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Radial Bias Alters Perceived Object Orientation

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Abstract

Orientation sensitivity is a fundamental property of the visual system, but not all orientations are created equal. For instance, radially oriented stimuli, aligned with a line intersecting the center of gaze, produce greater activity throughout the visual cortex and are associated with greater perceptual sensitivity compared with other orientations. Here, we discuss a robust visual illusion that is likely related to this preference. Using a continuous response measure, participants (N = 36 adults) indicated the gap position in a peripheral Landolt C placed in one of eight orientations and eight locations along four meridians (vertical, horizontal, 45°, 135°). The error distributions revealed that the perceived gap was attracted toward the radial axis. For instance, the gap in a regular C would often be wrongly perceived as tilted 45° corresponding to the oblique meridian where it was placed. These findings demonstrate an unsuspected early-vision influence on the perceived orientation of an object.

Keywords

visual perception, orientation sensitivity, radial bias

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Reporting a visual feature of an attended object may seem like a trivial task. However, to our surprise, all three authors, who have combined experience of more than 60 years as psychophysical observers, had trouble following instructions regarding the perceived orientation of an object during an attention experiment. The task was to report the gap position in a precued Landolt C. The display consisted of eight very briefly presented Landolt Cs placed along an imaginary circle, with gaps on the horizontal or the vertical axis (i.e., the polar angle of the gap was 0°, 90°, 180°, or 270°; see Fig. 1a). On occasion, we were very sure that we saw gaps along a diagonal axis, even though Landolt Cs were never presented with this orientation.

On closer investigation, we observed that we were more likely to perceive illusory slanting Landolt Cs when they were placed along the oblique meridians relative to fixation. The direction of the perceived rotations suggested that the gaps in the Landolt Cs were radially oriented, aligned with the meridian on which they were placed.

Ample research has shown that the visual system involves various visual field and orientation anisotropies. Visual performance is better along the horizontal than the vertical meridian and in the lower than the upper visual field (e.g., Altpeter et al., 2000; Barbot et al., 2021; Carrasco et al., 2001; Mackeben, 1999). Visual performance is also better for stimuli with cardinal than with oblique orientations (e.g., Appelle, 1972; Girshick et al., 2011). Most relevant to our findings, the visual system also has preferences for relative orientations. When simple stimuli, such as gratings or bars, are used, an increased sensitivity for radially (vs. tangentially) oriented stimuli, especially at more peripheral eccentricities, has been reported. Visual stimuli that are aligned with a line intersecting the fixation point are more easily seen or discriminated in psychophysical

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studies (Bennett & Banks, 1991; Rovamo et al., 1982; Sasaki et al., 2006; Temme et al., 1985; Westheimer, 2003, 2005). Neural studies also provided evidence for a radial-orientation bias in the retina, lateral geniculate nucleus (LGN), and cortex in cats and monkeys (Leventhal & Schall, 1983; Levick & Thibos, 1982; Schall et al., 1986) and more recently in the LGN (Ling et al., 2015) and cortex (Mannion et al., 2010; Sasaki et al., 2006) in humans. For example, Sasaki et al. (2006) compared contrast sensitivity to radially versus tangentially oriented sine gratings and reported greater sensitivity to the radial ones. Using both human and monkey functional MRI, they also demonstrated that radial orientations more strongly activated the visual cortex than tangential orientations did.

In short, there is strong evidence that the visual system prefers radial over tangential orientations. Can this preference alter the population coding of simple shapes, whereby a nonradially oriented object may appear rotated toward the radial axis? Our findings suggest so.

Here, we conducted two experiments. In Experiment 1, we tested naive participants ($N = 18$) on the extended version of the task in which we had experienced the visual illusion (Fig. 1b). In Experiment 2, we wanted to make sure that the results were not just the consequence of the cued-attention paradigm. Thus, we tested another group of participants ($N = 18$) on a simplified version of the task in which we removed the precuing and presented a single Landolt C target (Fig. 1c). In both experiments, participants clicked within one of two concentric response circles to indicate the gap position in the Landolt C as well as their confidence, using the inner circle for high-confidence responses and the outer circle for low-confidence responses (Figs. 1b and 1c). The target Landolt C was presented at one of eight peripheral locations (Fig. 2a, left), assuming one of eight orientations (Fig. 2a, right), making up a total of 64 different combinations (see Fig. S1 in the Supplemental Material available online for all 64 combinations).

The dependent measure of interest was error quantified as the angle between the actual and perceived gap positions (i.e., the mouse-click location). The target's relative orientation was coded as the relationship between the axis of the gap position in the target Landolt C and the radial axis on which the target Landolt C was placed. A relative orientation could be radial where the gap axis was aligned with the corresponding radial axis, tangential where the gap axis was orthogonal (90° away) to the corresponding radial axis, or in-between where the gap axis was obliquely related (i.e., 45° away) to the corresponding radial axis (see Fig. 2b for examples).

Statement of Relevance

Orientation sensitivity is a fundamental property of the visual system. Interestingly, for a given eccentrically viewed position, the visual system prefers some orientations over others. For instance, radially oriented visual stimuli—those that are aligned with a line intersecting the center of gaze—are more easily seen and discriminated. This is likely due to anatomical and physiological substrates in the early visual system. So far, this preference has been demonstrated only with low-level visual stimuli. By accident, we noticed a striking object-based illusion that is likely related to this preference. When presented with a horizontally or vertically oriented Landolt C, we sometimes saw a slanting Landolt C that appeared radial. We then systematically tested the illusion and replicated it with naive observers under various conditions. Our findings may be the first example of an object's perceived orientation being influenced by structural characteristics of the early visual system.

To show how a radial bias can account for the majority of the illusory perceived orientation, it is of special interest to consider the in-between condition (Fig. 2b, second and fourth columns). Here we would predict a preponderance of errors aligned with the nearby radial axis (45° away) in comparison with the orthogonal tangential orientation the same angular distance away (Fig. 2c).

In contrast, we reasoned that there would be no systematic bias in errors when the targets were already radially oriented (Fig. 2b, first column) or tangentially oriented (Fig. 2b, third column). In the radial case, we expected no biased pattern of errors because the targets were already aligned with the radial axis. In the tangential case, the nearest radial axis was twice as far away (90° away instead of 45°), and even if there were errors, they would be expected to be symmetrical because the angular distance in each direction was the same.

Experiment 1: Radial Bias Observed With a Precued Target

Method

Participants. Eighteen Brown University undergraduate students were recruited to participate in the study. All were right-handed and had normal or corrected-to-normal vision. Participants received partial course credit

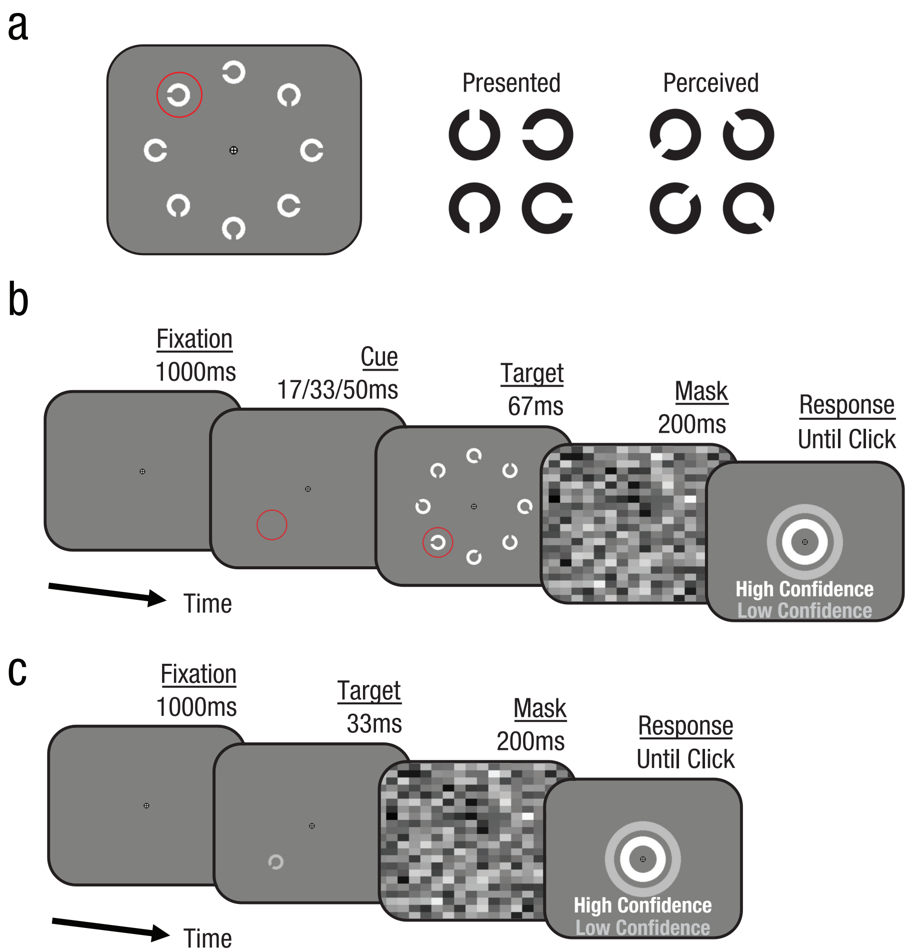

Fig. 1. Examples of stimuli and sequences of trial events. Stimuli (a) form the pilot experiment in which the authors experienced the illusion. The actual stimuli included Landolt Cs with openings along the horizontal or vertical axis. Authors experienced seeing gaps along the oblique axes in certain conditions. In Experiment 1, a precued-target Landolt C (b) was briefly presented in one of eight orientations and eight locations among seven nontarget Landolt Cs and was immediately masked. In Experiment 2, a single Landolt C (c) was presented. In both experiments, participants reported the gap position in the target Landolt C by clicking on a circle. They reported their confidence by clicking on one of two concentric response circles.

for their participation, which lasted approximately 1 hr. Our sample included all 18 participants (nine women, nine men) between the ages of 18 and 21 years (M = 19.5 years, SD = 0.71). The protocol was approved by the Institutional Review Board at Brown University. Participants gave informed consent and were treated according to the guidelines of the Institutional Review Board. Note that all authors piloting the task and colleagues who volunteered to pilot the task showed the hypothesized pattern of results. Thus, assuming this was a robust phenomenon, we simply aimed to have the same number of participants that a typical perception or attention experiment would. We then replicated the findings with slight modifications using the same number of new participants.

Stimuli and procedure. Stimuli were presented using a 13-in., 2.3-GHz MacBook Pro (with a 60-Hz screen) running MATLAB (Version R2016b) with Psychophysics Toolbox extensions (Version 3.0.14; Brainard, 1997; Kleiner et al., 2007; Pelli, 1997). All visual stimuli were white, red, or black on a light-gray background under normal lighting. The viewing distance was about 60 cm.

Each trial began with a fixation display consisting of a black cross on a white circle with a black outline (diameter = 0.26° of visual angle) placed in the center of the screen (see Fig. 2b for an example sequence of trial events). The fixation display was presented for 1,000 ms and was immediately followed by the cue display. The cue consisted of a red circle (diameter = 1.50° of

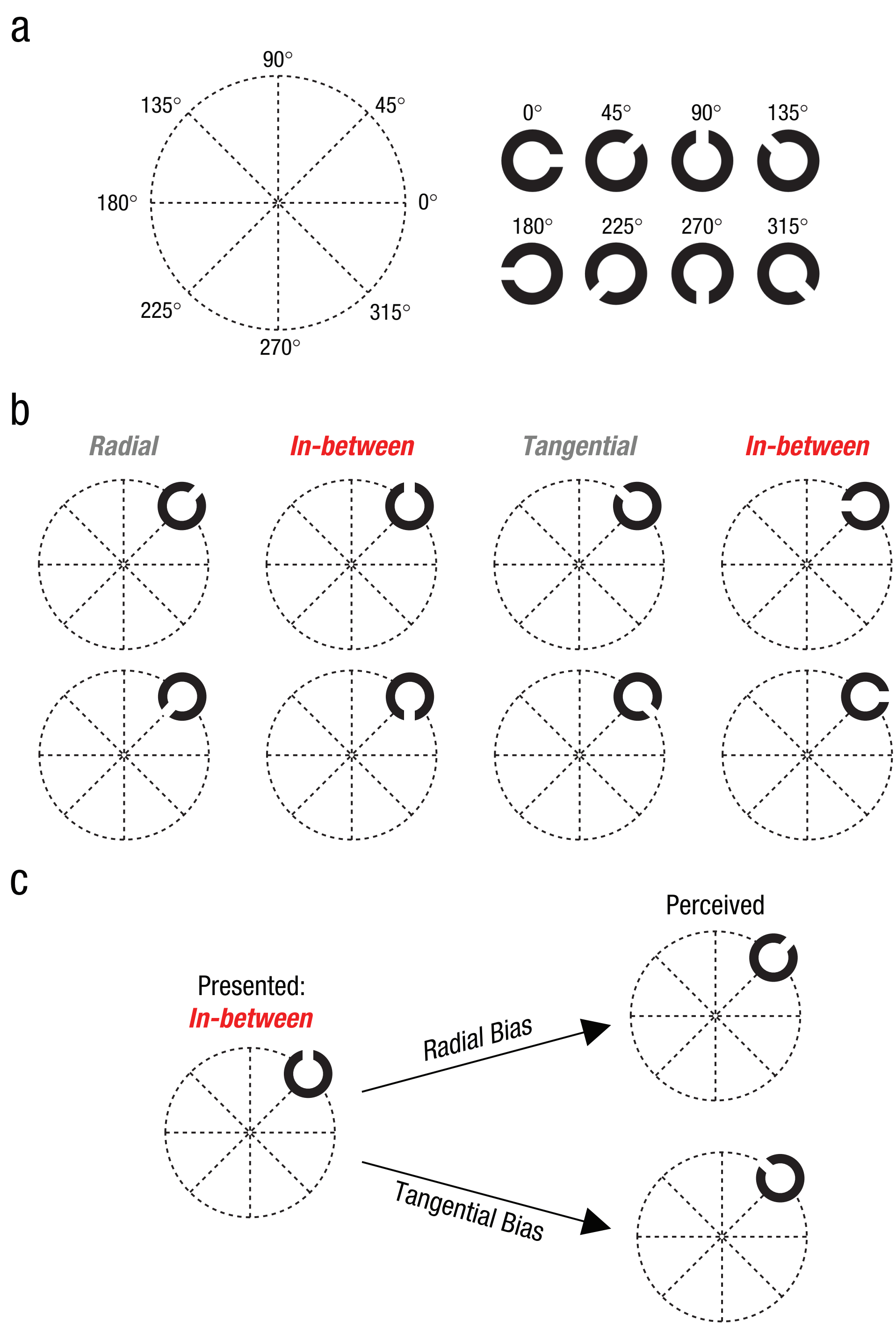

Fig. 2. Target locations and orientations. All possible target locations and target absolute orientations are shown in (a). All possible relative orientations for a specific target location (45°) are shown in (b). The target could be in radial, tangential, or in-between orientation relative to the meridian along which it was placed. Note that only eight combinations out of 64 are shown here. Depicted angular error for a presented in-between target predicted by a radial bias versus a tangential bias is shown in (c).

visual angle) and was presented in one of eight equally spaced locations on an imaginary circle (polar angle of stimulus location was 0°, 45°, 90°, 135°, 180°, 225°, 270°, or 315°) with a diameter of 4.94° of visual angle, centered on the fixation cross. The cue display was presented for 17, 33, or 50 ms (cue-lead time) and was immediately followed by the target display. The target was a white Landolt C (diameter = 0.75° of visual angle) among seven other nontarget Landolt Cs presented along the same imaginary circle around the fixation cross. The stroke width as well as the gap width of the Landolt C were one fifth of the diameter. The target Landolt C was always presented inside the cue. Landolt Cs were presented in one of eight orientations (the polar angle of the gap position in the Landolt C was 0°, 45°, 90°, 135°, 180°, 225°, 270°, or 315°). The orientations of the nontarget Landolt Cs were randomly chosen; the orientation of the target Landolt Cs was pseudorandomly chosen such that an equal number of trials with any combination of target location, target orientation, and cue-lead times was included and presented in a randomized order. The target display was presented for 67 ms. The target display was then immediately masked using a random noise pattern, presented for 200 ms.

Next, the response display was presented, which consisted of two concentric circles around the fixation cross—a smaller white circle with a diameter of 2.25° of visual angle and a larger gray circle with a diameter of 3.75° of visual angle. Instructions about the response were presented below the response circles, near the bottom of the screen, which read "High Confidence: Click on the white ring. Low Confidence: Click on the light gray ring. If you did not see the target at all, click on the fixation cross." The response display was presented until participants made their responses by clicking on the screen. After the response, the next trial began after an intertrial interval that varied between 1,300 and 1,700 ms.

Participants' task was to indicate the gap position in the target Landolt C by clicking on the response ring. They were told that the gap could be in various positions. Note that they were not explicitly informed of the fact that the gap would be in only one of eight positions. They were also asked to code their confidence level and were given the option to skip a trial if they did not see the target (in order to prevent wild guesses). Participants were instructed to keep their eyes on the fixation cross throughout the trial and not move their eyes to the target. The time between cue onset and target offset was also not long enough to allow for a saccade to target. Participants completed three blocks of trials, each of which included eight practice trials and 192 experimental trials. Participants were not given feedback either during practice or experimental trials. Participants were given an option to take a brief break every 5 min.

Data analysis. The dependent variable, error, could range between −180° and +180° to denote directionality. Positive errors (0° to 180°) indicated that the perceived gap was shifted clockwise relative to the actual gap, whereas negative errors (−180° to 0°) indicated that the perceived gap was shifted counterclockwise relative to the actual gap. We compared the error distributions across different relative orientations, which were radial, tangential, and in-between. Per participant, per relative orientation, we parsed errors ranging between −180° and +180° into 12 equal bins with a width of 30° and computed the proportion of responses in each bin. Thus, the group-averaged data presented here have equal contributions from each participant.

We reverse coded the error directions when necessary to align them (see details below). We then compared the proportion of responses at critical bins across different conditions using paired-samples *t* tests. We also compared the error distributions across confidence ratings (high and low confidence), the three cue-lead time conditions (17, 33, and 50 ms), and the meridians on which the target was placed (horizontal, vertical, and 45° and 135° oblique meridians). We opted for a replication with Experiment 2, with some modifications, for statistical rigor instead of conducting corrections for multiple comparisons.

Results

In Figure 3a, we present raw mouse-click data obtained from all 18 participants from a subset of trials (two out of 32 possible combinations for the in-between condition). In Figure 3a (top), the target Landolt C is placed along the 45° meridian, and its gap is in the 90° polar-angle position. The correct mouse-clicks are therefore along the top portion of the response circle, corresponding to a 0° error. Most of the clicks were near this value, thus falling within the ±15° error sectors. As predicted, there was also a disproportionate number of clicks within the +45° error sector corresponding to the target being perceived as radial, in contrast to the −45° error sector corresponding to the target being perceived as tangential.

In Figure 3a (bottom), we present the raw mouse-click data for the same Landolt C as the top figure but placed along the 90° meridian, making it a radially oriented target (two out of 32 possible combinations for the control condition). Because the Landolt C is already oriented radially, our hypothesis predicted no shift in perceived orientation and no particular bias in error directions. As can be seen, the errors are mostly around 0°. Unlike the top-row figure, they are symmetrically distributed around 0°, indicating no bias in the error distribution.

In Figure 3b, we present the histograms of errors separated by different relative orientations, collapsing across confidence ratings and cue-lead times. The red

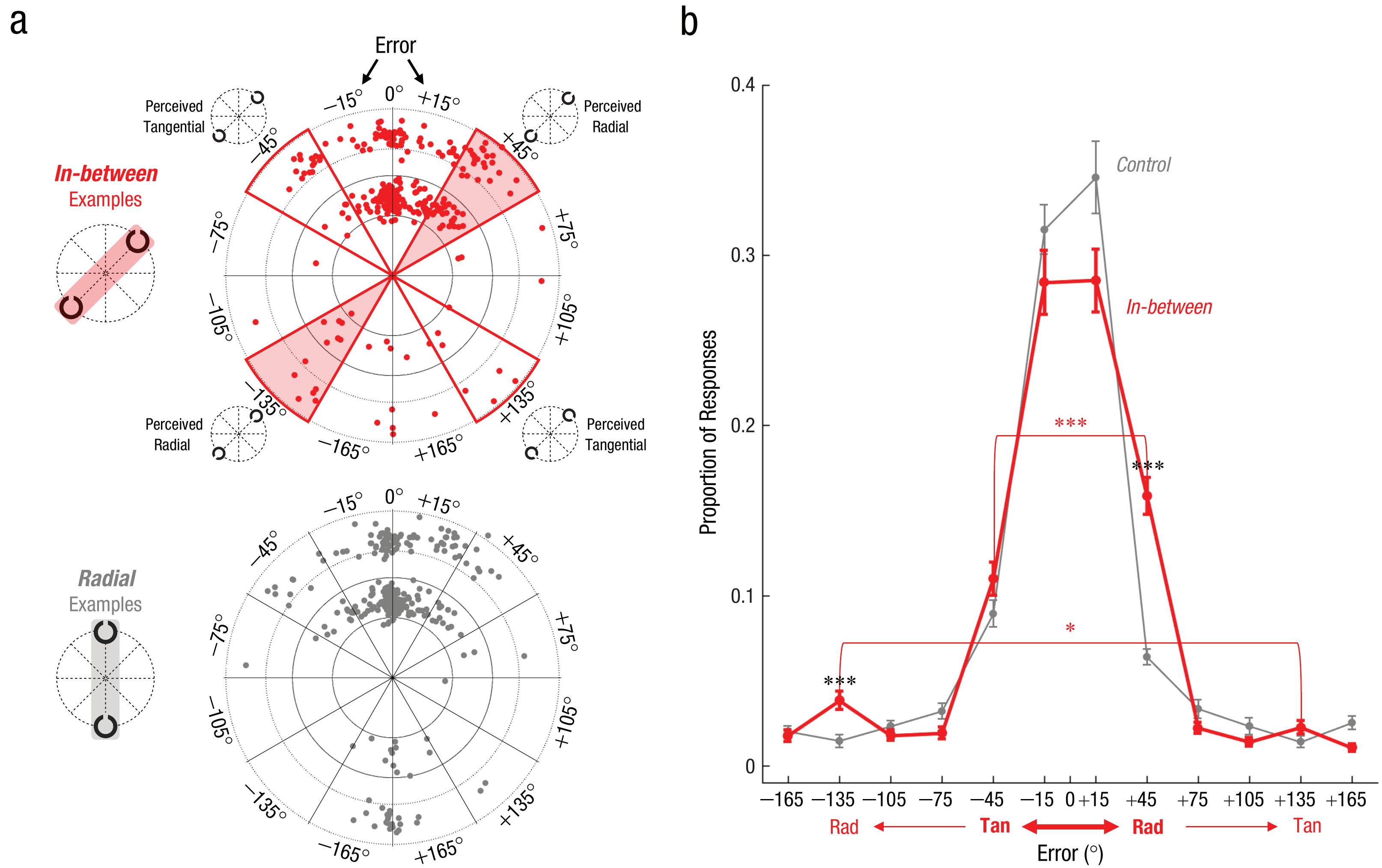

Fig. 3. Results of Experiment 1. Mouse-click data are illustrated in (a) for all 18 participants in Experiment 1 for the example conditions shown in Figure 2c. Targets that are in in-between orientation (top figure) or radial orientation (bottom figure) are shown. Each dot indicates where the participants clicked on the response circle. The concentric regions represent the high-confidence region (inner region enclosed by the first and second circles around fixation) and the low-confidence region (outer region enclosed by the third and fourth circles around fixation; see response-region details in Figs. 1b and 1c). The numbers in black indicate the error sectors (12 equal 30° sectors). When the target is in in-between orientation (top figure), there is an increased number of clicks along the corresponding radial axis (filled red sectors) compared with the corresponding tangential axis (unfilled red sectors). In contrast, when the target is in radial orientation (bottom figure), there is no preference for the ±45° and ±135° sectors. In (b), group mean error distributions are shown for all 64 combinations of target locations and target's absolute orientations, obtained from Experiment 1. Error bins plotted along the *x*-axis correspond to the error sectors shown in (a). The red distribution includes targets with in-between orientations; the gray distribution includes targets with radial and tangential orientations (control). Note the symmetry in the gray distribution and the asymmetry in the red distribution with elevated proportions of responses at +45° and –135°, indicating a radial bias. Data from all cue-lead times are included. Error bars represent ±1 *SEM*, adjusted for within-participants comparison (Morey, 2008; $^{*}p \le .05$, $^{***}p \le .0005$). Rad = radial; tan = tangential.

distribution in Figure 3b reflects all conditions in which the target is in the in-between orientation. Before averaging, we coded the error direction in the in-between conditions so that the target would become radial when rotated +45°, denoting this as the local radial direction. Thus, in the resultant distribution, a +45° error would mean that an in-between target was perceived to be radial; a −45° error would mean that an in-between target was perceived to be tangential.

As predicted, the resultant distribution was asymmetrical. The +45° error bin was elevated, indicative of a radial bias. No such elevation is seen in the tangential bin (−45°). Interestingly, and also as predicted, the error at the −135° bin was also elevated. This indicates that the in-between targets were perceived to be rotated not only +45° (the shortest rotation to become radial) but also the longer rotation (halfway around the circle), because this aligns the target radially as well. The raw data for this comparison can also be seen in Figure 3a (top), where there are more clicks in the shaded versus the open 135° red sectors.

The gray control curve in Figure 3b reflects all conditions in which the target orientation was either already radial or tangential with respect to the meridian on which it was placed. We collapsed the conditions in which the target was already radial or tangential into a combined control condition because the shapes of the error distributions were similar, and we made no specific predictions about a bias in error direction for either of the conditions. The resulting distribution was mostly symmetrical around 0°, meaning that there was no preferred direction of errors for these targets.

To quantify these observations statistically, we first contrasted the in-between and the control conditions at the critical error bins (Fig. 3b, black asterisks). The proportion of responses at the +45° and −135° bins were significantly greater for the in-between condition than for the control condition for +45°, $t(17) = 7.28$, $p < .0001$, $d = 1.72$, and for −135°, $t(17) = 4.92$, $p = .0001$, $d = 1.16$. Note that we contrasted the +45° (or −135°) error bin from the in-between condition with the combined ±45° (or ±135°) error bin from the control condition. The sign of the error in the control condition indicates only whether the error direction was clockwise or counterclockwise, so it is irrelevant for this particular comparison. This indicates that the same degree of error was more commonly observed when it corresponded to an in-between target being perceived as radial than when it corresponded to a radial or tangential target being perceived as in in-between orientation.

To directly test the asymmetry observed in the in-between condition, we contrasted the +45° and −45° bins as well as the −135° and +135° bins (Fig. 3b, red asterisks). The proportion of responses at the +45° bin was greater than −45°, $t(17) = 6.05$, $p < .0001$, $d = 1.43$, and that at the −135° bin was greater than +135°, $t(17) = 3.12$, $p = .006$, $d = 0.74$.

More specifically, when the target was presented in in-between orientation (equally away from being radial or tangential), participants perceived it as radial (+45° and −135° error bins) on 20% (SE = 1%) of the trials, whereas they perceived it as tangential (−45° and +135° error bins) on 13% (SE = 1%) of the trials. This indicates that among responses that corresponded to in-between targets being perceived as radial or tangential, radial occurred 61% of the time, whereas tangential occurred 39% of the time. If there were no bias, we would expect it to be 50%–50%.

This bias was present across different cue-lead times. We observed an overall decrease in error as the cue-lead times increased (see Fig. S2 in the Supplemental Material). Yet the prevalence of errors with a radial bias was present in all cue-lead times, suggesting that the additional benefits of attention were not sufficient to overcome the bias.

As for confidence ratings, on average, participants reported having high confidence on 58% (SE = 7%) of the trials, low confidence on 39% (SE = 7%) of the trials, and not seeing the target on 3% (SE = 1%) of the trials (i.e., "skip" trials). Thus, the majority of the responses were high-confidence responses. Notably, participants made errors in accord with radial bias with both high (Fig. S3a, left, in the Supplemental Material) and low confidence (Fig. S3a, right). Last, radial bias was present along all meridians except for the horizontal meridian (see Fig. S4 in the Supplemental Material). Notice that the fact that the bias was also observed along the vertical meridian indicates that the effect is not specific to the oblique meridians.

Overall, these results confirm our initial observation that radial-orientation bias could alter perceived object orientation. When a briefly presented object outside of fixation was oriented exactly between radial and tangential orientation with respect to the center of gaze, the visual system often incorrectly coded it as being radially oriented.

It is important to note that this pattern of results cannot be explained by a response bias in which participants click near the location of the Landolt C rather than in the gap position of the Landolt C. First, we do not observe the same tendency in the tangentially oriented targets (i.e., no prevalence of clicks with a 90° error). Second, the +45° or the −135° errors observed for the in-between targets, which reflect a radial bias, would mean 180° away from clicking near the target location for half of the in-between targets (e.g., consider a +45° error for the example Landolt-C target shown in Figure 3a, top, when it is located at the 225° polar-angle position, or a −135° error when it is at the 45° position).

Experiment 2: Radial Bias Observed With a Single Target

Method

Participants. Nineteen Brown University undergraduate students were recruited to participate in the study. All were right-handed and had normal or corrected-to-normal vision. Participants received partial course credit for their participation, which lasted approximately 1 hr. Data from one participant were excluded because they misunderstood the task and reported the location of the target rather than the gap position. Thus, our sample included 18 participants (11 women, 7 men) between the ages of 18 and 21 years (M = 18.8 years, SD = 0.92). The protocol was approved by the Institutional Review Board at Brown University. Participants gave informed consent and were treated according to the guidelines of the Institutional Review Board.

Stimuli and procedure. These were the same as in Experiment 1 with a few exceptions. First, we removed the cue and the nontarget Landolt Cs and presented a single Landolt C as the target. Second, to make the task more challenging (the single-target version of the task was noticeably easier than the cued-target version), we lowered the contrast of the target Landolt C by changing its color from white (red, green, blue [RGB] value: 255, 255, 255) to light gray (RGB: 191, 191, 191) while presenting it on the same medium-gray background (RGB: 128, 128, 128) and decreasing the duration of target presentation from 67 ms to 33 ms (see Fig. 2c). Participants completed two blocks of trials, each of which included eight practice trials and 256 experimental trials.

Data analysis. This was the same as Experiment 1.

Results

The results of Experiment 2 were essentially identical to those of Experiment 1, as reflected by the similarities between Figures 3 and 4. We conducted the same statistical comparisons as in Experiment 1. Across the in-between and control conditions, the proportions of responses at the +45° and −135° bins were significantly greater for the in-between condition than for the control conditions—for +45°: $t(17) = 4.85$, $p = .0002$, $d = 1.14$, and for −135°: $t(17) = 3.88$, $p = .001$, $d = 0.91$ (Fig. 4, black asterisks). In the in-between condition, the proportion of responses at the +45° bin was significantly greater than −45°, $t(17) = 3.22$, $p = .005$, $d = 0.76$, and the proportion of responses at the −135° bin was greater than at the +135° bin, $t(17) = 3.98$, $p = .001$, $d = 0.94$ (Fig. 4, red asterisks). More specifically, when the target was presented in in-between orientation, participants perceived it as radial (+45° and −135° error bins) on 19% (SE = 2%) of the trials, whereas they perceived it as tangential (−45° and +135° error bins) on 12% (SE = 2%) of the trials. This indicates that among responses that corresponded to in-between targets being perceived as radial or tangential, radial occurred in 61% of the trials whereas tangential occurred in 39% of the trials. If there were no bias, we would expect the breakdown to be 50%–50%.

As for confidence ratings, on average, participants reported having high confidence on 64% (SE = 5%) of the trials, low confidence on 33% (SE = 5%) of the trials, and not seeing the target on 3% (SE = 1%) of the trials (i.e., skip trials).

Similar patterns of confidence and meridian effects were observed as in Experiment 1. Participants made errors reflecting a radial bias both with high and low confidence ratings (Fig. S3b), and radial bias was present along all meridians except for the horizontal meridian (Fig. S4).

Discussion

Across two experiments, participants showed a tendency to preferentially perceive objects to be radially oriented when they were aligned at a 45° angle away from the corresponding radial axis. This bias was observed even on trials with high-confidence reports.

Prior studies have reported an increased sensitivity for radially compared with tangentially oriented lines and sine gratings using human psychophysics (e.g., Sasaki et al., 2006; Westheimer, 2003). A similar bias has been reported in anatomical and physiological studies. Research has shown that the dendritic fields of retinal ganglion cells are radially oriented (Leventhal & Schall, 1983), and this bias is also present in orientation-selective neural populations in both the LGN and V1 (Ling et al., 2015; Mannion et al., 2010) as well as in higher visual areas (Mannion et al., 2010).This pervasive bias would seem to be the likely source of the illusion observed here, in which a preference for radial orientations was manifested as an attraction of the object toward the radial axis rather than the tangential axis. Nevertheless, it is not immediately clear how greater neural representation of and perceptual sensitivity to radial orientations could lead to consistent misperception of the orientations of shapes as radial. One explanation is that when the visual information is impoverished because of very brief presentation, peripheral presentation, masking, and so on, orientation information becomes noisier. With the stronger weighting of radial orientations, the population coding of orientation may incorrectly skew toward radial.

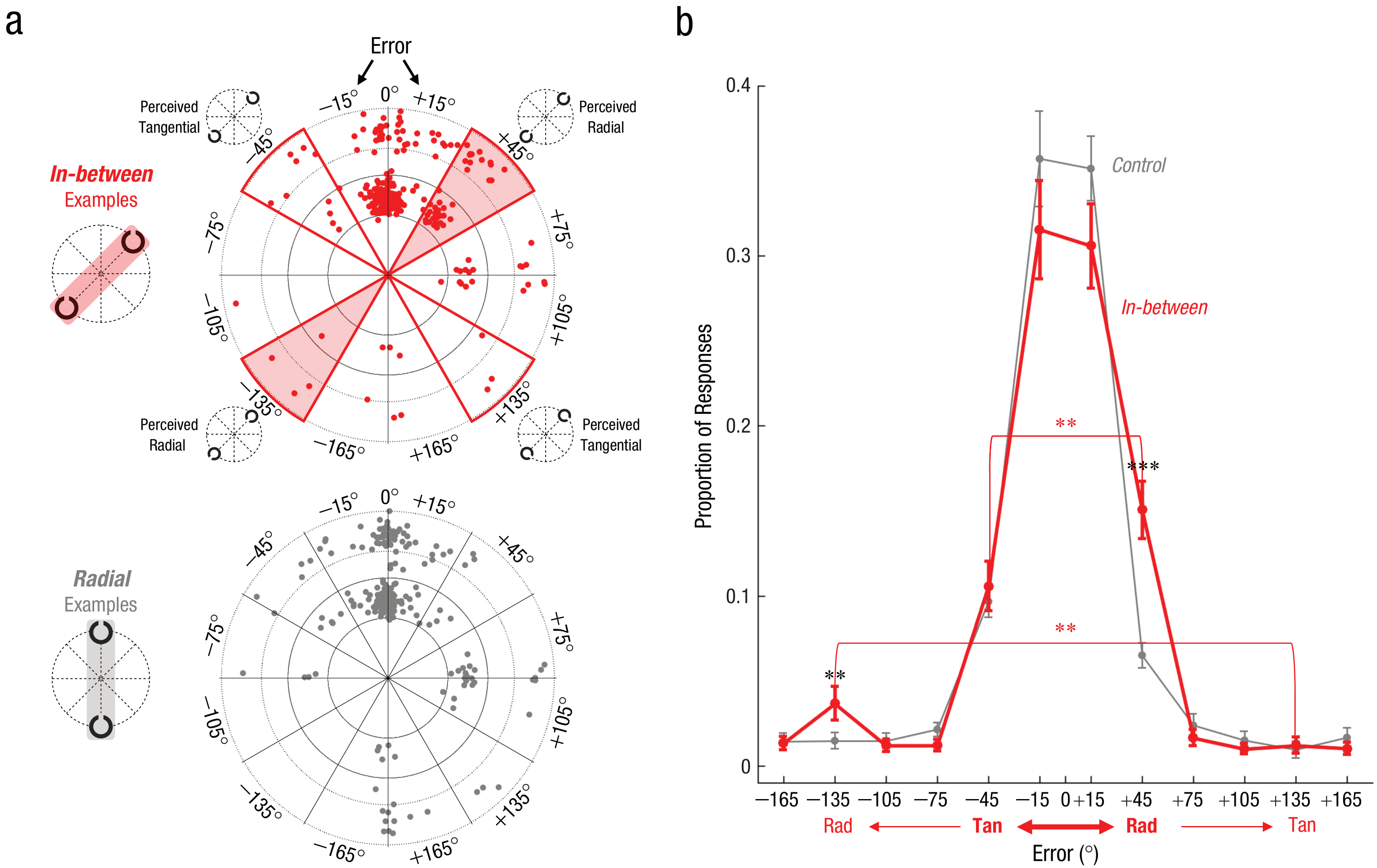

Fig. 4. Results of Experiment 2. Mouse-click data are illustrated in (a) for all 18 participants in Experiment 2 for the example conditions shown in Figure 2c. Targets that are in in-between orientation (top figure) or radial orientation (bottom figure) are shown. Each dot indicates where the participants clicked on the response circle. The concentric regions represent the high-confidence region (inner region enclosed by the first and second circles around fixation) and the low-confidence region (outer region enclosed by the third and fourth circles around fixation; see response-region details in Figs. 1b and 1c). The numbers in black indicate the error sectors (12 equal 30° sectors). When the target is in in-between orientation (top figure), there is an increased number of clicks along the corresponding radial axis (filled red sectors) compared with the corresponding tangential axis (unfilled red sectors). In contrast, when the target is in radial orientation (bottom figure), there is no preference for the ±45° and ±135° sectors. In (b), group mean error distributions are shown for all 64 combinations of target locations and target's absolute orientations, obtained from Experiment 2. Error bins plotted along the x-axis correspond to the error sectors shown in (a). The red distribution includes targets with in-between orientations; the gray distribution includes targets with radial and tangential orientations (control). Note the symmetry in the gray distribution and the asymmetry in the red distribution with elevated proportions of responses at +45° and −135°, indicating a radial bias. Error bars represent ±1 SEM, adjusted for within-participants comparison (Morey, 2008; ** $p \leq .005$, *** $p \leq .0005$). Rad = radial; tan = tangential.

Perceptual sensitivity increases as sensory information or stimulus representation becomes less noisy. In turn, the strength of a given bias, such as the horizontal-meridian advantage or the oblique effect, may decrease with increased sensitivity (e.g., Himmelberg et al., 2020; Tomassini et al., 2010). Consistent with this notion, while radial bias was present regardless of all cue-lead times, it tended to decrease with longer cue-lead times (see Fig. S2 for details). Similarly, although radial bias was present in both high- and low-confidence trials, it was smaller in high-confidence trials (see Fig. S3 for details). Last, in line with the horizontal-meridian advantage in visual performance (e.g., Barbot et al., 2021; Carrasco et al., 2001), radial bias was present along all meridians except for the horizontal meridian (see Fig. S4 for details).

Overall, the strength of this bias may depend on other factors that may change the amount of uncertainty in the stimulus representation, such as eccentricity (e.g., Malavita et al., 2021; Raemaekers et al., 2009; Rovamo et al., 1982), stimulus contrast, distribution of presented orientations, and (potentially) participant strategy, all of which may be explored by future researchers. Also, note that our sample consisted of university undergraduates with normal or corrected-to-normal vision, which may limit the generalizability of the findings. However, the fact that the phenomenon reported here is likely due to the structural characteristics of the early visual system and that all authors and colleagues who participated in the pilot experiment showed the effect, speaks to the likely generalizability of the findings.

In this article, we have presumed that the Landolt C stimuli were oriented along the axis of the gap, and we have reasoned that a biased population coding of orientation is the likely explanation for the observed radial bias. We confirmed our presumption by visualizing power at different orientations and spatial frequencies by calculating the fast Fourier transform (FFT) of the Landolt C stimulus for different orientations. In Figure S5 in the Supplemental Material, we present the FFT results for sample Landolt Cs with gaps in the 45° (first column) and 135° (second column) polar-angle positions; Gabor patches (third and fourth columns) are provided for comparison. In accordance with previous reports (e.g., Bondarko & Danilova, 1997), and as predicted, we found enhanced spectral energy along the axis that is orthogonal to that of the gap in the Landolt Cs (see Fig. S5b, first and second columns). Further, note that the orientation of the enhanced spectral energy observed for the 135° Landolt C (thin yellow line) is the same as that observed for the Gabor patches (yellow dots). When we consider how spectral energy contributes to our perception, it follows that the 135° Landolt C and the sample Gabor patches have the same orientation.

To conclude, we have demonstrated a new visual illusion: An object (Landolt C) was often seen in a nonveridical orientation, biased toward the case in which the gap was lined up with a radial line from the center of fixation. The visual system's increased sensitivity to radial orientations appears to be the substrate for this phenomenon.

Transparency

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Editor: Patricia J. Bauer
Author Contributions
All authors conceptualized and designed the study. M. Menceloglu collected and analyzed the data, prepared the figures, and drafted the initial manuscript. J. Song and K. Nakayama provided critical revisions. All authors revised the manuscript and approved the final version for submission.
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Open Practices
Data and materials have not been made publicly available, and the design and analysis plans for the experiments were not preregistered.

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Supplemental Material

Additional supporting information can be found at http://journals.sagepub.com/doi/suppl/10.1177/09567976221110243

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