

The temporal and spatial limits of compensation for fixational eye movements

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Abstract

High-fidelity eye tracking is combined with a perceptual grouping task to provide insight into the likely mechanisms underlying the compensation of retinal image motion caused by movement of the eyes. The experiments describe the covert detection of minute temporal and spatial offsets incorporated into a test stimulus. Analysis of eye motion on individual trials indicates that the temporal offset sensitivity is actually due to motion of the eye inducing artificial spatial offsets in the briefly presented stimuli. The results have strong implications for two popular models of compensation for fixational eye movements, namely efference copy and image-based models. If an efference copy model is assumed, the results place constraints on the spatial accuracy and source of compensation. If an image-based model is assumed then limitations are placed on the integration time window over which motion estimates are calculated.
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1. Introduction

Our eyes are constantly in motion. Even during periods of fixation our eyes produce a range of characteristic, oscillatory movements. This provides our visual system with a significant problem: It must somehow dissociate eye-based from real-world motion signals. One means of doing this involves subtracting a copy (efference copy) of the muscular control signals directed to the eye from the incoming retinal image, an idea which was first formally proposed in the 1950s (Sperry, 1950; von Holst & Mittelstaedt, 1950). In the case of saccadic eye movements (of which there are numerous identifiable types) there is certainly good evidence that such a signal is available to the visual system, even if it is not always utilized (Deubel, Schneider, & Bridgeman, 2002).

Although the efference copy model can account for the compensation of some forms of eye movement, it is unlikely that it could be used to counteract them all, especially those associated with periods of fixation. There are at least two reasons for thinking this: First, some eye movements may be due to spurious discharge in the ocular muscles, rather than being driven by a specific command signal. Second, motion of the retina may not be due to rotational eye movements, but rather to translational ones caused by motion of the head. An alternative to the efference copy model is that we estimate retinal motion by performing an optic-flow analysis on the retinal image itself. This has the advantage of integrating all forms of global motion in the image, irrespective of their source. However, it brings with it the disadvantage that it may, under certain circumstances, make mistakes. This potential for making mistakes has actually been offered as an explanation for certain types of visual motion illusions such as the jitter after-effect (Murakami & Cavanagh, 1998) and Leviant's Enigma (Mon-Williams & Wann, 1996).

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One image-based compensation model to have received considerable interest in recent years was put forward by Murakami and Cavanagh (1998). This model proposes that retinal motion is estimated on the basis of motion vectors drawn from numerous regions within the retinal image. A recent study of retinal cells in several vertebrate species has identified how such a subtraction process might be implemented in the eye (Ölveczky, Baccus, & Meister, 2003). Despite these theoretical and experimental advances, what has been lacking up until now is direct evidence for such a mechanism at work in humans. Instead, the direct evidence that does exist actually speaks against such a model. Studies conducted in the 60s and 70s looking at the compensation of fixational eye movements (e.g., Findlay, 1974; Matin, Matin, & Pearce, 1970), found no evidence for the correction of slower movements, and although Findlay (1974) did find some evidence for correction for microsaccadic movements, he attributed this to an efference copy model. The main element lacking from these earlier studies was a more detailed study of other forms of fixational eye movement. It has been known for many years that small amplitude, high-frequency movements of the eye take place during fixation (Bolger, Bojanic, Sheahan, Coakley, & Malone, 1999; Carpenter, 1988; Ratliff & Riggs, 1950), but they have often been thought of as being too small to affect perception. It is only relatively recently that debate on the topic has been reopened (Martinez-Conde, Macknik, & Hubel, 2004). This paper focuses on these low amplitude, high-frequency movements, and through a pair of experiments aims to establish spatial and temporal constraints on the two models of image motion compensation.

2. Experiment I

2.1. Introduction

The first experiment focuses on the temporal characteristics of retinal image motion compensation. The temporal characteristics are important because of a fundamental limitation of image-based motion compensation, namely its integration period. An image-based mechanism requires that compensation takes place over a narrow, but finite time-window, during which global retinal shift is estimated. If the compensation mechanism does contain an integration period of this type, it should be possible to identify the lower limit for the duration of the integration period using very briefly presented visual stimuli.

The stimulus used to search for this effect consisted of a grid of circular elements—see Fig. 1A. The perceptual grouping of elements within such grids was first studied by the early Gestalt psychologists. One of the most comprehensive studies of this effect was made by Wertheimer (1923), who measured how grouping is affected by introducing minor irregularities to the arrangement of grid elements. In particular, Wertheimer described how subjects tend to report seeing a grid as containing rows of elements

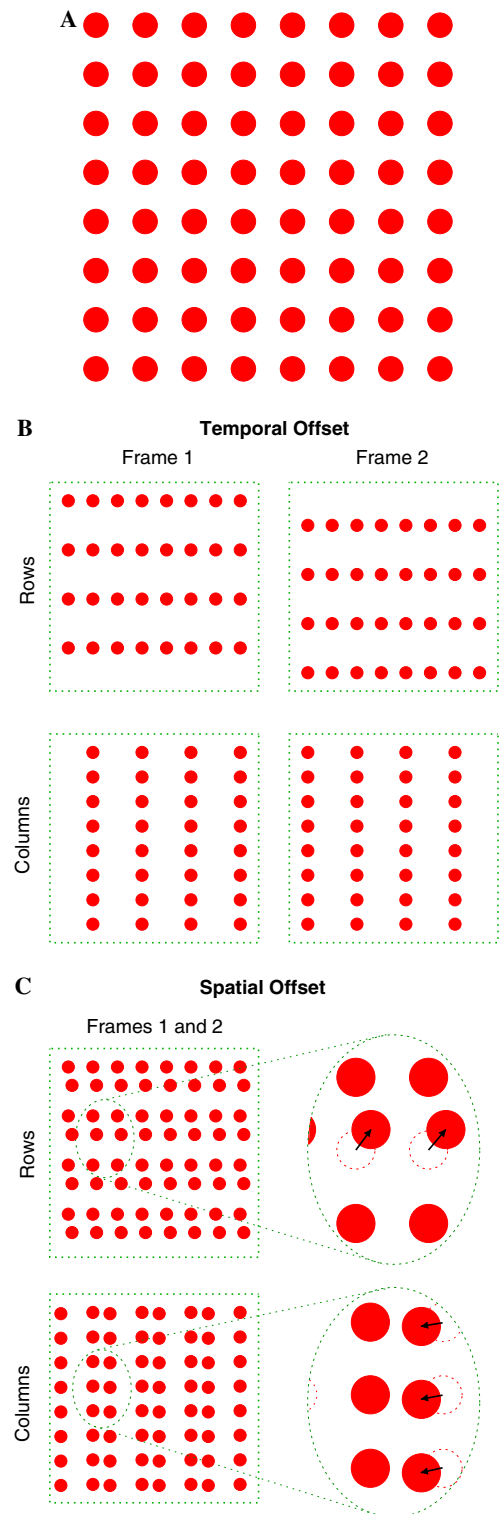


Fig. 1. Summary of the two presentation regimes used in the experiments. (A) The regular stimulus grid. (B) The asynchronous presentation paradigm used in Experiment I. Alternate rows (or columns) were shown in alternate frames on the CRT screen. (C) The synchronous condition used in Experiment II. All 64 grid discs appeared simultaneously, but with alternate rows (or columns) displayed with a small, randomly oriented spatial offset relative to the reference frame of the grid. The magnified sections on the right indicate the direction and magnitude of the displacement in each example case. The pale, dotted frames appear for illustrative purposes only and did not form part of the actual stimulus.

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