

LAST BUT NOT LEAST

The riddle of the Rotating-Tilted-Lines illusion

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Abstract. Gori and Hamburger (2006, *Perception* 35 853–857) devised a new visual illusion of relative motion elicited by the observer's motion. We propose that the systematic error of direction discrimination found by Lorenceau et al (1993, *Vision Research* 33 1207–1217) can explain this illusion. The neural correlate of such a systematic error with respect to the two types of neurons in the primary visual cortex, namely end-stopped and contour cells, is discussed.

Gori and Hamburger (2006) presented the Rotating-Tilted-Lines illusion (RTLI) (figure 1). Moving back and forth in front of this pattern makes the circle of lines appear to rotate, respectively, in a clockwise and counterclockwise direction.

Orientation of the lines seems to be the main factor in eliciting the illusory motion in RTLI. Gurnsey et al (2002) highlighted how also in the Pinna–Brelstaff illusion (Pinna and Brelstaff 2000) the low-frequency orientation of the micropatterns is crucial for the illusory motion, and suggested direction-selective neurons as a neutral substrate of this perceived rotation. They reduced the Pinna–Brelstaff pattern to a circle of Gabor patches; no ends of the lines were left, which perfectly served the purpose of their study. Unlike this, the RTLI is composed of simple lines having extra cues of line ends,

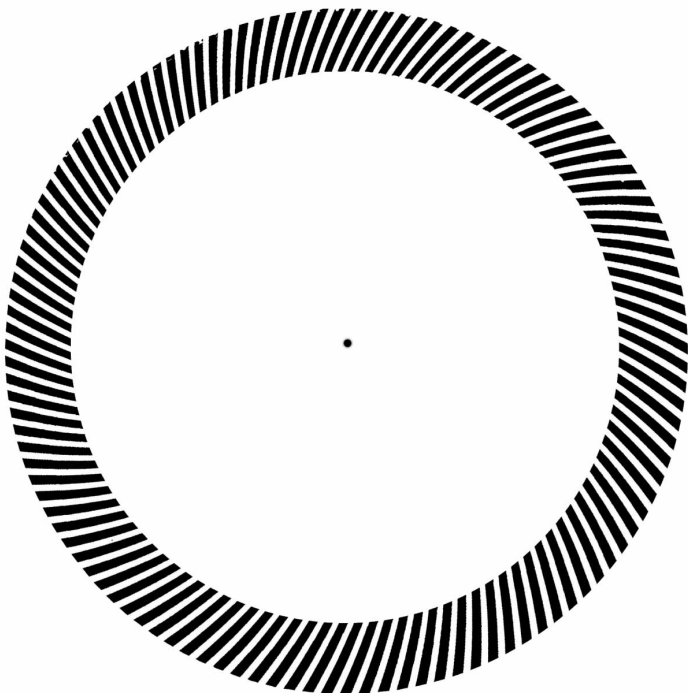


Figure 1. The Rotating-Tilted-Lines illusion.

which aid correct motion detection compared with the ambiguous motion signal in the middle of the lines. The origin of the RTLI illusory phenomenon may be understood by considering the competition between motion signals originating from two different motion-processing units as well as ambiguous and unambiguous motion signals originating from the stimulus geometry. Indeed, Lorenceau et al (1993) investigated a systematic error in direction discrimination of lines moving obliquely relative to their orientation. Two different units are supposed to be involved in this misperception of direct discrimination. Some motion-processing units input the motion signal within a line (we shall name them contour units). These units will face the aperture problem: the velocity signal that will be received from such units will be orthogonal to line orientation and thus inconsistent with the true direction of motion. Motion-processing units of the second type input motion signals from terminators and therefore can signal the true direction of motion (Grossberg and Mingolla 1993). Symmetrical or asymmetrical end-stopped neurons (Pack et al 2003; Yazdanbakhsh and Livingstone 2006) could signal the correct line-end motion. These two types of motion-processing units are depicted in figure 2. The subjects' misperception of line directions could happen because the overall response of the contour units overcomes the response to terminator motion. Approaching the RTLI we have an expansion motion of the circle on the retina (figure 3). The motion of every single line composing the circle is analyzed by n contour units and n end-stopped units. The end-stopped units signal the correct direction of motion (figure 2a, solid black arrows in figure 3), while the n contour units signal a direction which is different from the veridical motion signal available at the line endings (figure 2b, dashed gray arrows in figure 3). The ratio between the overall response of end-stopped units and contour units determines the final signaled direction.

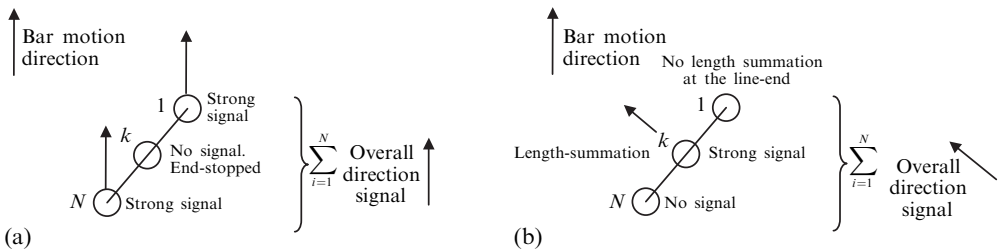


Figure 2. Two types of motion-processing units: (a) end-stopped cells (E); (b) contour units (C).

The end-stopped and contour units E_i^k and C_i^k signal orientation k at location i along the bar (figure 2). The overall activity of each set of E and C units for each orientation is determined by:

$$E^k = \sum_{i=1}^N E_i^k \quad (1)$$

$$C^k = \sum_{i=1}^N C_i^k \quad (2)$$

In expressions (1) and (2), the overall end-stopped and contour units which signal orientation k for each bar are calculated as the sum of the oriented units along the bar. The net result of such calculation for a bar with orientation k_0 moving in a certain direction is shown in figure 2 for expressions (1) and (2).

As can be seen in figure 2a, the end-stopped cells around the ends of the lines (in figure 2a, units 1 and N) are the active units, because they are not end-stopped by the full length of the line over their receptive field, as is the case for the units signaling the middle of the line. The latter, having the full length of the line over them, show decreased or no activity.

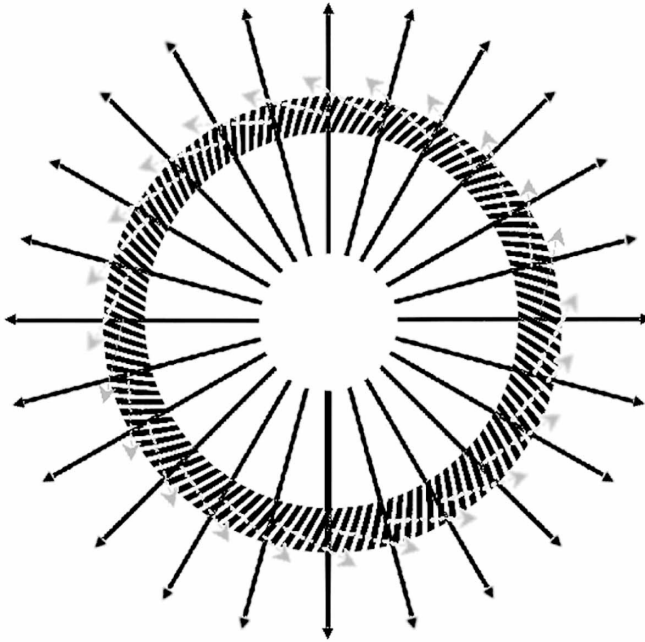


Figure 3. Expansion motion of the circle on the retina. The correct direction of motion is analyzed by end-stopped units (black arrows) while the contour units (dashed gray arrows) signal a direction different from the veridical motion signal.

Therefore the units close to the end of the line show activity as they are not fully stopped by the full length of the line; on the contrary, all the units within the line have exceeded the optimal length for their activation and do not contribute in the sum represented by equation (1). The contour units get their optimal input within the line. Owing to their length-summing nature, they get less input at the line ends, because they are not exposed to the full length of the lines.

In summary, the net result of equation (1) would be that shown in figure 2a together with that shown in figure 2b. The weighted sums of end-stopped and contour units then determine the final direction of motion.

The average would be weighted more toward the contour units than the end-stopped units, given that the length of the line is large enough to weigh the sum in equation (2) above that in equation (1). In this case, the subject will see that the illusory rotation becomes stronger. Given the schema depicted in figure 2, and the involvement of the end units in the end-stopped group to signal the correct motion of the line, the only chance for this group to bias the weighted average more toward itself would be to use short line elements, because in short lines the activities of the 1st and N th unit in the end-stopped group are balanced by the lack of activities of the middle contour units which do not produce any input (figure 4). According to Lorenceau et al

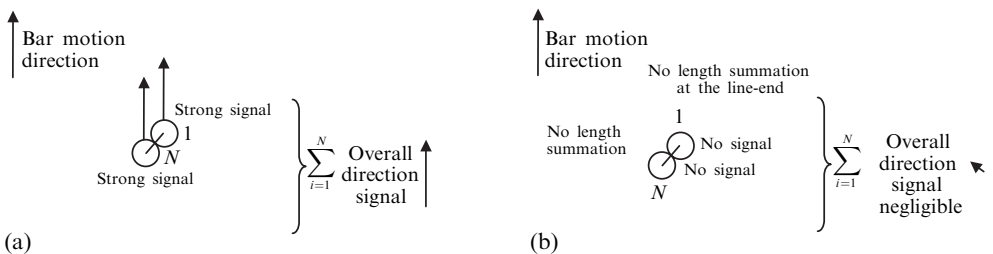


Figure 4. The effect of short lines.

(1993), the line length should have an effect on the strength of the illusory motion. With very short lines the illusory rotation disappears (Gori and Hamburger 2006). This is interpretable as a case where the activity of the contour units is not sufficient to bias the weighted activity toward them compared with the end-stopped units (figure 4). On the other hand, the illusion is enhanced when the lines are longer (figure 2b).

On inverting the orientation of the lines in RTLI, the observers report an inversion of illusory rotation (Gori and Hamburger 2006). This is in accord with our explanation, because the motion direction signaled by the contour units is then inverted. Also, the illusion disappears if the lines are arranged radially. In this case only terminator motion is present; no motion is signaled by the contour units. Informal observations show that the strength of the illusion seems to be the function of the length of the lines: a small variation in length affects the strength of the illusion. This is consistent with the above explanation because the number of active contour units increases with longer lines (figure 2b). Finally an RTLI composed of dashed lines reduces drastically the illusory motion (figure 5). This can be derived from the same explanation.

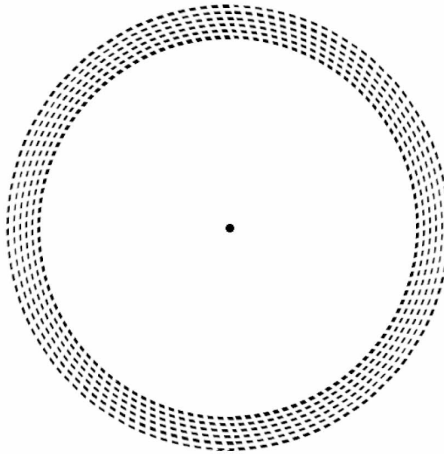


Figure 5. Dashed lines reduce illusory motion in RTLI.

Here we offer a direct ‘visual’ and ‘intuitive’ aid to interpret the Pinna–Brelstaff illusion. The Gabor-patch version (Gurnsey et al 2002) shows the importance of the ambiguous-motion signal by using just one type of motion detectors rather than distinguishing two types of neural units. In this respect their approach has the benefit of minimal assumptions as regards the number of units, and provides the simplest description of the phenomenon. Our assumption of two units was borrowed from the findings of single-cell electrophysiology, and offers an attempt to reconcile the existence of different units and the psychophysical percept. To confirm the involvement of the end-stopped neurons we tested fifteen subjects. The task was to choose which pattern presented the strongest illusory effect between that in figure 1 and that in figure 6, giving a confidence rating for the choice.

All subjects reported that figure 6 showed the strongest illusory effect with the maximum confidence rating. The pattern in figure 6 generated almost no signal for the end-stopped neurons owing to the blurred edges. Only the contour units would be involved in the generation of this percept. The difference in strength between the two patterns supports the involvement of end-stopped neurons in the RTLI. End stopping, as an aspect stemming from electrophysiology, provides another visual hint of the underlying mechanism.

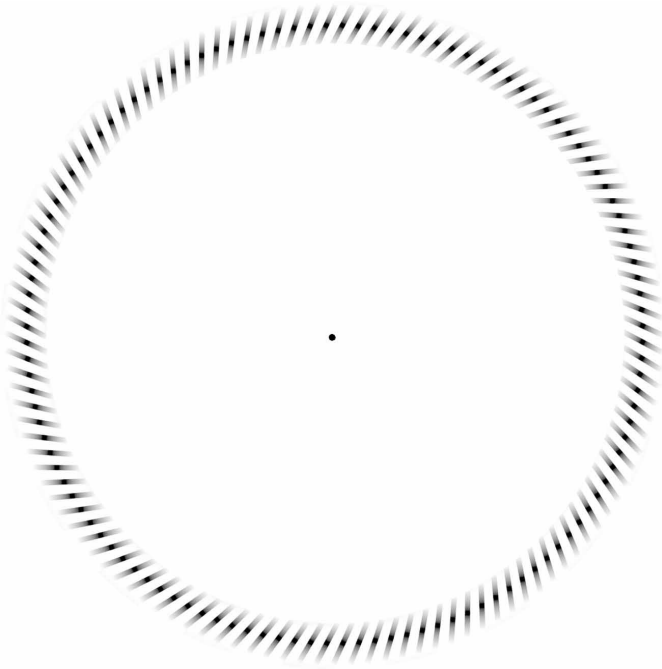


Figure 6. RTL produced by short lines with blurred edges.

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