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Perception of opposite-direction motion in random dot kinematograms

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Abstract

Computational models of motion perception suggest that the perceived direction of weak motion signals may sometimes be directly opposite to the true stimulus motion direction. However, this possibility cannot be assessed by using standard 2AFC motion discrimination paradigms because two opposite directions of motion were used in most studies (e.g., leftward vs. rightward). We were able to obtain robust evidence of opposite-direction motion reports by using a random-dot-kinematogram (RDK) paradigm in which the motion direction varied over 360° and observers were asked to estimate the exact motion direction. These opposite-direction motion reports were replicable across multiple display types and feedback conditions, and observers had greater confidence in their opposite-direction responses than in true guess responses. When we fed RDKs into a computational model of motion processing, we found that the model estimated substantial motion activity in the direction opposite to the coherent stimulus direction, even though no such motion was objectively present in the stimuli, suggesting that the opposite-direction motion perception may be a consequence of the properties of motion-selective neurons in visual cortex. Together, these results demonstrate that the known properties of the visual system may lead to reports of motion that are directly opposite to the true direction.

Keywords

motion perception; opposite direction; RDK; continuous direction estimation

Introduction

Perceptual decisions often involve integrating information over both space and time. This is especially true of global motion perception (e.g., perceiving the average direction of a school of fish despite variations in the direction of individual fish within the school). To understand this type of perception, researchers typically use random dot kinematograms (RDKs), in

which some dots move coherently in a single direction and other dots move randomly (Kim & Shadlen, 1999; Roitman & Shadlen, 2002). The ability of observers to report the direction of the coherent motion typically increases as the percentage of coherently moving dots increases. This experimental paradigm has been used for many decades to study both specific mechanisms of motion perception (Braddick, 1980; Julesz, 1971) and general principles of decision making (Gold & Shadlen, 2007).

One important characteristic of typical RDKs is that temporal smearing of the stimulus can produce the perception of *streaks*, perceived line segments oriented along the axis of motion (Geisler, 1999). These streaks are known to influence motion perception (e.g., Apthorp, Cass, & Alais, 2011; Burr & Ross, 2002; Geisler, Albrecht, Crane, & Stern, 2001) because a streak is equally consistent with the true direction of motion and the opposite direction. Although a neural circuit has been proposed for disambiguating the true direction from the opposite direction (Geisler, 1999), it is possible that this disambiguation fails on a substantial fraction of trials. In addition, studies on Glass pattern have shown that local pairs of random dots in a dynamic random-dot display can induce the global pattern of 'line orientations' (Glass, 1969; Nankoo, Madan, Spetch, & Wylie, 2012). This suggests that observers could perceive the opposite of true stimulus motion direction in RDKs.

However, this hypothetical opposite-direction motion perception cannot be detected in most studies using RDKs because most studies have required observers to choose between two opposite directions of motion (e.g., leftward vs. rightward; Britten, Shadlen, Newsome, & Movshon, 1993; Gold & Shadlen, 2007). In these tasks, it is impossible to distinguish between a complete failure to extract motion information and extraction of the correct axis of motion but incorrection perception of the direction along this axis. Popular computational models of perceptual decision making are based on this type of discrete choice task, and those models attribute the opposite-direction reports to the lack of direction evidence, biases in motion perception, or the lapses of attention (Gold & Shadlen, 2007) but not to a genuine perception of the opposite direction of motion.

The present study sought to find evidence that RDKs may lead to incorrect motion reports that are opposite to the true direction of motion rather than being random. Toward that end, we used a continuous direction estimation task with a 360° range of motion directions (see Figure 1). In pilot experiments that were conducted for a different purpose, we noticed that we and our participants frequently perceived the dots to be moving in the direction opposite to the true direction of coherent motion (Bae & Luck, 2019) (see also, Wang et al., 2015). We therefore designed the present experiments to determine whether this preliminary observation reflected a robust and replicable aspect of motion perception, which would have implications both for the mechanisms of motion perception and for the interpretation of perceptual decision-making experiments.

In Experiment 1, we examined opposite-direction motion perception under two levels of motion coherence and stimulus duration. If the illusion were simply a result of motion adaptation (as in the *waterfall illusion*; Crane, 1988), we would expect the rate of opposite-direction responses to increase as the stimulus duration increased. In Experiment 2, we used a different monitor type and changed the contrast polarity from white-on-black to

black-on-white to minimize physical persistence artifacts. In Experiment 3, we provided feedback about the true direction of motion after each report to ensure that participants were not confused about the task. In Experiment 4, observers indicated the confidence of each report so that we could determine whether opposite-direction reports were made with high confidence, which would suggest that these reports reflect conscious perception of the opposite-direction motion rather than an unconscious bias in guessing. Finally, we fed our stimuli into a mathematical model of motion processing (Kiani et al., 2008) that is based on the spatiotemporal tuning of neurons in area MT (Movshon et al., 1988) to determine whether substantial opposite-direction neural activity would be expected on the basis of the known properties of the visual system.

To preview our results, we found that observers made a significant number of opposite-direction reports in all four experiments, that they frequently made these errors with high confidence, and that the model of motion-related activity in area MT also yielded strong opposite-direction activity.

Experiment 1

Method

Participants.—Twenty-four college students (20 women, 4 men) between the ages of 18 and 30 with normal or corrected-to-normal visual acuity participated for course credit. An a priori power analysis was performed, using data from an electrophysiological study with a nearly identical task (Bae & Luck, 2019), and this analysis indicated that a sample size of 12 would be sufficient to have .9 power for detecting the presence of above-chance opposite-direction responding. We selected, a priori, a larger sample size of 24 so that we could have more precise estimates of the effects. The study was approved by the UC Davis Institutional Review Board and the Arizona State University Institutional Review Board.

Stimuli and procedure.—Stimuli were generated in Matlab (The Mathworks, Inc.) using PsychToolbox (Brainard, 1997; Pelli, 1997). Stimulus presentation scripts used in this study are available online at https://osf.io/fexmg. The stimuli were presented at 60 Hz on an LCD monitor (Dell U2412M) at a viewing distance of 70 cm. We confirmed the timing of the stimuli using an external photosensor (see Online Supplementary Material for a detailed characterization). The background of the display was set to white (87.6 cd/m^2), and a black circular disk (5° diameter, $< .1$ cd/m^2) was continuously visible at the center of the display except during the intertrial interval. Dots were presented in white (87.6 cd/m^2, 0.15° diameter) within the black disk.

The motion stimulus was generated online using a popular RDK algorithm (Roitman & Shadlen, 2002), with one small modification as described below. On each trial, the RDK consisted of a 300- or 1000-ms sequence of video frames. At the beginning of the trial, 336 dot locations were randomly distributed across a virtual aperture with a diameter of 20°, centered on the black disk, yielding an average density of 21.4 dots per square degree per second. However, a given dot was visible only when it was inside the 5° black disk. During the motion presentation, each dot was sent to the video display for one video frame (16.67 ms) and was then replotted in a new location after a 2-frame delay. The overall set of 336

dots was divided randomly into three sets, and one set was visible in each video frame. Thus, although a given dot was visible on only one of every three frames, one third of the dots were visible in every frame.

On every trial, the direction of coherent motion was chosen as a continuous value between 0° and 360° (see below). The speed of coherent motion was always 6°/s. The coherence level was randomly chosen on each trial to be 25% or 50%. When a given dot was replotted, it had a 25% or 50% chance (depending on the coherence level) of shifting by 0.3° in the direction of coherent motion for that trial. Otherwise, the dot was replotted at a random location within the 20° virtual aperture. When the new position of a dot was outside this aperture, that dot was replotted at a random location on the circumference of the aperture to maintain the dot density. However, this update was not visible to participants because only the dots within the 5° black disk were visible to participants.

The use of a smaller visible area within the larger virtual aperture was the one change we made in the standard RDK algorithm (Roitman & Shadlen, 2002). We made this change to avoid the possibility that the frequent appearance of new dots on the circumference of the aperture might somehow induce the perception of opposite-direction motion. We obtained nearly identical results in pilot experiments that did not include this change in the RDK algorithm, but our final experiments used the modified algorithm out of an abundance of caution.

As illustrated in Figure 1, each trial began with a 500-ms presentation of a red fixation dot (0.5°, 28.4 cd/m^2) at the center of the black disk, followed by a 300-ms or 1000-ms presentation of the RDK. Participants were instructed to attend carefully to the direction of motion during the entire motion period. At the end of the RDK, the fixation dot turned green (60.5 cd/m^2) to indicate that the observer should report the exact motion direction for that trial using the mouse. Once the participant started moving the mouse, a green probe dot appeared at a point on the circumference of the aperture that was in line with the position of the mouse cursor. A green line connecting the central dot and the probe dot was presented to indicate the direction. The orientation of the line was continuously updated as the mouse position changed, and participants adjusted the line until it matched the perceived direction of motion for that trial. They finalized the report by clicking a mouse button. This was followed by a 500-ms intertrial interval during which the display was blank.

To determine the direction of motion on a given trial, we first randomly selected a motion direction bin from twenty-four bins of discrete motion directions (from 7.5° to 352.5°, in steps of 15°). We then added a random value to select a random direction within the ±15° range of the selected bin. This procedure guaranteed that the actual distribution of motion directions would be relatively uniform for every observer in every condition, but any direction across the entire 360° space was possible.

Each session began with a minimum of 16 practice trials. During each practice trial, the participant's report on a given trial was followed by a 500-ms red line corresponding to the actual motion direction. This feedback stimulus was used to ensure that the participants understood how to report the perceived motion direction. Each participant completed a total

of 480 trials (120 trials for each of the four combinations of coherence and duration, with 5 trials per direction bin for each condition, in random order). The session was divided into 6 blocks of 80 trials.

Data Analysis.—For each trial, we computed the *response error*, defined as the angular difference between the true motion direction and the reported motion direction (i.e., true direction minus reported direction). The distributions of response errors for each condition, aggregated over participants, are shown in Figure 2a.

We used two different approaches to quantify the proportion of opposite-direction reports, one based on a *mixture model* and one that was model-free. Both approaches yielded the same basic pattern of results. For the sake of simplicity, we describe the model-free results here and provide a description of the mixture model and associated results in online supplementary materials.

In the model-free approach, we first counted the number of trials with responses that were approximately opposite to the true direction of motion ($180 \pm 30°$ error, shown as the red areas in Figure 1b), and divided that number by the total number of trials to compute the proportion of opposite-direction responses ($P_{Opposite}$). Responses in this opposite-direction range could sometimes be guesses rather than reflecting an actual perception of the opposite direction, so we used responses that were approximately orthogonal to the true direction ($90 \pm 15°$ and $-90 \pm 15°$ error, shown as the blue areas in Figure 1b) to estimate the guessing rate. We counted the number of orthogonal direction responses and divided that number by the total number of trials to compute the proportion of orthogonal direction responses ($P_{Orthogonal}$). Note that both the opposite-direction range and the orthogonal-direction range span $60°$, and uniform guessing would therefore be expected to yield equal numbers of reports in these two ranges. Consequently, the difference between $P_{Opposite}$ and $P_{Orthogonal}$ was used to estimate the proportion of true opposite-direction perceptions, which we termed $P_{Opposite-Orthogonal}$[1]. This is actually a conservative measure, because there is a greater probability that an imprecise perception of the true direction of motion would lead to a response in the orthogonal-direction range than in the opposite-direction range.

$P_{Opposite-Orthogonal}$ was not normally distributed according to the Shapiro-Wilk normality test (Shapiro & Wilk, 1965). Consequently, we used non-parametric permutation testing instead of parametric statistics. For the sake of simplicity, we mainly compared $P_{Opposite-Orthogonal}$ with chance (= 0) in each condition separately and then applied a false discovery rate (FDR) correction for multiple comparisons (Benjamini & Hochberg, 1995). In a given permutation test, we compared the mean $P_{Opposite-Orthogonal}$ across observers with a null distribution determined by randomly permuting the labels for the opposite- and orthogonal-direction trials within each observer and then computing the opposite-minus-orthogonal difference score. This permutation reflects the null hypothesis that the number of opposite-direction reports, and the number of orthogonal direction reports are samples from the same population, so taking the opposite-minus-orthogonal difference score should be the

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[1]All the analysis reported here is on POpposite-Orthogonal. We provide the data for the two types of reports separately in online supplementary materials.

same as taking the orthogonal-minus-opposite difference score. We iterated this permutation procedure 10,000 times to construct an empirical null distribution, and the *p* value for the test was calculated as the percentile relative to this null distribution. An observed $P_{Opposite-Orthogonal}$ was considered statistically significant if it fell in the top or bottom 2.5% of the null distribution (i.e., a 2-tailed test with alpha = .05) after the FDR correction. This was done for each combination of motion coherence and duration separately.

Experiment 1 used a 2 x 2 factorial design with factors of duration (300-ms vs. 1000-ms) and coherence (25% versus 50%). To examine the main effect of duration with a permutation test, we simply averaged $P_{Opposite-Orthogonal}$ across the two coherence levels and compared the difference between the two durations to an empirical null distribution created by permuting the duration labels. To examine the main effect of coherence, we averaged $P_{Opposite-Orthogonal}$ across the two durations and compared the difference between the two coherence levels to an empirical null distribution created by permuting the coherence labels. We then calculated *p* values by comparing the observed differences with the relevant empirical null distributions, as described for the initial set of permutation tests. The interaction effect in our 2 x 2 factorial design was not theoretically important, so we did not perform a test of this effect.

Note that we also conducted conventional one-sample *t* tests and a conventional 2 x 2 ANOVA on the data, and the pattern of significance was identical to that obtained by permutation testing (see online supplementary material).

Results and Discussion

Figure 2a shows the distribution of response errors for each combination of motion coherence and duration. Overall, most response errors were centered around zero, and the distributions were broader for the lower coherence level and the shorter duration. This is exactly what would be expected if perception was less precise when less motion information was available (because of lower coherence or shorter duration). In addition to the bell-shaped cluster of response errors, there were also larger errors (>60°), especially when the coherence was low or the duration was brief. However, the distributions were clearly non-monotonic, with an increase in likelihood for errors near 180° (directly opposite to the true direction of motion) and more errors near 180° than near ±90°. This "bump" in opposite-direction reports is clearly visible in Figure 2a for all four combinations of coherence and duration, even in the condition with 50% coherence and a 1000-ms duration, in which very few errors were made between 60° and 150°. Moreover, opposite-direction responses were just as evident at the 300-ms duration as at the 1000-ms duration, ruling out the possibility that they are a consequence of adaptation of the stimulated direction (because adaptation should be stronger for the longer stimulus duration).

The rate of true opposite-direction perceptions was quantified as $P_{Opposite-Orthogonal}$, which accounts for the fact that random errors will occasionally occur near 180°. Figure 2b shows $P_{Opposite-Orthogonal}$ averaged across participants for each combination of motion coherence and duration. $P_{Opposite-Orthogonal}$ was significantly greater than zero in all four conditions (p <.0001 for each condition). When averaged across the four conditions, every single one of the 24 observers exhibited evidence of opposite-direction perception (i.e., a positive value

for P$_{Opposite-Orthogonal}$). These results demonstrate that observers reported the opposite of the true direction substantially more often than would be expected by guessing. See online supplementary material for converging results from the mixture model analysis.

We found no significant difference in P$_{Opposite-Orthogonal}$ between the 300- and 1000-ms durations after collapsing across coherence levels (p = .4134). We also found no significant difference between the 25% and 50% coherence levels after collapsing across durations (p = .0886). We are not claiming that perception of opposite-direction motion is completely unaffected by coherence or duration (i.e., that the null hypothesis is true); some effect might be obtained with more statistical power, more sensitive measures, or more extreme manipulations of coherence or duration. However, the present results make it clear that substantial levels of opposite-direction perception are present across this range of coherence levels and durations.

Although opposite-direction reports clearly occurred more than orthogonal direction reports, they were still rare compared to reports near the true direction of motion. For example, in the 50% coherence, 300-ms condition, 72% of reports were within ±30° of the true direction, whereas 11% of errors were within ±30° of the opposite direction and 2.8% of errors were within ±30° of the two orthogonal directions. Across all conditions, opposite-direction perceptions (i.e., grand average of P$_{Opposite-Orthogonal}$) were present on approximately 7.8% of trials. We have provided videos of several trials from this condition and Matlab scripts for demo displays at https://osf.io/fexmg. Thus, although all 24 participants reported the opposite direction more often than would be expected by chance, opposite-direction reports were relatively rare. This distinguishes the opposite-direction motion perception phenomenon from typical visual illusions, in which the nonveridical perception is present most or all of the time.

In the next set of 3 experiments, we replicated the finding of above-chance opposite-direction motion responses with reversed luminance contrast (i.e., black dots on a white aperture) on a CRT monitor (Experiment 2), with response feedback after each report (Experiment 3), and with confidence ratings (Experiment 4).

Experiment 2

It is important to rule out the possibility that the opposite-direction reports in Experiment 1 were a result of visible persistence of the dots in the RDK displays. For example, the actual duration of a stimulus on an LCD might be different from the duration of the signal coming from the computer's video card (see Supplementary Online Material for the empirically measured duration of the stimuli). In addition, white dots on a black background could have potentially produced weak but visible persistence, and this may have contributed to the perception of opposite-direction motion. To rule out these possibilities, Experiment 2 used the same motion direction estimation task as in Experiment 1 but with a CRT monitor and black dots on a white disk.

Method

A new group of 24 college students (21 women, 3 men) participated in Experiment 2. The method was identical to that of Experiment 1 except that we used a CRT monitor (Samsung Syncmaster 793DF, 60 Hz refresh rate) instead of an LCD monitor, and we reversed the contrast so that black dots were presented on a white disk (on a black background) instead of white dots on a black disk (on a white background as shown in Figure 3a; see online supplementary materials for measurements of the temporal profile of the CRT monitor).

Results and Discussion

Figure 3b shows the distribution of response errors for each combination of motion coherence and duration in Experiment 2. The probability of opposite-direction motion perception ($P_{Opposite-Orthogonal}$) is shown in Figure 3c. The results of a mixture model analysis are reported in online supplementary materials.

Figure 3c shows that $P_{Opposite-Orthogonal}$ was significantly greater than zero in all four conditions of Experiment 2 (p < .0001 in each condition). Averaged across the four conditions, 21 out of the 24 observers exhibited evidence of opposite-direction perception (i.e., a positive value for $P_{Opposite-Orthogonal}$). As in Experiment 1, we found no significant effect of motion coherence (p = .6927) or duration (p = .6072) on opposite-direction motion perception in this experiment. These results rule out the possibility that the opposite-direction reports were a consequence of artifacts in the stimulus presentation.

Experiment 3

Experiment 3 was designed to rule out an alternative explanation for the opposite-direction motion perception observed in Experiments 1 and 2. Although participants received response feedback on each trial during the practice session of Experiment 1 and 2, it is possible that participants were occasionally confused about how to report the direction of perceived motion. That is, the task requires participants to orient the response line toward the *destination* of the dots, but participants might have instead aligned the response line toward the *source* of the dots. To make sure they fully understood the task throughout the entire duration of the session, Experiment 3 provided response feedback on every trial during the entire session.

Method

A new group of 24 college students (21 women, 3 men) was tested. The method of Experiment 3 was identical to that of Experiment 1 except that the participant received feedback about the true direction of motion on each trial. Specifically, as soon as the observer clicked the mouse button to confirm the response on a given trial, a red line indicating the true motion direction was presented for 500 ms (Figure 4a).

Results and Discussion

Figure 4b shows the distribution of response errors for each combination of motion coherence and duration in Experiment 3. The probability of opposite-direction motion

perception (P$_{\text{Opposite-Orthogonal}}$) is shown in Figure 4c. The result of a mixture model analyses are reported in online supplementary materials.

Opposite-direction reports were evident in all four conditions of Experiment 3 (Figure 4c). Specifically, observers made significantly more opposite-direction reports than orthogonal-direction reports in all four conditions (p < .0001 in each condition), and all 24 observers showed a positive value for P$_{\text{Opposite-Orthogonal}}$ (averaged across the four conditions). We found no significant main effect of motion coherence (p = .0652) or duration (p = .5858).

Experiments 4

Experiments 1–3 provided clear evidence that observers report the opposite direction of motion more than would be expected by chance and confirmed that this effect is not a result of stimulation artifacts or task confusion. However, the opposite-direction reports were fairly rare, occurring on approximately 10% of trials. Do these reports reflect an actual conscious perception of motion in the opposite of the true direction, or do they reflect an unconscious bias that influences performance when participants are unsure of the direction of motion?

When we, the authors, view the stimuli, we often have a very clear conscious perception of a direction of motion that is the opposite of the true direction. We have provided videos so that interested readers can experience this for themselves (https://osf.io/fexmg). However, because opposite-direction reports are relatively rare, it is difficult to rely on such subjective reports to establish whether observers consciously perceive the opposite direction of motion.

Experiment 4 therefore examined this question more rigorously by requiring participants to report their confidence in the reported direction on every trial (Figure 5a). If opposite-direction reports reflect an unconscious bias that occurs when participants are unsure of the direction of motion, then they should be no more confident when their report is approximately 180° from the true direction than when their report is approximately 90° from the true direction. If anything, confidence should be lower for 180° than for 90° given that 90° errors are more likely to reflect a simple imprecision in the motion perception. However, if opposite-direction reports reflect a conscious perception of the opposite direction of motion, then participants should be more confident when they make opposite-direction reports than when they make orthogonal-direction reports.

One might argue that reports of confidence are inherently subjective, making the confidence reports difficult to interpret. However, if participants report a higher level of confidence for opposite-direction reports than for orthogonal-direction reports, then they must be having a different experience when they report the opposite direction than when they report the orthogonal direction. That is, if participants have equivalent phenomenological experiences on these two types of trials, they could not report different levels of confidence.

Method

A new group of 24 college students (23 women, 1 man) participated in Experiment 4. The method of Experiments 4 was identical to that of Experiment 1 except that observers

reported their confidence – either "I am pretty sure" or "I am not sure" – by pressing a button on a keyboard after each motion direction report (Figure 5a).

Results and Discussion

Figure 5b shows the distribution of response errors in each condition of Experiment 4. The probability of opposite-direction motion perception ($P_{Opposite-Orthogonal}$) is shown in Figure 5c. The results of a mixture model analysis are reported in online supplementary materials.

In Experiment 4, we again replicated the finding of above-chance opposite-direction motion perception in all four conditions (p < .0001; Figure 5c), with all 24 observers showing a positive value for $P_{Opposite-Orthogonal}$ (averaged across the four conditions).

To examine whether observers were more confident when their reports were near the opposite direction compared to the orthogonal direction, we collapsed the data across all four conditions[2] and computed the difference between the proportion of "I am pretty sure" trials and the proportion of "I am not sure" trials separately for opposite-direction reports and for orthogonal direction reports. We found that participants reported "I am pretty sure" on 25% (SEM = 7.5%) of the trials with an opposite-direction report and on only 5% (SEM = 8.6%) of trials with an orthogonal direction report. This difference was statistically significant in a paired *t* test (t(23) = 7.226, p < .0001, two-tailed).

These results demonstrate that the participants were more confident in their opposite-direction reports than in reports that were presumably guesses (i.e., orthogonal-direction reports). This result is consistent with the proposal that opposite-direction reports often reflect a conscious perception of the opposite direction of motion and is not entirely an unconscious response bias that occurs when participants are unsure about the direction of motion.

Low-Level Motion Energy Analysis

We next examined whether our finding of more opposite-direction than orthogonal-direction reports might be related to the known properties of low-level motion processing systems in the brain. Specifically, we used the mathematical model of Kiani et al. (2008) to estimate the amount of motion energy that would be coded by MT neurons in the true motion direction, in the opposite direction, and in the two orthogonal directions (see also Bollimunta et al., 2012). This model is given a video of the RDK and asked to report the amount of perceived motion energy in a specific direction. The motion energy is determined by the luminance contrast between the background (i.e., black) and the dot stimuli (i.e., white) after applying a spatiotemporal filter. Specifically, the model passes the RDK through a combination of a Gaussian-like spatial filter and a temporal impulse response function in the specified direction and filters out energy along any other directions. The local motion energies at each point in the image across the time is computed by convoluting the filter across the space, and the global motion energy is computed by summing the local motion energies. Because the

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[2]We collapsed across the four conditions because there were no opposite direction reports or orthogonal direction reports for some participants in some conditions (e.g., 50% coherence with 1000 ms duration). Consequently, confidence ratings were not defined for those cases.

spatiotemporal filters used in this analysis are consistent with a spatiotemporal passband of MT neurons (Movshon et al., 1988), this mathematical model has been used to approximate the spatiotemporal response profiles of neurons in area MT for RDK displays (Kainai et al., 2008).

The actual videos used in Experiments 2–4 were provided to the model. The model does not report a single motion direction in 360°, as the observers in our experiment were asked to do. Instead, one queries the amount of energy in a particular direction. We therefore asked the model to compute the motion energy in each of 4 directions: The actual direction of motion for the video (0°), the opposite direction (180°), and the two orthogonal directions (-90° and +90°). Only the portion of the trial corresponding to the RDK was provided to the model in a given video. Figure 6 shows the model's estimated motion energy (in arbitrary units) for each combination of motion coherence and duration, averaged across time points for 120 videos (each representing a single trial).

We found that the estimated motion energy in area MT for the true direction was greater than the estimated motion energy for both the opposite direction (by 4.5%) and the two orthogonal directions (by 15.6%) in all four conditions. More importantly, in all four conditions, motion energy for the opposite direction was greater than motion energy averaged across the two orthogonal directions (by 10.5%). We conducted statistical testing on these results using t tests with FDR correction for each combination of motion coherence and duration. Table 1 summarizes the statistical results. These results indicate that our finding of more opposite-direction than orthogonal-direction reports in human observers is consistent with the known properties of the primate motion processing system as implemented in this computational model.

General Discussion

In four experiments, we demonstrated that participants frequently report the opposite of the true direction of motion in a display containing a mixture of coherent and random motion. These opposite-direction reports were present across a range of coherence levels and stimulus durations, and they were not a consequence of the specific display device, the contrast polarity, or a lack of training or feedback. Moreover, the observers were more confident when they made opposite-direction reports than when they made orthogonal-direction reports, suggesting that the opposite-direction reports reflected a conscious experience of opposite-direction motion and not an unconscious bias in guessing. We also found that the opposite-direction reports were no more frequent for a longer RDK duration than for a shorter RDK duration, ruling out the possibility that the opposite-direction perception was caused by motion adaptation. Together, these results demonstrate that RDKs produce the perception of opposite-direction motion on a small but significant proportion of trials.

Although our model-free analysis did not find a significant impact of motion duration and motion coherence on the rate of opposite direction reports, a more sophisticated mixture model analysis (see Supplementary material) showed a significant reduction in opposite-direction reports in the trials with longer motion duration (Experiments 2 and 4)

and higher motion coherence (Experiments 1, 3, and 4). These results suggest that more perceptual evidence and better motion signals help disambiguate the true and opposite motion directions. However, we do not make a strong conclusion about the effect of motion duration and motion coherence on the basis of this result because we only tested two levels of motion duration and coherence. Future research is necessary to more systematically investigate factors that influence on the rate of opposite direction motion perception.

The finding that observers reported higher confidence for opposite-direction responses than for orthogonal-direction responses in Experiment 4 suggests that the opposite-direction reports arise during perception rather than being a decision-stage effect. However, we provided only two different levels for the confidence reports in that experiment, so we cannot conclude that the confidence levels for the opposite-direction responses were as high as for the true-direction responses. In addition, the opposite-direction responses were relatively rare (approximately 10% of trials), whereas most perceptual illusions are present most of the time. Also, unlike bistable perceptual phenomena such as binocular rivalry and the Necker cube, our informal observations suggest that perception does not alternate back and forth between the true and opposite directions. In addition, informal observations indicate that the perceived direction does not appear to be reliably influenced by attempts at voluntary control. Nonetheless, people who view the displays often report a strong phenomenological experience of motion in the opposite direction, as would be expected for a perceptual effect. Additional research will be needed to determine whether opposite-direction motion perception represents a genuine perceptual illusion.

We suspect that opposite-direction motion perception has been present in studies using RDKs for decades, but there was no way for researchers to detect this effect in standard two-choice paradigms (e.g., leftward vs. rightward motion), because the perception of opposite-direction motion is indistinguishable from uninformed guessing in such tasks. The present results suggest that errors in traditional binary decision tasks can arise from two distinctly different sources, namely guesses in the absence of a clear perception of motion and confident-but-erroneous perceptions of the incorrect direction of motion. It would be difficult to account for these two different types of errors in models of perceptual decision-making that are based on a simple implementation of the drift-diffusion model, but the generalized version of this model (Ratcliff et al., 2016) could potentially account for them. Thus, the present results suggest a need to update models of perceptual decision-making.

Interestingly, evidence for an opposite-direction bias has recently been observed in a binary choice RDK paradigm (Wu, Rothwell, Spering & Montagnini, 2021). In this study, observers performed a RDK motion discrimination task in between trials of smooth pursuit eye movements. When the smooth pursuit trials were predominantly in one direction, reports of motion in the RDK displays were biased in the opposite direction. However, it is not clear whether this probability-based effect occurs as a result of the same mechanisms as the opposite-direction motion reports observed in the present study, in which each direction of motion was equally likely.

The present study was not designed to investigate the specific mechanisms underlying opposite-direction motion perception, but we obtained a hint about the source of this effect

by feeding our stimuli into a mathematical model of motion processing based on the spatiotemporal tuning of neurons in area MT (Kiani et al., 2008). This model indicated that MT neurons would respond as if substantially more motion energy were present 180° to the true direction of motion (even though there was not greater objective energy at 180° than at ±90° in our stimuli). Thus, the perception of opposite-direction motion on a fraction of trials is broadly consistent with the known properties of MT neurons (and their inputs from V1 neurons). Note that this opposite-direction activity in the model did not require a decision stage, providing more reason to believe that the present results occurred during perception rather than being a result of a decision mechanism.

The opposite-direction motion energy appears to be a result of the temporal dynamics of the model, in which the energy from a given dot is spread over time by the temporal impulse response filter in the model. If the perceived time of a given dot is uncertain, then there is some probability that the order of occurrence of a dot in two corresponding frames will be misperceived, leading to the perception of motion in the opposite of the true direction (but not in one of the orthogonal directions). This is one possible mechanism that could produce the perception of opposite-direction motion.

However, it is also possible that motion streaks—which are not explicitly represented in the model—might also play a role. That is, the appearance of multiple consecutive dots along a line can create the appearance of orientation, but without indicating which direction the dots are moving along this line. The mechanism that disambiguates between the true direction and the opposite direction (Geisler, 1999) might occasionally fail, leading to perception of motion in the opposite direction. Additional research will be needed to determine the actual mechanism underlying opposite-direction motion perception.

Yet another alternative mechanism would be inhibition around the orthogonal directions, which would artificially create a "bump" at the opposite direction. However, if this were the case, then trials with a higher coherence level should have exhibited greater rate of opposite-direction reports (because the motion signal and any accompanying inhibition would be stronger). However, we found no significant main effect of coherence on the proportion of opposite direction reports. Indeed, the model-based analysis showed a reduction in opposite-direction reports on high-coherence trials. Although some inhibition might have been present, these results indicate that is not the main cause of our findings.

Lastly, the proportion of opposite-direction motion responses may be influenced by the exact algorithm used to create coherent motion in the RDKs. In the present study, the coherence was defined in a probabilistic manner: some percentage of dots moved in a specific direction whereas the remaining dots were randomly displaced within the aperture. However, the coherence can also be defined in a more continuous manner by having a probability distribution of the direction of individual dot motion. Future research should investigate how these different RDK algorithms impact the opposite-direction motion reports.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgements

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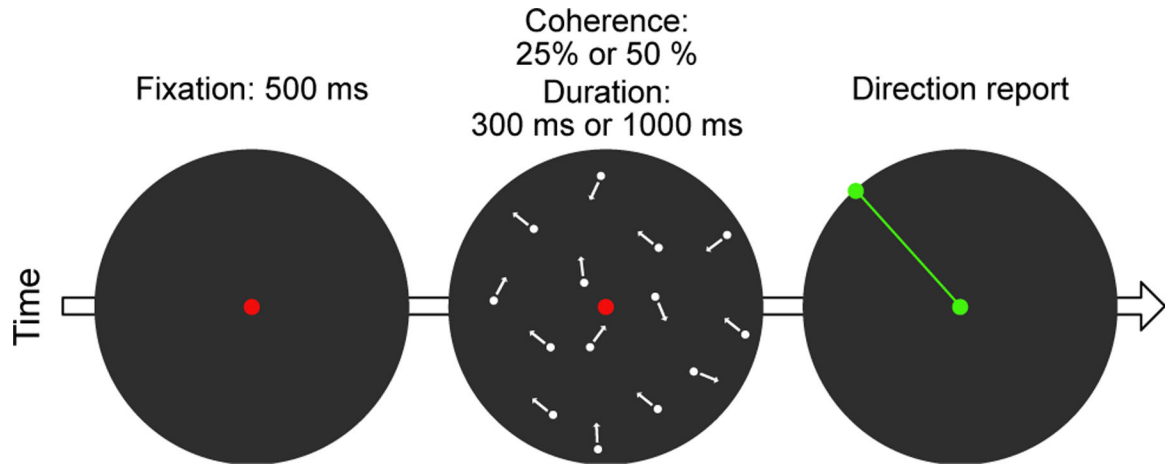
Figure 1.
Task used in Experiment 1. On each trial, participants fixated the central red dot for 500 ms and saw a random dot kinematogram (RDK) for 300 ms or 1000 ms with a direction randomly sampled from the 360° space. Motion coherence was either 25% or 50%. After the RDK ended, the central dot turned green, indicating that a direction report should be made. Participants adjusted the green line until it matched the perceived motion direction, and then they submitted their report by clicking the mouse button.
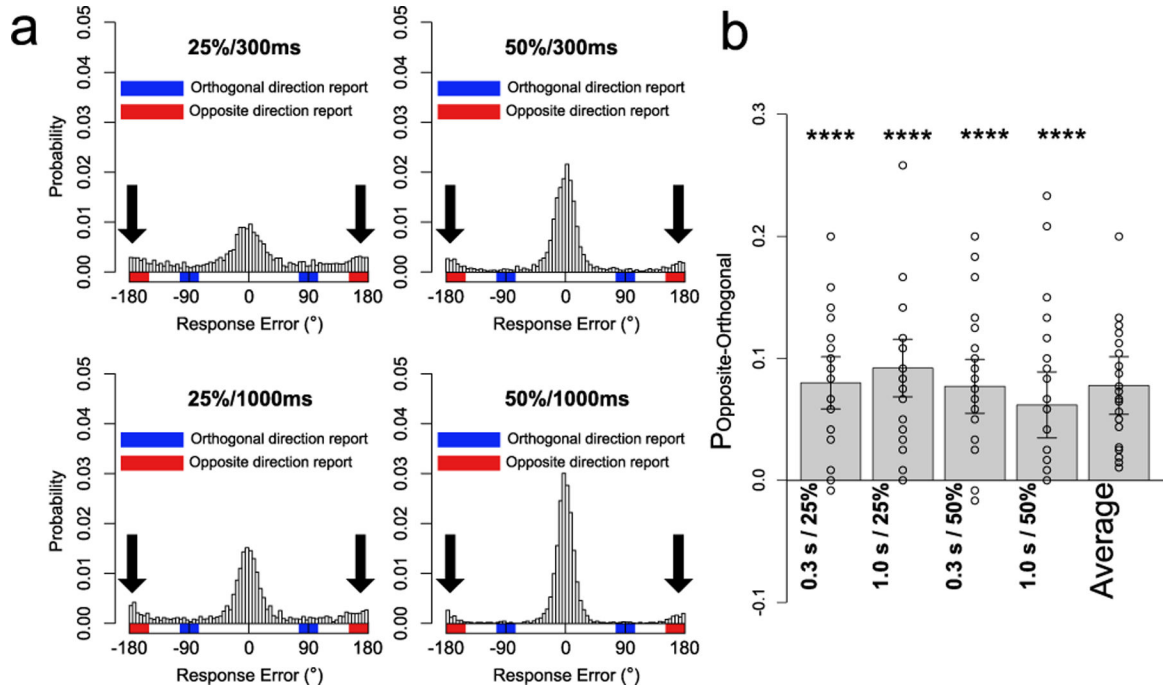
Figure 2.

(a) Distribution of response errors for each combination of motion coherence and duration. Opposite-direction responses can be seen as increases in probability near 180° (indicated by arrows) in each of the distributions. Trials with response errors within the blue areas (60° combined width) were categorized as orthogonal-direction reports, and trials with response errors within the red areas (60° combined width) were categorized as opposite-direction reports. The difference between the rate of opposite-direction reports and the rate of orthogonal-direction reports, $P_{Opposite-Orthogonal}$, was used to estimate the rate of true opposite-direction reports. (b) Average rate of opposite-direction reports ($P_{Opposite-Orthogonal}$) for each combination of motion coherence and duration, and for the average across the combinations. Error bar indicates 95% confidence intervals. Circles represent individual participants.**** = p < .0001 as indicated by permutation testing.
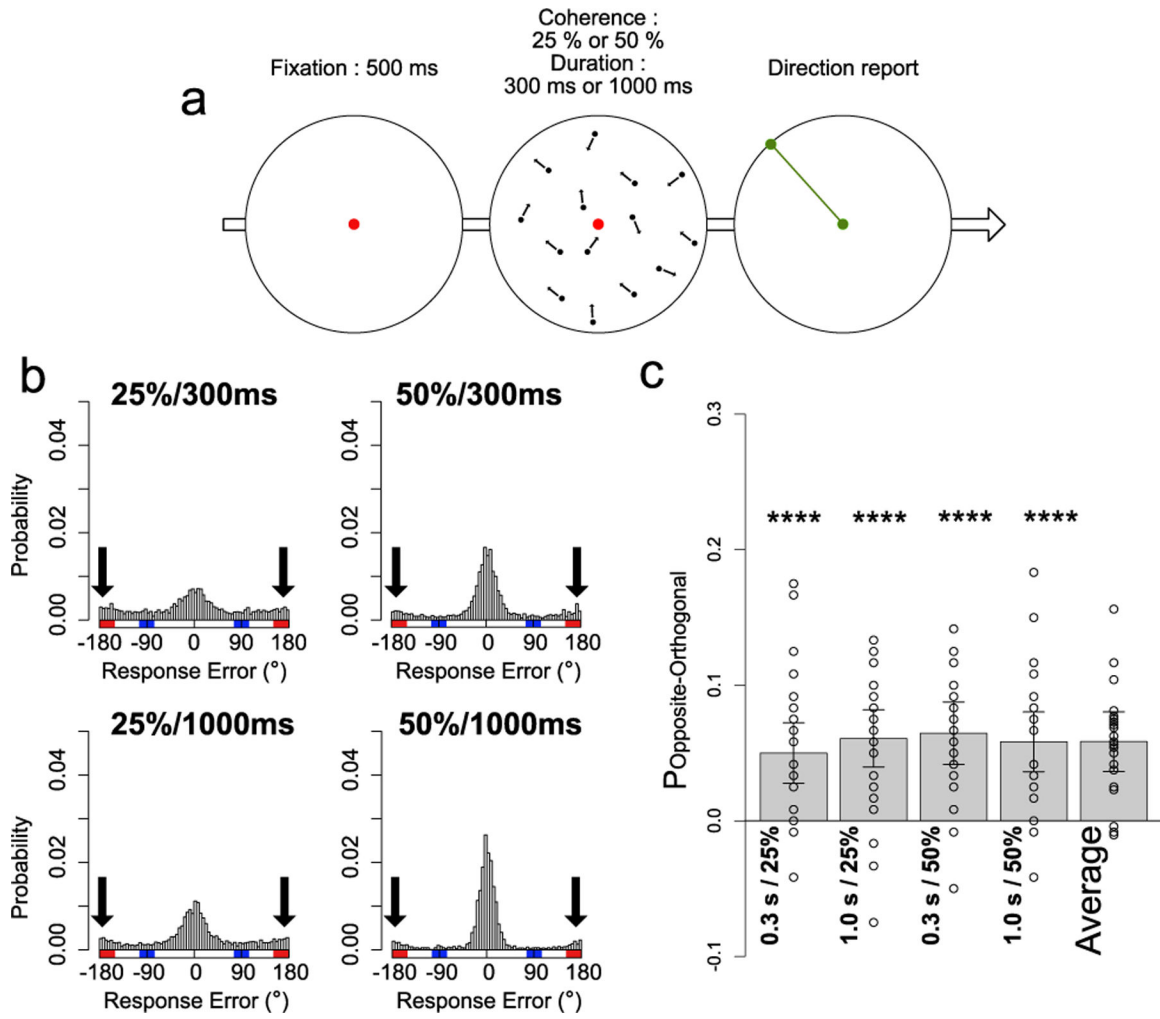
Figure 3.
(a) Task used in Experiment 2. The task was identical to Experiment 1 except that black dots were presented on a white disk via a CRT monitor. (b) Distribution of response errors for each combination of motion coherence and duration. Opposite-direction reports were evident (indicated by arrows) in all four conditions. (c) Average rate of opposite-direction reports ($P_{Opposite-Orthogonal}$) for each combination of motion coherence and duration, and for the average across the combintations. Error bar indicates 95% confidence intervals. Circles represent individual participants. **** = p < .0001 as indicated by permutation testing.
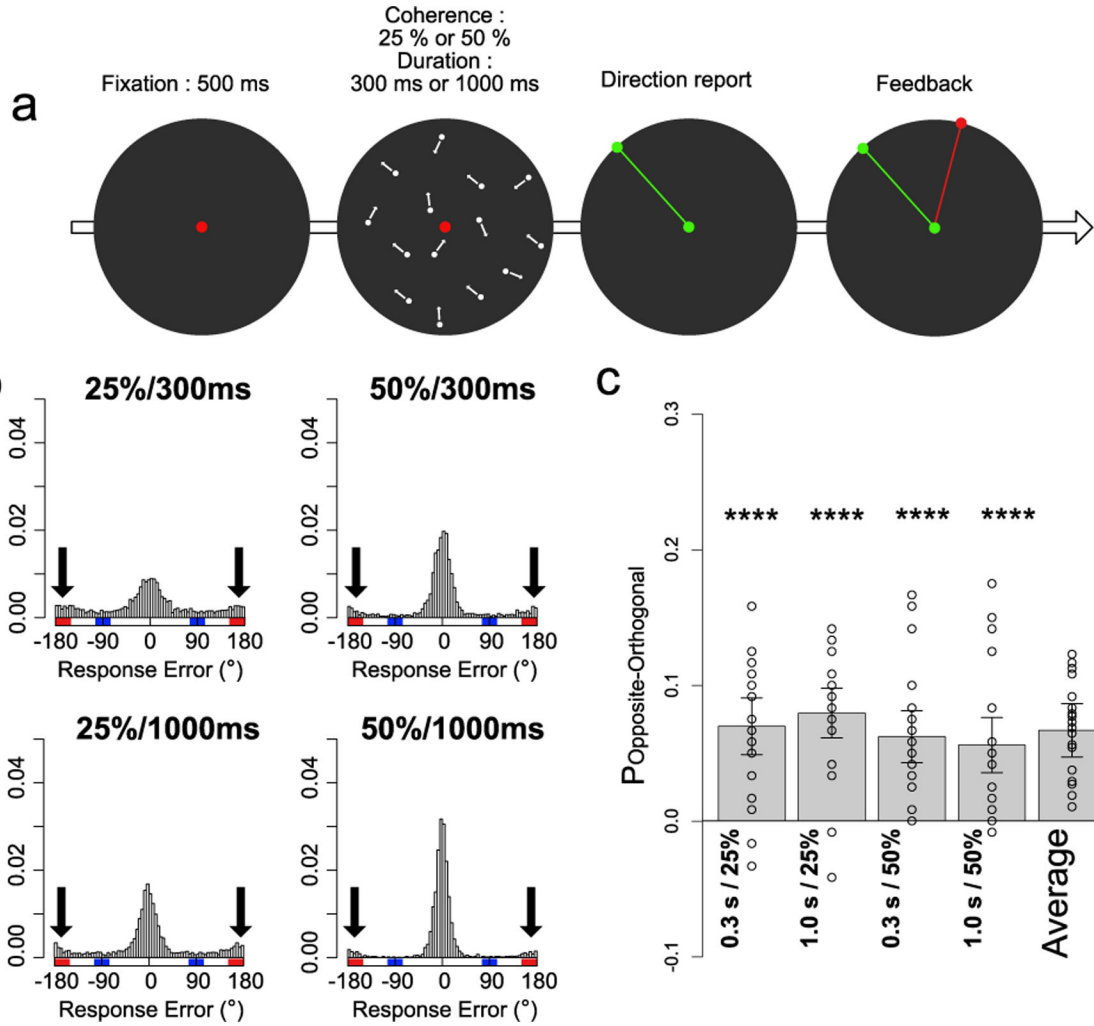
Figure 4.
(a) Task used in Experiment 2. The task was identical to that used in Experiment 1 except that a feedback stimulus indicating the true motion direction (red line in the figure) was provided for 500 ms after each direction report. (b) Distribution of response errors for each combination of motion coherence and duration. Opposite-direction reports were evident (indicated by arrows) in all four conditions. (c) Average rate of opposite-direction reports ($P_{Opposite-Orthogonal}$) for each combination of motion coherence and duration, and for the average across the combintations. Error bar indicates 95% confidence intervals. Circles represent individual participants. **** = p < .0001 as indicated by permutation testing.
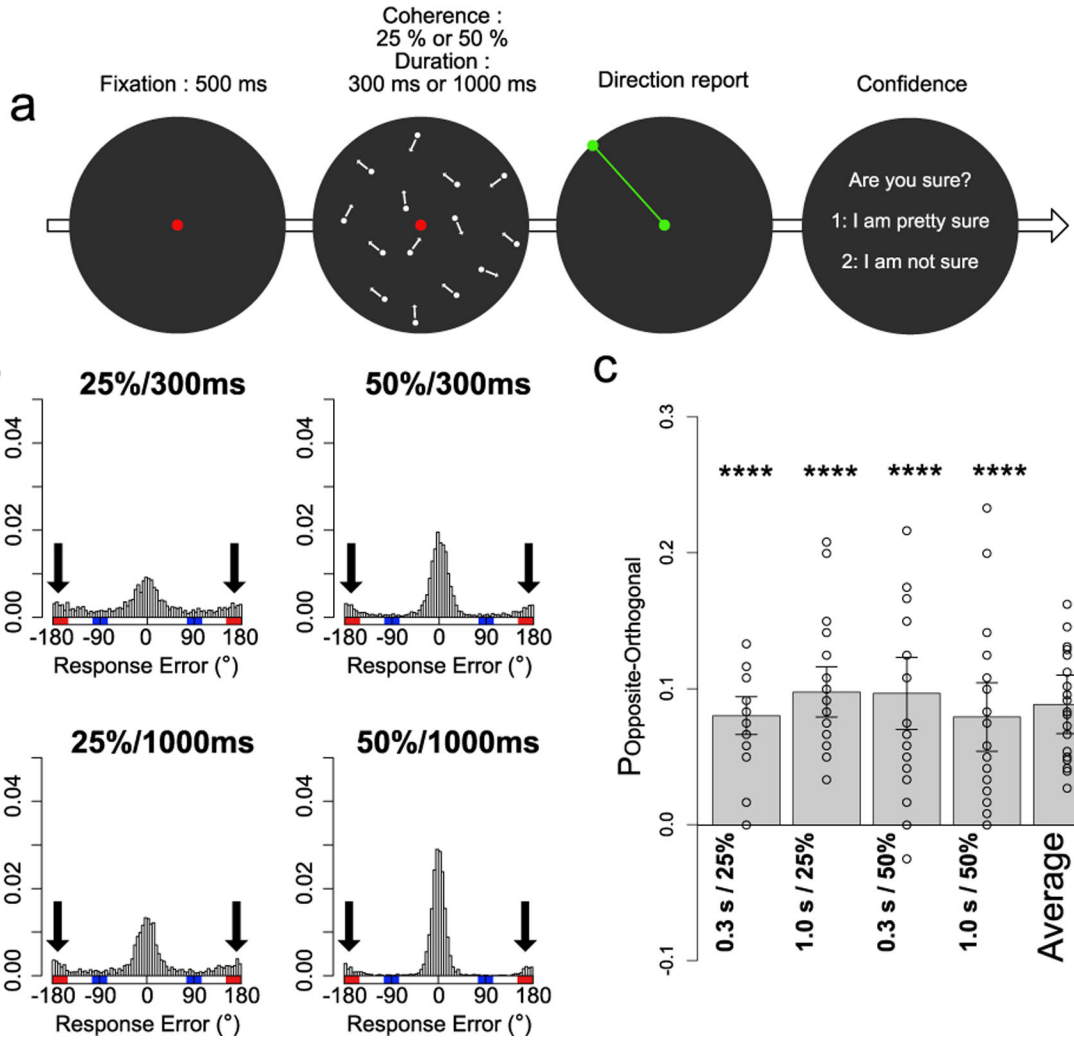
Figure 5.
(a) Task used in Experiment 4. The task was identical to that used in Experiment 1 except that participants were required to report their confidence after each direction report. (b) Distribution of response errors for each combination of motion coherence and duration. Opposite-direction reports were evident (indicated by arrows) in all four conditions. (c) Average rate of opposite-direction reports (POpposite-Orthogonal) for each combination of motion coherence and duration, and for the average across the combintations. Error bar indicates 95% confidence intervals. Circles represent individual participants. **** = p < .0001 as indicated by permutation testing.
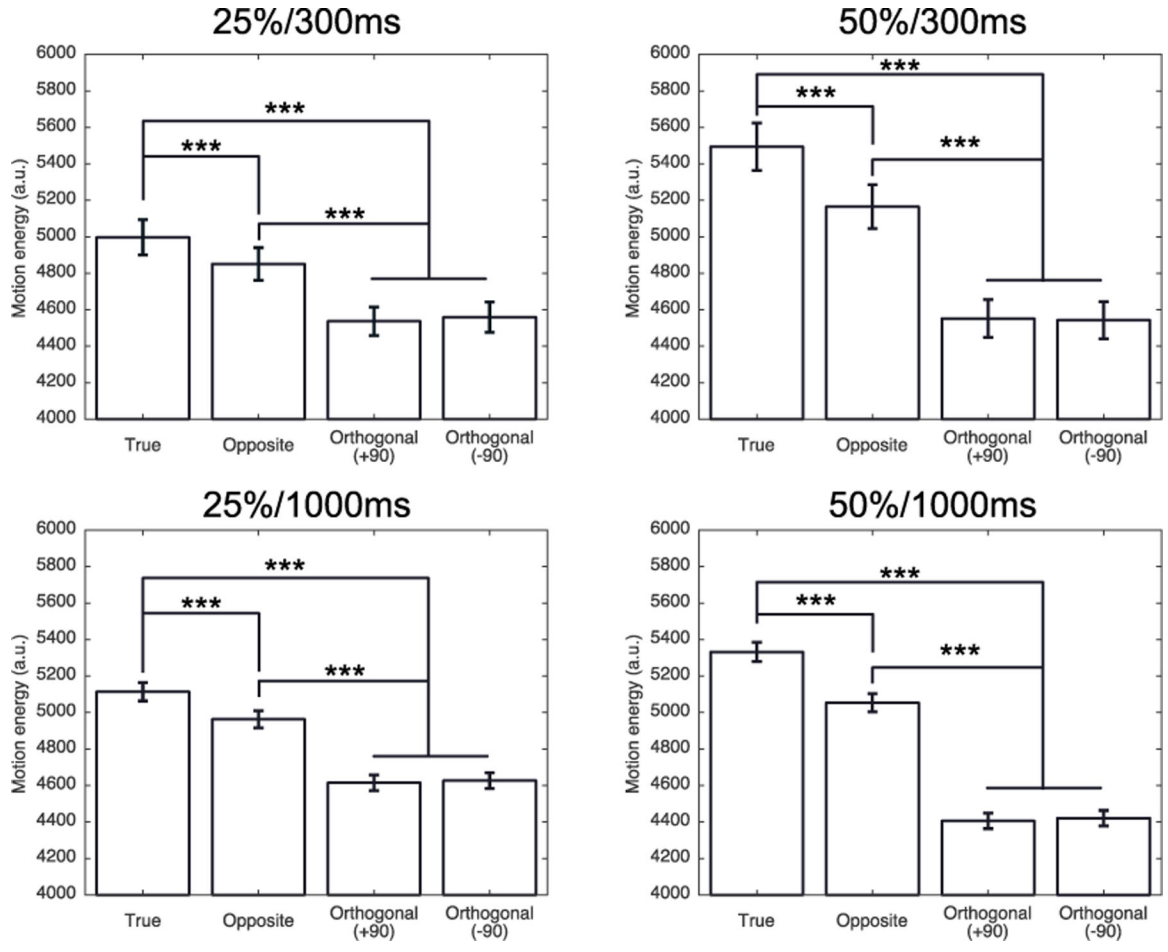
Figure 6.
Estimated motion energy in area MT for the true direction, the opposite direction, and the two orthogonal directions averaged across time points for RDK trajectories in each combination of motion coherence and duration (based on the exact stimuli used in Experiments 2–4). Error bars represent ±1 S.E of the mean. *** < .001

Table 1.

t tests for motion energy

Coherence/Duration	Comparisons	t	P
25% / 300 ms	true direction vs. opposite direction	t(119) = 5.296	< .001
	true direction vs. average of orthogonal directions	t(119) = 15.442	<.001
	opposite direction vs. average of orthogonal directions	t(119) = 12.602	<.001
25% / 1000 ms	true direction vs. opposite direction	t(119) = 12.673	< .001
	true direction vs. average of orthogonal directions	t(119) = 40.311	<.001
	opposite direction vs. average of orthogonal directions	t(119) = 34.201	<.001
50% / 300 ms	true direction vs. opposite direction	t(119) = 8.597	< .001
	true direction vs. average of orthogonal directions	t(119) = 23.791	<.001
	opposite direction vs. average of orthogonal directions	t(119) = 19.940	<.001
50% / 1000 ms	true direction vs. opposite direction	t(119) = 18.031	< .001
	true direction vs. average of orthogonal directions	t(119) = 59.232	<.001
	opposite direction vs. average of orthogonal directions	t(119) = 47.377	<.001