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Anisotropic visual awareness of shapes

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ABSTRACT

While object perception may feel instantaneous, it is an iterative process in which information is accumulated until ambiguity about identity and location is resolved. In theory, awareness of an object should depend on how efficiently this process occurs. Therefore, objects with inherently weak visual representations should be more susceptible to perceptual disruption. We tested this hypothesis by examining the perception of aspect ratio, a 2D feature of shapes with anisotropic representation (circular shapes are less robustly represented than elongated shapes in high-level visual areas). Observers viewed a target shape shown for 20-ms within an array of ellipses. The target, which varied from flat to tall, was either masked or unmasked. Observers indicated the target's aspect ratio and if it was visible. Observers reported seeing elongated shapes far more often than circular shapes, but only on trials with object-substitution masking. This effect replicated across five control experiments, even though the shapes were identical in basic image attributes (e.g., contrast, area). Our findings demonstrate that shapes with extreme aspect ratios are more readily available to awareness than shapes with ambiguous dimensionality. More generally, this work supports theories of object processing which suggest that strength of visual representation gates access to awareness.

1. Introduction

In the visual world, objects can have a variety of forms and may be seen from a multitude of perspectives. Thus, the number of two-dimensional shape patterns projected on the retina is nearly unlimited. Interestingly, the visual system is equipped to represent some variations of shapes more than others. The neural representation of aspect ratio (the width of a pattern relative to its height), for example, is highly anisotropic. In particular, the majority of cells in inferotemporal cortex (IT) respond most strongly to extremely flat or tall shapes (Kayaert, Biederman, Op de Beeck, & Vogels, 2005). One benefit of this unequal representation is heightened sensitivity for discriminating aspect ratios around the category boundary—in this case, shapes that are only slightly flat or tall (Regan & Hamstra, 1992; Suzuki, 2005). Here, we propose a paradoxical consequence of aspect ratio's anisotropic organization in terms of visual awareness.

Objects are generally detected before they are discriminated. And before objects are detected, the visual system accumulates information about their locations and structures over time (Perrett, Oram, & Ashbridge, 1998). Some accounts of object processing propose that this process of refinement generally continues until a detailed interpretation of an object is established, so that only after ambiguity about location and identity is resolved does awareness of the object occur (e.g., Di Lollo, Enns, & Rensink, 2000; Enns, 2004; Enns & Di Lollo, 1997). Accordingly, objects that have inherently noisy or weak representation will take more time to surpass this threshold, and therefore should be less likely to be seen during visual masking. Across seven experiments, we tested our hypothesis that, as a consequence of the imbalanced tuning profiles of IT neurons, visual masking will more effectively interrupt awareness of shapes with circular aspect ratios than shapes with extreme aspect ratios.

Aspect ratio is a simple but important visual feature, crucial for interpreting information such as the two-dimensional shapes of objects (Biederman, 1987; Marr & Nishihara, 1978) and faces (Young & Yamane, 1992). It may also resolve three-dimensional rotations of objects (Biederman & Kalocsai, 1997), as extreme aspect ratios can indicate that a circular object is being seen from an oblique vantage point, and thus has potential to inform depth perception in general (Treisman & Gormican, 1988). Aspect ratio is a mid-level visual feature—more complex than orientation, but less complex than facial identity—that has singular cells dedicated to its neural representation. This direct encoding of aspect ratio (Op de Beeck, Wagemans, & Vogels, 2003; Stankiewicz, 2002) begins in intermediate stages of vision (e.g., V4; Dumoulin & Hess, 2007) and occurs along with other global shape attributes in IT (e.g., Kayaert et al., 2005). At the neural population level, aspect ratio has been described in the context of an opponent-coding

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scheme (Regan & Hamstra, 1992; Suzuki, 2005), although recent work suggests a multi-channel approach may be more appropriate (Dickinson, Morgan, Tang, & Badcock, 2017; Storrs & Arnold, 2017).

What is relevant in this investigation is that extreme aspect ratios are a priority for the visual system. In terms of neural representation, tall and flat aspect ratios are encoded more robustly than circular aspect ratios, both in the number of neurons and strength of response in IT (Kayaert et al., 2005). Anisotropic representation is also maintained in the encoding of aspect ratio of faces (Freiwald, Tsao, & Livingstone, 2009). This prioritization is evident in examinations of visual perception as well. During brief viewing, perceived aspect ratios of shapes are distorted away from circular values (Suzuki & Cavanagh, 1998). Shapes with extreme aspect ratios even stand out among circles, whereas the converse is not true (Treisman & Gormican, 1988). Treisman and Gormican proposed that the visual system only weakly supports the perception of what they referred to as "standard values" (i.e., circles), and instead emphasizes more extreme variations of shape. We extended this framework beyond visual discrimination, predicting that extreme shapes should have privileged access to awareness, and that circular shapes should be more susceptible to visual masking. We aimed to test this hypothesis using object-substitution masking (OSM).

OSM is a unique type of masking (e.g., Enns, 2004; Enns & Di Lollo, 1997) in which four dots are typically shown flanking a briefly-presented object, then allowed to trail on screen for a short amount of time. Like other types of masking, OSM can disrupt object discrimination or even render a target inaccessible to awareness. Unlike other types of masking, however, OSM probably does not involve inhibitory interactions or the addition of noise, and is instead thought to work primarily by disrupting re-entrant processing between high- and low-level visual areas (e.g., extrastriate areas and V1; Boehler, Schoenfeld, Heinze, & Hopf, 2008; Pascual-Leone & Walsh, 2001; although see Bridgeman, 2006; Poder, 2012). According to seminal accounts of OSM, the visual system updates object representations iteratively over time, using the initial feedforward sweep of processing to build a sort of working hypothesis about an object's appearance and location (e.g., Enns, 2004). Via feedback activity, often from higher- back to lower-level visual areas, this hypothesis is checked against current visual input and revised, potentially via multiple cycles of processing. Once ambiguity about the object is resolved, it is made available to visual awareness.

This OSM framework clearly implies that more iterations through this system of processing should be required for awareness of stimuli with inherently weaker initial neural representation. We utilized the anisotropic representation of aspect ratio to test this prediction. Because both the signal strength and number of cells responding to shapes with circular aspect ratios are weak, we suspected that, during brief viewing, these shapes would produce fragile representations in feedforward processing, thereby requiring more iterative processing. We thus predicted that compared to shapes with elongated forms, ellipses with circular aspect ratios should exhibit increased susceptibility to object-substitution masking. By this account, we suggest that an object's visibility may not be dictated just by its relevance, salience, or basic visual attributes, but also by biological factors that bias initial visual representations.

2. Experiment 1

2.1. Materials and methods

2.1.1. Observers

We conducted a power analysis for a general effect of masking on visual awareness using data from a previous investigation with the same ellipse stimuli and a similar masking procedure (Sweeny, D'Abreu, Elias, & Padama, 2017). Assuming the same large effect size from this previous work (d = 0.88), we determined that we would need

a sample of 19 observers to obtain power of 0.95 (1–ß). We thus set our stop rule for the first six experiments in this investigation at twenty. All experimental protocols in this investigation were approved by the Institutional Review Board at the University of Denver and were carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki). Twenty observers gave informed consent to participate either as volunteers or for course credit. All reported normal or corrected-to-normal vision. Sixteen observers were tested in one hour sessions on two separate occasions, and four observers were only able to participate in one session.

2.1.2. Stimuli

Displays were shown on an 18" CRT monitor with a refresh rate of 100-hz via a Macintosh computer running MATLAB and the Psychophysics toolbox (Brainard, 1997). We used a stimulus set from a previous investigation (Sweeny et al., 2017). This set included 11 ellipses, each drawn with gray (19.00 cd/m², 0.4°-thick) lines. These ellipses differed in terms of their aspect ratios (log values: -0.374, -0.311, -0.221, -0.131, -0.043, 0.0, +0.043, +0.131, +0.221, +0.311, and +0.374), but were equivalent in area. The diameter of a circular ellipse was 2.51°, and the width (or height) of the widest (or tallest) ellipse was 3.8° of visual angle. Ellipses were treated with a Gaussian blur with a 2.0-pixel radius to reduce aliasing.

Ellipses were presented in groups of four. Each ellipse was presented along an iso-acuity orbit (Rovamo & Virsu, 1979) around the fixation point (Fig. 1). This ensured that, regardless of their positions on the screen, all shapes would be seen with the same visual acuity, 5.01° from the fixation point. Three ellipses always had nearly circular aspect



Fig. 1. (A) A typical trial sequence from Experiment 1. Each trial contained four ellipses. Three distractor ellipses had relatively circular aspect ratios while the target ellipse had a randomly selected aspect ratio ranging from extremely flat to extremely tall. Each target ellipse was surrounded by a quartet of black masking dots, cueing it as the ellipse to be rated. On *masking trials*, the dots remained on the screen after the offset of the ellipses. On *no-masking* trials, all of the dots offset with the rest of the stimuli and were followed by a blank screen. (B) Examples of response options from the aspect-ratio matching screen, which did not include a circular option.

ratios.¹ The aspect ratio of the fourth ellipse in each group was randomly selected from the 11 values listed above, including the circular option. The location of this target ellipse was randomized on each trial. The target ellipse was always displayed surrounded by a quartet of masking dots that either offset with the ellipses or trailed the offset of the target ellipse for an additional 240-ms. The four masking dots (visual angle = 0.7°, luminance = 0.84 cd/m^2) were each equidistant (2.51°) from the center of the target ellipse. All stimuli were presented on a grey background (RGB = 170, 170, 170, luminance = 41.46 cd/m²) around a central blue fixation cross subtending a visual angle of 0.7°.²

2.1.3. Procedure

Each observer was directed to sit 57-cm from a monitor in a dimlylit room. The experiment began with an automated demonstration of four example trials. Each trial began with a blank screen with a fixation cross presented for a random duration between 800- and 1500-ms to prevent anticipation of the onset of the stimuli. Observers were asked to fix their gaze on the cross, but to expand their attention to the corners of the screen. An array of four ellipses (plus the masking dots) was then presented for 20-ms. We used this brief presentation time to prevent observers from making saccades to the cued ellipses. The four black masking dots surrounding the target indicated to observers which of the four shapes they should evaluate. On trials with no masking, the dots disappeared simultaneously with the ellipses, while on masking trials, the dots lingered for 240-ms. Previous investigations have shown that feedback activity tends to arrive in early visual areas with a latency of 80-120-ms (Jannati, Spalek, & Di Lollo, 2013) and that the timing of this reentrant activity is related to the effectiveness of OSM (Kotsoni, Csibra, Mareschal, & Johnson, 2007). Thus, according to re-entrant accounts of OSM, our 240-ms lag time should have induced strong masking during late stages of object representation (Enns. 2004). Including masking dots to offset with the target in the no-masking condition was important for controlling for possible effects of crowding (Kahan & Enns, 2010).

On every trial, the fixation cross lingered on a blank screen after the dots disappeared, again for a duration randomly selected between 800and 1500-ms. Text then appeared directing observers to indicate how many ellipses they perceived, either by pressing the left key (to indicate that only three were visible) or the right key (to indicate that four were visible). Next, a magnitude-matching screen directed observers to select an ellipse with an aspect ratio that most closely matched that of the cued ellipse. Observers were asked to provide this aspect ratio judgment regardless of whether or not they reported having seen the target ellipse. We excluded a circle from this screen to preclude observers who were not confident about their response from selecting a circle by default. Each of these response screens was presented until observers made their key-presses. Observers also had the option of pressing the 'x' key to indicate that they had experienced a lapse of attention, blinked, or were otherwise unaware of the entire ellipse display. This aborted the current trial, omitting it from the dataset. The first block of testing included 500 trials. The directions were shortened in the second block of testing, allowing for 600 trials to be completed. Observers were given a break every fourth of the way through each block.

3. Results

3.1. Aspect-ratio discrimination

Before conducting our main analyses, we first examined sensitivity for making flat-vs-tall discriminations in terms of proportion correct (Fig. 2A). We expected that aspect ratio discrimination in the masking condition would be impaired relative to the no-masking condition, and that sensitivity for discriminating aspect ratio would be best when the target ellipse had a more extreme aspect ratio. We conducted a repeated-measures ANOVA with factors of OSM (no masking and masking) and shape (flat: ellipses 1-5; and tall: ellipses 7-11). As expected, we found a main effect of OSM, F(1, 19) = 38.38, p < .001, $\eta_p^2 = 0.67$, and a main effect of shape, F(9, 171) = 68.44, p < .001, $\eta_p^2 = 0.78$.³ We also found an interaction between OSM and shape, F(9, 171) = 68.44, p < .001, $\eta_p^2 = 0.78$.³ We also found an interaction between OSM and shape, F(9, 171) = 68.44, p < .001, $\eta_p^2 = 0.78$.³ We also found an interaction between OSM and shape, F(9, 171) = 68.44, p < .001, $\eta_p^2 = 0.78$.³ We also found an interaction between OSM and shape, F(9, 171) = 68.44, p < .001, $\eta_p^2 = 0.78$.³ We also found an interaction between OSM and shape, F(9, 171) = 68.44, p < .001, $\eta_p^2 = 0.78$.³ We also found an interaction between OSM and shape, F(9, 171) = 68.44, p < .001, $\eta_p^2 = 0.78$.³ We also found an interaction between OSM and shape, F(9, 171) = 68.44, p < .001, $\eta_p^2 = 0.78$.³ We also found an interaction between OSM and shape, F(9, 171) = 68.44, p < .001, $\eta_p^2 = 0.78$.³ We also found an interaction between OSM and shape, F(9, 171) = 68.44, p < .001, $\eta_p^2 = 0.78$.³ We also found an interaction between OSM and shape, F(9, 171) = 68.44, $\eta_p^2 = 0.78$.³ We also found an interaction between OSM and shape, F(9, 171) = 68.44, $\eta_p^2 = 0.78$.³ We also found an interaction between OSM and shape, F(9, 171) = 68.44, g = 0.78.³ We also found an interaction between OSM and shape and g = 0.78.³ We also found an interaction between OSM and g = 0.78.³ We also found an interaction between OSM and g = 0.78.³ We also found an interaction between OSM and g = 0.78.³ We also found an interaction between OSM and g = 0.78.³ We also found an interaction between OSM and g = 0.78.³ We also found an interaction between OSM and g = 0.78.³ We also found an interaction between OSM and g = 0.78.³ We also found an interaction between OSM and g = 0.78.³ We also found an interaction between OSM and g = 0.78.³ We also found an interaction between OSM and g = 0.78.³ We also found an interaction between OSM and g = 0.78.³ We also fou 171 = 6.415, p < .001, $\eta_p^2 = 0.25$. The main effect of OSM confirmed that masking degraded discrimination of flat-vs-tall aspect ratios. The main effect of shape indicated that tall-vs-flat discrimination was best for more elongated targets. These analyses were not the primary focus of our investigation, but they are useful because they confirm that (1) the masking in our design was successful, and (2) observers were sensitive to the subtle aspect ratio differences between the shapes.

3.2. Shape awareness

Our main objective was to examine how reports about the target shape's visibility (i.e., subjective awareness) depended on OSM and aspect ratio. We expected that awareness of the target ellipse would be disrupted in the masking condition relative to the no-masking condition. More importantly, we predicted that masking would disrupt awareness of the target ellipses more readily when these shapes had less elongated aspect ratios compared to more extreme aspect ratios. We conducted a repeated-measures ANOVA with factors of OSM (no masking and masking) and shape (1-11, including the circular target). In this analysis, we used the proportion of trials where observers reported seeing the target shape as our dependent variable. As expected, we found a main effect of OSM, F(1, 19) = 18.38, p < .001, $\eta_p^2 = 0.49$, and a main effect of shape, F(10, 190) = 8.66, p < .001, $\eta_p^2 = 0.31$. We also found an interaction between OSM and shape, F (10,190) = 10.96, p < .001, $\eta_p^2 = 0.37$. The main effect of OSM confirmed that masking disrupted awareness of the target ellipse (Fig. 2B). The main effect of shape indicated that awareness of the target ellipse was disrupted more easily when it had a less elongated aspect ratio. The interaction was especially important because it revealed that less elongated shapes were not simply more difficult to see. Rather, all shapes were equally visible in the absence of masking, but when OSM was present, it was especially effective at disrupting awareness of less elongated shapes.

3.3. Aspect-ratio discrimination, masking, and awareness

We also evaluated aspect ratio discrimination as a function of both the presence of masking dots and each observer's visual awareness on a trial-by-trial basis. We examined three types of trials: (1) trials in which masking dots offset with the shapes and observers reported seeing the target ellipse (i.e., there was no masking—*no-masking/aware trials*), (2) trials in which masking dots lingered after the shapes offset, but observers reported being aware of the target (i.e., masking failed, in terms

¹ Due to a technical error that occurred only in Experiment 1, the three distractor ellipses had aspect ratios that were nearly, but not perfectly circular (log AR -0.043, choice #5 on the magnitude matching screen). This was corrected in subsequent experiments and did not appear to influence our results in any meaningful way since we replicated our main findings several times.

² For purposes related to a different investigation, auditory stimuli were presented with the initial ellipse display, offset by 30-ms. Observers were told to ignore the sounds, which had no effects on target recognition or shape rating.

³ Discrimination performance was better for flat shapes than tall shapes throughout our investigation. This may have been because of a bias to report flat aspect ratios, which has been shown previously (Lindermann, 1955; Suzuki & Cavanagh, 1998). This was not important for understanding our main results regarding visual awareness, thus we do not discuss it further.



Fig. 2. Discrimination and subjective awareness of shapes based on trial type (no masking and masking) and aspect ratio of the cued ellipse from Experiment 1. (A) Proportion correct for determining whether the target ellipse was flat or tall across 10 target-ellipse aspect ratios, shown separately for the no-masking and masking conditions. (B) Proportion of trials in which observers reported seeing the target ellipse, shown separately for the 11 target aspect ratios and for the no-masking and masking conditions. (C) Proportion correct for making flat/tall discriminations (averaged across 10 target aspect ratios) on *no-masking/aware, masking/aware,* and *masking/unaware trials*. The error bars in panels A–C represent ± 1 *SEM* with baseline individual variability across the data points removed (i.e., repeated-measures error bars).

of visual awareness—*masking/aware trials*), and (3) trials in which masking dots lingered after the shapes offset and the target was not visible to observers (i.e., successful masking—*masking/unaware trials*).⁴

Overall, we found that visual awareness was the key factor in evaluating shapes (Fig. 2C). Aspect ratio discrimination was worse in the masking/unaware condition (M = 59.2%, SD = 13.2%) compared to both the no-masking/aware condition (M = 81.3%, SD = 4.7%), t (19) = 6.91, p < .001, d = 1.77, and the masking/aware condition (M = 82.0%, SD = 6.58%), t(19) = 6.29, p < .001, d = 1.71.⁵ Interestingly, a one-sample *t*-test confirmed that even though disruptions of awareness degraded performance in the masking/unaware condition, shape discrimination on these trials was still greater than chance-level performance (i.e., 50% correct), t(19) = 3.12, p < 0.01, d = 0.69. These analyses suggest that the simple presence of masking dots alone did not disrupt shape discrimination. Flat/tall judgements were only impaired when observers reported not being able to see the target.

4. Experiment 2

It is possible that weaker masking of the most elongated ellipses in Experiment 1 could have been because their end-points were further away from the masking dots. In Experiment 2, we rotated the ellipses by \pm 45° but maintained the positions of the masking dots. This ensured that, compared with the less elongated shapes, the contours of the most elongated shapes would be closer to the masking dots. Previous work demonstrated that masking of global shape properties is not based simply on proximity (Habak, Wilkinson, Zakher, & Wilson, 2004). We thus predicted that we would find the same pattern of results as in Experiment 1, which would suggest that weaker masking of the extreme shapes is instead a matter of their robust representation.

4.1. Materials and method

4.1.1. Observers

Twenty observers gave informed consent to participate either as volunteers or for course credit. All reported normal or corrected-tonormal vision. 4.1.2. Stimuli and procedure

All stimuli and procedures were identical to those from Experiment 1 with the exception that all ellipses were tilted either -45° (i.e., counter-clockwise; ellipses 1–5) or 45° (i.e., clockwise; ellipses 7–11) (Fig. 3A). Treisman and Gormican (1988) showed that more efficient search for extreme aspect ratios occurs even when they are rotated away from cardinal orientations. We thus did not expect our manipulation to disrupt the underlying representation of the shapes in a meaningful way. Observers made coarse judgements about orientation (left versus right) as well as more nuanced evaluations of aspect ratio. The experiment was run in the same session as Experiment 3 (but in a different block) with 500 trials and a break at the half-way point.

5. Results

5.1. Aspect-ratio discrimination

As in Experiment 1, we began by examining observers' sensitivity for making flat-vs-tall judgements of the target ellipses (Fig. 3B). We conducted a repeated-measures ANOVA with factors of OSM (no masking and masking) and shape (flat: 1–5; and tall: 7–11). As expected, we found a main effect of OSM, F(1, 18) = 21.78, p < .001, $\eta_p^2 = 0.55$, and a main effect of shape, F(9, 168) = 24.1, p < .001, $\eta_p^2 = 0.56$. We also found an interaction between OSM and shape, F(9, 168) = 2.27, p = .02, $\eta_p^2 = 0.11$. As in Experiment 1, these results confirm that masking was effective and observers were attentive to the aspect ratios of the shapes even when the ellipses were rotated.

5.2. Shape awareness

We next examined how each observer's reports about the target shape's visibility depended on OSM and aspect ratio (Fig. 3C). We conducted a repeated-measures ANOVA with factors of OSM and shape, using the proportion of trials where observers reported seeing the target shape as the dependent variable. We found a main effect of OSM, *F*(1, 18) = 31.64, *p* < .001, $\eta_p^2 = 0.64$, and a main effect of shape, *F*(10, 186) = 17.84, *p* < .001, $\eta_p^2 = 0.49$. As in Experiment 1, we found an interaction between OSM and shape, *F*(10, 186) = 12.73, *p* < .001, $\eta_p^2 = 0.41$. This suggests that the findings from Experiment 1 cannot simply be explained by the proximity of the edges of each target ellipse to the masking dots.

⁴ We did not evaluate trials in which masking dots offset with the shapes and yet observers still did not report seeing the target. We suspected that performance in these trials, which were rare, simply reflected lapses in attention.

⁵ Effect sizes for within-subject comparisons here and in subsequent analyses were corrected for dependence among means (Morris & Deshon, 2002).



Fig. 3. A typical stimulus array, as well as discrimination, and subjective awareness of shapes based on trial type (no masking and masking) and aspect ratio of the cued ellipse in Experiment 2. (A) The target ellipse was either rotated to the left or right so that the contours of the extreme shapes were closer to the masking dots. (B) Proportion correct for determining whether the target ellipse was flat or tall across 10 target-ellipse aspect ratios, shown separately for the no-masking and masking conditions. (C) Proportion of trials in which observers reported seeing the target ellipse, shown separately for the 11 target aspect ratios and for the no-masking and masking conditions. The error bars in panels B and C represent ± 1 *SEM* with baseline individual variability across the data points removed (i.e., repeated-measures error bars).

5.3. Aspect-ratio discrimination, masking, and awareness

As in Experiment 1, we evaluated aspect ratio discrimination as a function of both the presence of masking dots and each observer's visual awareness on a trial-by-trial basis. Again, we found that visual awareness was the key factor in evaluating shapes. Aspect ratio discrimination was worse in the masking/unaware condition (M = 55.85%, SD = 10.3%) compared to both the no-masking/aware condition (M = 83.61%, SD = 8.19%), t(19) = 4.9, p < .001, d = 2.66, and the masking/aware condition (M = 84.44%, SD = 10.81%), t(19) = 8.36, p < .001, d = 2.09. As in Experiment 1, a one-sample *t*-test confirmed that shape discrimination in the masking/unaware condition was still greater than chance-level performance, t (19) = 2.54, p = .02, d = 0.57.

6. Experiment 3

The rationale behind Experiment 3 was similar to that from Experiment 2. We rotated the quartets of masking dots by 45° so that they formed a diamond-configuration around the target shapes, which

were stretched horizontally or vertically as in Experiment 1 (Fig. 4A). This ensured that the contours of the more elongated shapes were closer to the masking dots. Again, we predicted that we would find the same pattern of results as in Experiment 1, which would suggest that weaker masking of the extreme shapes is not simply a matter of proximity to the masking dots.

6.1. Materials and method

6.1.1. Observers

Twenty observers gave informed consent to participate either as volunteers or for course credit. All reported normal or corrected-tonormal vision.

6.1.2. Stimuli and procedure

All stimuli and procedures were identical to those from Experiment 1 with the exception that the masking dots were rotated around the target ellipse by 45° (Fig. 4A). The experiment was run in the same session as Experiment 2 (but in a different block) with 600 trials and a break at the half-way point.



Fig. 4. A typical stimulus array, as well as discrimination, and subjective awareness of shapes based on trial type (no masking and masking) and aspect ratio of the cued ellipse in Experiment 3. (A) The group of masking dots was rotated so that they were closer to the contours of the extreme shapes. (B) Proportion correct for determining whether the target ellipse was flat or tall across 10 target-ellipse aspect ratios, shown separately for the no-masking and masking conditions. (C) Proportion of trials in which observers reported seeing the target ellipse, shown separately for the 11 target aspect ratios and for the no-masking and masking conditions. The error bars in panels B and C represent ± 1 *SEM* with baseline individual variability across the data points removed (i.e., repeated-measures error bars).



Fig. 5. A typical stimulus array, as well as discrimination, and subjective awareness of shapes based on trial type (no masking and masking) and aspect ratio of the cued ellipse in Experiment 4. (A) The distractor ellipses had randomly selected variations of extreme aspect ratios so that circular targets would be distinct. (B) Proportion correct for determining whether the target ellipse was flat or tall across 10 target-ellipse aspect ratios, shown separately for the no-masking and masking conditions. (C) Proportion of trials in which observers reported seeing the target ellipse, shown separately for the 11 target aspect ratios and for the no-masking and masking conditions. The error bars in panels B and C represent ± 1 *SEM* with baseline individual variability across the data points removed (i.e., repeated-measures error bars).

7. Results

7.1. Aspect-ratio discrimination.

As in Experiment 1, we began by examining sensitivity for making flat-vs-tall judgements of the target ellipses (Fig. 4B). We conducted a repeated-measures ANOVA with factors of OSM (no masking and masking) and shape (flat: 1–5; and tall: 7–11). As expected, we found a main effect of OSM, *F*(1, 19) = 27.65, *p* < .001, $\eta_p^2 = 0.59$, and a main effect of shape, *F*(9,171) = 21.91, *p* < .001, $\eta_p^2 = 0.54$. We also found an interaction between OSM and shape, *F*(9, 171) = 2.11, *p* = .03, $\eta_p^2 = 0.1$.

7.2. Shape awareness

Next, we examined how each observer's reports about the target shape's visibility depended on OSM and aspect ratio (Fig. 4C). We conducted a repeated-measures ANOVA with factors of OSM and shape, using the proportion of trials where observers reported seeing the target shape as the dependent variable. As expected, we found a main effect of OSM, F(1, 19) = 22.7, p < .001, $\eta_p^2 = 0.54$, and a main effect of shape, F(10, 190) = 8.54, p < .001, $\eta_p^2 = 0.31$. As in Experiment 1, we found an interaction between OSM and shape, F(10, 190) = 4.56, p < .001, $\eta_p^2 = 0.19$. This pattern of results suggests that again, the findings from Experiment 1 cannot simply be explained by the more extreme ellipses breaking the illusory border created by the masking dots in OSM.

7.3. Aspect-ratio discrimination, masking, and awareness

We evaluated aspect ratio discrimination as a function of both the presence of masking dots and each observer's visual awareness on a trial-by-trial basis. Two observers did not contribute data to each of the awareness conditions (*no-masking/aware, masking/aware, and masking/unaware*), so we removed them from this analysis. Again, we found that visual awareness was the key factor in evaluating shapes. Aspect ratio discrimination was worse in the masking/unaware condition (M = 51.97%, SD = 11.86%) compared to both the no-masking/aware condition (M = 82.85%, SD = 7.89%), t(17) = 8.57, p < .001, d = 2.07, and the masking/aware condition (M = 82.53%, SD = 11.32%), t(17) = 7.82, p < .001, d = 1.86. These results mirror those from Experiments 1 and 2 with one exception. A one-sample *t*-test showed that shape discrimination on successful masking trials was not

greater than chance-level performance, t(18) = 0.72, p = .48, d = 0.17.

8. Experiment 4

We conducted an additional experiment to examine whether strong masking of the less elongated ellipses in Experiments 1–3 occurred because of their similarity to the distractor shapes, which were always circles. Similarity between target and distractor shapes is known to impair performance in other visual tasks, like search (Foster & Savage, 2002), and is thus important to examine in the current context. In this experiment, we used ellipses with flat and tall aspect ratios as the distractor shapes. We predicted that we would find the same pattern of results as in Experiments 1–3, which would suggest the extremely flat and tall ellipses were not more difficult to mask simply because they stood out among a group of circles.

8.1. Materials and method

8.1.1. Observers

Twenty observers gave informed consent to participate either as volunteers or for course credit. All reported normal or corrected-tonormal vision. The experiment was run in the same session as Experiment 6 (but in a different block) with 500 trials and a break at the half-way point.

8.1.2. Stimuli and procedure

All stimuli and procedures were identical to those from Experiment 1 except instead of using three circles as the non-target ellipses, random selections of extreme ellipses (ARs: -0.374 and 0.374) were displayed (Fig. 5A).

9. Results

9.1. Aspect-ratio discrimination

We began by examining sensitivity for making flat-vs-tall judgements of the target ellipses (Fig. 5B). We conducted a repeated-measures ANOVA with factors of OSM (no masking and masking) and shape (flat: 1–5; and tall: 7–11). As expected, we found a main effect of OSM, F(1, 19) = 53.43, p < .001, $\eta_p^2 = 0.74$, and a main effect of shape, F(9, 171) = 9.51, p < .001, $\eta_p^2 = 0.33$. Unlike in the previous experiments, we did not find an interaction between OSM and shape, F(9,171) = 1.58, p = .125, $\eta_p^2 = 0.08$.

9.2. Shape awareness

Our primary analysis examined how reports about the target shape's visibility depended on OSM and aspect ratio with a repeated-measures ANOVA (Fig. 5C). As expected, we found a main effect of OSM, F(1, 19) = 13.68, p < .01, $\eta_p^2 = 0.42$, and a main effect of shape, F(10, 190) = 2.54, p < .01, $\eta_p^2 = 0.12$. As in Experiment 1, we found an interaction between OSM and shape, F(10, 190) = 2.63, p < .01, $\eta_p^2 = 0.12$. These results suggest that the strong masking for circular shapes in Experiments 1–3 cannot be *entirely* accounted for by similarity to the distractor shapes. It may occur on top of a "pop-out" effect, and in fact the unique pattern of strong masking for circular shapes appears to have been larger in Experiments 1–3, but specific comparisons across experiments was not our goal.

9.3. Aspect-ratio discrimination, masking, and awareness

We again evaluated aspect ratio discrimination as a function of both the presence of masking dots and each observer's visual awareness on a trial-by-trial basis. We removed two observers who did not contribute data to each of the awareness conditions (*no-masking/aware, masking/aware,* and *masking/unaware*). Again, we found that visual awareness was the key factor in evaluating shapes. Aspect ratio discrimination was worse in the masking/unaware condition (M = 44.12%, SD = 13.51%) compared to both the no-masking/aware condition (M = 74.48%, SD = 9.75%), t(17) = 7.76, p < .001, d = 1.8, and the masking/aware condition (M = 66.69%, SD = 13.51%), t(17) = 5.47, p < .001, d = 1.32. As in Experiment 3, a one-sample *t*-test showed that shape discrimination on successful masking trials was not greater than chance-level performance, t(17) = 1.85, p = .08, d = 0.44. These results are similar to those found in Experiment 1.

10. Experiment 5

Previous work has shown that OSM is strongest when masking dots are more similar to the target (e.g., having a shared orientation; Goodhew, Edwards, Boal, & Bell, 2015). Additionally, the encoding of aspect ratio is relatively independent of an object's size (Regan & Hamstra, 1992). It is thus possible that the circular aspect ratio of the masking dots made the circular targets easier to mask in Experiments 1–4. This is reasonable, since cells in IT are organized according to their similarity in two-dimensional shape, and contain numerous short-range inhibitory connections (Fujita & Fujita, 1996; Wang, Fujita, & Tamura, 2002) that could, in theory, produce strong interference between shapes with similar aspect ratios (Suzuki & Grabowecky, 2002). In Experiment 5, we used masking dots with tall aspect ratios to test if similarity to the masking dots was responsible for our previous results, in which case the tall targets should be most easily masked. Instead, we predicted the same pattern of results as in Experiments 1–4.

10.1. Materials and method

10.1.1. Observers

Twenty observers gave informed consent to participate either as volunteers or for course credit. All reported normal or corrected-tonormal vision. The experiment was run in the same session as Experiment 6 (but in a different block) and had 300 trials with a break at the half-way point.

10.1.2. Stimuli and procedure

All stimuli and procedures were identical to those from Experiment 1 except instead of using masking dots with circular aspect ratios, we used masking dots with aspect ratios identical to those of the tallest ellipses in our stimulus set (log AR: 0.374) (Fig. 6A).

11. Results

11.1. Aspect-ratio discrimination

We began by examining sensitivity for making flat-vs-tall judgements of the target ellipses (Fig. 6B). We conducted a repeated-measures ANOVA with factors of OSM (no masking and masking) and shape (flat: 1–5; and tall: 7–11). As expected, we found a main effect of OSM, F(1, 19) = 26.18, p < .001, $\eta_p^2 = 0.58$, and a main effect of shape, F(9, 171) = 43.02, p < .001, $\eta_p^2 = 0.69$. We also found an interaction between OSM and shape, F(9, 171) = 5.33, p < .001, $\eta_p^2 = 0.22$. These results simply confirm that masking was effective and observers were attentive to the aspect ratios of the shapes even when the masking dots had extremely tall aspect ratios.

11.2. Shape awareness

Next we examined how each observer's reports about the target shape's visibility depended on OSM and aspect ratio (Fig. 6C). We conducted a repeated-measures ANOVA with factors of OSM and shape, using the proportion of trials where observers reported seeing the target shape as the dependent variable. As expected, we found a main effect of OSM, F(1, 19) = 19.1, p < .001, $\eta_p^2 = 0.5$, and a main effect of shape, F(10, 190) = 3.47, p < .001, $\eta_p^2 = 0.15$. As in Experiment 1, we found an interaction between OSM and shape, F(10, 190) = 3.54, p < .001, $\eta_p^2 = 0.16$. This pattern of results, which mirrored those from the previous experiments, suggest that our main findings cannot simply be explained by the shapes of the individual masking dots.

11.3. Aspect-ratio discrimination, masking, and awareness

We next evaluated aspect ratio discrimination as a function of both the presence of masking dots and each observer's visual awareness on a trial-by-trial basis. For the fifth time, we found that visual awareness was the key factor in evaluating shapes. Aspect ratio discrimination was worse in the masking/unaware condition (M = 52.44%, SD = 3.99%) compared to both the no-masking/aware condition (M = 69.37%, SD = 3.0%), t(20) = 3.7, p < .01, d = 0.84, and the masking/aware condition (M = 71.12%, SD = 2.62%), t(20) = 4.11, p < .001, d = 0.94. A one-sample *t*-test showed that shape discrimination on successful masking trials was not greater than chance-level performance, t(20) = 0.61, p = .55, d = 0.14.

12. Experiment 6

We conducted an exploratory investigation using orientation to examine the generalizability of our effect beyond aspect ratio. There is some evidence that orientation perception is anisotropic (e.g., the oblique effect; Appelle, 1972; Girshick, Landy, & Simoncelli, 2011), and representation in V1 has been shown to favor horizontal and vertical orientations (e.g., Li, Peterson, & Freeman, 2003). However, these kinds of effects can be quite complex; depending on an object's location relative to fixation, uneven neural response can be eliminated or even reversed (Mannion, McDonald, & Clifford, 2010). We thus expected that contrary to Experiments 1-5, when we examined the strength of OSM for masking a variety of orientated Gabor patches across the peripheral locations in our design, each orientation would be equally effected by OSM. Such a finding would rule out a simple explanation that any stimuli nearby a category boundary may have limited access to visual awareness, and instead suggest some specificity of our effect for the perception of aspect ratio.

12.1. Materials and method

12.1.1. Observers

Twenty observers gave informed consent to participate either as



Fig. 6. A typical stimulus array, as well as discrimination, and subjective awareness of shapes based on trial type (no masking and masking) and aspect ratio of the cued ellipse in Experiment 5. (A) Masking dots always had extremely tall aspect ratios. (B) Proportion correct for determining whether the target ellipse was flat or tall across 10 target-ellipse aspect ratios, shown separately for the no-masking and masking conditions. (C) Proportion of trials in which observers reported seeing the target ellipse, shown separately for the 11 target aspect ratios and for the no-masking and masking conditions. The error bars in panels B and C represent ± 1 *SEM* with baseline individual variability across the data points removed (i.e., repeated-measures error bars).

volunteers or for course credit. All reported normal or corrected-tonormal vision. The experiment was run in the same session as Experiment 4 (but in a different block) with 500 trials and a break at the half-way point.

12.1.2. Stimuli and procedure

Stimuli and procedures were identical to those from Experiment 1, except observers viewed and evaluated Gabor patches instead of ellipses (Fig. 7A). Observers were first asked to report if they perceived 3 or 4 patches on each trial, and then indicate the rotation of the target patch cued by masking dots in the same fashion as Experiments 1–5. Observers indicated the target's degree of rotation from -45 to 45° , in 10-degree increments, using a magnitude matching screen similar to those from Experiments 1–5 (excluding the "vertical" option with 0° rotation). Each array contained three patches rotated by 0° and a target patch with one of 11 randomly selected rotations (-45° , -35° , -25° , -15° , -5° , 0°, 5°, 15°, 25°, 35° and 45°). As in the previous experiments, this target patch was surrounded by four circular masking dots. Each Gabor patch subtended a visual angle of 2.41° and had a spatial frequency of 2.9 cycles per degree (cpd). Gabors appeared against the same gray background as the other stimuli.

13. Results

13.1. Orientation discrimination

Similar to aspect ratio discrimination in Experiments 1–5, we examined sensitivity for judging whether the target was tilted to the left or to the right (Fig. 7B). We conducted a repeated-measures ANOVA with factors of OSM (no-masking and masking) and orientation (left: -45° to -5° ; and right: 5° to 45°). We found a main effect of OSM, F(1, 19) = 5.01, p < .05, $\eta_p^2 = 0.21$, and a main effect of orientation, F(9, 171) = 10.05, p < .001, $\eta_p^2 = 0.35$. We did not find an interaction between OSM and orientation, F(9, 171) = 1.3, p = .24, $\eta_p^2 = 0.06$. These results confirm that masking was effective and observers were attentive to the nuanced differences in orientation.

13.2. Orientation awareness

Next, we examined how each observer's reports about the target object's visibility depended on OSM and orientation (Fig. 7C). We conducted a repeated-measures ANOVA with factors of OSM and orientation, using the proportion of trials where observers reported seeing the target object as the dependent variable. We did not find a main



Fig. 7. A typical stimulus array, as well as discrimination, and subjective awareness of orientated patterns based on trial type (no masking and masking) and orientation of the cued pattern in Experiment 6. (A) Oriented Gabor patches replaced the elliptical targets and distractors. (B) Proportion correct for determining whether the target-patch was tilted to the left or right across 10 target orientations, shown separately for the no-masking and masking conditions. (C) Proportion of trials in which observers reported seeing the target patch, shown separately for the 11 target orientations and for the no-masking and masking conditions. The error bars in panels B and C represent \pm 1 *SEM* with baseline individual variability across the data points removed (i.e., repeated-measures error bars).



Fig. 8. Subjective awareness of shapes based on the global aspect ratio of the masking dots (depicted above each panel), trial type (no masking and masking), and the aspect ratio of the cued ellipse in Experiment 7. The three panels show the proportion of trials in which observers reported seeing the target ellipse when the quartet of masking dots had (A) a globally-flat configuration, (B) a globally-balanced, "square" configuration, and (C) a globally-tall configuration. The error bars represent ± 1 *SEM* with the baseline individual variability across the data points removed (i.e., repeated-measures error bars).

effect of OSM, *F*(1, 19) = 2.18, *p* = .16, $\eta_p^2 = 0.10$, nor did we find a main effect of orientation, *F*(10, 190) = 0.82, *p* < 0.61, $\eta_p^2 = 0.04$. We also did not find an interaction between OSM and orientation, *F*(10, 190) = 0.99, *p* = 0.45, $\eta_p^2 = 0.05$. The weak main effect of masking here is not surprising, since relative to 2D shapes, oriented patches have been shown to be somewhat resistant to OSM (Goodhew et al., 2015). More important, target orientation had no impact on reports of visibility, suggesting that masking is not simply more difficult for more extreme stimuli.

13.3. Orientation discrimination, masking, and awareness

Finally, we evaluated orientation discrimination as a function of both the presence of masking dots and each observer's visual awareness on a trial-by-trial basis. We removed three observers who did not contribute data to each of the three awareness conditions. Again, we found that visual awareness was the key factor in evaluating objects. Orientation discrimination was worse in the masking/unaware condition (M = 59.17%, SD = 11.01%) compared to both the no-masking/ aware condition (M = 71.54%, SD = 16.52%), t(16) = 2.57, p = .02, d = 0.82, and the masking/aware condition (M = 72.96%, SD = 15.89%), t(16) = 3.12, p < .01, d = 0.93. A one-sample *t*-test confirmed that even though disruptions of awareness degraded performance in the masking/unaware condition, orientation discrimination on these successful masking trials was still greater than chance-level performance, t(16) = 3.43, p = < 0.01, d = 0.83.

14. Experiment 7

Similarity between masking dots and targets influences the effectiveness of OSM (Goodhew et al., 2015). It may be that the implied global shape of a set of masking dots (e.g. a square) may also contribute to the effectiveness of masking a target. The global aspect ratio of each quartet of masking dots in our experiments, thus far, was always balanced, with a 1-to-1 height-to-width ratio. Consequently, the similarity of the more circular targets to the global aspect ratio of each masking quartet could have led these shapes to be most effectively masked in our experiments. Such an alternative account would be consistent with the object-updating interpretation of OSM, in which the success of masking depends on the visual system's ability to resolve the quick succession of target and mask as belonging to different objects (Enns, Lleras, & Moore, 2009; Enns & Oriet, 2007; Goodhew, 2017; Moore & Enns, 2004). In Experiment 7, we varied the global arrangements of our quartets of masking dots into flat, tall, and square aspect ratios to test if similarity between the implied aspect ratio of the masking dots and the targets was responsible for our main finding. We did not suspect that this would be the case, and instead predicted the same pattern of results as in Experiments 1-4.

14.1. Materials and method

14.1.1. Observers

Thirty observers gave informed consent to participate either as volunteers or for course credit. We increased our sample size by 50% because we wanted increased power to measure a potentially subtle effect of congruency between the global aspect ratio of the masking dots and the target shapes, if one did in fact exist. All observers reported normal or corrected-to-normal vision. The experiment included 540 trials with three breaks.

14.1.2. Stimuli and procedure

All stimuli and procedures were identical to those from Experiment 1 except that, instead of only displaying quartets of masking dots with a globally-balanced aspect ratio, we also displayed quartets of re-positioned masking dots with global aspect ratios matched to those of a moderately flat and moderately tall ellipse from our stimulus set (log AR: -/+0.221). Fig. 8A–C display the three global configurations of masking dots. Additionally, we only displayed target ellipses 3, 6, and 9 (log ARs of -0.221, 0.0, and +0.221) consistent with the global aspect ratios of the masking dots. Distractor ellipses were always circles.

15. Results

We streamlined the analysis in Experiment 7 and only examined how each observer's reports about the target shape's visibility depended on OSM, the shape's aspect ratio, and the global aspect ratio of the masking dots (Fig. 8). We conducted a repeated-measures ANOVA with factors of OSM (no masking and masking), the target shape's aspect ratio (flat, circular, tall), and the global aspect ratio of the masking dots (flat, balanced, tall), using the proportion of trials where observers reported seeing the target shape as the dependent variable. As expected, we found a main effect of OSM, F(1, 29) = 31.14, p < .001, $\eta_p^2 = 0.52$, and a main effect of shape, F(2, 58) = 18.07, p < .001, $\eta_p^2 = 0.38$. The main effect of the global aspect ratio of the masking dots was not significant, F(2, 58) = 2.88, p = 0.06, $\eta_p^2 = 0.09$, although this trended in the direction of slightly stronger masking when the global aspect ratio was balanced (i.e., "square"). This makes sense since the dots were slightly closer to the target in this condition compared with the new globally-flat and tall configurations. As in Experiment 1, we found an interaction between OSM and target shape, F(2, 58) = 11.69, p < .001, $\eta_p^2 = 0.29$. Most important, the interaction between OSM, target shape, and global aspect ratio of the masking dots was not significant, F(4, 116) = 1.07, p = 0.37, $\eta_p^2 = 0.04$.

If congruency between the global aspect ratio of the masking dots and the target were responsible for the strong masking of circles in our previous experiments, then we would have observed strongest masking for (1) flat shapes when the global configuration of the masking dots was flat (Fig. 8A), and (2) tall shapes when the global configuration of the masking dots was tall (Fig. 8C), especially in the masking condition. Clearly, this did not occur. Instead, in the masking condition, we found the same pattern of weakened visual awareness when the target had a circular aspect ratio, regardless of the global configuration of the masking dots (the proportion of trials in which observers indicated awareness of the target was significantly lower on trials with circular targets compared to flat and tall targets in each global masking configuration, all p's < .01). This pattern of results suggests that our main findings cannot simply be explained by an effect of the globally implied shape causing lateral inhibition of the more similar circular target shapes.

16. Discussion

We evaluated how aspect ratio influences an object's access to visual awareness. We found that shapes with circular aspect ratios were more easily suppressed from awareness than extremely flat or tall shapes. This only occurred in the presence of object-substitution masking, indicating that circular shapes were not simply more difficulty to see, but were instead more susceptible to perceptual disruption. We replicated this effect across several control experiments while also ruling out alternative explanations unrelated to aspect ratio.

This investigation is unique in that we examined the outcomes of anisotropic representation not just for visual discrimination, which has been the focus of previous work, but also in terms of a more elementary process—visual awareness. We showed that an object's accessibility to consciousness can be predicted by the way the brain encodes its basic 2D structure, a surprising explanation compared with lower-level sources of visibility such as contrast, luminance, or area, which were all controlled for here. Our results were perceptual—observers did not simply use the difficulty of making flat-vs-tall discriminations as a proxy for reporting awareness, in which case the no-masking and masking conditions would have produced the same pattern of results. Our effect was also persistent, replicating across a variety of control experiments which targeted other explanations, such as proximity and similarity of the target to the masking dots, and similarity to the distractor shapes.

Our results confirm a previously untested pillar of the object-substitution framework—that strength of representation should gate access to visual awareness. According to this account, object representations are built iteratively by revising perceptual hypotheses about an object's identity and location via feedback activity across high-level and lowlevel visual areas (Di Lollo et al., 2000; Enns, 2004). Crucially, objects with weak initial representation should require the most iterative processing before they are made available to awareness, and should thus be more susceptible to masking. We suggest that because of the anisotropic organization of aspect ratio, the resulting weaker neural representation of circular shapes led to a strengthened effect of masking. Our findings are consistent with growing evidence that OSM works by disrupting feedback processing (Boehler et al., 2008; Enns, 2004; Goodhew, Dux, Lipp, & Visser, 2012; Jannati et al., 2013; Kotsoni et al., 2007).

Some accounts of OSM argue that it disrupts perception (and

awareness) via lateral inhibitory interactions (Bridgeman, 2006; Macknik & Martinez-Conde, 2007; Põder, 2012). According to this framework, our effect could have been due to inhibitory interactions from the masking dots to the target shape that could have operated prior to, or independent of, feedback activity. We examined this possibility by manipulating the proximity of the masking dots to the target in Experiments 2 and 3. Shapes that were closest to the masking dots were the *least* likely to be suppressed from awareness. Similarly, we were also able to rule out effects of inhibition due to similarity between the target and masking dots in Experiments 4 and 5. We also demonstrated in Experiment 7 that similarity between the global configuration of the masking dots and the target shape cannot have accounted for our results. Therefore, we consider our results as consistent with the iterative account of object substitution and inconsistent with accounts based on lateral inhibition.

Our investigation also illustrates the importance of considering distinct types of phenomenology that can occur during OSM (Gellatly, Pilling, Cole, & Skarratt, 2006; Harrison, Rajsic, & Wilson, 2016; Sweeny et al., 2017). Elimination of visual awareness often coincides with masking, so much so that the two phenomena are sometimes conflated, yet masking need not eliminate detection of an object altogether. Measuring detection and discrimination separately and sorting data according to subjective awareness on a trial-by-trial basis is thus very important. By taking this approach, we showed across several experiments that the presence of masking dots alone is not sufficient to disrupt discrimination of a shape's aspect ratio. Rather, disruptions of visual awareness must co-occur.

Further research is needed to determine how the effect we have demonstrated here relates to the processing of aspect ratio at the population level, which presumably operates according to a central-tendency framework. Some suggest that aspect ratio is opponent coded, whereby average responses from just two populations of flat-tuned and tall-tuned neurons are compared (Regan & Hamstra, 1992; Suzuki, 2005). More recent work suggests that aspect ratio is multi-channel coded, with individual channels of cells tuned to numerous aspect ratios, including circles (Dickinson et al., 2017; Storrs & Arnold, 2017). Although an opponent-coding framework seems more intuitively compatible with our results, we suspect that a multi-channel system could still be viable so long as circular-tuned channels are either less prevalent than extreme-tuned channels, or are more inhibited during initial viewing (which is consistent with findings of aspect ratio exaggeration during brief presentations; Suzuki & Cavanagh, 1998).

Consideration of our results in a broader context is also important. Our effects did not generalize to the perception of orientation. Yet we suspect that the type of results we have shown here may not be limited to aspect ratio and may occur for other mid-level visual features such as curvature, skew, and taper, or even more complex visual patterns. We thus hope to frame the current work not just as a study of shape perception, but also as an example of how 2D patterns can be used to understand general principles of object perception and awareness in general. We also think it is important to be careful when relating our findings to neurophysiological research with primates (e.g., Kayaert et al., 2005). While we do not provide direct evidence that anisotropic representation (in terms of cell number and firing rate) is responsible for our effect, the parallel between our results and the selectivity of aspect ratio encoding at the single-cell level is striking, and in our opinion offers a parsimonious explanation. More generally, our work is an example of how psychophysics can complement neurophysiological research to uncover the mechanisms of visual perception (e.g., Cohen, Rhee, & Alvarez, 2016; Sweeny, Grabowecky, Paller, & Suzuki, 2009).

Aspect ratio is a basic 2D shape feature with highly anisotropic neural representation. Our findings suggest that there are consequences to this kind of organization not just in terms of visual discrimination, but for visual awareness as well. For extreme aspect ratios, this means resistance to masking, increased salience, and in turn, privileged access to awareness compared to more subtle aspect ratios nearby the category boundary.

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