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Research Report

A model of encoding and decoding in V1 and MT accounts for motion perception anisotropies in the human visual system

Ariel Rokem[a], *Michael A. Silver*[a,b,*]

[a]*Helen Wills Neuroscience Institute, University of California, Berkeley, USA*
[b]*School of Optometry, University of California, Berkeley, USA*

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ABSTRACT

We used the motion aftereffect (MAE) to psychophysically characterize tuning of motion perception in the human visual system. The function relating MAE strength and the range of directions present in the adapter stimulus provides information regarding the width of direction tuning of motion adaptation. We compared the directional anisotropy in MAE tuning width to the well-known oblique effect in motion direction discrimination. In agreement with previous research, we found that subjects had lower motion direction discrimination thresholds for cardinal compared to oblique directions. For each subject, we also estimated MAE tuning width for a cardinal and an oblique direction by measuring the strength of the MAE for adapter stimuli containing different directional variances. The MAE tuning width was smaller for the cardinal direction, suggesting a fundamental similarity between motion direction discrimination and tuning of the MAE. We constructed a model of encoding of motion stimuli by V1 and MT and decoding of stimulus information from the cells in area MT. The model includes an anisotropy in the representation of different directions of motion in area V1. As a consequence of the connections implemented in the model, this anisotropy propagates to cells in MT. Model simulations predicted an oblique effect for both direction discrimination thresholds and MAE tuning width, consistent with our experimental results. The model also concurs with a recent report that the magnitude of the oblique effect for direction discrimination is inversely proportional to the directional variance of the stimulus. The agreement between model predictions and empirical data was obtained only when the model employed a maximum likelihood decoding algorithm. Alternative decoding mechanisms such as vector averaging and winner-take-all failed to account for the psychophysical results.

1. Introduction

Performance in visual tasks is often asymmetric, depending on the location, orientation, and/or motion direction of visual stimuli. In some cases, these differences in performance may stem from asymmetries that exist in the natural environment and can provide insight into the developmental origins of perceptual and behavioral asymmetries (Dakin et al., 2005). In

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* *Corresponding author*. 360 Minor Hall, #2020, School of Optometry, University of California, Berkeley, CA 94720-2020, USA. Fax: +1 510 643 5109.
E-mail address: masilver@berkeley.edu (M.A. Silver).
URL: http://argentum.ucbso.berkeley.edu (M.A. Silver).

Abbreviations: MAE, motion aftereffect; RDK, random dot kinetogram

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addition, these asymmetries may be used to illuminate the mechanisms of neural encoding and decoding underlying the performance of visual tasks. In this work, we have used anisotropies in motion perception to investigate encoding and decoding of motion stimuli by the human visual system.

Thresholds for perceptual tasks performed on moving stimuli or on oriented stimuli are often lower for stimuli with orientation or direction of motion that is parallel to the cardinal axes (up/down, left/right) than for stimuli oriented or moving along the oblique directions (the off-cardinal diagonals), a phenomenon referred to as the oblique effect (Appelle, 1972). This behavioral anisotropy probably stems from a more robust representation of cardinal orientations in the visual system. Furmanski and Engel (2000) and Furmanski et al. (2004) showed that the oblique effect in detection of low-contrast gratings (lower detection contrast threshold for cardinal than for oblique orientations) was correlated with a difference in the magnitude of primary visual cortical fMRI responses to presentation of cardinal and oblique gratings. In addition, in a large sample of cat primary visual cortical neurons, randomly sampled in many different experiments, there were more cells preferring cardinal than cells preferring oblique orientations (Li et al., 2003). In motion perception, thresholds for discriminating two similar motions of direction are higher when the stimuli are centered at oblique directions compared to cardinal directions (Ball and Sekuler, 1982; Dakin et al., 2005; Gros et al., 1998). By analogy with the oblique effect for stimulus orientation, we assume that the oblique effect for motion perception is also based on an anisotropy in the representations of different motion directions in the visual system. A significant proportion of cells in primary visual cortex is not only orientation-selective but also direction-selective (De Valois et al., 1982, 2000; Hubel and Wiesel, 1959; Peterson et al., 2004). The preferred direction and preferred orientation are always approximately orthogonal in macaque V1 cells, based on responses to moving bar stimuli (Albright, 1984). 2D motion direction information may not always be available to the cell, due to the aperture problem (Horn, 1986). However, when 2D motion direction information is available to V1 neurons, preferred direction is independent of stimulus orientation (Pack et al., 2003). Therefore, it is reasonable to assume that there are more cells in V1 that show a preference for cardinal motion directions than cells that prefer oblique directions. Moreover, the average orientation tuning width of primary visual cortical neurons tuned to cardinal orientations was smaller than the average tuning width of those tuned to oblique orientations (Li et al., 2003). Therefore, the average tuning width of motion selectivity is likely to be smaller for cells representing the cardinal directions compared to cells preferring oblique motions, though this has not yet been tested experimentally in primary visual cortex.

We used two tasks to characterize the oblique effect in motion perception. The first, a motion direction discrimination task, exhibited an oblique effect in direction discrimination threshold and was used to identify the cardinal direction associated with lowest discrimination threshold and the oblique direction associated with highest threshold in each of our subjects. We then measured the tuning width of motion adaptation for these two directions. Estimates of the tuning width were obtained by measuring the strength of adaptation (magnitude of the motion aftereffect, or MAE) following prolonged viewing of a field of coherently moving dots in one of the two directions. Previous work has shown that the magnitude of the MAE for random dot kinetogram (RDK) adapter stimuli was greater when the adapter stimulus included a moderate range of directions compared to a single direction of motion (Hiris and Blake, 1992). Thus, the relationship between MAE strength and the range of directions in the adapter stimulus allows estimation of the width of direction tuning of motion perception.

In our experiments, the RDK adapting stimuli were generated by assigning a direction to each dot from a distribution of directions centered on either a cardinal or oblique direction. The variance of this distribution determines the directional variance of the stimulus. Our results show that like motion direction discrimination performance, the tuning width of motion adaptation also exhibited an oblique effect: direction tuning was sharper for cardinal adapter stimuli than for oblique stimuli.

We constructed a computational model of encoding and decoding of motion information by cells in areas V1 and MT that accounts for the observed oblique effects in motion direction discrimination and tuning width of motion adaptation. The model contains a set of V1 units with feedforward connections to a set of MT units. The V1 units are anisotropic in their representation of motion: V1 cells representing cardinal directions are more numerous, and their directional tuning widths are narrower than the tuning widths of V1 cells representing oblique directions. The tuning properties of MT cells are then inherited through feedforward projections from V1 cells.

Information about stimulus motion direction is then decoded from the activity in the entire population of MT cells (as in Pouget et al., 2000). The decoding method is based on a maximum likelihood procedure (Jazayeri and Movshon, 2006). Our model quantitatively accounts for the observed psychophysical results, generating oblique effects for motion discrimination and for motion adaptation tuning width. It also agrees with previous findings that the oblique effect for motion discrimination is only present for stimuli with low directional variance (Dakin et al., 2005).

Our modeling results demonstrate that oblique effects in motion perception could arise from a combination of an anisotropy in the encoding of the stimulus by the visual system and a decoding mechanism that employs a statistically optimal strategy to read out this information. This suggests that complex perceptual phenomena such as the oblique effect should be understood as a consequence of specific encoding and representation schemes as well as specific decoding strategies employed by the brain.

2. Results

2.1. *The oblique effect in motion direction discrimination*

To compare perceptual abilities for different directions of motion, we employed a motion direction discrimination task. Subjects viewed an annulus centered at the fixation point and containing a random dot kinetogram (RDK). For each trial, two