

# Anisotropies in judging the direction of moving natural scenes

Steven C. Dakin

Institute of Ophthalmology, University College London,  
London, UK



Deborah Apthorp

School of Psychology, University of Sydney,  
Sydney, Australia



David Alais

School of Psychology, University of Sydney,  
Sydney, Australia



Although visual systems are optimized to deal with the natural visual environment, our understanding of human *motion perception* is in large part based on the use of artificial stimuli. Here, we assessed observers' ability to estimate the direction of translating natural images and fractals by having them adjust the orientation of a subsequently viewed line. A system of interleaved staircases, driven by observers' direction estimates, ensured that stimuli were presented near one of 16 reference directions. The resulting error distributions (i.e., the differences between reported and true directions) reveal several anisotropies in global motion processing. First, observers' estimates are biased away from cardinal directions (*reference repulsion*). Second, the standard deviations of estimates show an "oblique effect" being ~45% lower around cardinal directions. Third, errors around cardinal directions are more likely (~22%) to approach zero than would be consistent with Gaussian-distributed errors, suggesting that motion processing minimizes the *number* as well as *magnitude* of errors. Fourth, errors are similar for natural scenes and fractals, indicating that observers do not use top-down information to improve performance. Finally, adaptation to unidirectional motion modifies observers' bias by amplifying existing repulsion (e.g., around cardinal directions). This bias change can improve direction discrimination but is not due to a reduction in variability.

Keywords: motion—2D, structure of natural images, temporal vision

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## Introduction

In the past few decades, analysis of the statistics of real-world scenes has suggested that the human visual system is optimized to code the spatial information present in natural images (Field, 1987; Simoncelli & Olshausen, 2001). Although a considerable amount of research has explored the perception of static natural scenes (e.g., Baddeley & Hancock, 1991; Gallant, Connor, & Van Essen, 1998; Hansen, Essock, Zheng, & DeFord, 2003), considerably less is known about the processing of dynamic natural scenes. It seems that the statistical properties of natural movies can shape neural processing systems (Betsch, Einhauser, Körding, & König, 2004; Dong & Atick, 1995; Simoncelli & Olshausen, 2001; van Hateren & Ruderman, 1998; Zanker & Zeil, 2005). Bartels, Zeki, and Logothetis (2008) applied flow-field analysis to natural movies to derive estimates of local (object) motion, global (self- or camera) motion, and a residual measure (e.g., due to illumination change). fMRI activation measured by Bartels et al. during free viewing of movies reveals that early visual areas are activated by

residual change, but that MT+ responds to object motion (in a contrast-dependent manner) while medial posterior parietal cortex (mPPC) responds in a contrast-invariant manner to global flow, consistent with it being important for determining self-heading.

The latter study highlights a significant difficulty for the psychophysical study of moving natural scenes. To quantify observer error, the true state of the signal must be known, and the "ground truth" for motion within complex environments is generally not known. Without this information, it is hard to evaluate predictions of optimal coding strategies within such environments and compare them to human performance. The approach of Bartels et al. assumes that flow-field estimates reflect the true motion structure of the stimulus, which is likely appropriate for a free viewing study where data are pooled across many stimulus presentations, but which may be less suitable for studies quantifying error on a trial-by-trial basis. Another innovative approach has been to avoid natural scenes and instead analyze the motion structure of synthetic scenes (Tversky, 2008), but the disadvantage of this approach is the lack of meaningful structure in such stimuli, which may contribute to our ability to determine

direction of motion. In this paper, we opted to establish ground truth by applying synthetic translation to a single calibrated natural-scene image in a variety of directions. Although global translation of a scene is only an approximation to naturally arising motion (which, e.g., contains motion parallax), knowing the true underlying motion does allow us to perform detailed analysis of direction discrimination errors.

It has long been known that discrimination of oblique orientations is less precise than discrimination of cardinal (horizontal or vertical) orientations (Appelle, 1972; Heeley & Timney, 1988). Similarly for motion, observers are more precise at fine direction discrimination (i.e., reporting whether a stimulus is clockwise or anticlockwise of a reference direction) for motions near the cardinal directions ( $0^\circ$ ,  $90^\circ$ ,  $180^\circ$ , or  $270^\circ$ ) than they are for oblique directions (Ball & Sekuler, 1979, 1980; Dakin, Mareschal, & Bex, 2005a, 2005b; Gros, Blake, & Hiris, 1998; Heeley & Buchanan-Smith, 1992; Krukowski, Pirog, Beutter, Brooks, & Stone, 2003). Interestingly, this oblique effect only applies to discrimination and not detection performance (at least in dot patterns; Gros et al., 1998). In plaids, it is pattern motion, and not component motion, that determines the oblique effect (Heeley & Buchanan-Smith, 1992). Generally, the oblique effect is thought to result from low-level tuning properties of orientation-sensitive neurons, with oblique orientations and motion directions being underrepresented relative to cardinal directions (Li, Peterson, & Freeman, 2003; McMahan & MacLeod, 2003). It has been suggested that this uneven distribution of neural sensitivities is due to the statistical properties of the natural environment, which exhibit a similar bias to vertical and horizontal (Essock, Haun, & Kim, 2009; Keil & Cristobal, 2000), and consequent underrepresentation of the obliques. However, an oblique effect for direction discrimination with natural images is yet to be established.

Previously, Dakin et al. (2005a) used a noise paradigm to determine that poor discrimination around oblique directions is *local* in nature: it affects the precision with which the directions of individual elements are encoded but not how well they are integrated across space. The particular pattern of sensitivity loss associated with oblique motion, expressed in a polar format, resembled a fat “X”; low discrimination thresholds are observed only within a few degrees of the cardinal directions. The authors went on to compare this pattern of results with the local motion statistics of natural movies, using a video shot from the point of view of an individual walking through an urban environment. This revealed that there was substantially less energy at oblique than cardinal directions and that local energy profiles had broader directional bandwidths (i.e., standard deviations) away from the cardinals. This paper made several predictions, notably that the representation of global direction should be prone to the effects of anisotropies

in the earlier motion coding stage. Specifically, distributions around cardinal directions should: first, have lower standard deviations, and second, be more leptokurtic.<sup>1</sup>

Judgments of direction are not only more variable at oblique directions, they are also less accurate (Loffler & Orbach, 2001). Observers required to judge the absolute direction of motion of a moving dot pattern are biased, typically away from the cardinal directions. This tendency is known as *reference repulsion* (Loffler & Orbach, 2001; Rauber & Treue, 1998) where it is assumed that observers use the cardinal directions (up, down, left and right) as implicit “reference” directions, even in the absence of an explicit reference boundary. Jazayeri and Movshon (2007) recently observed a systematic bias in observers’ estimates of motion direction in a fine discrimination task. Their observations were well explained by a model of sensory decoding in which the most informative signals are those from neurons tuned away from the discrimination boundary; such signals are preferentially weighted in a fine discrimination task, but not in a coarse (up–down) task. Jazayeri and Movshon’s (2007) model asserts that the direction channels used for motion perception will depend on the task. If this is the case, then so-called “reference repulsion” should not be seen in absolute judgments of direction, since the task is not a binary discrimination task. The “off-channel” neurons are only more informative if a decision must be made regarding the direction of motion with respect to a boundary (clockwise/anticlockwise of the boundary); the most informative neurons in an absolute direction judgment must be those tuned to the direction itself, since they are maximally responsive. On the other hand, it is possible that observers may compute absolute direction based on some internal representation of cardinal directions (up/down and left/right), in which case reference repulsion might still be seen for directions near the cardinals.

Although absolute direction judgments have been used previously in various motion studies (e.g., Alais, Wenderoth, & Burke, 1994; Kim & Wilson, 1996; Loffler & Orbach, 2001; Marshak & Sekuler, 1979; Nichols & Newsome, 2002; Yo & Wilson, 1992), the shape of the distributions of observers’ responses has never been examined. Most motion models, like many models used to explain other perceptual effects, assume that the error in the underlying sensory information has a Gaussian distribution. However, if the oblique effect in direction perception is to be fully understood, it is important to have information regarding the form of the underlying error distributions. Indeed, this is essential for any explanation proposing that percepts or decisions arise from information from neighboring channels, for the simple reason that changes in the mean, kurtosis, or skew of the two neural populations can all produce the same outcome (see Figure 1). In the experiments reported below, we use absolute direction judgments across a range of 16 directions

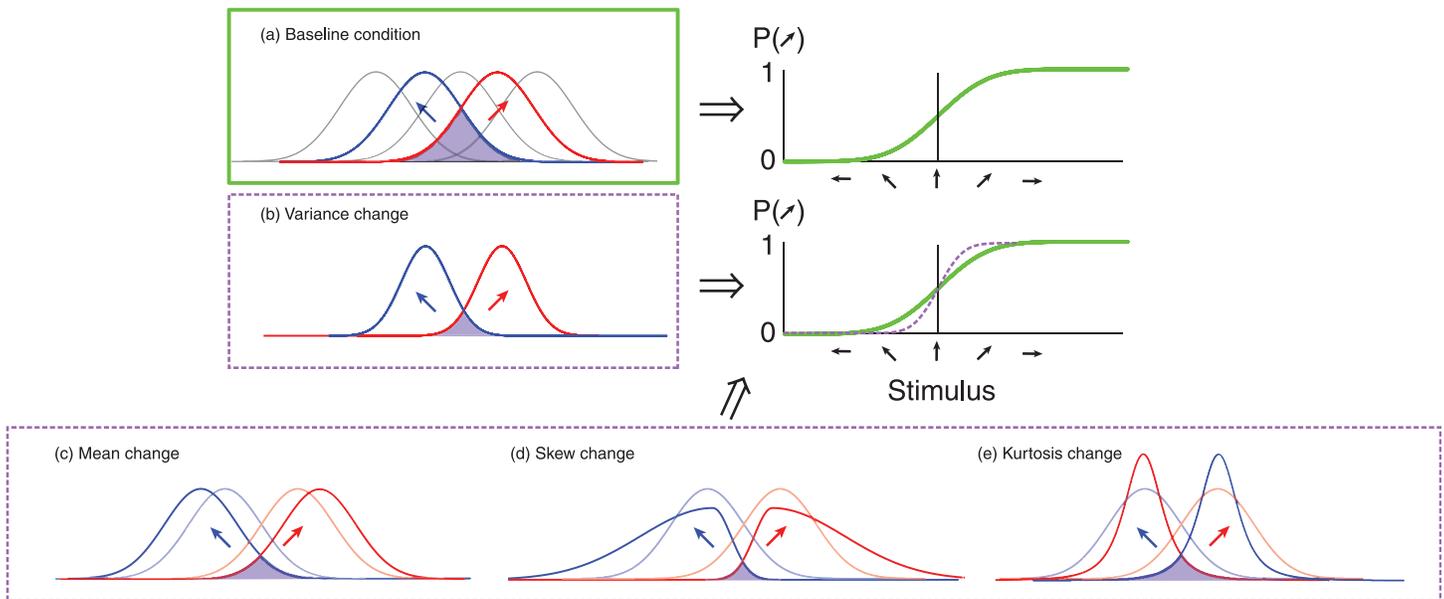


Figure 1. (a) We generally assume that observers' performance of a 2AFC "clockwise versus anticlockwise of vertical" discrimination is determined by a representation limited by Gaussian direction uncertainty. Performance is determined by the extent of overlap between the red and blue channel profiles (shaded) that encode information just off the reference direction, which predicts discrimination performance (green line). (b) When performance improves, we assume it is because the *variance* of their representation has been reduced, leading to less overlap (shaded region) between channels and correspondingly steeper psychometric functions (dashed line). (c–e) However, changes in other statistical properties of the observers' representation of direction could also lead to less overlap between channels and steeper psychometric functions. For example (c) could explain why prolonged adaptation—which leads to pronounced repulsion in perceived direction away from the adapter—can produce improved discrimination under some circumstances. Note that mixtures of these effects could also serve to cancel one another out.

to determine the shape of the underlying error distributions and to find out whether the form of distributions depends on stimulus direction.

## General methods

### Subjects

In [Experiment 1](#), observers were the three authors (SCD, DMA1, and DMA2) and one naive subject (MB). All have normal or corrected-to-normal vision and are experienced psychophysical observers. For the second adaptation experiment, we recruited an additional naive subject (DK) who is also psychophysically experienced with normal vision.

### Apparatus

Experiments were run under the MATLAB programming environment (MathWorks) using software from the PsychToolbox (Brainard, 1997; Pelli, 1997). Stimuli were presented on a Mitsubishi Diamond Pro 2020U CRT monitor calibrated with a ColourCal photometer and

linearized in software using a look-up table. The display operated at a resolution of  $1024 \times 768$  pixels and a frame refresh rate of 75 Hz. The display had a mean (background) and maximum luminance of 50 and 100  $\text{cd/m}^2$ , respectively.

### Stimuli

Stimuli consisted of a moving natural scene ([Figure 2](#)) generated by applying synthetic translational motion (4 deg/s) to either a natural image or a fractal with a dimension matched to the slope (averaged across orientation) of the power spectrum of our natural scene. We did this because we observed the overrepresentation of vertical and horizontal structures (due to the presence of the ground-plane and gravitational effects) in our scene (Coppola, Purves, McCoy, & Purves, 1998; Dakin et al., 2005a, 2005b). Our fractals, on the other hand, were strictly isotropic so that any anisotropies in observers' judgment of direction of such scenes could not be attributable to the orientation structure of the source image. Both source and fractal images were normalized to have maximal Michelson contrast, that is, minimum and maximum values were scaled between 0.0 and 1.0, respectively. The speed used (4 deg/s) was picked to be

close to the values used in Gros et al. (1998; 5.6 deg/s) and Loffler and Orbach (2001; 3.5 to 5.6 deg/s). We would predict that directional accuracy would improve at faster speeds, but that this would be due to oriented “motion streaks” providing helpful orientation cues (Geisler, 1999).

Stimuli were 15-frame movies that took 200 ms to display at the monitor’s frame rate of 75 Hz. Motion was generated in hardware using the OpenGL capabilities of the graphics card (NVIDIA GeForce 7300 GT) accessed via the PsychToolbox (Brainard, 1997; Pelli, 1997). The method used to select the directions in which stimuli moved, on a trial-by-trial basis, is described in the Procedure section below.

The source natural image was image “imk00183.iml” from the Van Hateren calibrated image database (<http://www.kyb.mpg.de/bethge/vanhateren/index.php>; van Hateren, 2007). We wanted our stimuli to present observers with a task whose difficulty was representative of the challenge the visual system faces in estimating the direction of motion of complex natural scenes. To this end, we set about first estimating the degree of directional ambiguity present when a subset (200 images) of the van Hateren image set was translated in directions from 0 to 360° (Figures 2c and 2d).

We assume that the primary source of ambiguity in observers’ ability to determine the direction of a natural scene will be the well-known “aperture problem.” Because motion-selective neurons in the primary visual cortex are able only to signal direction perpendicular to their preferred direction, the speed and direction of a straight contour passing through their receptive field is intrinsically ambiguous. For this reason, images dominated by edge structure present a particular difficulty that images dominated by texture do not. We therefore computed a metric for the degree to which a natural image was dominated by edges or texture. Specifically, we generated a large number of 15-frame movies by translating a given scene at 4 deg/s (the speed to be used in our psychophysical experiment) at directions densely sampled around the clock. We superimposed the frames of each movie to generate a “motion-streak” image, which we then convolved with a bank of Gabor filters (with peak spatial frequency set to 128 cycles/image) in quadrature phase. The sum of squares of the pair was used to estimate energy as a function of orientation for a given direction of translation. Sample histograms are presented in Figure 2d, where each vertical slice is a histogram for a single motion direction where vertical position codes image orientation (which has been phase shifted to match the motion direction). Thus, a narrow horizontal line in this representation (Figure 2d, top left) indicates that the orientation energy (“streaks”) arising from translation closely matched the direction of motion (with the usual  $\pm\pi$  ambiguity). This is consistent with scenes being dominated by texture, whereas images that are dominated by edge structure (Figure 2c, lower right) generate

histograms whose orientation structure (both the mean and the range) is much more dependent on the direction of motion in which they are translated (Figure 2d, lower right). We took the covariance of these histograms as a simple index of directional ambiguity. The image eventually selected fell near the middle of the range of values computed and was also selected to contain both texture and edge information and to avoid the presence of specularities that can dominate the gray-level range in linearized natural scenes.

## Procedure (no adaptation)

Observers fixated centrally on a continuously visible marker and were presented with a 200-ms movie sequence, after which they were required to adjust the orientation of an on-screen indicator line—using the computer mouse—to match the perceived direction of motion that had just been presented. No time limit was enforced, although observers generally indicated their choice within 1–2 s. Observers were permitted to move their eyes freely during the response phase.

A run consisted of sixteen interleaved blocks of 32 trials, and observers performed between 4 and 8 runs of each condition. Each block drove a separate adaptive staircase (QUEST; Watson & Pelli, 1983) that estimated direction discrimination performance around a particular reference direction, with a total of 16 reference directions tested (0°–337.5° in linear steps of 22.5° where 0° is horizontal rightward motion). QUEST generates a single stimulus value, the response to which will, based on a Bayesian model observer, minimize uncertainty on QUEST’s subsequent estimate of threshold. QUEST generates only a single value (e.g., 5°), which we used to determine the magnitude of the difference between the direction of stimulus motion and a given reference direction. The sign of the motion stimulus was selected randomly (i.e., a QUEST-generated value of 5° could lead to a cue of 85° or 95° in the 90° reference direction condition), so that both sides of the reference direction were sampled.

Figure 3 illustrates how we converted the observers’ (essentially analog) responses into digital (clockwise versus anticlockwise) responses that were used to drive the QUEST threshold estimation procedure. *Note that this procedure was used only to sample an informative range of directions around a given reference direction.* For a given reference direction, QUEST generated a motion cue value (which we assigned a random sign relative to the reference). In Figure 3a, that motion cue is positive (i.e., clockwise of the reference). The motion cue is presented to the observer who estimates its direction with an analog response (*report*). In this case, their report is clockwise of the reference direction (computed using Equation 1 below), and this is classed a correct response that would lead QUEST to reduce cue size on the subsequent trial. In

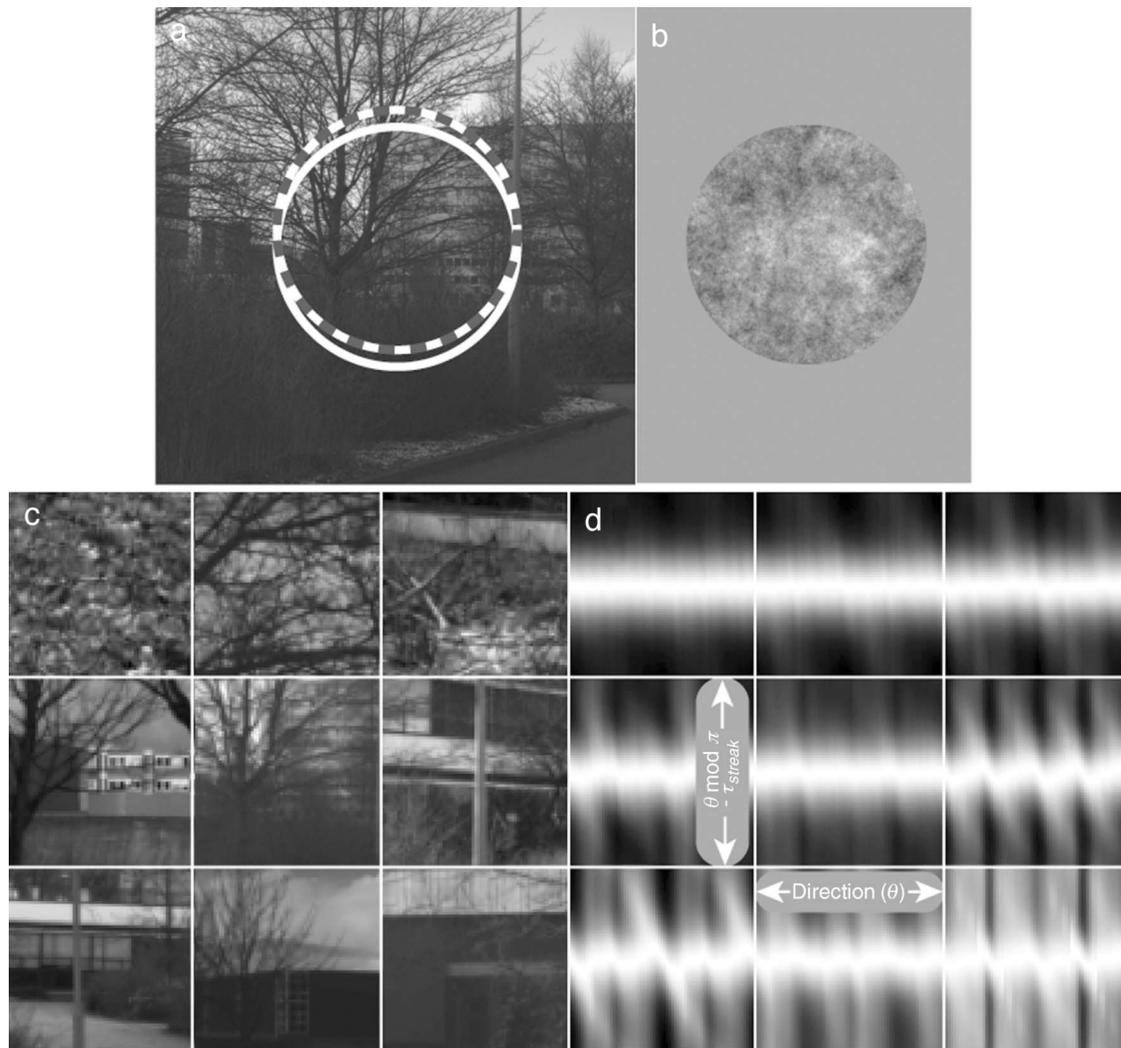


Figure 2. (a) The natural image used in psychophysical experiments. On each frame of the stimulus movie, a portion of a large image was revealed through a two-dimensional raised cosine window. By offsetting the image on each frame, we generated translational motion behind a static aperture. Here the solid and dashed lines depict the portion of the image revealed in frames 1 and 2, respectively, i.e., the resulting movie depicted downward motion. (b) A fractal with a similar fractal dimension to (a). The image was selected to be typical in terms of the ambiguity of its direction under synthetic translation. We estimated motion ambiguity by assessing the degree to which stimuli were prone to the “aperture problem.” (c) Nine images ordered (from top left to bottom right) in decreasing consistency of orientation structure (“streaks”) that arise when the image is translated in different directions, and the resulting frames superimposed. (d) Histograms of filter energy as a function of motion direction ( $\theta$ ) and streak orientation ( $\tau_{streak}$  normalized to the difference between itself and motion direction) for images in the corresponding locations in (c). The x-axis shows direction of motion (0 to 360°). The y-axis shows deviation of motion streaks from motion direction (−90 to +90°). Images with uniform textures (e.g., top left of (c)) make streaks that align closely with motion direction (leading to a horizontal band in the resulting histogram) but for images dominated by edges (e.g., bottom right of (c)) there are large deviations of oriented streaks from the direction of motion (due to the aperture problem) leading to irregular structure in the resulting histogram. We used the histograms to compute a measure of “streak consistency” and selected a source image that fell in the center of the range, i.e., one that contained both texture and edges.

Figure 3b, a negative cue is presented, but the observer’s report is clockwise (positive) of the reference direction and this is classed as an incorrect response (leading to an increase in cue size). In brief, observers’ responses are correct only if they are the same “side” of the reference as the true/cued direction. On each trial, we record (a) the reference direction, (b) the cued direction, and (c) the reported direction. The difference between true and

reported directions ( $\theta_{error}$ ) will form the basis of our analysis below.

Note that the primary goal of the QUEST procedure was to concentrate stimulus directions at informative points relative to the reference directions. We elected not to simply present stimuli at predetermined directions to avoid subjects being able to use this information strategically in making their judgments (e.g., “it looked

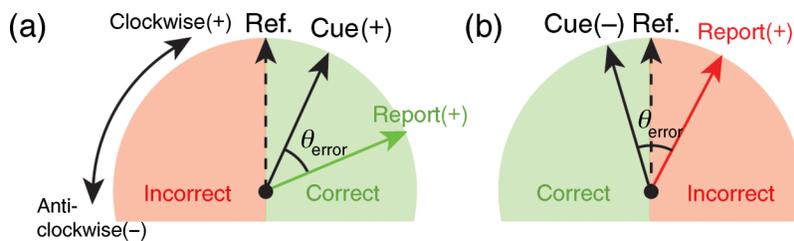


Figure 3. Schematic representation of our task. (a, b) Subjects were presented with a particular direction of motion (*Cue*) and made a judgement of its direction (*Report*) by adjusting the orientation of a subsequently viewed line. The error in their report ( $\theta_{\text{error}}$ )—the signed difference between the presented direction and the subjects’ report—was recorded and was the primary measure of performance analyzed below. The sign of their report with regard to a particular reference direction (*Ref.*; unknown to the observer) was used solely to drive the QUEST staircase procedure. In this way, the staircase concentrated the motion cues on informative directions *around a particular reference direction*.

near-vertical, I know one of the test directions is vertical, I will report vertical...”). We used QUEST rather than simply randomizing direction (on a trial-by-trial basis) so that we could more efficiently concentrate stimuli on directions that were close to the subjects’ discrimination threshold for a given reference direction. Indeed, in similar experiments (using “apertured” natural stimuli; Kane, Bex, & Dakin, [submitted](#)) using random cue directions, we report similar patterns of results to those reported below.

## Procedure (adaptation)

The procedure for the adaptation experiment was essentially the same as described above except that the first trial of every sequence was preceded by a 30 s adapting sequence of the stimulus moving rigidly in one direction (either  $135^\circ$  or  $90^\circ$ , depending on the block). Subsequent trials were preceded by a 3 s top-up adaptation. We also elected not to test the full  $0\text{--}337.5^\circ$  range, since pilot data indicated that adaptation effects were confined to a range around the adapting direction. Consequently, we spaced nine test directions more finely at  $\pm 15^\circ$ ,  $\pm 7.5^\circ$ ,  $\pm 3.75^\circ$ ,  $\pm 1.87^\circ$ , and  $0^\circ$  relative to the adapting direction.

## Analysis

Below we analyze the subjects’ distributions of *errors* using variety of summary circular statistics. The simplest way to compute the (signed) difference between two directions is to use a complex polar representation:

$$\Delta\theta = -i \ln \left( \frac{e^{i\theta_1}}{e^{i\theta_2}} \right). \quad (1)$$

For a true/cued direction  $\theta_{\text{true}}$  and a given estimated direction  $\theta_{\text{est}}$ , we use [Equation 1](#) to compute a signed

directional error  $\theta_{\text{error}}$ . In this paper, we will adhere to the convention that  $0^\circ$  indicates rightward horizontal motion,  $90^\circ$ , upward vertical motion,  $180^\circ$  leftward horizontal motion, etc. To remain consistent with this convention, positive errors are anticlockwise, and negative errors are clockwise, of the true direction.

We divided all observers’ trials for a given image condition into 16 blocks. Each block was centered on  $\theta_{\text{block}}$  ( $0^\circ, 22.5^\circ, \dots, 337.5^\circ$ ) and data were derived from trials when  $\theta_{\text{true}}$  fell in the corresponding range:  $0^\circ \pm 11.25^\circ, 22.5^\circ \pm 11.25^\circ, \dots, 337.5^\circ$ . Blocks contained between 75 and 311 samples (depending on observer and direction). For each block, we summarized the distribution of signed directional errors between the true and estimated directions (estimated as above) using the following statistics (Mardia & Jupp, 2000). The mean direction ( $\bar{\theta}$ ) is defined as

$$\bar{\theta} = \begin{cases} \tan^{-1}(\bar{S}/\bar{C}) & \text{if } \bar{C} \geq 0 \\ \tan^{-1}(\bar{S}/\bar{C}) + \pi & \text{if } \bar{C} < 0 \end{cases}, \quad (2)$$

where

$$\bar{S} = \frac{1}{n} \sum_{j=1}^n \sin\theta_j \quad \text{and} \quad \bar{C} = \frac{1}{n} \sum_{j=1}^n \cos\theta_j. \quad (3)$$

In Matlab,  $\bar{\theta}$  may be computed using  $\text{atan2}(\bar{S}, \bar{C})$ . Below, we typically plot the mean directional bias, which is simply the directional error between  $\bar{\theta}$  and  $\theta_{\text{block}}$  for a given block. Thus when presented with vertical upward motion ( $90^\circ$ ) if observers systematically reported  $95^\circ$  ( $5^\circ$  anticlockwise of the reference), then their bias would be  $+5^\circ$ .

The second summary statistic we use is the circular standard deviation ( $\sigma_\theta$ ). The mean resultant length

$$R = \sqrt{\bar{S}^2 + \bar{C}^2}, \quad (4)$$

can be transformed into the circular variance

$$V = 1 - R, \quad (5)$$

because we are dealing with unit vectors,  $0 \leq V \leq 1$ . Mardia and Jupp (2000) show that this measure can be transformed into a measure of circular standard deviation using

$$\sigma_\theta = \sqrt{-2\ln(1 - V)}, \quad (6)$$

which takes on the values  $[0, \infty]$ . Mardia and Jupp (2000) go on to define circular skewness as

$$\gamma_\theta = \frac{\bar{R}_2 \sin(\bar{\theta}_2 - 2\bar{\theta})}{(1 - \bar{R})^{3/2}}, \quad (7)$$

and circular kurtosis as

$$\kappa_\theta = \frac{\bar{R}_2 \cos(\bar{\theta}_2 - 2\bar{\theta}) - \bar{R}^4}{(1 - \bar{R})^2}, \quad (8)$$

where  $\bar{\theta}_p$  and  $\bar{R}_p$  denote the sample mean direction and sample mean resultant length of  $p\theta_1, \dots, p\theta_n$ . Skewness quantifies the degree of asymmetry of a distribution—i.e., the difference in a distribution's slope either side of its peak—with positive and negative skews indicating that the slope is steeper clockwise or anticlockwise of the peak, respectively. Positive kurtosis indicates that a distribution is more “peaky” (leptokurtic) than a Gaussian distribution, and negative kurtosis that is “flatter/more uniform” (platykurtic).

Note that we shifted and scaled the numerical estimates from Equations 7 and 8: our skew measure was  $-\frac{\gamma_\theta}{2\sqrt{2}}$  and our kurtosis measure was  $3 + \frac{\kappa_\theta}{2}$ . We did this to bring these measures into correspondence with linear estimates of skewness and kurtosis for low variance distributions, i.e., where wrapping is not a significant issue. Thus, for a Laplace (double exponential) distribution, both the standard linear kurtosis and our scaled circular kurtosis are 6.0. Because we did this, and because our error distributions always fell within the range  $\pm 45^\circ$  (no subjects ever made a larger error across all conditions), non-circular summary statistics will produce similar values to those reported below.

## Experiment 1: Perceived direction of motion in natural scenes

In the first experiment, we asked observers to adjust the orientation of a line to match the perceived direction of

motion of a rigidly translating image: either a natural scene or a spatially unstructured fractal pattern. Below, we analyze and compare observers' errors in judging the direction of these two kinds of image.

## Results

Figure 4 presents polar histograms of (a) presented and (b) reported directions of a moving fractal in the 16 conditions tested (pooled across the sign of the stimulus motion cue within a given block) across all runs performed by one subject (DMA1). Color of shading indicates the reference direction around which measures were taken (the key is in the lower left corner of (a)). The white or black thick lines inset in the center of Figures 4a and 4b plot the summary histograms of all directions presented or reported, respectively, pooled across blocks. Figure 4c plots the specific pattern of errors made by observer DMA1 in the 16 interleaved conditions tested, pooled across all runs. Each histogram plots binned data (blue points) along with the best-fitting wrapped Gaussian function, for direction estimates made by subjects when the true direction of motion fell within  $\pm 11.25^\circ$  of the block direction (bold type, inset top left in each plot). Note that error distributions are narrower and taller around cardinal ( $0^\circ$ ,  $90^\circ$ ,  $180^\circ$ , and  $270^\circ$ ) than other directions. The fact that observers' estimates are less variable around these directions accords with the known oblique effect for direction discrimination (reviewed in the Introduction section).

That the observers' task was to set a line's orientation to match the perceived motion direction leads to the question of whether the superior performance with patterns moving along cardinal directions could be attributable to better orientation acuity at cardinal orientations. However, it is unlikely that orientation acuity could set the limit on observers' performance because it is much more precise than motion acuity at both cardinal and oblique orientations/directions (Appelle, 1972; Gros et al., 1998; Westheimer, 2003). For this reason, most of the variance in our measurements must reflect the contribution of the motion system. With this said, it is still possible that the two “oblique effects” are related. Indeed, Xu, Collins, Khaytin, Kaas, and Casagrande (2006) reported that the higher representation of cardinal than oblique orientations in V1 of owl monkey is mirrored in MT, which they suggest may be the neural underpinning of the oblique effect for motion.

Inset into each plot in Figure 4c is a table of four statistics indicating the mean (bias), standard deviation, skew, and kurtosis of each corresponding data set. These statistics are plotted, as a function of the cue motion direction (within a block), in Figures 4d–4g. Two notable features emerge from this individual's data, in addition to reduced variability on judgments around cardinal directions. First, reports are biased, falling in the range  $\pm 10^\circ$ ,

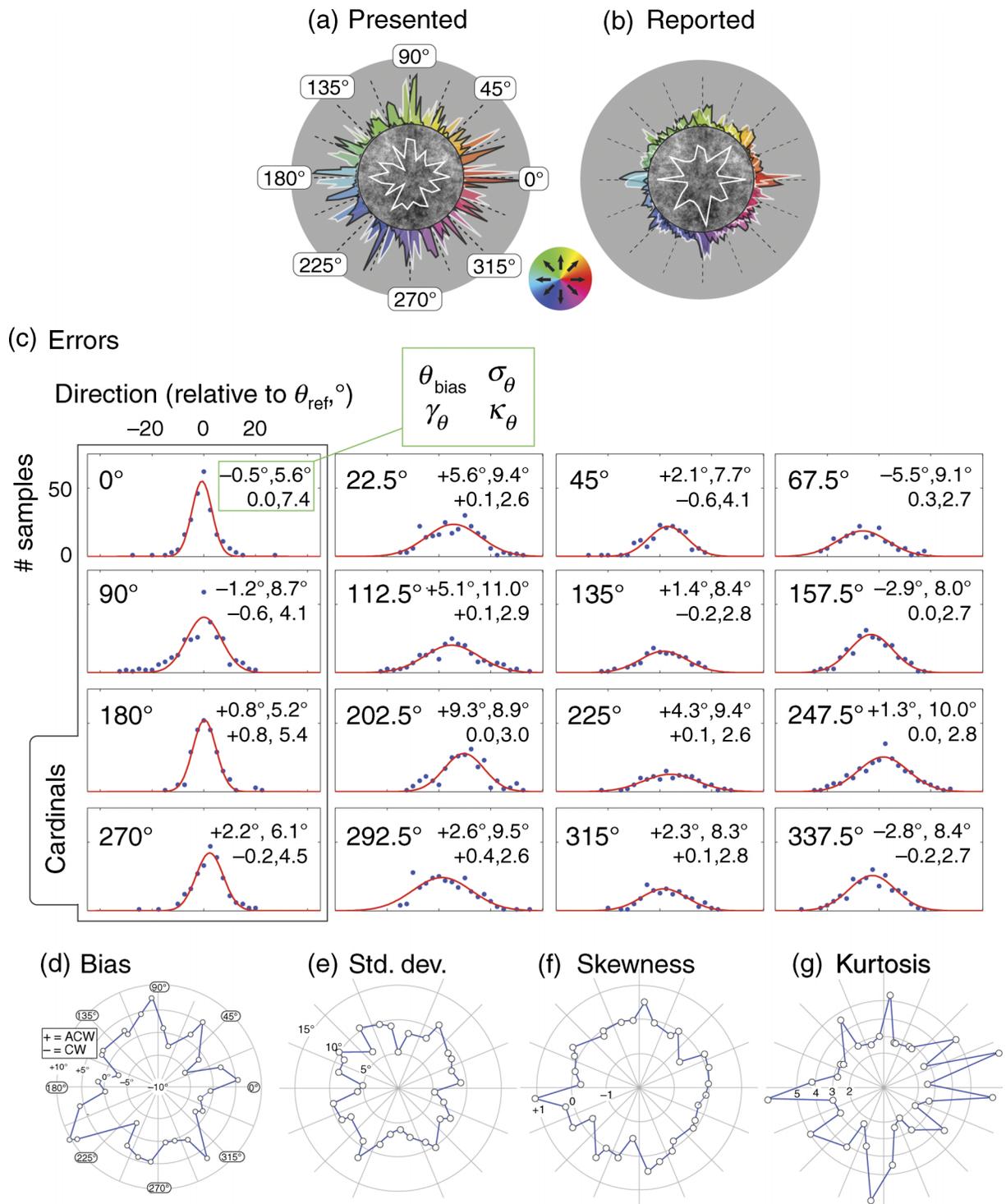


Figure 4. Data for fractal patterns. Colored regions are histograms (2° bin width) of directions (a) presented and (b) reported over 3392 trials by observer DMA1. Dashed black lines show the reference directions used to position the stimulus directions; histograms outlined in black and white are for stimuli presented clockwise or anticlockwise of the reference, respectively. These data are blocked by condition, but the white insets in the center of each plot are histograms (6° bin width) of directions, presented or reported, respectively, across all conditions. (c) Histograms of signed errors between DMA1’s report and the true direction of motion in each of the 16 reference direction conditions. Blue symbols are data, the red line is the best-fitting wrapped Gaussian, and the legend in each plot gives the bias, standard deviation, skew, and kurtosis of each distribution. (d–g) Plots of these four statistics for this subject’s data, as a function of the stimulus direction.

which is substantial given that variability is between  $\sim 5^\circ$  (cardinals) and  $\sim 10^\circ$  (obliques). Second, Figures 4f and 4g show that while errors are symmetrically distributed around the true directions, those errors are not consistently Gaussian-distributed but are more “peaky” around cardinal directions. This is important since the use of two-alternative forced choice procedures to assess direction discrimination makes assumptions about the nature of observers’ errors, including that they will be Gaussian-distributed (Figure 1). These data indicate that this assumption is being violated for this task.

Figure 5 pools summary statistics of error distributions from four subjects’ direction judgments made with the translating fractal image. We note a generally similar pattern of results to those observed in individual data (Figures 4d–4f) although some features of the results are now clearer. In particular, the bias data, plotted in Figure 5a, are again in the range  $\pm 10^\circ$  and tend to approach  $0^\circ$  on the cardinal direction. They also tend to be

negative (more clockwise) for slightly clockwise directions and positive (more anticlockwise) for directions slightly anticlockwise of cardinal directions. This is *reference repulsion* (Rauber & Treue, 1998): observers are likely to be using the cardinals as an internal “standard” for their judgments, and because the most informative channels for performing the task tend to be located slightly clockwise and anticlockwise of the cardinal reference, this can bias the appearance of the stimulus (Jazayeri & Movshon, 2007). Our results are not as clear as those from Rauber and Treue (superimposed in Figure 5a in orange), as our data indicate reliable repulsion only around  $90^\circ$  and  $180^\circ$ . However, we note that Rauber and Treue pooled across 11 subjects to gain their effect and that others have failed to find reliable reference repulsion effects at all (Wiese & Wenderoth, 2008).

To what extent might the findings in Figure 5 be determined by the nature of the stimulus, and how much

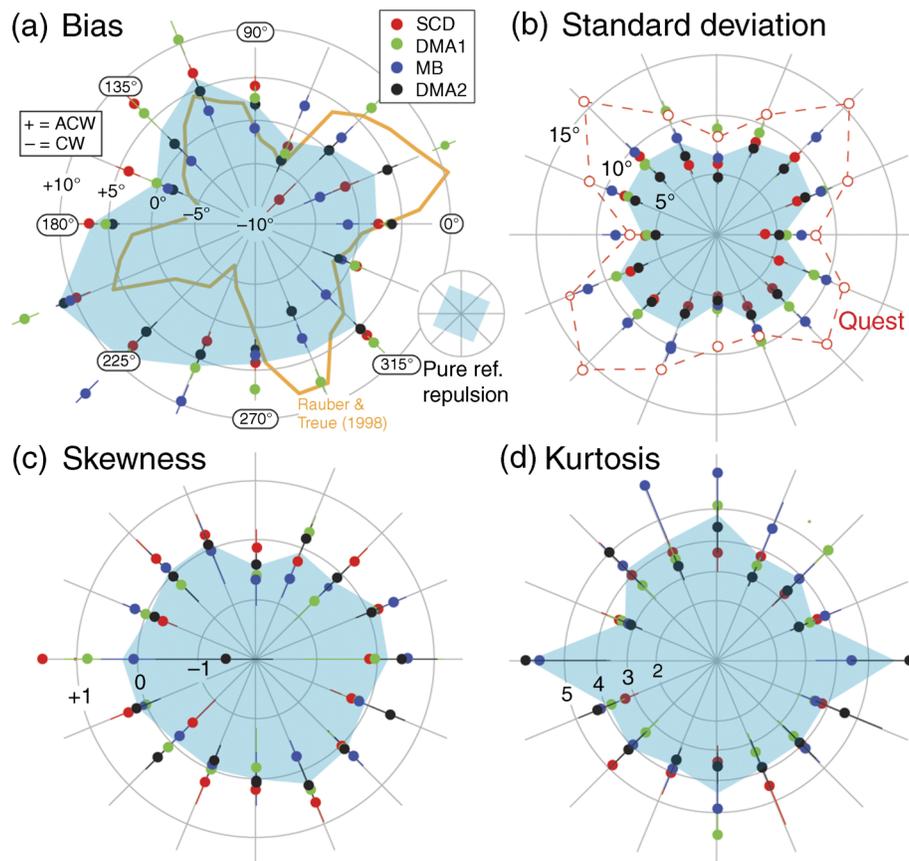


Figure 5. Four statistical moments of all observers’ error distributions for judging the direction of a translating fractal pattern. Symbols show estimates derived from individual observers’ data (direction errors relative to the true/cued direction), error bars indicate 95% confidence intervals on those estimates derived using a bootstrap, and shaded regions indicate mean values across subjects. (a) Directional bias tends to be positive when just clockwise, or negative when just anticlockwise, of cardinal directions indicating that subjects were prone to “reference repulsion” (orange line; Rauber & Treue, 1998). (b) Two estimates of precision: open symbols show the estimate of discrimination threshold (across subjects) derived from the QUEST adaptive staircase procedure, while filled symbols show the standard deviations of observers’ distributions of direction judgments. Note that both estimates are lowest on the cardinal directions, a manifestation of the well-known oblique effect, but that QUEST tends to systematically overestimate threshold. (c) Skewness is near zero across direction. (d) Kurtosis (the “peakiness” of the error distribution where 3.0 is Gaussian) is markedly elevated on the cardinal axes.

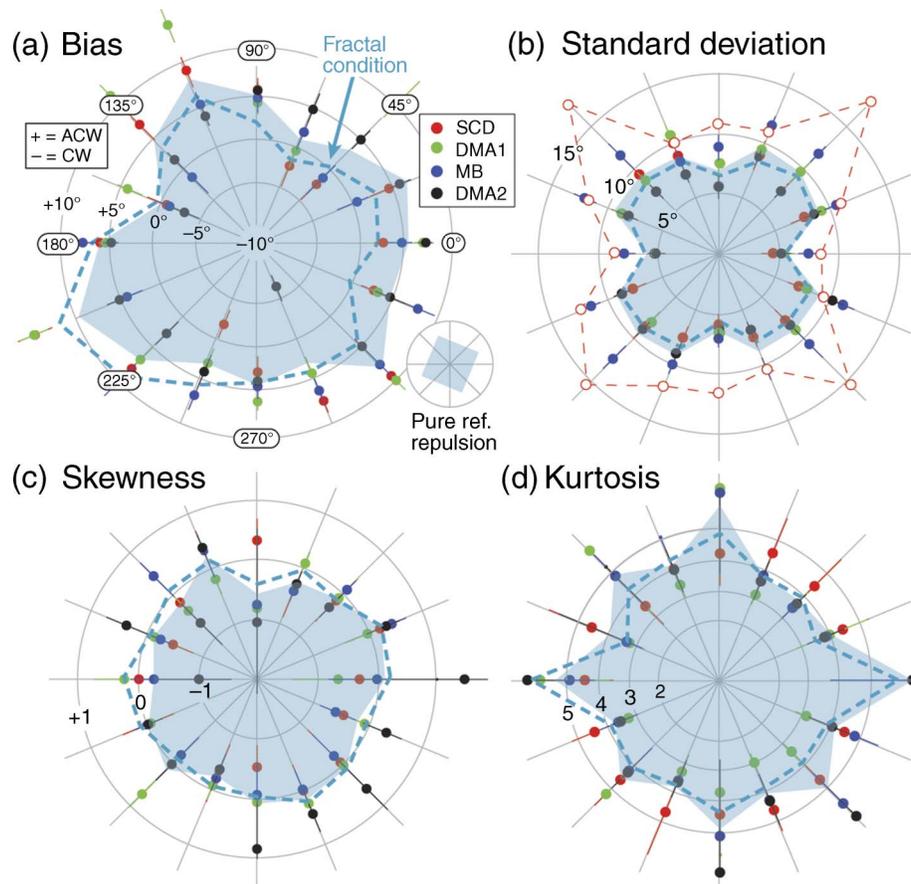


Figure 6. As for Figure 5, except that the translating image is a natural scene rather than a fractal. Note the high level of consistency with most measures from the fractal image data in Figure 5 (shown by the blue dashed line), except that the natural scene elicits error distributions with consistently higher kurtosis.

by the observer? To find out, we also measured absolute direction judgments for translating natural images. Such stimuli allow us to study two additional factors that may contribute to direction judgments under more natural conditions. Although natural scenes contain extended contour structure and may therefore potentially suffer from the aperture problem, they also offer the opportunity for the observer to use top-down information to constrain their judgments (using recognizable visual objects, etc.). Results for natural images are plotted in Figure 6 and show a very high level of agreement with performance measured with the drifting fractals (superimposed as blue dashed lines). The very similar results suggest that the pattern of results observed above is linked to the observer and not the stimulus. The natural image data show a near-identical pattern of bias, similar variability ( $6.2^\circ$  on the cardinals and  $9.1^\circ$  on the obliques, an average elevation of 45%), skewness is again minimal (averaging  $-0.06$ ), and kurtosis is generally slightly higher (4.5 on the cardinals compared to 3.2 on the obliques). In Figures 5 and 6, the standard deviation estimate averages  $7.8^\circ$  (group average, pooling over all directions). Therefore, the variability of direction judgments for natural images and fractal patterns are very similar, although several times higher than 2AFC

discrimination thresholds (82% correct) obtained with translating dot patterns moving in cardinal directions (Dakin et al., 2005a, 2005b).

## Experiment 2: Effect of adaptation on perceived direction of motion in natural scenes

In the last experiment, we described the pattern of errors that observers make when judging the absolute direction of a translating image. In this experiment, we investigated the effect of prolonged adaptation to a moving natural scene on those error distributions. Our reason for looking at adaptation was to address the long-standing issue of what the mechanism of adaptation is, and by extension to consider whether it might confer functional benefits on the observer. As outlined in the Introduction section (see Figure 1), analysis of data based on binary forced choice discrimination may misattribute any improvement in performance following adaptation to a reduction in

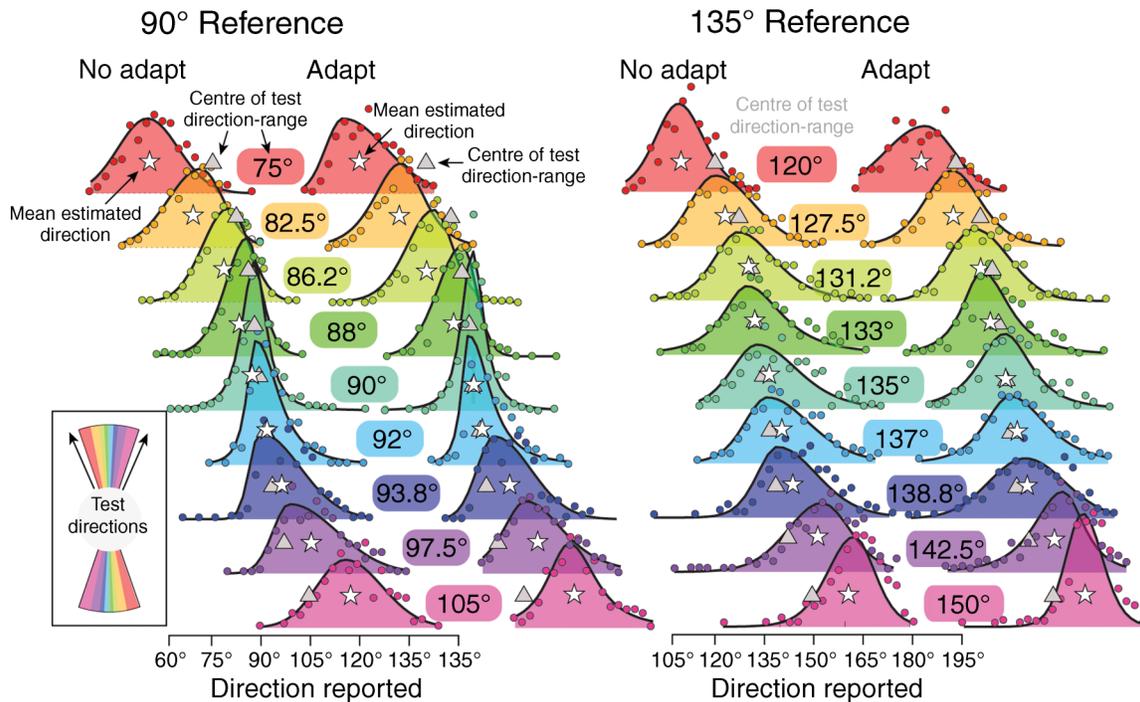


Figure 7. Effect of adapting to cardinal (left side) and oblique (right side) directions on subsequent direction estimation. The x-axis is the absolute test direction, and data show the pooled frequency with which the five observers reported a direction of motion given a test direction indicated by the figures shown in the colored boxes. Raw data (filled circles) have been fit with a 5-parameter asymmetric Pearson distribution. For each row of the figure, the triangles indicate the true test direction and the stars the mean direction reported (i.e., over the color-shaded histogram, key to colors is boxed in the lower left). The magnitude of offset between the stars and triangles is an indication of the amount of “reference repulsion.” Note that the left distributions around 90° (teal-colored) are substantially narrower and more “peaky”—both before and after adaptation—than the corresponding distributions on the right (i.e., centered on 135°). Note also that the distributions on the left (e.g., 97° and 88°) tend to be skewed such that the tail is longer pointing away from the true direction; that is when the mean is to the left/clockwise of the true direction the skew is negative and that when the mean is to right/anticlockwise of the true direction the skew is positive. Fewer systematic changes in skew are evident in the 135° condition (e.g., note the switch in sign of skew between distributions centered on 139° and 143° in the unadapted 135° condition).

variability in the underlying representation of direction, when it may instead be due to a change in mean, kurtosis, or skew of direction information. In this experiment, we again use absolute direction estimation, this time to reveal the effect that adaptation has on subjects’ distributions of direction judgments.

### Results

Direction estimates, pooled across all five observers, are plotted in Figure 7. Raw data (filled circles)—the number of times observers reported a given direction as a function of the true direction—have been fit (using the Matlab `fmins` function) with a five-parameter wrapped asymmetrical type VII Pearson distribution. The probability density function for a standard type VII Pearson distribution is defined (Pearson, 1916) as

$$p(\theta) = \frac{1}{\alpha B(m - \frac{1}{2}, \frac{1}{2})} \left[ 1 + \left( \frac{\theta - \mu}{\alpha} \right)^2 \right]^{-m}, \quad (9)$$

where  $B$  is the Beta function (evaluated using a numerical approximation in Matlab) and

$$\alpha = \sigma \sqrt{2m - 3}, \quad (10)$$

where  $m$  controls the kurtosis of the distribution ( $m > 3/2$ ). The parameter  $\sigma$  and  $\mu$  control the mean and standard deviation of the distribution. An asymmetric prediction is derived by generating two distributions with a common mean and kurtosis (the first and second free parameters), but with different standard deviations ( $\sigma_1$  and  $\sigma_2$ , the third and fourth parameters), matching the peaks of the two distributions and joining the left component of one distribution with the right of the other, at the point of the mean. The final (fifth) parameter is an overall scaling factor. Note that these distributions are fit only for graphical purposes: all statistics of kurtosis, etc., reported below are computed from the raw data not from the parameters of the fit.

The resulting fits (Figure 7, shaded regions) generally provide very good characterizations of the data. Two

general points emerge from inspection of these data. First, we observe some similarities and differences between these distributions and the data collected in [Experiment 1](#). Distributions of direction judgments around  $90^\circ$  are still narrower and more peaky than around  $135^\circ$ . We again see reliable repulsion of the mean reported direction of the test (stars) compared to its true direction (triangles). However, this effect is now evident both around  $90^\circ$  and  $135^\circ$ . This is interesting because we did not observe reliable direction repulsion around  $135^\circ$  in [Experiment 1](#) (see [Figures 5](#) and [6](#)); if anything the trend was for attraction toward  $135^\circ$ . There are two possible explanations for this. First, we sampled test directions much more coarsely ( $22.5^\circ$  steps from  $0$  to  $347.5^\circ$ ) in [Experiment 1](#) compared to here ( $\pm 15^\circ$ ,  $\pm 7.5^\circ$ ,  $\pm 3.75^\circ$ ,  $\pm 1.87^\circ$ , and  $0^\circ$ ), so that we may have simply missed the fine structure of the observers' bias around  $135^\circ$ . Second, the direction repulsion effects we see (in the pooled data) may in some sense be defined relative to the center of the range of directions presented. This makes sense if the observers are using this direction as an implicit reference relative to which they make their (absolute) judgments of direction. We return to this point in the [General discussion](#) section. An interesting difference with the data from [Experiment 1](#) concerns the skew of the distributions. In [Experiment 1](#), distributions of reported directions were fairly symmetrical (i.e., skew was on average  $0$ ) whereas here we see pronounced skew of some distributions (e.g., with a  $94^\circ$  test). The direction of this skew is such that the longer tails tend to point away from the true direction. We return to this point below when we compare quantitative estimates of skew across conditions.

A second point to be drawn from [Figure 7](#) is that distributions change subtly after adaptation to  $90^\circ$  motion (left set of plots) but less so with adaptation to  $135^\circ$  motion (right set). In particular, the distributions shift away from the  $90^\circ$  adapting direction (compare the separation of stars—the mean of each distribution—with triangles—the true test direction, before and after adaptation) but less so from  $135^\circ$ . Adaptation does not appear to change other features of the distributions (such as their width).

We next consider statistical properties of the observers' distribution of direction estimates before and after adaptation. The effect of adapting to  $90^\circ$  and  $135^\circ$  on subjects' direction estimates are plotted in [Figures 8](#) and [9](#), respectively. Considering first the unadapted performance for  $90^\circ$  plotted in [Figure 8](#) (open symbols, dashed lines), we observe broadly similar patterns of results to those described above for [Experiment 1](#). However, the finer sampling of direction used in this experiment (9 values between  $\pm 15^\circ$ ) has revealed two points very clearly. First, there is a sigmoidal pattern of bias ([Figure 8](#), left column), which indicates a pronounced “reference repulsion” (Raubert & Treue, 1998). Observers' direction judgments reveal that they effectively “exaggerate” the clockwise or anticlockwise directions when presented with motion that is slightly off the cardinal axis. It is

interesting to note how smoothly this repulsion increases as one moves only a few degrees either side of the cardinal direction, and that it returns to veridical (i.e., returns to the unit slope line) at about  $\pm 15^\circ$  from vertical. The second point to emerge clearly from these data is the modest but systematic modulation of skew around  $90^\circ$  ([Figure 8](#), third column), which we did not detect using the coarser sampling of test directions in [Experiment 1](#). Specifically, subjects' distributions for directions just either side of the cardinal are skewed with opposite skew sign (compare distributions for  $84^\circ$  and  $96^\circ$  tests in [Figure 7](#)). The switch in skew sign around the cardinal is consistent with the bias underlying the reference repulsion effect, which also switches in sign around the cardinal direction. The other two statistics plotted in [Figure 8](#) show that there is a dip in the standard deviation around  $90^\circ$  showing that there is an oblique effect of similar magnitude to that of [Experiment 1](#) (see [Figures 5](#) and [6](#)) as well as a robust peak in the kurtosis of direction distributions near the cardinal direction.

Turning to the adapted performance for  $90^\circ$  ([Figure 7](#), filled symbols, solid lines), there is no clear evidence that adaptation alters any of these statistics, with the exception of bias. This is consistent with the well-known repulsive effects of adaptation on perceived direction (Levinson & Sekuler, 1976). What is new here is that our data (column 1) indicate that the bias change from adaptation arises from an *amplification* of underlying direction repulsion (i.e., present before adaptation). For example, the tendency to see directions that are slightly clockwise of  $90^\circ$  as further clockwise than is veridical is exaggerated by adaptation (and vice versa for anticlockwise directions). This effect is present but subtle for subject SCD but is pronounced for MB. The modulation of skew around  $90^\circ$  (with equal and opposite signs) observed in the unadapted condition is also seen after adaptation. Although the skew effect is not altered by adaptation, the replication of this subtle effect is striking.

Another interesting aspect of the data is that there was no change in the standard deviation of direction distributions following adaptation. These data argue the notion that adaptation might reduce variability in the representation of motion direction that could explain established improvements in discrimination around the adapted direction (Phinney, Bowd, & Patterson, 1997). We shall see in the simulations below ([Figure 9](#)) that a change in bias is sufficient to produce a robust improvement in 2AFC discrimination performance.

[Figure 8](#) plots an identical analysis of direction errors after subjects adapted to motion in a non-cardinal direction ( $135^\circ$ ). Looking first at the no-adapt conditions (open symbols, dashed lines), we observed less reference repulsion for  $135^\circ$  than for  $90^\circ$  (but still substantially more than reported in [Experiment 1](#)) and confirmed the oblique effect in that standard deviations are greater for  $135^\circ$  than for  $90^\circ$  and exhibit a clear peak around  $135^\circ$ . Data for the higher order statistics of skew and kurtosis

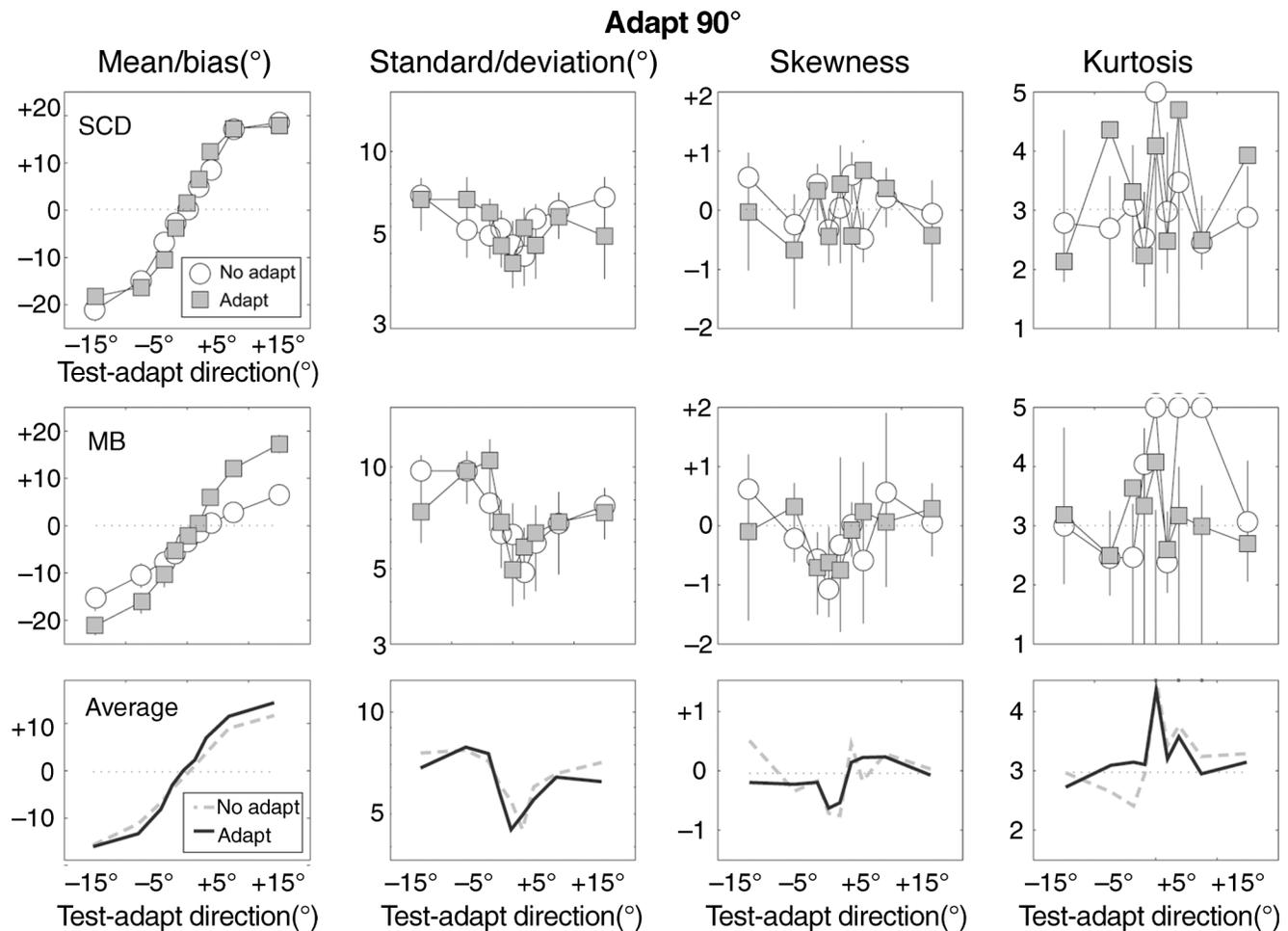


Figure 8. Effect of adapting to a cardinal direction on subsequent direction estimation. The abscissa shows the actual test direction relative to the 90° adapter (adapt minus test); the ordinate shows perceived test direction (relative to the adapter). The four summary statistical descriptions of subjects' errors are plotted for two subjects and the average across all five observers. Note that the reference repulsion effect (the sigmoidal modulation of bias around 90°) is amplified with adaptation (particularly in MB) but that generally other statistics remain largely unaffected.

are more variable and show no systematic change. Turning to the adaptation data (filled symbols, solid lines), we again see that standard deviation is not reduced by adaptation (consistent with adaptation to 90° directions), and reference repulsion is not modulated by adaptation.

Finally, we can use the subjects' error distributions to predict their performance on a 2AFC discrimination task, assuming independent representation of the directions presented in the two intervals. We ran a Monte Carlo simulation to simulate psychometric functions, which are presented in Figure 10. The simulation shows that adaptation to 90° results in a statistically significant improvement (based on *t*-tests of the bootstrapped estimates of the  $\sigma$  parameter of the psychometric functions) in four of the five subjects (all but DMA1) and that adapting to 135° produces improvement in only one of the subjects (DMA2). The reliable improvement in discrimination following adaptation to 90° is interesting because it occurred even though the variability of

direction judgments was not altered by adaptation. As the group averages in Figure 8 show, the primary effect of adaptation was to alter bias, not standard deviation. This simulation demonstrates that adaptation can lead to improved discrimination due to changes in bias.

## General discussion

In two experiments, we have characterized the distributions of absolute direction judgments made by observers viewing translating natural scenes. Using large numbers of observations (each subject made between 1024 and 2048 direction judgments per distribution), we were able to characterize the first four statistical moments of each distribution, that is, the mean, standard deviation, skew, and kurtosis. We compiled distributions

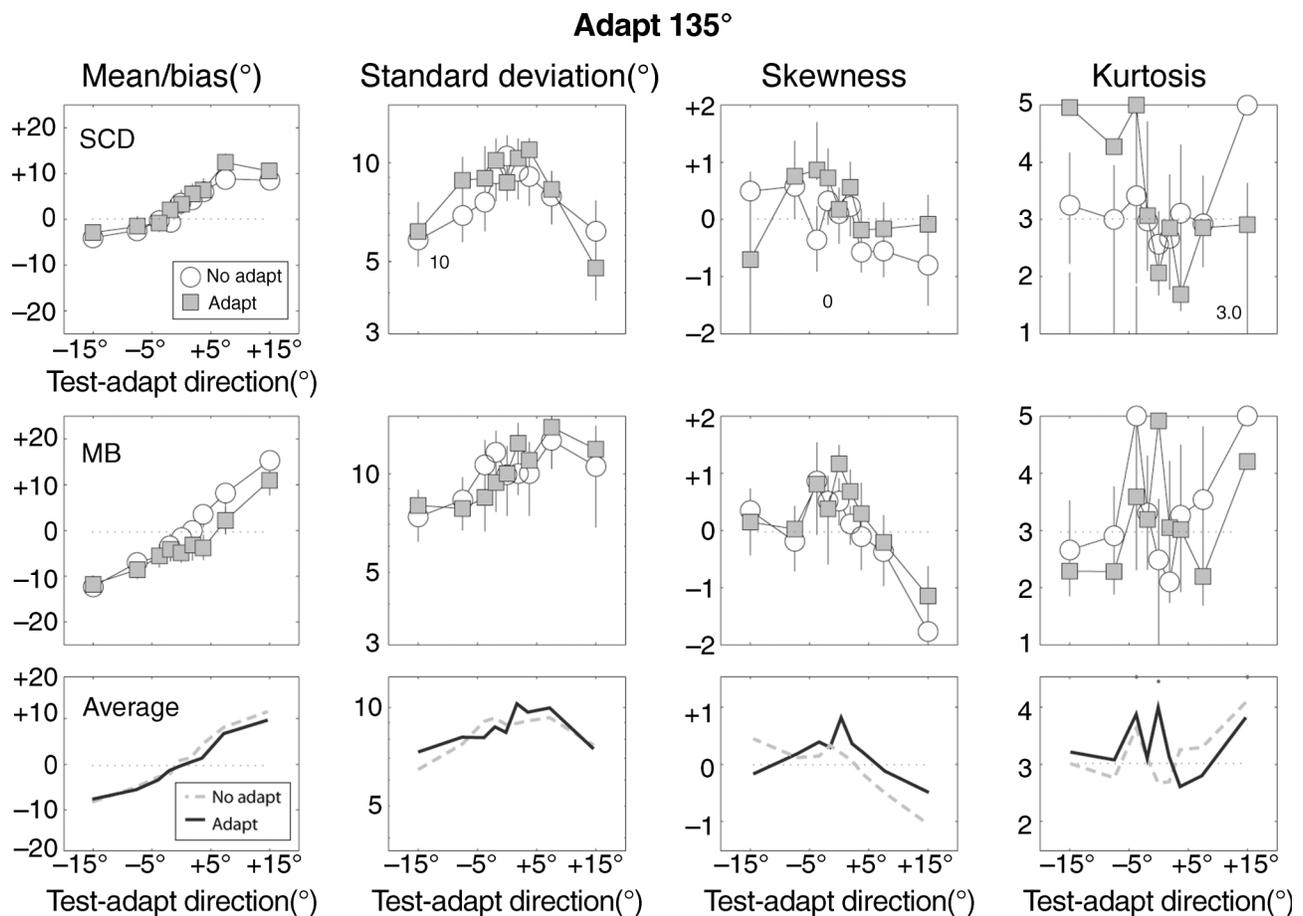


Figure 9. As for Figure 8, except the adapting direction is to a non-cardinal direction (135°). Again summary statistical descriptions of subjects' errors are plotted for individual subjects and the average. There is a much more modest reference repulsion effect around 135°, which is not greatly shifted under adaptation. No other systematic effects of adaptation are apparent in the other statistics.

for 16 directions equally spaced around the clock in [Experiment 1](#), and for 9 directions finely spaced around a cardinal (90°) or an oblique (135°) direction in [Experiment 2](#). Measurements made in [Experiment 2](#) were made with and without prior adaptation to the cardinal or oblique direction.

Looking at [Experiment 1](#), the clearest result concerned the variation in standard deviation over direction. Standard deviation was lowest for cardinal directions, and for a narrow range either side of the cardinals, and was elevated elsewhere, revealing a broad region subject to the “oblique effect.” The other clear effect concerned kurtosis, with distributions on the cardinals having elevated kurtosis values above the value of 3.0, which indicates a perfect Gaussian form. Values above 3.0, such as observed on the cardinals, indicate a leptokurtic or “peaky” shape with a disproportionate number of near-zero values. Finally, there was a tendency for the mean of distributions close to the cardinal directions to be pushed away from the cardinal. This tendency to perceive directions close to the cardinals as being further from the cardinal than they truly are is known as “reference repulsion” (Raubert & Treue, 1998) although in our case

since no reference was present on screen we infer that observers use the cardinal directions as implicit references when making judgments of absolute direction.

Turning to [Experiment 2](#), we measured how perception of motion in the cardinal or oblique directions was affected by preadaptation to those directions. The test directions around these two standard directions were finely spaced (9 directions spanning  $\pm 15^\circ$ ) and clearly showed a systematic effect of reference repulsion around the cardinal direction ([Figure 8](#), left column), an effect that was enhanced by adaptation. In this experiment, unlike in the last, we do observe reference repulsion around the oblique ([Figure 9](#), left column), but adaptation exerts less influence. The fine spacing of test directions also revealed an interesting change in skew. The skew value departs from zero (a value indicating symmetry) for directions close to 90° and does so with equal and opposite magnitude either side of 90°. This skew effect was constant between adapt and no-adapt conditions. Together with the dip in standard deviation for the cardinal direction, and the increase in kurtosis at the same direction (replicating the kurtosis result from [Experiment 1](#)), these data describe a narrow, peaky

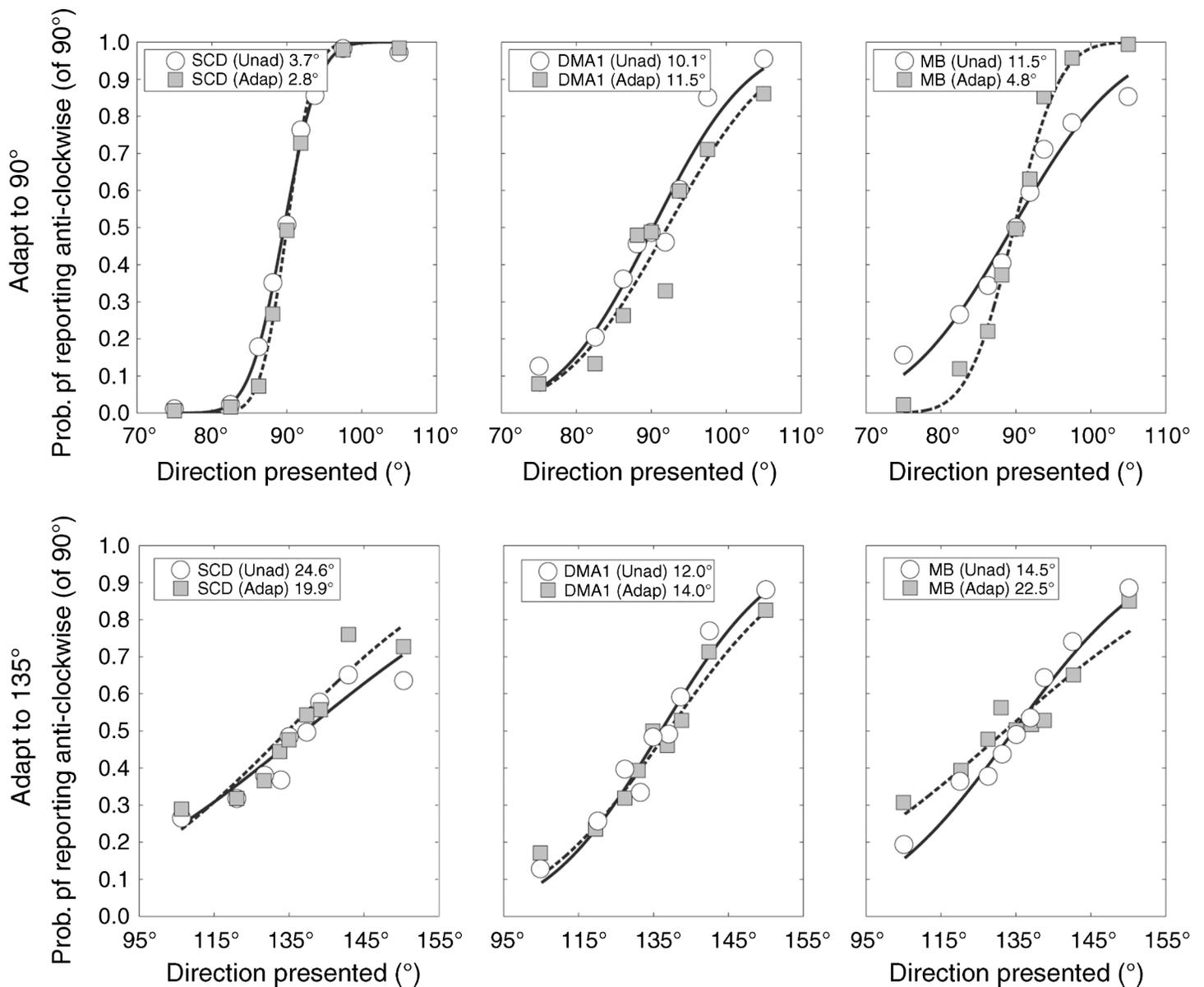


Figure 10. Predicted psychometric functions from a Monte Carlo simulation based on three subjects' error distributions from the adaptation experiment. The top row shows predictions for 90° adapters, the bottom row for 45° adapters, and the boxed caption shows the predicted threshold in degrees.

distribution centered on the cardinal, flanked on each side by skewed and slightly broader distributions (Figure 7). As shown in Figure 7, the flanking distributions have their steep sides bordering the narrow and peaky cardinal distribution and their shallow side trailing off more gradually toward oblique directions. Adaptation in the cardinal direction has the effect of shifting these skewed distributions away from the cardinal but leaves them otherwise unaffected.

One very interesting observation to emerge from Experiment 1 is that estimates of directional precision varied quite dramatically depending on the procedure used to quantify it. Figures 5b and 6b plot two estimates of precision: the standard deviation of the direction distributions

compiled from our absolute direction judgments and the estimate of precision produced by the QUEST adaptive staircase procedure (recall that QUEST was used as a tool to sample the directions presented around each of the 16 directions used in Experiment 1). The open symbols and dashed lines in Figures 5b and 6b show the group average estimate of discrimination threshold derived from QUEST, while outer limits of the shaded region show the standard deviations of observers' distributions of judged direction. Although both measures agree qualitatively, in that both produce estimates that are lowest in the cardinal directions (the well-known oblique effect), they differ markedly in quantitative terms. The precision estimate (i.e., standard deviation) from QUEST tends systematically

to overestimate the precision of the empirically obtained distributions.

The difference between the two measures of precision is significant because one is empirically derived from actual distributions while the other (QUEST) is theoretically derived. That is, QUEST is driven by subjects' discrimination performance, which in turn is supposed to reflect underlying variability in the observers' representation of the stimulus attribute. Crucially, this approach assumes that observers are unbiased and display Gaussian-distributed errors. That is, the assumed underlying distribution has a bias of 0 and a kurtosis of 3. The data from our empirically derived direction distributions plotted in Figures 5 and 6 show that this is not true of observers and for this reason the use of thresholds derived from QUEST are not a true reflection of observer variability. Our method produces a standard deviation estimate of  $7.8^\circ$  (the group average, pooling over all directions), while the QUEST estimate is  $11.8^\circ$ . Therefore, the assumptions underlying QUEST lead to an overestimation of the empirical standard deviation by a factor of 1.5, and this tendency was exaggerated in the oblique directions where the overestimation increased to a factor of 2.

Another interesting point to emerge from Experiment 1 is that the resolution of direction appears to be poorer using our absolute direction task on natural or fractal patterns than previous studies have found. The average standard deviation in the cardinal directions is  $\sim 6.5^\circ$  (see Figures 5 and 6) and is several times higher than the discrimination thresholds obtained with translating dot patterns moving in cardinal directions ( $\sim 1.25^\circ$ ) using a 2AFC task and 82% correct thresholds (Dakin et al., 2005a, 2005b). Why should previously reported thresholds be so much lower than the variability in our observers' direction distributions suggest? One possibility is that it is due to the different stimuli used in these studies. This

seems unlikely as the translating patterns in both studies were broadband in spatial frequency and directional structure, and both were composed of unambiguously translating two-dimensional texture. Moreover, natural scenes are presumably optimal for visual processing and performance on the fractal pattern was just as good (cf., Figures 5 and 6). A more likely possibility is that 2AFC performance, assumed to depend only on underlying variance, can exploit other statistical properties, such as kurtosis and skew, to improve thresholds. On this point, our results are revealing. For kurtosis (where Gaussian has a value of 3.0), off-cardinal distributions are strongly Gaussian (fractal pattern:  $k = 3.0$ ,  $s = 0.26$ ; natural scene:  $k = 3.0$ ,  $s = 0.27$ ), whereas on the cardinal directions kurtosis rises to 4.3 ( $s = 0.67$ ) for fractals and 4.5 ( $s = 0.35$ ) for natural scenes. Our data also reveal that skewed distributions lie next to the cardinals (Figure 7, bottom of third column), which may be critical as flanking distributions play a key role in improving discrimination (Jazayeri & Movshon, 2007; Regan & Beverly, 1985). When the elevation in kurtosis on the cardinals (indicating “peaky” distributions) is combined with skewed flanking distributions (see Figure 9b), we consider there is ample scope for statistics other than simple variance to drive 2AFC performance lower than variance-only models would predict.

The point regarding elevated kurtosis on the cardinals is summarized in Figure 11, which replots directional errors from the fractal condition of Experiment 1 (pooling across subjects) in three directional categories: cardinal ( $0^\circ$ ,  $90^\circ$ ,  $180^\circ$ ,  $270^\circ$ ), principal oblique directions ( $45^\circ$ ,  $135^\circ$ ,  $225^\circ$ , and  $315^\circ$ ), and other oblique directions ( $22.5^\circ$ ,  $67.5^\circ$ ,  $112.5^\circ$ ,  $157.5^\circ$ ,  $202.5^\circ$ ,  $247.5^\circ$ ,  $292.5^\circ$ ,  $337.5^\circ$ ). All errors have been normalized to zero mean and unit standard deviation; thus the only differences between distributions must be attributable to higher statistical properties of the

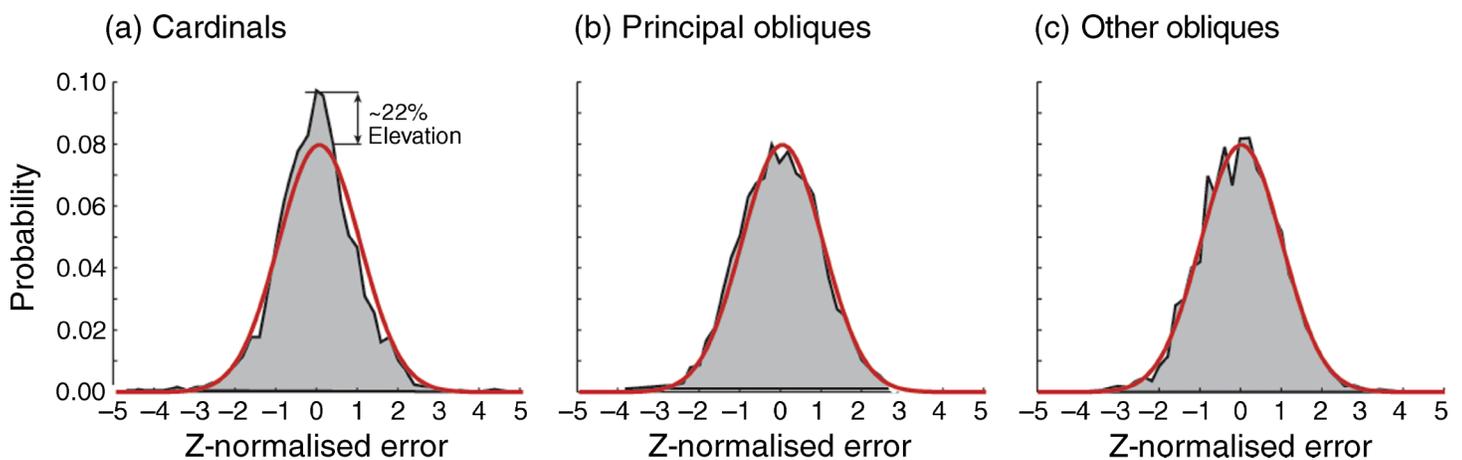


Figure 11. Errors from the fractal noise condition, normalized to have zero mean and unit standard deviation, pooled across all subjects in the direction conditions indicated. Note that data from the cardinal conditions are “peakier” than the Gaussian prediction (red line) and that deviation from normality leads to around 22% higher probability of near-zero errors in the cardinal case *even when variance and bias of the data have been equated*.

error distributions. The red curves plot a Gaussian with unit standard deviation and zero mean. Note that around the cardinal directions the proportion of near-zero errors is substantially higher than the Gaussian model predicts. This “cardinal effect” is on the order of 20% or so. Looking at the variability of observers’ errors in estimating direction within these three categories, we observe an “oblique effect.” That is, comparing the cardinals with the pooled oblique directions, there is an increase of ~45% in standard deviation for both fractals and natural scenes. This is substantially lower than previous estimates of the oblique effect of nearer a 100% increase (Dakin et al., 2005a, 2005b). Again, for the same reasons as noted above, this overestimate may be due to the contribution of statistics other than variability, which do not form part of standard 2AFC modeling of thresholds.

The results of these two experiments are relevant to related work by Dakin et al. (2005a). They investigated direction discrimination using an equivalent noise paradigm and concluded that poor discrimination around oblique directions was due to precision limitations in local motion processing, rather than to limitations at the global pooling stage. The authors proposed a channel model of human direction discrimination based on wrapped Normal channel profiles, Poisson/multiplicative noise, and maximum likelihood estimation. This model could account for fine discrimination of clockwise/anticlockwise directions in the presence of directional variability and predicted that the representation of global direction should reflect the anisotropies in the earlier local motion stage. Specifically, they plotted the combined (population) response of a set of filters derived from natural motion statistics and predicted that distributions of responses around cardinal directions should have lower standard deviations and should be more leptokurtic or “peaky.” The results discussed here clearly confirm these predictions and confirm that absolute direction judgments (global perceptual output) do reflect earlier local motion anisotropies. Moreover, by collecting a large number of absolute direction estimates we were able to compile distributions and to describe their first four statistical moments (mean, standard deviation, skew, and kurtosis) and to describe how they vary across a 360° range of directions. Apart from confirming kurtotic “peaky” distributions at the cardinals, and a rather narrow band of high precision centered on the cardinals (the fat-“X” pattern in Figures 5b and 6b), there also appears to be modest skew in distributions just adjacent to the cardinal. This effect was only measurable with the finer spacing of test directions employed in Experiment 2; the intrinsic “blurring” of responses induced by the motion-energy filtering stage used by Dakin et al. (2005a) meant that these authors were unable to make specific predictions concerning skew over this range.

Finally, a comparison with earlier data estimating oblique effects and directional precision using 2AFC methods reveals estimates that differ substantially from

the distribution statistics reported here, suggesting that some or all of these higher order statistics may be involved in perceptual judgments, in contrast to standard models of 2AFC performance that consider only variability.

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Corresponding author: Steven C. Dakin.

Email: s.dakin@ucl.ac.uk.

Address: Institute of Ophthalmology, University College London, Bath Street, London EC1V 9EL, UK.

## Footnote

<sup>1</sup>Kurtosis refers to the “peakedness” of a distribution. A high kurtosis (“leptokurtic”) distribution has a taller, sharper peak than a Gaussian distribution, with broad light tails. A low kurtosis (“platykurtic”) distribution has a lower, more rounded peak, with heavy narrow tails.

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