Eye Movements: Illusions in Slow Motion

A recent study has shown that a range of different motion illusions occurring during smooth pursuit eye movements can be explained as optimal percepts based on a simple model derived from the Bayesian statistical framework.

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Illusions occur in all domains of the perceptual system. These include pictorial illusions, illumination illusions, or motion illusions. Intuitively, such illusions are considered a failure of the perceptual system. A closer look, however, often reveals the opposite: using the Bayesian statistical framework it has been demonstrated several times that such illusions can actually be viewed as instances of optimal perceptual performance [1–4]. To appreciate this, we have to understand that human perception can be well described as a probabilistic process. This is because noisy and often ambiguous sensory information builds the basis for the inference of the percept. To constrain the range of possible interpretations of the noisy sensory information, the brain may use prior knowledge about the statistical regularities of the environment. The Bayesian statistical framework provides a principled method for optimally combining prior knowledge with noisy sensory evidence as encoded in the likelihood function. The result of this combination is the most reliable and accurate estimate of the underlying environmental property. Maximizing reliability and accuracy seems a desirable goal for many perceptual-motor tasks. Illusions explained by this framework may therefore be considered manifestations of optimal perceptual performance.

In 2002, Weiss et al. [1] used this Bayesian framework to explain a class of motion illusions that occur during fixation when the eyes are still. One example of such a motion illusion is that low contrast stimuli are perceived to be moving more slowly than high contrast stimuli, even when the velocities are actually the same. Weiss et al. [1] suggested that these illusions could be explained by a prior for slow motion centered at zero velocity: such a prior is a reasonable assumption because, in statistical terms, objects tend to be stationary or to move only slowly. When such a slow-motion prior is combined with sensory evidence, the prior information receives increasingly more weight the less reliable the sensory evidence becomes. Low contrast stimuli provide less reliable motion signals compared to high contrast stimuli, so in combination with the slow-motion prior, low contrast stimuli are perceived to have a lower velocity. As Weiss et al. [1] showed, such a prior quantitatively predicts these kind of motion illusions. Using empirical methods Stocker and Simoncelli [5] have inferred the shape of this prior, thereby confirming the slow-motion assumptions made by Weiss et al. [1].

In a paper in this issue of *Current Biology*, Freeman et al. [6] extend this framework to active perception and a class of motion illusions occurring during smooth pursuit eye movements. Among those illusions are the Filehne Illusion [7], in which a stationary background object appears to move, and the Aubert-Fleischl Phenomenon [8,9], where pursuit stimuli appear to be slower. Compared to the eye static illusions considered by Weiss et al. [1], the situation here is complicated by the existence of eye movements. Thus, in addition to the retinal motion information, there is a non-zero eye movement signal. The question therefore arises how these signals are combined with the prior for slow motion. To account for the illusions, Freeman et al. [6] convincingly demonstrate that the slow-motion prior is first integrated with an estimate of pursuit target motion and an estimate of relative motion, before those are summed into the final motion percept (Figure 1). The illusions arise because both estimates can be differently reliable, so that the prior has a differential influence on these estimates before they are summed. The alternative, that the estimates are first summed and integrated with the prior only later, cannot account for the illusions, because such a model would not allow the estimates to be weighted differentially.

The paper by Freeman et al. [6] makes several significant contributions. Foremost, it provides a common Bayesian framework to understand a whole class of motion illusions occurring during smooth pursuit eye movements. Previously, different, seemingly ad hoc accounts, which most often assumed biased perceptual estimates, were necessary to explain these illusions. The common framework presented by Freeman et al. [6] should thus help to significantly simplify the literature. More importantly, however, this framework should enable us to predict further perceptual phenomena of active motion perception. For example, it will be interesting to see whether this account can explain motion illusions in other domains of active perception as well, such as illusions during head movements or locomotion. For example, it is known that retinal motion is perceived to be slower during walking as compared to standing still, a phenomenon that Durgin et al. [10] called ‘subtraction’. Also in the haptic (touch) domain, kinesthetic and tactile motion signals have to be combined into a coherent motion percept representing movement in the world. It would be interesting to see whether similar motion illusions as found in vision also occur in the haptic modality.

In motion perception and many other domains, Weber’s law, which states that the discrimination performance is proportional to the magnitude of the signal, fails at low signal values. Instead of evoking an early non-linearity to model this behavior, which is done by most traditional models (for example [5,11,12]), Freeman et al. [6] show that, in the Bayesian framework, Weber’s law and its breakdown can be explained by a prior acting on sensory signals with variable internal noise. This is a key idea that might help to bring the different modeling approaches currently existing into line. It further demonstrates the diversity of the Bayesian approach in providing a general framework for understanding phenomena in human perception.

To confirm this modeling approach, however, it remains to be seen how consistently the variable noise can be
characterized and whether this approach can be used also in other domains where different priors might exist.

From a modeling point of view Freeman et al. [6] provide interesting insights into the level at which prior information interacts with sensory evidence. They mainly distinguish two implementations of Bayesian models: in the first, the sensory estimates are summed and then combined with the prior information; in the second, each sensory estimate is first combined with the prior and then summed. Evidence for the latter comes predominantly from accounts for the Filehne illusion. The handling of the level at which the priors operate and what the consequences are for perception are not only of theoretical interest, but may also hint at the way the Bayesian computations are implemented neuronally in the brain. Up to now, however, our knowledge about how such computations are represented in the human brain is very limited. There are some first indications from computational neuroscience that probability distributions used for the Bayesian computations — priors, likelihoods — may be implemented in neuronal population codes [13,14]. There is also some recent evidence from monkey physiology that Bayes-optimal integration of visual and vestibular estimates of perceived direction of motion may be conducted in populations of neurons in area MSTd of the monkey brain [15].

One major problem that we face currently with the Bayesian approach is that the prior distributions, which are used to represent the statistics of the sensory signals derived from the environment, are merely postulated. The reason for this is that they are not easily measurable. Future research needs to address how priors can be determined, measured, or manipulated independently. There are several ways to achieve this. One method entails the study of how priors are learned in one context and then to investigate how the learning of these priors is transferred to other situations or tasks. This has successfully been demonstrated by Adams et al. [16], who adapted the light-from-above prior in one context and demonstrated transfer of the learning effect to another context and task, thereby undoubtedly demonstrating the updating of a priori knowledge [16]. Alternatively, one can indirectly infer the prior by varying the reliability of the signal estimates using a method proposed by Stocker and Simoncelli [5]. Ideally, such an inferred prior distribution should then be compared to the statistics of the environment as measured independently by some physical measurement method. Recently, this approach has been employed by Burge et al. [17] for the visual perception of depth at an occluding contour. In their experiments, Burge et al. [17] found a good qualitative agreement between the empirically inferred prior and the physically measured statistics of the environment. Future research must strive to demonstrate such correspondence between postulated priors and the statistics of the

Figure 1. The motion illusion analysed by Freeman et al. [6].
(A) Perceptual situation. Pursuit target object moving in front of the background. (B) Integration model. Upper panel: combination of pursuit target motion signals (T) with slow-motion prior (P) according to Bayes rule. This results in the posterior distribution with the maximum a posteriori estimate T'. Middle panel: combination of relative motion signals (R) with slow-motion prior (P) resulting in maximum a posteriori estimate R'. Lower panel: sum of T' and R', which results in the Filehne illusion, with the background apparently in motion.

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environment in order to justify the Bayesian approach to human perception.

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Mitosis: Taking the Measure of Spindle Length

Recent studies have investigated the mechanisms responsible for setting spindle length — and how spindle length changes over the course of development.

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You started life as a single fertilized egg and, after multiple divisions, the number of cells in your body is now one hundred times larger than the number of stars in the galaxy. The DNA in your cells originated from that first cell, propagated through rounds of duplication and segregation. This division of your genetic material continues to occur inside you about ten million times per second. An error could give rise to a cancer that will kill you. How can one cellular structure, the mitotic spindle, so accurately partition DNA in your various cells and tissues? A partial answer is that the premise of the question is wrong: it’s not that one spindle functions repeatedly, rather the spindles are incorporated into centrosomes, microtubule nucleating centers located at the spindle poles. While components of spindles have been studied in detail, we still do not know how these constituents work together to form spindles.

Many models of spindle organization have been devised. These can roughly be divided into two classes: mechanical models and dynamical models. Mechanical models propose that spindle morphology and size result solely from a balance of forces, with pushing by some factors, such as motor proteins and polymerizing microtubules [3], counteracted by resistance from other elements, such as opposing motors, microtubule rigidity [4], or chromosome stiffness [5]. These mechanical models are reminiscent of elasticity theory of simple physical structures like soap bubbles, whose shape is governed by a balance of surface tension and internal pressure. Dynamical models posit that spindle structure arises from the self-organization of the spontaneous activity of the constituent microtubules, motor proteins, and regulatory factors. Examples of dynamical models include the suggestion that spindle length is set by proteins that induce a length-dependent microtubule depolymerization [6], or the distance a microtubule slides during its lifetime [7].

An influential class of dynamical models is that spindle structure is