms to provide stability will be one of the main challenges for future research.

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DOI: 10.1016/j.cub.2010.03.033

Sperm Competition: Discrimination Isn't Always Bad

Observing sperm in competition has been limited by our ability to discriminate between males' sperm. Recent work has overcome this obstacle, while another study reports on seminal fluid with very specific spermicidal activity, suggesting discrimination is easy for some.

Kensuke Okada and David J. Hosken*

It was Geoff Parker who first realised that competition between males did not cease at mating [1] and while it took some years for the rest of us to appreciate the depth of Parker's insights, there is now widespread awareness of the importance of sperm competition, and of post-copulatory sexual selection in general. Sperm competition selects on many traits, including primary sexual characters previously viewed as being unaffected by sexual selection, and the most thoroughly studied of these is testis size. Testis size variation has been investigated across and within species, and almost without exception, the higher the risk of sperm competition, the greater the investment in testes [2,3], much as Parker predicted. As phenotypic responses to selection through sperm competition have become clearer, investigations of post-copulatory male–male competition have increasingly focussed on mechanisms, and this is where two recent papers make their impact [4,5].

Inferring mechanism often involved employing mathematical models to test potential explanations for patterns of paternity-sharing, and Parker's pet insect, the yellow dung fly, has been particularly well studied using this approach. In yellow dung flies, males mating last typically have a fertilization advantage, but this advantage can be eliminated by forcing males to stop copulating before they otherwise would [6]. This, and other evidence, suggested males were displacing rival sperm from storage with their own ejaculates, a notion supported by models [7]. Two investigations that attempted to observe sperm movement within females largely confirmed this, but also corrected some erroneous detail of precisely how displacement occurred [8,9]. These two studies were important because they showed that observation of ejaculates within females is the best way to understand sperm competition mechanisms, but both were very low-tech, which limited the inferences that could be drawn from them.

Studies of another sperm competition model, *Drosophila melanogaster*, had also directly observed sperm within females, but because of the genetic tools available for *Drosophila*, they could employ transgenic males that produced sperm with fluorescent tails [10,11]. Using labelled sperm greatly increased our ability to observe interactions between rival ejaculates inside the female, and while these studies seemed to confirm previous inferences about sperm competition mechanisms in these flies, direct assessment of sperm behaviour, number and position within females was very difficult because the tagged sperm-tails fluoresced so much. Additionally, transgenic males often produced far fewer sperm than non-transgenic males, which compromised their utility. As a result, many questions remained unanswered, such as how many sperm were stored and where, and do the different female sperm-stores have different functions? Partly as a result of these ambiguities, debate continued over the precise mechanisms involved in generating the second male fertilization advantage observed in *D. melanogaster*.

Now, work by the Pitnick lab [4] using more specific labelling of sperm, has finally clarified precisely what occurs inside female *D. melanogaster* when they mate with two males [4].