

# Reversal of apparent rotation in the Enigma-figure with and without motion adaptation and the effect of T-junctions

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## Abstract

We studied the time course of apparent rotation and directional reversal in Leviat's Enigma figure. On average, periods of clockwise rotation lasted 5.0 s as opposed to 4.4 s for counter-clockwise rotation, resulting in an average reversal frequency of 6.4 within 30 s. At the beginning of a trial, clockwise rotation was perceived almost twice as often as counter-clockwise rotation. This bias could be shifted by previous adaptation to a black-and-white rotating sector disk, suggesting a neural interaction between real motion and illusory motion. We further studied Enigma-type motion on a chromatic bar superimposed onto a black-and-white linear grating. Illusory motion was strongest when the bar was oriented at 90 deg to the grating lines and became progressively weaker with a decrease in angle. This suggests that T-junctions formed by the radial rays impinging onto the colored rings of the Enigma figure are instrumental for eliciting the rotary motion and may rule out a low-level sensory origin of the illusion.

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**Keywords:** Enigma illusion; Illusory motion; Motion aftereffect; T-junction; Terminators

## 1. Introduction

In 1981, Leviat devised a figure that elicits spontaneous perception of rotary motion in the absence of real motion. The figure consists of a black and white ray pattern with narrowly spaced radial lines onto which three chromatic rings are superimposed (Fig. 1). The spurious rotation seen on the rings gave rise to the name *Enigma*.

The number of rays in Leviat's figure was 120 and the duty cycle between black and white lines was 1:1.5 (Leviat, 1996). For an explanation of the illusion, Gregory (1993) suggested transient changes of accommodation and rapid eye movements. As an alternative, Mon-Williams and Wann (1996) proposed that optical aberration in conjunction with small eye movements produces Phi-motion between the radial lines of the Enigma figure leading to illusory motion on the rings.

Fermüller, Pless, and Aloimonos (1997) put forward a computational model based on 3D-motion. Their idea was that certain two-dimensional patterns may be interpreted in terms of three-dimensional motion. Within this context the spatial structure of the Enigma figure is assumed to represent a copoint vector field. The radial lines of the pattern are perpendicular to the copoint vectors while the rings are tangential. In order to support their theory, the authors showed that patterns similar to the Enigma figure produce illusory motion. However, this happens only when the motion vectors belong to the copoint vector fields, and not to other or to multiple classes.

To test for ocular artifacts, Zeki (1994) and Hamburger and Spillmann (2005) immobilized the crystalline lens with a cycloplegic. In addition, the latter authors produced a long-lasting afterimage of the Enigma figure by illuminating the stimulus with an intense photoflash. Under both conditions subjects reported seeing illusory motion in the Enigma figure. Thus, the apparent rotation cannot be accounted for by accommodative fluctuations

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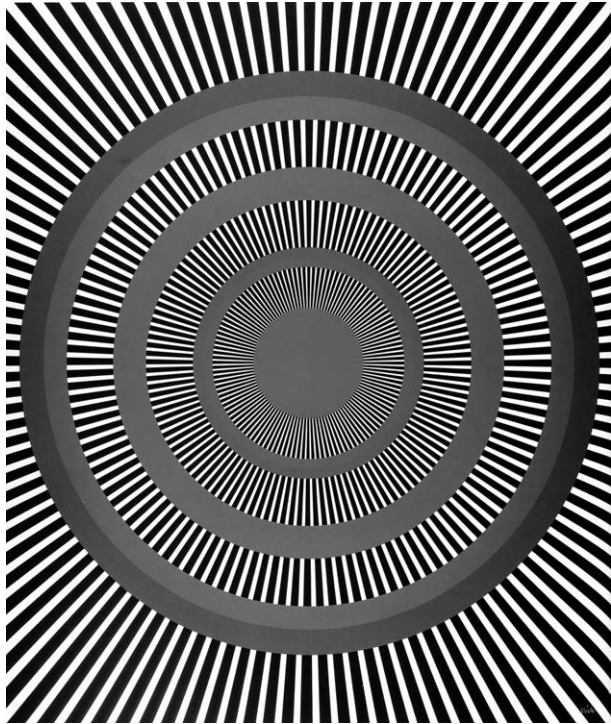


Fig. 1. Enigma figure by Isia Leviant (1981, cited in Leviant, 1996). Rotary motion alternating between clockwise and counter-clockwise direction may be perceived on the three chromatic annuli.

of the lens or image shifts on the retina, although the latter may enhance the illusion. There must be an additional factor. Another observation that speaks against an ocular artifact is the periodical change from clockwise to counter-clockwise rotation (Leviant, 1996). This reversal in direction suggests an involvement of higher-level processes.

Assuming a cortical origin Hamburger and Spillmann (2005) tested the influence of T-junctions and found that the illusory rotation became weaker, when the rays were replaced with short slashes or strings of dots. A reduction in strength was also obtained when the lines were arbitrarily tilted in opposite directions relative to the rings (by 25 deg). These findings were interpreted in terms of orthogonal terminators being instrumental for the induction of rotary motion.

In the present study, we were interested in both the spatial and the temporal properties of the Enigma illusion. First, we measured the duration for clockwise versus counter-clockwise rotation by recording the time between reversals of perceived rotation direction (Experiment 1). Next, we asked whether the onset and initial direction of rotation could be influenced by previous adaptation to real rotation (Experiment 2). Finally, we tested the strength of illusory motion in a simplified version of the Enigma composed of a chromatic bar superimposed onto a linear grating stimulus, when the angle between the bar and the grating lines was systematically varied (Experiment 3).

## 2. Experiment 1: Time course of illusory rotation

Here, we investigated the temporal behavior of apparent rotation in the Enigma illusion. The duration of clockwise versus counter-clockwise rotation was measured by recording the time when the apparent motion reversed its direction. We were also interested if the reversal time was comparable to that of other bistable illusions.

### 2.1. Methods

#### 2.1.1. Subjects

Seven naïve subjects (mean age 28 yrs; SD = 7.1) participated in the study. All had normal or corrected-to-normal visual acuity and normal color vision (tested with the Ishihara pseudo-isochromatic plates).

#### 2.1.2. Stimuli

Leviant's Enigma figure as reproduced by Livingstone (2002) served as a stimulus (Fig. 1). The background of the figure subtended  $14.8 \times 14.8$  deg. The outer ring had a radius of 5.65 deg; it was 1 deg wide and was composed of two different shades of purple. The middle ring had a radius of 3.85 deg; it was 0.7 deg wide and was composed of purple and red. The inner ring had a radius of 2.3 deg; it was 0.4 deg wide and was composed of two different shades of red. A small point in the center of the stimulus was used for fixation.

#### 2.1.3. Procedure

Subjects were seated 1 m away from a 21 in.-monitor (Sony Multiscan 6520) having a resolution of  $1344 \times 1008$  pixels and a refresh rate of 120 Hz. A chin rest was used to stabilize the head; fixation was binocular. Subjects first familiarized themselves with the Enigma illusion including the spontaneous reversals of motion direction. Thereafter they were exposed to the stimulus for 30 s. The task was to press the Enter-key on the keyboard of the computer as soon as the illusory motion was seen. Key #1 was pressed for counter-clockwise motion and key #9 for clockwise rotation. The time intervals between key presses defined motion duration in one or the other direction. Measurements were repeated 5 times for each ring and subject in a random order. Thus, the total number of test periods was 105 (5 repetitions  $\times$  3 rings  $\times$  7 subjects). The time interval between successive trials was 1 min. The experiment was performed in a dark room.

## 2.2. Results

The responses for all 7 observers were normalized to 100%. In Fig. 2, the percentage of cumulated responses for clockwise rotation is plotted as a function of time after stimulus onset. (Responses for counter-clockwise motion may be derived by subtracting the percentage for clockwise rotation from 100). Results for each ring are given by a different curve. All three curves show an oscillatory behavior

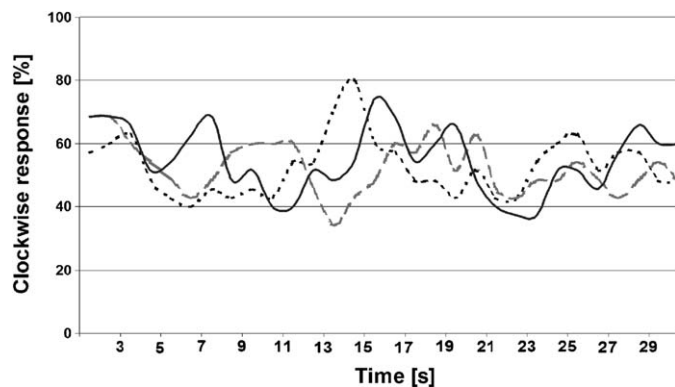


Fig. 2. Time course of clockwise rotation (given in percent) in the Enigma figure for each of the three rings (solid curve, outer ring; dashed curve, middle ring; and dotted curve, inner ring). Each curve is based on averaged responses obtained in 35 trials, 5 trials for each of the 7 subjects. Bin width was 1 s.

with occasional phase shifts; however, these differences between the rings are not significant (Kruskal–Wallis test = 1.75,  $p = 0.417$ ). Also, the dynamic oscillations are much the same within and between subjects.

On average, illusory motion was first perceived after a delay of 2.1 s (SD = 1.2 s) following stimulus exposure. Mean duration of uninterrupted clockwise rotation was 5.0 s while that for counter-clockwise rotation was 4.4 s. This translates into a mean number of directional reversals of 6.4 (SD = 2.5), with minor differences among the three rings (ANOVA repeated measure  $F_{2,102} = 0.38$ ). The number of reversals decreased monotonically from a mean of 2.38 in the first 10 s to 2.16 in the second and 1.86 in the last.

When analyzing the data, we found a strong bias at the beginning of a trial in favor of seeing clockwise motion (64.8%) vs. counter-clockwise motion (35.2%). Also, the total number of responses for all rings and subjects cumulated over 30 s was somewhat higher for clockwise rotation than for counter-clockwise rotation (53.54% vs. 46.46%).

In addition to these quantitative results, subjects reported that the direction of rotation on the three rings was not always the same. For example, while perceived rotation on one ring may have been in the clockwise direction, on the other two it was in the opposite direction, etc. Also, rotation in both directions could occasionally be seen simultaneously on the same ring, clockwise on one shade of color and counter-clockwise on the other. Finally, perceived speed was reported to be faster on the inner ring than on the middle and outer rings.

### 2.3. Discussion

The time lag of about 2 s preceding the onset of rotary motion suggests that whatever mechanism is responsible for the apparent rotation in the Enigma illusion requires a minimum time of stimulation to produce the effect. The average duration of 4.7 s (5.0 s for clockwise

direction vs. 4.4 s for counter-clockwise direction) for apparent rotation further suggests an internal “clock” that switches the percept from one to the opposite motion direction. Such a switch is unlikely due to involuntary eye movements, but may reflect saturation or adaptation not unlike the known reversals in other bi-stable figures. There are several studies on bi-stable motion illusion consistent with this interpretation. For example, Duffy and Wurtz (1997) and Paolini et al. (2000) presented electrophysiological evidence from single cell studies in monkey that both motion onset and abrupt changes in flow trajectory are followed by peaks in the response of MSTd neurons. In line with these results Tolias, Smirnakis, Augath, Trinath, and Logothetis (2001) obtained in an fMRI study with nonhuman primates an adaptation of BOLD response in motion sensitive areas during unidirectional rotation of a visual motion stimulus, whereas sudden direction changes were followed by a peak in the BOLD response. Moreover, Sterzer, Russ, Preibisch, and Kleinschmidt (2002) found in their fMRI study transient activation in the human motion complex in response to perceived sudden changes in motion direction during observation of the wagon-wheel illusion. They suggested an adaptation of motion sensitive neurons during continuous visual motion stimulation that is followed by an increase in activity when motion direction changes. The similarities between these two bistable motion illusions, Enigma and the wagon-wheel illusion, show spontaneous reversals from clockwise to counter-clockwise rotation and vice versa. This supports our assumption of physiological mechanisms underlying the spontaneous reversal of motion direction. The gradual decrease of the reversal rate within the same inspection period may similarly result from directional adaptation or tiring of the observers.

Eye movements have also been ruled out as a factor for the wagon-wheel illusion (Sterzer et al., 2002). Instead, transient fMRI-activation was found in area hMT+/V5 correlated with sudden changes in perceived motion direction. It would be interesting to check whether a similar correlation holds also for the Enigma illusion.

Table 1 based on a survey by Strüber and Stadler (1999) summarizes the rate of reversals and mean duration for various static bistable phenomena. Results for the Enigma figure (first column) and the wagon-wheel illusion (second column) are almost identical. Results for the static percepts are in the same order of magnitude, although durations for the Enigma illusion are consistently longer and reversals fewer than for the other illusions. However, there is excellent agreement with the mean duration of 4.7 s obtained for the wagon-wheel illusion.

We have no explanation for the directional bias (clockwise > counter-clockwise) at the beginning of a trial or the slight bias for clockwise rotation over the entire inspection period. Handedness is not likely to be a factor as a compar-

Table 1  
Mean number of spontaneous reversals and mean duration (in s) for each percept in various static bistable illusions

	Enigma illusion	Wagon-wheel illusion	Necker cube		
Mean number of reversals	6.4	6.4	8.2		
Mean duration of one percept	4.7	4.7	3.7		
	Rock's chef/dog	Schröder's staircase	Rubins vase/faces	Maltese cross	
Mean number of reversals	9.1	11.7	13.3	10	
Mean duration of one percept	3.3	2.6	2.3	3	

Data for the Enigma illusion (this study) and wagon-wheel illusions (from Sterzer et al., 2002) are given for comparison. Results have been adjusted for 30 s of observation. (From Strüber and Stadler, 1999.)

ison between right-handed and left-handed subjects in a small sample of 5 vs. 2 observers showed no difference. No evidence of handedness was found either by MacKay (1957) who studied “complementary motion” in a radial ray pattern and reported an even greater directional bias of 75% for clockwise vs. 25% for counter-clockwise rotation. In an informal observation, one of the authors (S.G.) noticed little or no effect of focused attention on reversal rate.

### 3. Experiment 2: Adaptation to real rotation

Here, we asked whether the direction of illusory motion could be influenced by prolonged adaptation to physical rotation prior to viewing the Enigma figure. In this way, we hoped to find out whether real and illusory motion perception interact within the same neuronal circuitry.

#### 3.1. Method

##### 3.1.1. Subjects

Six naïve subjects (mean age 26 yrs;  $SD = 2.5$ ) participated in the experiment.

##### 3.1.2. Stimuli

For motion adaptation a black-and-white sector disk (Kleiner, 1878) spinning either clockwise or counter-clockwise was displayed on the face of the monitor. The disk had the same radius as the outer ring of the Enigma figure (5.65 deg). Michelson contrast was 98.4% and there were a total of 62 sectors. Speed of rotation was 12 deg/s (0.03 rps). This speed was chosen because it yielded the longest motion aftereffect. Fixation was in the middle of the disk.

##### 3.1.3. Procedure

Adapting time was 30 s. Immediately after adaptation to the sector disk, the Enigma figure was displayed for 15 s, during which period subjects reported the beginning as well as the direction of the apparent rotation by key press. There were 4 measurements for each of the 3 rings in each adapting direction. The total number of test periods was 144 (4 repetitions  $\times$  3 rings  $\times$  2 adapting directions  $\times$  6 subjects). The time interval between successive trials was 1 min.

The mean duration of the resulting motion aftereffect measured under these conditions was 9.2 s ( $SD = 3.2$ ). Since the first reversal of the illusory rotation in Experiment 1 occurred on average after 6.8 s (2.1 s initial delay plus 4.7 s mean duration), any influence of the preceding adaptation to the real motion should be reflected in a shift of the initial direction bias towards the motion aftereffect.

#### 3.2. Results

Mean time required for perceiving the rotary motion after adaptation to real motion was 3.7 s ( $SD = 2.4$  s), which is significantly longer than the time lag for the motion onset (2.1 s) found in Experiment 1 (Fig. 3). There were no significant differences between the onset delays observed with clockwise adaptation and counter-clockwise adaptation ( $t_{71} = 0.61$ ,  $p = n.s.$ ). However, there was a major shift of the response bias at the beginning of a trial. After adapting to clockwise rotation, 31.9% of the responses were clockwise and 68.1% counter-clockwise. In comparison, after adapting to counter-clockwise rotation, 80.6% of the initial responses were clockwise and only 19.4% counter-clockwise. These results are significantly different from the 64.8% to 35.2% ratio found without adaptation

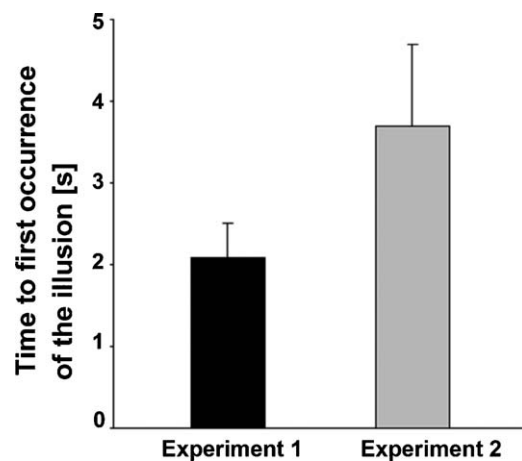


Fig. 3. Time lag for first occurrence of illusory rotation on the rings of the Enigma figure without and with adaptation to real motion. Data are averages from 105 (Experiment 1) and 144 (Experiment 2) trials. The bars give the standard error.

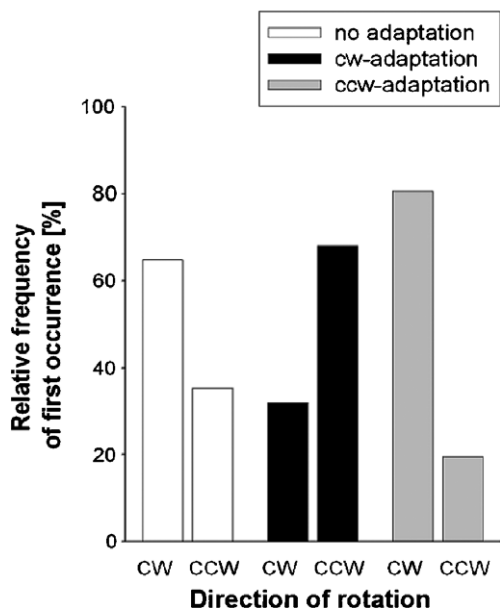


Fig. 4. Relative frequency of first occurrence of clockwise and counter-clockwise rotation without and with adaptation to real motion in one or the other direction (see inset). Data represent 105 trials for “no adaptation” and 72 trials for each direction of “adaptation.”

(Fig. 4). The relative preference for seeing clockwise rotation prevails even after adaptation.

### 3.3. Discussion

Results show that the motion aftereffect resulting from adaptation to a rotating sector disk delays the onset of apparent motion in the Enigma illusion from 2.1 to 3.7 s and also changes the directional bias towards the motion aftereffect. Specifically, previous adaptation to clockwise motion resulted in a 32.9% increase for counter-clockwise responses, while adaptation to counter-clockwise adaptation resulted in a 15.8% increase for clockwise responses. Thus, clockwise adaptation had an effect that was twice as strong as counter-clockwise adaptation, consistent with the initial directional bias found in Experiment 1.

We do not think that this result can be accounted for by a change of attention. It is true that the motion aftereffect attracts attention (Huk, Ress, & Heeger, 2001). However, all subjects could readily distinguish between the global motion aftereffect that became immediately visible in the motion-adapted area of the Enigma figure and the apparent rotation on the three rings that emerged a few seconds thereafter.

From earlier observations we know that the motion aftereffect typically is strongest during the first 4 s after offset of the adapting stimulus, whereafter it rapidly declines and disappears. This is about the same time (3.7 s) that we measured for the onset of the Enigma illusion following adaptation to the sector disk. We therefore cannot rule out that the strong motion aftereffect masked and captured the weaker rotary motion on the rings delaying its onset and

shifting the directional bias. On the other hand, the motion aftereffect might have interfered with the illusory motion because it has access to the same neural circuitry that mediates the Enigma illusion. This assumption would be consistent with the finding by Sterzer et al. (2002) that both real motion and illusory motion in the wagon-wheel figure produce activity in the same cortical area, MT+/V5 (occipitotemporal junction). PET-activation in motion sensitive cortical areas recorded in response to the Enigma figure (Zeki, Watson, & Frackowiak, 1993) would also favor a neuronal interpretation. Meanwhile, it has been shown that in addition to motion, the effect of attention of fMRI-activity needs also to be taken into account (Huk et al., 2001).

### 4. Experiment 3: T-junctions

To probe for an explanation of the Enigma illusion, we here asked whether and to what extent the illusory rotation requires orthogonal rays impinging on a closed annulus. Fermüller et al. (1997) report that in a large quadrant of the original Enigma figure (their figure 8a) illusory motion in both directions continued to be seen within the segment. We extended this observation by reducing the segment to one eighth of a circle and still observed motion. Therefore, a closed annulus is not necessary for eliciting the Enigma illusion. Furthermore, Fermüller et al. (1997) used a linear grating pattern with six horizontally oriented gray bands intersecting the grating lines at right angles (their figure 8b). Under these conditions illusory streaming motion was still present on the bands. Thus, curvature is not a requirement either. This is confirmed by the grainy motion seen in the undulating street pattern of DeRays (1976), as illustrated in Fig. 5.

All these patterns have in common that the inducing lines impinge at right or near-right angles onto the narrow interspace on which the illusory motion is seen. We therefore asked whether a 90 deg angle is critical for eliciting the illusory motion. The hypothesis was that T-junctions might be crucial for obtaining the illusory motion. To test for the effect of T-junctions, we superimposed a straight, bicolored

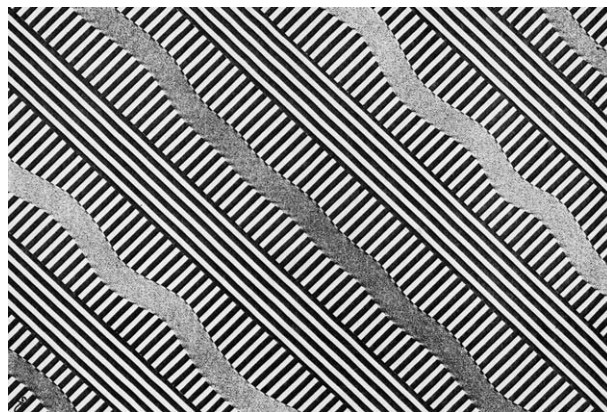


Fig. 5. Street pattern by DeRays. Note the illusory motion of the grainy “dust” on the undulating streets.

bar comparable to the outer ring of the Enigma figure onto a black-and-white grating and systematically changed the angle between the bar and the grating lines.

#### 4.1. Methods

##### 4.1.1. Subjects

Eleven naïve subjects (mean age 30 yrs; SD = 4.8) participated in the study.

##### 4.1.2. Stimuli

Six stimuli were presented, each composed of a black-and-white vertical grating and a bar with two shades of purple superimposed onto it. The grating had a spatial frequency of 1.7 cpd similar to the outermost set of radial lines in the Enigma figure and subtended 19.3 (height) × 29 deg (width). The black lines were again 1.5 times as wide as the white interspaces. The intersecting bar was 19.3 deg long and 1.4 deg wide. Fixation was 3.8 deg away from the center of the bar and orthogonal to it. The angle between the bar and the grating lines was randomly varied in steps of 18 deg from 90 (orthogonal) to 0 deg (parallel).

##### 4.1.3. Procedure

Subjects were seated 40 cm away from the stimulus. The task was to rank-order the six different stimuli according to strength of the illusory motion seen on the chromatic bar. We used print-outs on paper, laid out in a random sequence, so that stimuli could be viewed and compared simultaneously. The results for all 11 subjects were then assigned to a scale ranging from 0 to 5 points. The pattern with the strongest illusory motion was assigned 5 points, whereas the pattern with the weakest illusory motion was assigned 0 points. This arbitrary scale was expressed as a percentage of the total.

#### 4.2. Results

All subjects reported fast streaming motion streaks shuttling back and forth on the bar, comparable to the illusory

motion on the 45 deg sector mentioned earlier. Fig. 6 plots the strength of this motion as a function of the angle between the chromatic bar and the grating lines. Illusory motion increases linearly with increasing angle. The determination coefficient of the regression line was  $R^2 = 0.99$  and the Bartlett  $\chi^2$  is significant ( $\chi^2_1 = 13.98$ ;  $p < 0.001$ ).

#### 4.3. Discussion

Results show that T-junctions are a strong factor in eliciting illusory motion. Whereas the illusory motion was judged most salient (83.7%), when bar and gratings lines were oriented at right angles, it was least salient (7.3%), when the chromatic bar was oriented parallel to the grating. In fact, many subjects reported that in the latter case there was almost no motion. The progressive decrease in strength may depend on the reduction in figure-ground segregation and depth-ordering that may also affect the illusion. However, even these two factors cannot explain, how orientation signals from the terminators of the grating lines are transformed to produce rotary (and reversing) motion on the bar.

End-stopped neurons as a candidate mechanism for generating orthogonal motion have recently been shown to lack orientation specificity (Pack, Livingstone, Duffy, & Born, 2003) and therefore no longer qualify for an explanation. We are therefore back to MacKay (1957, 1961), who described “complementary” afterimages, similar to the streaming motion in the Enigma figure, in radial, concentric, and grating patterns. He hypothesized that “the system tends to favor the direction at right angles to the regular contours, suggesting a theoretical model of form-perception in which directions at right angles are treated by the system as competitive” (MacKay, 1957). Visual neurons suitable for this task remain to be identified.

#### 5. Conclusion

The perceived reversal of illusory rotation in Leviant’s Enigma figure with time follows an oscillatory pattern, irrespective of the retinal eccentricity of the rings. Initial rotation in the clockwise direction outweighed by far rotation in the counter-clockwise direction; clockwise rotation also lasted longer than counter-clockwise rotation. Our findings demonstrate that this directional bias is influenced by previous adaptation to real rotation suggesting that the same higher-level processes that subserve the perception of real motion may also mediate illusory motion.

Our study shows a strong influence of T-junctions in line with previous results by Hamburger and Spillmann (2005). This dependency on angle rules out a low-level origin. A locus in the cortex is also evident from the PET-study by Zeki et al. (1993), who found activation in response to the Enigma illusion in motion sensitive cortical areas; and from the fMRI-study by Sterzer et al. (2002) reporting transient fMRI-activation in the same area correlated with directional motion reversals. Thus, combining psychophysics and

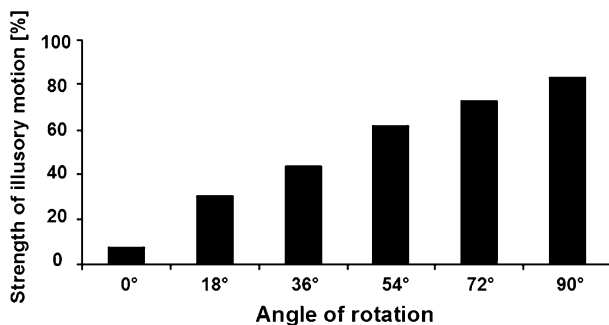


Fig. 6. Strength of illusory motion as a function of the angle between a chromatic bar and the grating lines. Stimuli were rank-ordered according to strength and assigned to a scale ranging from 0 to 5 points. The results of 11 subjects were then cumulated and expressed as a percentage of the total ( $\Sigma = 55$ ).

brain imaging in future studies may provide us with better insight into the nature of this illusory motion phenomenon.

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### References

- Duffy, C. J., & Wurtz, R. H. (1997). Multiple temporal components of optic flow responses in MST neurons. *Experimental Brain Research*, *114*, 472–482.
- Fermüller, C., Pless, R., & Aloimonos, Y. (1997). Families of stationary patterns producing illusory movement: insights into the visual system. *Proceedings of the Royal Society of London Series B*, *264*, 795–806.
- Gregory, R. L. (1993). A comment: MacKay rays shimmer due to accommodation changes. *Proceedings of the Royal Society of London Series B*, *253*, 123.
- Hamburger, K., & Spillmann, L. (2005). New insights into ‘Enigma’. *JOV*, *5*(8), 61a (Abstract), <<http://journalofvision.org/5/8/61/>>.
- Huk, A. C., Ress, D., & Heeger, D. J. (2001). Neuronal basis of the motion aftereffect reconsidered. *Neuron*, *32*, 161–172.
- Kleiner, A. (1878). Physiologisch-optische Beobachtungen. *Pflügers Archiv für die gesamte Physiologie des Menschen und der Tiere*, *18*, 542–573.
- Leviant, I. (1996). Does ‘brain-power’ make Enigma spin? *Proceedings of the Royal Society of London Series B*, *263*, 997–1001.
- Livingstone, M. S. (2002). *Vision and art: The biology of seeing*. New York: Harry N. Abrams Inc.
- MacKay, D. M. (1957). Moving visual images produced by regular stationary patterns. *Nature*, *180*, 849–850.
- MacKay, D. M. (1961). Interactive processes in visual perception. In W. Rosenblith (Ed.), *Sensory communication* (pp. 339–355). Cambridge, MA: MIT Press.
- Mon-Williams, M., & Wann, J. P. (1996). An illusion that avoids focus. *Proceedings of the Royal Society of London Series B*, *263*, 573–578.
- Pack, C. C., Livingstone, M. S., Duffy, K. R., & Born, R. T. (2003). End-stopping and the aperture problem: two-dimensional motion signals in macaque V1. *Neuron*, *39*, 671–680.
- Paolini, M., Distler, C., Bremmer, F., Lappe, M., & Hoffmann, K. P. (2000). Responses to continuously changing optic flow in area MST. *Journal of Neurophysiology*, *84*, 730–743.
- Sterzer, P., Russ, M. O., Preibisch, C., & Kleinschmidt, A. (2002). Neural correlates of spontaneous direction reversals in ambiguous apparent visual motion. *Neuroimage*, *15*, 908–916.
- Strüber, D., & Stadler, M. (1999). Difference in top-down influences on the reversal rate of different categories of reversible figures. *Perception*, *28*, 1185–1196.
- Tolias, A. S., Smirnakis, S. M., Augath, M. A., Trinath, T., & Logothetis, N. K. (2001). Motion processing in the macaque: revisited with functional magnetic resonance imaging. *Journal of Neurosciences*, *21*, 8594–8601.
- Zeki, S. (1994). The cortical Enigma: a reply to Professor Gregory. *Proceedings of the Royal Society of London Series B*, *257*, 243–245.
- Zeki, S., Watson, J. D. G., & Frackowiak, R. S. (1993). Going beyond the information given: the relation of visual motion to brain activity. *Proceedings of the Royal Society of London Series B*, *252*, 215–222.