Radial bias for orientation and direction of motion modulates access to visual awareness during continuous flash suppression

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Two types of radial bias have been demonstrated in the primate visual cortex: for orientation and for direction of motion. Considering that a visual neuron's directional selectivity is generally perpendicular to its preferred orientation, it is counterintuitive that radial biases for orientation and direction of motion coexist in retinotopic cortex including primary visual cortex. The current study measured the influence of radial bias for orientation and direction of motion on the access to visual awareness during continuous flash suppression. Strength of static and moving target stimuli, inferred by time to breakup of suppression, was modulated by the orientation and motion direction of the suppressed target stimulus according to its spatial location, indicating radial biases for both orientation and motion direction. However, orientation dominated over direction of motion when they were perpendicular to each other. These results indicate that, first, orientation-specific neural responses may be stronger than direction-specific neural responses at the stage of visual processing where interocular suppression is resolved. Second, the preferential processing of both orientation and direction of motion may result from anisotropic distribution of orientation- and direction-selective cells. Third, the neural substrate of the radial direction bias may reflect an orientation-specific neural response induced by fast-moving random dot patterns.

Introduction

The oblique effect, which refers to preferential processing of cardinal orientations (vertical and horizontal) compared to oblique orientations, suggests that not all orientations are processed equally (Campbell, Kulikowski, & Levinson, 1966; Furmanski & Engel, 2000; Heeley & Timney, 1988). This preferential processing of cardinal orientations is observed in peripheral vision (up to 20° eccentricity) as well as in foveal vision (Vandenbussche, Vogels, & Orban, 1986; Westheimer, 2003), indicating an isotropic cortical distribution of orientation preference for the cardinal orientations. On the other hand, the preferential processing of radial orientations over tangential orientations in extrafoveal vision has been reported in numerous psychophysical studies (Bennett & Banks, 1991; Berardi & Fiorentini, 1991; McGraw & Whitaker, 1999; Westheimer, 2003) and functional neuroimaging studies (Freeman, Brouwer, Heeger, & Merriam, 2011; Mannion, McDonald, & Clifford, 2010; Sasaki et al., 2006). This compelling evidence for a radial orientation bias suggests an anisotropic cortical organization for orientation processing across multiple retinotopic cortical areas.

Radial directions of motion (both centrifugal and centripetal) also have been shown to be processed preferentially compared to circular or spiral motion (Beardsley & Vaina, 2005; Malek, Mendoza-Halliday, & Martinez-Trujillo, 2012; Parker & Alais, 2007, but also see Morrone, Burr, Di Pietro, & Stefanelli, 1999). This radial direction bias over tangential direction of motion is also supported by anisotropic motion responses in the retinotopic cortex (Raemaekers, Lankheet, Moorman, Kourtzi, & van Wezel, 2009). However, it is puzzling that radial biases for both orientation (Sasaki et al., 2006) and direction of motion (Raemaekers et al., 2009) are found in the same retinotopic cortex, including the primary visual cortex. This is because the direction selectivity of a neuron in the early visual cortex is known to be perpendicular to its orientation preference. The preferred motion direction of a visual neuron is usually perpendicular to its preferred orientation (Albright, 1984; De Valois, Yund, & Hepler, 1982), because direction of motion can be signaled unambiguously only when the orientation is perpendicular to the direction of motion. If there were an anisotropic

cortical preference for radial orientation, we would predict a tangential rather than a radial-motion direction bias. Thus, radial biases for orientation and motion direction are difficult to reconcile at the same level of visual processing.

In the current study, the strength of a radial bias in orientation and direction of motion was compared using an interocular suppression paradigm. When two different images of equivalent strength are presented separately to each eye, perception alternates between the two images; this phenomenon is called *binocular rivalry* (Blake & Logothetis, 2002). In *continuous flash suppression* (CFS), dynamically changing, contour-rich patterns are presented to one eye and a to-be-suppressed target stimulus is presented to the other eye. In this configuration, the target image is rendered invisible for an extended duration (sometimes more than 10 s) due to a strong suppressive effect of the dynamically changing pattern presented to the other eye. However, the suppression induced by CFS eventually breaks up, and the target image is perceived consciously. Consistent with Levelt's theory on binocular rivalry (Levelt, 1965), a strong stimulus breaks up suppression more quickly than a weak stimulus. The strength of the suppressed stimulus can be defined by physical image characteristics, such as overall contrast (Stein, Hebart, & Sterzer, 2011; Yang, Zald, & Blake, 2007). The elapsed time until suppression breaks up is considered an estimate of the strength of neural response induced by the target stimulus (Stein et al., 2011).

The aim of this study was to resolve the apparent conflict from the counterintuitive evidence for radial biases in orientation and direction of motion. If a radial orientation or motion direction induces a stronger neural response in a specific retinotopic area, the breakup of suppression during CFS will occur faster compared to a tangential orientation or direction when the stimulus is presented at the visual location corresponding to the specific retinotopic area in the visual cortex.

General methods

Participants

Ten naïve observers who had normal or corrected-to-normal vision participated in each of the five following experiments for a class credit; thus, there were a total of 50 participants. All participants provided their informed consent to participate in the experiment. The Florida Atlantic University Institutional Review Board approved the protocol.

Apparatus, stimulus, and procedure

Stimuli were presented on a Sony CPD-G520, 21" CRT display (100 Hz frame rate). The presentation of the stimuli and the collection of behavioral responses were controlled by Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) operating in Matlab (Mathworks). Stimuli were presented to observers positioned 90 cm from the CRT monitor, which had a luminance that was linearized from "black" (0.5 cd/m^2) to "white" (110 cd/m^2). A four-mirror stereoscope was used to present the stimuli binocularly. Detailed information about the stimuli and experimental procedure are described in each experiment section.

Experiment 1: Radial orientation bias under CFS

Experiment 1 was designed to test whether the radial bias in orientation modulates access to visual awareness during CFS. If a radial orientation induces stronger neural responses compared to a tangential orientation in the early visual cortex (Sasaki et al., 2006), the radially-oriented grating will break up suppression and reach visual awareness faster than the grating oriented perpendicular to the radial orientation.

Stimulus and procedure

The target stimulus was a sinusoidal grating with two different orientations, $\pm 45°$ from vertical. The spatial frequency was set to 3 cycles/°. The grating was masked by a Gaussian envelope to fit within a 2° square aperture with a smooth outline. The target grating was presented in one of four apertures to one eye. The square apertures were arranged in a 2×2 array (Figure 1a). The suppressors, dynamically changing Mondrian-like patterns, were presented in all four apertures to the other eye. Each suppressor was composed of 200 rectangular patches with random sizes. The luminance of each patch was randomly assigned, but within a predetermined range whose maximum and minimum values were used to compute contrast of the suppressors. The mean luminance of the suppressors was fixed at 55 cd/m^2, which was identical to the luminance of the background. During stimulus presentation, participants were instructed to maintain their fixation on the central fixation checkers. The distance between central fixation and the center of each square aperture was 2°.

During the first two seconds of stimulus presentation, the contrast of the target stimulus was increased from 0 to its maximum contrast (30% Michelson contrast) with a fixed mean luminance (55 cd/m^2) to
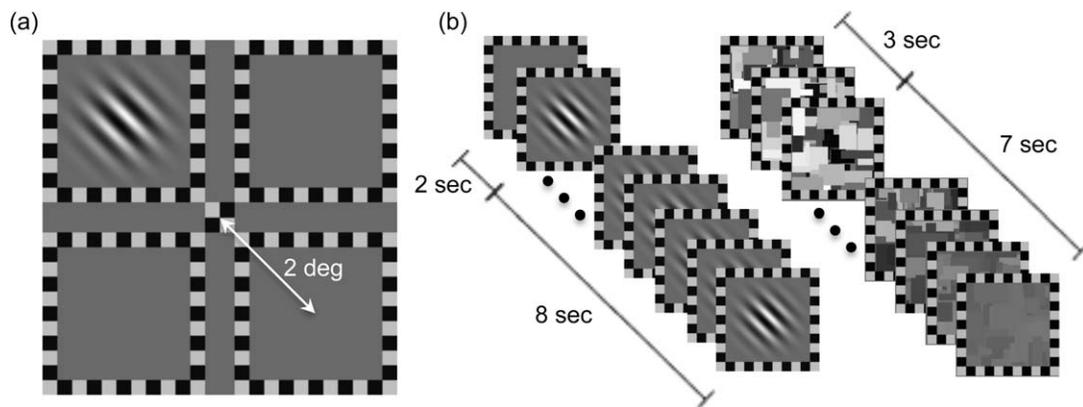
Figure 1. (a) Schematic diagram of the stimulus presentation. In this example, a target grating is presented in the top-left aperture. (b) The sequence of stimulus presentation for one trial. Only one of four apertures, where the target was presented, is shown here. Left panels show the target grating, and right panels show the suppressor.

prevent breakup of suppression due to a transient signal caused by abrupt onset of the target stimulus (Figure 1b). The contrast then remained constant until the target was detected by breaking up the suppression or until the end of presentation time (total 10 s). The contrast of the suppressor stimuli was at a maximal level for the first 3 s and then slowly decreased to 0 over the remaining 7 s. Reducing the contrast of the suppressor does not guarantee that the suppression will be broken during the 10-s stimulus presentation. However, it was expected to decrease the number of trials in which the target stimulus did not break up the suppression, since the relative strength of the target stimulus increased through reduction of the contrast of the suppressor.

Each trial began with pressing the space bar on the keyboard. Participants were instructed to report the orientation of the target grating as quickly and accurately as possible whenever they could identify the orientation. To report the orientation of the grating, participants pressed number 1 on the keyboard for left-tilted grating and number 2 for right-tilted grating. The relative orientation of the target grating to the display

(radial vs. tangential) was defined by the location of where the grating was presented. For example, the left-tilted grating was defined as radial when it was presented either in the top-left aperture (as shown in Figure 1a) or in the bottom-right aperture. The same grating was defined as tangential when it was presented either in the top-right or bottom-left aperture.

Results and discussion

Response times (RTs) were defined throughout as the time from stimulus onset to the breakup of suppression. Mean RTs in seconds ($\pm$ standard error of the mean) for the two relative orientations (radial vs. tangential) are shown in Figure 2. A paired comparison revealed that the radial orientation broke up suppression significantly faster than the tangential orientation, when the target gratings were presented at 2° eccentricity, $t(9) = 4.57$, $p < 0.001$. This result is consistent with the radial orientation bias shown in human psychophysics (Bennett & Banks, 1991; Westheimer, 2003) and functional magnetic resonance imaging (fMRI) studies (Sasaki et al., 2006; Mannion et al., 2010). Although the physical contrast of the target grating was fixed, the radial orientation resulted in an earlier breakup of suppression. This result provides indirect evidence for an anisotropic representation of orientation in the visual cortex.
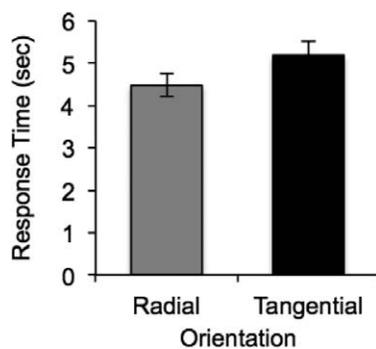

Figure 2. Results of Experiment 1. Mean response times ($\pm$ standard error) for target gratings with radial (gray) and tangential (black) orientations.

Experiment 2: Radial direction bias under CFS

The findings from Experiment 1 confirmed that a radial orientation bias affected how fast a static target broke up suppression and reached visual awareness.
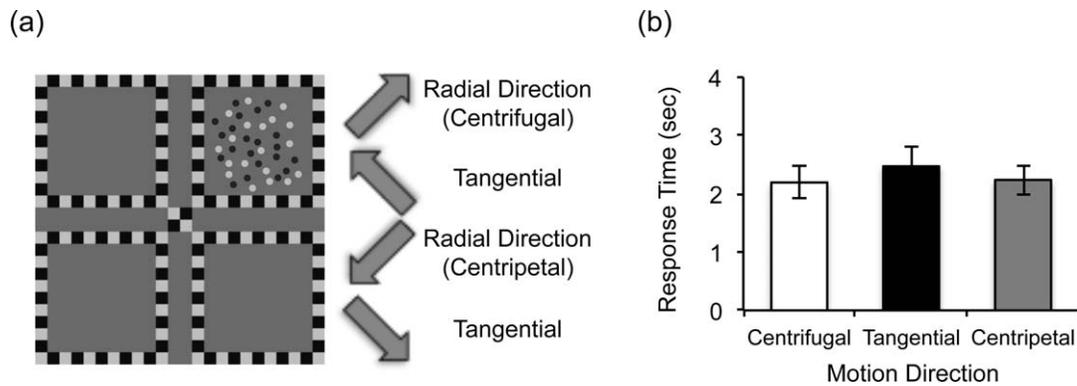
(a)

(b)

Figure 3. (a) Schematic diagram of the stimulus presentation for Experiment 2. Depicted is the target stimulus (random dot pattern) in the upper right of the four possible quadrants. Gray arrows indicate the four potential configurations for motion direction of the random dots. (b) Mean RTs ($\pm$ standard error) for target random dot stimuli moving in centrifugal (white), tangential (black) or centripetal (gray) directions.

The aim of Experiment 2 was to test whether the same radial bias existed in the motion domain. If radial direction of motion induces a stronger neural response than tangential direction of motion, a pattern moving in a radial direction will break up suppression faster than a pattern moving in a tangential direction.

Stimulus and procedure

The target stimuli were random dot patterns, moving in one of four directions (45°, 135°, 225°, and 315°). They were composed of 50 dark and light dots, each with a diameter of 0.08°. The lifetime of each dot was 200 ms and the speed was set to 2°/s. All dots were presented within a circular aperture (2° diameter) filling one quadrant of the 2 × 2 array of square apertures (Figure 3a). During the first two seconds of stimulus presentation, the contrast of the target stimulus was increased from 0 to its maximum contrast (30% contrast). The contrast then remained constant until the target was detected by breaking up the suppression or until the end of presentation time (total 10 s). The suppressor stimulus was the same as described in Experiment 1.

The experimental procedure was similar to that of Experiment 1 with the exception of the response choices. Participants pressed one of four numeric keys (1: bottom-left, 2: bottom-right, 4: top-left, and 5: top-right, each corresponding to a direction of motion) on the numeric keypad located on the right side of a keyboard. Participants were instructed to report the direction of motion of the random dot pattern as quickly and accurately as possible whenever they could identify the direction of motion. The direction of motion was defined by the location where the random dot pattern was presented within the array of four

apertures. For example, the 45° angle motion (top-right direction) was defined as radial-centrifugal direction when it was presented in the top-right aperture (Figure 3a) because it resembled a top-right quarter-sector of a centrifugal optic-flow pattern motion. The same direction of motion presented in the bottom-left aperture was defined as radial-centripetal because it resembled a bottom-left quarter-sector of a centripetal optic-flow pattern motion. When presented in either the top-left or the bottom-right aperture, it was defined as tangential.

Results and discussion

The RTs for the different directions of motion are shown in Figure 3b. A one-way analysis of variance (ANOVA) revealed that direction of motion significantly affected the time until breakup of suppression, $F(2, 18) = 7.08$, $p = 0.004$. Follow-up contrast tests confirmed that tangential direction of motion significantly increased time until breakup of suppression compared to centrifugal, $F(1, 9) = 15.21$, $p = 0.004$, and centripetal direction of motion, $F(1, 9) = 5.46$, $p = 0.044$. RTs between centrifugal and centripetal directions of motion did not differ significantly, $F(1, 9) = 0.50$, $p = 0.50$.

Consistent with the prediction based on the radial direction bias, random-dot patterns moving in a radial direction broke up suppression faster than the same patterns moving in a tangential direction. However, there was no difference in the response time between outward direction (consistent with centrifugal direction) and inward direction (consistent with centripetal direction). This result is inconsistent with the strong dominance of centrifugal motion over centripetal motion during binocular rivalry between two random
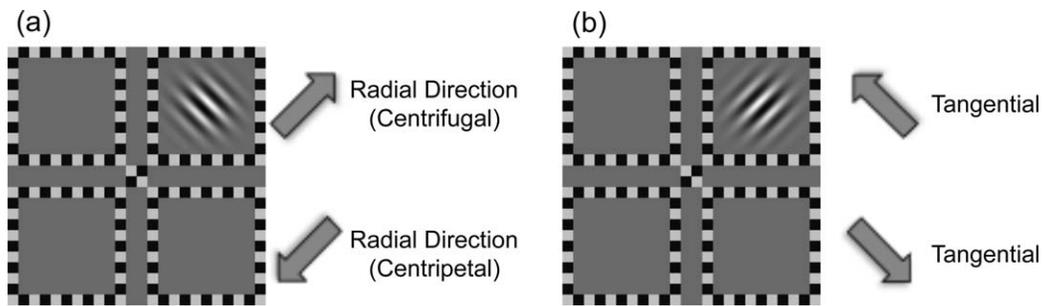
Figure 4. Schematic diagram of the stimulus presentation for Experiment 3. (a) Target grating drifting in radial directions (centrifugal and centripetal). (b) Target grating drifting in tangential directions.

dot motion patterns (Malek et al., 2012). However, there are clear differences in the stimuli used in their experiment. In Malek et al. (2012), conventional optic-flow patterns with the expanding and contracting random-dot-motion were presented foveally. Therefore, dots were moving radially in all directions (360°) and the focus of expansion (FOE) was clearly visible, which is critical for the optic-flow perception. In the current study, on the other hand, dots were moving only one direction (translational motion) and also presented 2° away from the foveal fixation. Thus, there was no FOE, and no clear perception of optic-flow pattern motion. This result is consistent with an fMRI study showing that the hemodynamic response to centrifugal and centripetal motion was similar at an eccentricity of 2° (Raemaekers et al., 2009), which is equivalent to the current display conditions. Another possible explanation is that faster access to visual awareness for radial directions of motion compared to tangential direction of motion might be mediated by an orientation-specific neural response rather than a direction-specific neural response. If orientation-specific neural responses mediated the RT difference, there would be no difference between centrifugal and centripetal directions of motion, since both would induce the same orientation-specific response.

Experiment 3: Orientation versus motion

Experiment 2 revealed that direction of motion affected the time for the suppressed random dot motion stimulus to reach visual awareness, supporting a radial bias for direction of motion. However, a random dot pattern moving coherently in one direction could contain orientation-specific information parallel to the direction of motion. Fast-moving, randomly distributed dots can induce an orientation signal due to the temporal integration window of about 100 ms described for early visual processing stages (Snowden &

Braddick, 1989). The orientation signal created by the "smeared" trail left behind a moving object, called the "motion streak" (Geisler, 1999), is parallel to the direction of motion. To test which radial bias, orientation, or direction of motion predominantly modulates access to visual awareness, drifting gratings instead of random dot patterns were employed in Experiment 3. The motion direction of a drifting grating is always perpendicular to the grating's orientation. Thus, if radial biases for orientation and direction of motion are equally strong, there will be no difference in the time until breakup of suppression between a grating moving in radial direction (tangential orientation) and in tangential direction (radial orientation).

Stimulus and procedure

The sinusoidal gratings were identical to the ones used in Experiment 1, except that the gratings were drifting in one of four directions (45°, 135°, 225°, and 315°) at a speed of 2 cycles/s. The relative direction of motion of the grating was defined by the location within the 2 × 2 array. For example, the 45° angle motion (toward the top-right) was defined as radial-centrifugal when the grating was presented in the top-right aperture since it resembled a top-right quarter-sector of a concentric ring pattern, moving in a centrifugal (expanding) direction. The 225° angle motion (toward the bottom-left) was defined as radial-centripetal when the grating was presented in the same top-right aperture. In both cases, the orientation of the grating was tilted left (45°) from vertical and perpendicular to the direction of motion (Figure 4a). For tangential motion, radially oriented gratings drifted perpendicular to the orientation of the grating (Figure 4b). The task was the same as Experiment 1, in which participants reported the orientation of the moving grating as quickly and accurately possible by pressing the left or right arrow key.
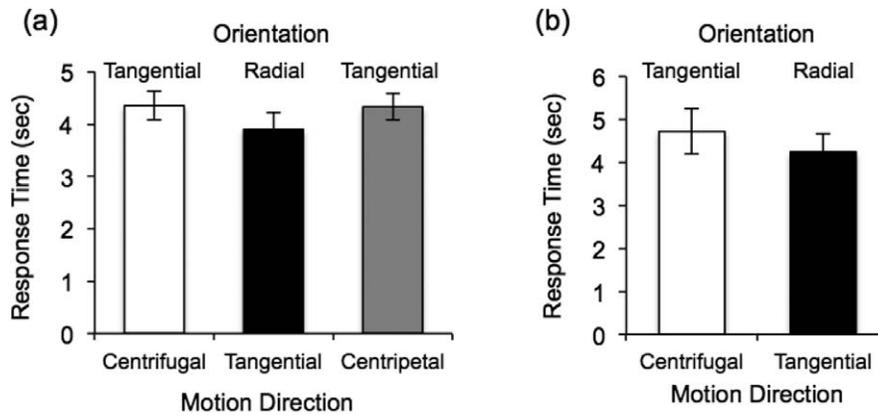
Figure 5. Mean RTs (± standard error) for different configurations of motion direction (bottom) and orientation (top) from Experiment 3 (a) and Experiment 4 (b).

Results and discussion

Again, the RTs until breakup of suppression were measured for different combinations of motion and orientation (Figure 5a). A one-way ANOVA revealed that motion direction significantly affected the time until breakup of suppression, $F(2, 18) = 5.74$, $p = 0.012$. However, unlike the random dot moving patterns, the gratings moving tangentially (radial orientation) broke up suppression earlier than both centrifugal and centripetal motion. Follow-up contrast tests showed that tangential direction of motion broke up suppression significantly faster than did centrifugal. $F(1, 9) = 6.00$, $p = 0.037$) or centripetal motion, $F(1, 9) = 8.61$, $p = 0.017$. RTs were not significantly different between centrifugal and centripetal directions of motion, $F(1, 9) = 0.04$, $p = 0.85$, which is consistent with the results of Experiment 2.

When a grating was drifting in a tangential direction, the orientation of the grating was radial to the center of fixation. On the other hand, when the grating was drifting either in a centrifugal or centripetal direction, the orientation of the grating was perpendicular to the radial orientation. The faster breakup of suppression for tangential directions of motion is contrary to the results from Experiment 2. This indicates that orientation largely determines the time of breakup of suppression for grating stimuli. Evidently, the difference in the time of breakup of suppression between centrifugal (tangential orientation) and tangential (radial orientation) directions of motion was not significantly different from that observed in Experiment 1 with no motion, $t(18) = 1.06$, $p = 0.30$. An alternative explanation is that the faster breakup of suppression for radial motion observed in Experiment 2 may be mediated by orientation-specific neural responses induced by motion streak rather than direction-specific neural responses. Although the current study cannot separate the effect of orientation-specific from direc-

tion-specific neural responses, it raises the question of whether the directional bias observed in previous studies (Malek, Mendoza-Halliday, & Martinez-Trujillo, 2012; Raemaekers et al., 2009) can be understood in the same manner.

Experiment 4: Control experiment

In Experiment 3, participants were instructed to report the orientation of the suppressed gratings while the gratings drifted in one of four directions. It could be argued that these results can be attributed to the specifics of the task (reporting the orientation), since participants focused on the orientation rather than the direction of motion. To test this hypothesis, participants were instructed to report the direction of motion in a control experiment. The stimulus setting was identical to Experiment 3, but the response mode was identical to Experiment 2, in which participants reported the direction of motion by using four numeric keys. Since no significant difference between centrifugal and centripetal directions of motion was found in both Experiment 2 and 3, only centrifugal and tangential directions of motion were tested in this control experiment.

RTs for this experiment are shown in Figure 5b. Paired comparisons revealed that radial orientation (tangential motion) broke up suppression faster than tangential orientation did (centrifugal motion), $t(9) = 2.67$, $p = 0.026$. This result suggests that the dominant influence of radial orientation bias over direction of motion cannot be attributed to the influence of attention to a specific visual feature. Feature-based attention posits that neural signals for a visual feature, such as direction of motion, can be enhanced by deploying attention to that specific visual feature (Saenz, Buracas, & Boyton, 2002; Treue & Martinez-Trujillo, 1999). Further, attention can affect processing
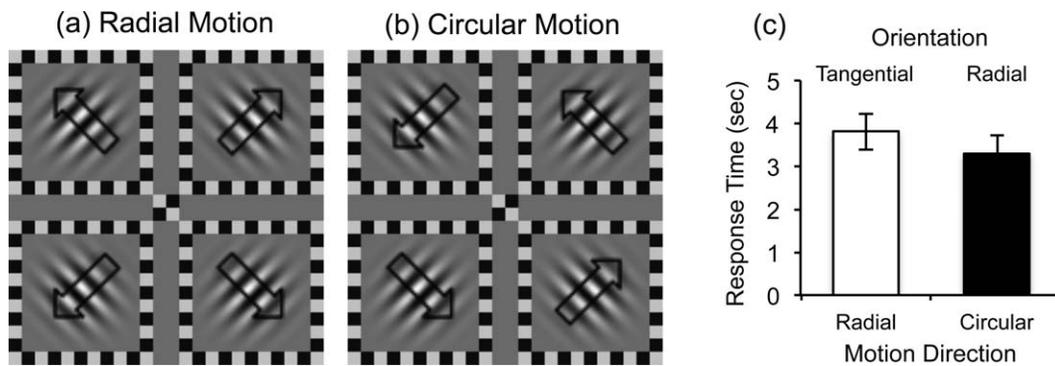
Figure 6. Schematic diagrams of the radial motion pattern (a), and the circular motion pattern (b), for Experiment 5. Black arrows indicate the four directions of motion. (c) Mean RTs ($\pm$ standard error) for radial motion (white) and circular motion (black).

of a visual stimulus when it is suppressed from visual awareness by CFS (Shin, Stolte, & Chong, 2009; Yang, Hong, & Blake, 2010). In the current experiment, the radial orientation bias was still strong enough to modulate the strength of the target stimulus even when participants were instructed to report the direction of motion.

Experiment 5: Radial bias over circular motion

Results from Experiment 3 and 4 suggest that orientation-specific responses dominantly modulate access to visual awareness of a moving pattern. It has been shown that both centrifugal and centripetal motions are more dominantly perceived compared to a circular motion during binocular rivalry (Malek et al., 2012). On one hand, the longer period of dominance for centrifugal and centripetal motion than that for circular motion evidences preferential processing of optic-flow patterns. On the other hand, predominance of centrifugal/centripetal motion over the circular motion may reflect radial direction bias over tangential directions as shown in the current study since the circular motion, when divided into four quadrants as in the current study, resembles tangential directions of motion. If this is the case, it is also possible that the predominance of radial motion over circular motion may be mediated by orientation-specific neural responses rather than by motion-specific neural response as shown in Experiments 3 and 4. Experiment 5 tested this hypothesis.

The sinusoidal gratings identical to the ones used in Experiments 3 and 4 were presented in all four quadrants to create either radial motion or circular (rotational) motion. Radial motion was depicted by arranging the gratings in tangential orientations in every quadrant and drifting in radial (outward) direction (Figure 6a). Circular motion was created by arranging the gratings in radial orientations in every quadrant and drifting in tangential directions as shown in Figure 6b. As described in Experiment 3, orientation-specific signals and direction-specific signals induced by the stimuli were perpendicular each other. The experimental procedure was identical to the Experiment 3, except that participants were instructed to report the direction of motion, either expanding or counter-clockwise, by pressing either the number 1 or 2 key. The difference in sensitivity between centrifugal and centripetal direction of motion was not of interest in this study, so only the centrifugal direction of motion was tested.

RTs for this experiment are shown in Figure 6c. Paired comparisons revealed that radial orientation (circular motion) broke up suppression faster than tangential orientation (radial motion) did, $t(9) = 2.83$, $p = 0.020$. Consistent with Experiment 3, where a drifting sinusoidal grating was presented in only one quadrant, the radial orientation bias dominantly modulated access to visual awareness, compared to the radial direction bias. Thus, this result suggests that preferential processing of radial motion over circular motion induced by random dot patterns (Malek et al., 2012) may be mediated by orientation-specific neural responses rather than motion-specific neural responses.

General discussion

The present study shows that the radial bias for orientation modulates access to visual awareness during CFS (Experiment 1). In the extra-foveal region (2° eccentricity), static gratings with radial orientations broke up suppression earlier than did gratings with tangential orientations. Moving random dot patterns also broke up suppression earlier when they were moving in a radial direction compared to a tangential direction, suggesting a possible radial bias for direction of motion (Experiment 2). However, when orientation

and direction of motion were perpendicular to each other, orientation information predominantly affected the time to overcome the suppression effect (Experiments 3, 4, and 5).

Based on the assumption that a strong stimulus breaks up the interocular suppression induced by CFS earlier than a weak stimulus does (Stein, Hebart, & Sterzer, 2011; Yang, Zald, & Blake 2007), the current results suggest that radial orientation and direction of motion are stronger than are tangential orientation and direction of motion. This is also consistent with neuroimaging studies showing that radial orientation (Furmanski & Engel, 2000; Sasaki et al., 2006) and direction of motion (Raemaekers et al., 2009) induce stronger BOLD signals compared to tangential orientation and direction.

It cannot be concluded whether there is a cortical anisotropy for direction of motion, because supporting evidence is based on studies that use random dot motion patterns. Fast-moving random dot patterns can leave a neural trace that results in motion streak (Geisler, 1999). Orientation-specific information from motion streak is supported by orientation-specific masking (Apthorp, Cass, & Alais, 2010) and fMRI studies with pattern classification (Apthorp, et al., 2013). This raises the question of whether the radial bias for direction of motion is truly based on a cortical anisotropy or is caused by orientation-specific neural responses induced by the motion streak. In other words, it is possible that the radial bias for direction of motion observed in this study (Experiment 2) and a human fMRI study (Raemaekers et al., 2009) resulted from the radial orientation bias induced by motion streaks. Our results showed a consistent dominance of orientation over direction of motion when the orientation and direction of motion of a grating are perpendicular to each other (Experiments 3, 4, and 5). If a radial bias for both orientation and direction of motion independently affected access to visual awareness, the influence of the radial orientation should be reduced when the grating is drifting in a perpendicular direction, which was not the case in the current study.

Alternatively, radial biases for both orientation and direction of motion likely exist, but the radial orientation bias is stronger than the directional bias at the cortical level, where interocular suppression is resolved. It has been intensively debated where in the visual processing stream binocular rivalry is resolved. One theory posits that binocular rivalry results from competition between monocular neurons receiving signals from only one eye (Blake, 1989; Lee & Blake, 2004; Polonsky, Blake, Braun, & Heeger, 2000; Tong & Engel, 2001). This theory places resolution of interocular suppression at the earliest stage of cortical visual processing. Others propose that binocular rivalry is resolved at later stages of visual processing and reflects

competition between incompatible images rather than competition between monocular neurons (Leopold & Logothetis, 1996; Logothetis, Leopold, & Sheinberg, 1996). The current consensus incorporates both theories, that is, binocular rivalry involves neural competition at multiple stages of visual processing (Blake & Logothetis, 2002; Tong, Meng, & Blake, 2006). CFS, on the other hand, is mediated by continuously triggered transient signals from one eye (Tsuchiya & Koch, 2005), which indicates that CFS may be mainly mediated by mechanisms operating at early stages of visual processing (Hong & Blake, 2009). It is difficult to directly compare the strength of neural response between two fundamental visual features, orientation and direction of motion. However, the dominant influence of the radial orientation bias over the radial direction of motion bias suggests that orientation-specific neural responses dominate at early stages of visual processing.

Evidence for preferential processing for centrifugal and centripetal motions is somewhat mixed. On one hand, it has been reported that the primate visual system is more sensitive to centrifugal than to centripetal motion (Duffy & Wurtz, 1991a, 1991b; Graziano, Andersen, & Snowden, 1994; Maloney, Watson, & Clifford, 2013; Saito et al., 1986; Tanaka, Fukada, & Saito, 1989; Xiao, Barborica, & Ferrera, 2006). This biased sensitivity for centrifugal over centripetal direction of motion is also consistent with an ecological point of view. The motion pattern created by forward movement consists of expanding optic flow (Crowell & Banks, 1993; Freeman, Harris, & Tyler, 1994), which also informs of a potential collision (Franconeri & Simons, 2003; Hassenstein & Hustert, 1999). On the other hand, a significant number of studies support preferential processing of centripetal over centrifugal direction of motion (Badcock & Khuu, 2001; Edwards & Badcock, 1993; Giaschi, Zwicker, Young, & Bjornson, 2007; Raymond, 1994; Shirai, Kanazawa, & Yamaguchi, 2006). In the current study, no preferential processing between centrifugal and centripetal motion directions was observed. However, because the stimuli used in the current study were translational (moving in one direction) motion patterns, they did not clearly represent either expanding or contracting perception, which is prominent in the optic-flow pattern.

Conclusion

The current study investigated the influence of radial bias for orientation and direction of motion on access to visual awareness during CFS. The perceptual strength of static and moving target stimuli, as

measured by the time until breakup of suppression, was modulated by their orientation and direction of motion. Preferential processing of both orientation and direction of motion (in moving random dot patterns) may result from anisotropic distribution of orientation- and motion-selective neurons in several cortical visual areas. However, the influence of orientation exceeded that of motion direction when they were perpendicular to each other, suggesting that orientation-specific neural responses were stronger than direction-specific neural responses at the stage of visual processing where interocular suppression is resolved. In addition, the neural substrate of the radial direction bias, enhanced sensitivity to radial direction of motion, in early visual cortex may reflect an orientation-specific neural response induced by the fast-moving random dot patterns.

Keywords: orientation anisotropy, visual awareness, motion anisotropy, motion streak, continuous flash suppression

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