Representation of Illusory and Physical Rotations in Human MST: A Cortical Site for the Pinna Illusion

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Abstract: Visual illusions have fascinated mankind since antiquity, as they provide a unique window to explore the constructive nature of human perception. The Pinna illusion is a striking example of rotation perception in the absence of real physical motion. Upon approaching or receding from the Pinna-Brelstaff figure, the observer experiences vivid illusory counter rotation of the two rings in the figure. Although this phenomenon is well known as an example of integration from local cues to a global percept, the visual areas mediating the illusory rotary perception in the human brain have not yet been identified. In the current study we investigated which cortical area in the human brain initially mediates the Pinna illusion, using psychophysical tests and functional magnetic resonance imaging (fMRI) of visual cortices V1, V2, V3, V3A, V4, and hMT+ of the dorsal and ventral visual pathways. We found that both the Pinna-Brelstaff figure (illusory rotation) and a matched physical rotation control stimulus predominantly activated sub-area MST in hMT+ with a similar response intensity. Our results thus provide neural evidence showing that illusory rotation is initiated in human MST rather than MT as if it were physical rotary motion. The findings imply that illusory rotation in the Pinna illusion is mediated by rotation-sensitive neurons that normally encode physical rotation in human MST, both of which may rely on a cascade of similar integrative processes from earlier visual areas. *Hum Brain Mapp* 37:2097–2113, 2016. © 2016 Wiley Periodicals, Inc.

Key words: visual illusion; Pinna illusory rotation; rotary motion perception; area MST; hMT+; fMRI

INTRODUCTION

The mismatch between perception and reality reflects the constructive nature of human vision and provides valuable insight into the mechanisms of perception [Eagleman, 2001;

Gregory, 1972; Komatsu, 2006; Murray and Herrmann, 2013; von der Heydt et al., 1984; Wertheimer, 1912]. A celebrated example is the Pinna-Brelstaff figure [Pinna and Brelstaff, 2000], which elicits vivid illusory rotation with to and fro motion of the head in the absence of physical

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rotary motion of the stimulus (Fig. 1A). The stimulus figure consists of two concentric rings formed by small rhombi, whose edges are either bright or dark and slanted in opposite directions (to the right or left). This illusory perception of counter rotating rings is known as the Pinna rotary illusion. Psychophysical studies have already shown that the arrangement and orientation of the local inducers in the rings are crucial for the perception of illusory rotation [Gurnsey and Page, 2006; Pinna and Brelstaff, 2000]. When the edges are rearranged and there is no slant, the illusion is absent (Fig. 1B). Although the Pinna illusion is a well-known example of a global percept derived from integration of local visual cues [Bayerl and Neumann, 2002; Fermüller and Malm, 2004; Gurnsey and Page, 2006; Gurnsey et al., 2002; Mather, 2000], the exact visual areas mediating the illusory rotary perception in the human brain have not yet been identified.

fMRI studies have demonstrated that non-motion illusions such as the misperception of contours, angles and surfaces are represented in human ventral visual cortices V1, V2, and V4, respectively [Fang et al., 2008; Mendola et al., 1999; Meng et al., 2005; Schwarzkopf et al., 2011; Sperandio et al., 2012; Stanley and Rubin, 2003]. In contrast, motion illusions such as the waterfall illusion [Tootell et al., 1995a], the flash-drag effect [Maus et al., 2013], and the rotating snakes illusion [Ashida et al., 2012] have been attributed to the human MT complex (hMT+). hMT+ is a large area composed of at least two subareas with potentially different functions: areas MT and MST [Amano et al., 2009; Dukelow et al., 2001; Huk et al., 2002; Kolster et al., 2010]. Single-cell recording in macaques has revealed that physical rotary motion is initially encoded by rotation-sensitive neurons in area MST of the dorsal visual pathway [Duffy and Wurtz, 1991; Graziano et al., 1994; Saito et al., 1986; Tanaka et al., 1989; Tanaka et al., 1993]. Furthermore, in comparison with MT, MST is much less retinotopic because its neurons have very large receptive fields which typically ranging its size from a quadrant to the whole visual field. Therefore MST neurons are capable of forming global representations by integrating from a large visual field. Here we hypothesize

that the illusory perception of the global rotary motion in the Pinna-Brelstaff figure originates in subarea MST of hMT+.

We launched a combined psychophysical and fMRI protocol to test this hypothesis in a group of 17 healthy volunteers. A variety of stimulus parameters in the perception of Pinna illusory rotation was first examined psychophysically outside the scanner. The test results were then used to determine the most suitable stimulus conditions for eliciting vivid Pinna illusory rotation in all subjects in the fMRI scanner. Using a classic block-design stimulus paradigm (Fig. 1C), we applied the general linear model (GLM) to analyze blood oxygenation level dependent (BOLD) signals in various hierarchical visual areas along the dorsal and ventral visual pathways activated by the Pinna-Brelstaff figure. Specifically, we asked where the illusory rotary perception occurs in the visual brain by examining the magnitude (% change of BOLD signals) and spatial localization of BOLD signals elicited by the expansion of the Pinna-Brelstaff figure. For control conditions, we used a figure exhibiting real physical rotation with a matching speed to the illusory rotation in addition to physical expansion and a figure showing the physical expansion only (Fig. 1C). We applied a standard condition-wise subtraction of the expansion components, and significant BOLD activations were seen mostly in hMT+ under both physical and illusory rotation conditions. Moreover, we found that these cortical activations were predominantly located in a sub-region MST of hMT+ with similar response amplitudes. The fMRI evidence thus suggests that it is subarea MST, not subarea MT in hMT+ that mediates the Pinna illusory rotation in a way similar to physical rotation, implying the same neuronal circuits with the active recruitment of rotation-sensitive neurons responsible for seeing both physical rotation and illusory rotation.

MATERIALS AND METHODS

Seventeen healthy volunteers (11 males and 6 females) with normal or corrected-to-normal vision and aged 22–30 years were recruited for both the psychophysical and fMRI study. Psychophysical and fMRI scan protocols were approved by the Biomedical Research Ethics Committee, Shanghai Institutes for Biological Sciences, Chinese Academy of Sciences. All subjects had given written consent to the procedure in accordance with institutional guidelines and the Declaration of Helsinki.

Psychophysics Experiment

All visual stimuli were generated in MATLAB using Psychtoolbox functions [Brainard, 1997; Pelli, 1997]. The Pinna-Brelstaff figure (Fig. 1A) and its derived patterns were presented on a 19-inch LCD monitor (Philips 190E2 plus, 1440 × 900, 60 Hz), 50 cm in front of the subject

Abbreviations

EO	Expansion only
FA	Flip angle
GE-EPI	Gradient echo, echo-planar imaging
GLM	General linear model
IPS	Intraparietal sulcus
IR	Illusory rotation
MPRAGE	Magnetization-prepared-rapid-acquisition-gradient-echo
MST	Medial superior temporal
ROI	Region of interest
STS	Superior temporal area

Figure 1.

Experimental stimuli and fMRI experiment paradigm. **A**, The Pinna-Brelstaff figure. In the experiment radial expansion was used to simulate the effects of head movement. Fixation was on the central black dot. **B**, Modified control stimulus. The rhombi are changed to squares and the bright and dark edges are juxtaposed. **C**, The sequence illustrates a complete run in the fMRI scanner for three stimulus conditions as specified. Black arrows denote expansion for all three conditions, yellow arrows direction of physical rotation. Eight cycles were included in one scan session.

whose head rested on a chin rest. The subject's eye position was monitored by an infrared image eye tracker system (iSCAN ETL-200, ISCAN Inc.). Since the subject was not allowed to move in the scanner, we simulated the to and fro head movement normally required for perceiving the Pinna illusion by increasing and decreasing the initial diameter of the stimulus and animation step size. The effects of two critical parameters in the perception of Pinna illusory rotation were thus examined: viewing distance and heading speed of the subjects towards the Pinna-Brelstaff figure.

Previous experiments by other groups [Fermüller and Malm, 2004; Gurnsey and Page, 2006; Gurnsey et al., 2002;

Mather, 2000; Pinna and Brelstaff, 2000] have shown that this simulation method produced illusory rotary motion comparable to that seen in the free viewing condition. We also mounted an LCD screen on a linear track driven by a step motor to generate the to and fro movement and tested the effects of the two variables outside the scanner. The results obtained under physical motor drive and simulated situations were comparable, enabling us to use simulated movement for eliciting the Pinna illusion. We tested the effect of simulated viewing distance for 8 distances, ranging from 20 to 160 cm in 20 cm step, and the effect of 17 simulated heading speeds ranging from 0 to a maximum of 160 cm/s in 10 cm/s step. Stimulus duration was fixed at 1 s in all cases. The detailed stimulus parameters used in our study are summarized in Table I. Radii and side lengths in the table are specified by their visual angles, which were increased by an appropriate amount when mimicking the forward motion of the subject toward the Pinna-Brelstaff figure. Backward motion was not used to generate the Pinna illusion in our study.

All trials were randomly interleaved within one block. The speed of apparent rotation in the Pinna-Brelstaff figure was determined in each subject by performing a matching task. Specifically, a set of 10 stimuli with varying physical rotation speeds of 0, 2, 4, 8, 12, 16, 20, 24, 28, 32°/s was simultaneously presented right after the Pinna-Brelstaff pattern disappeared. The radii of the inner and outer rings of the matching stimuli were 3.4 and 4.6 deg, respectively. The ten matching stimuli were denoted by letters A-J and presented in two rows simultaneously on the screen with different rotation speeds. From top left to lower right, matching speed increased monotonically. Subjects were instructed to select one of the 10 physically rotating stimuli that most closely resembled the speed of illusory rotation by pressing the corresponding letter for that physical stimulus and then pressing the Enter key. All subjects finished the choosing of a physical stimulus with a speed matching to that he/she perceived in the Pinna-Brelstaff figure within 5–10 s. During each trial, subjects maintained fixation within a 2 by 2° window; trials with excessive eye movements were discarded.

TABLE I. Parameters of stimulus used in the psychophysical experiments

Number of rhombuses of inner ring	28
Number of rhombuses of outer ring	34
Radius of inner ring (to center of rhombus)	4.2°
Radius of outer ring (to center of rhombus)	5.6°
Radius of fixation point	0.1°
Side lengths of rhombus	0.55° and 0.59°
Angle between the two sides (acute)	68.2°

fMRI Stimulus Paradigm

Stimuli were projected onto a translucent screen (45 × 35 cm in length and width) mounted on the rail of the scanner at a distance of 100 cm from the eye with an effective visual angle of 19.8°. A complete stimulus paradigm for fMRI experiment consisted of three sessions: retinotopic mapping, functional localization of hMT+/MT/MST, and Pinna illusion. In retinotopic mapping session, we used stimuli consisting of wedges and rings for the retinotopic mapping of V1-V4, the same as described in previous studies [Engel et al., 1997; Engel et al., 1994; Sereno et al., 1995; Wandell et al., 2007]. Essentially, two opposite wedges with 22.5° polar angle and 9.4° radii, rotating by 45° every 4 seconds in a clockwise or counter-clockwise manner, were used for the visual field polar angle test. For the eccentricity test, we used rings that expanding or contracting by 2.5° every 4 seconds with a minimal (1.9°) and maximal (9.4°) radius. The width/thickness of the ring was kept constantly at 1.25° during the expansion or contraction period. Both wedges and rings were black-white checkerboard patterns flickering at a contrast reversal rate of 8 Hz on a gray background. The luminance of the background was equal to the average of the black and white checks. Next, spatial localizers used in previous studies [Dukelow et al., 2001; Huk et al., 2002] were applied here for the functional mapping of hMT+/MT/MST. In short, to functionally localize hMT+, 1500 randomly distributed white dots with radius of 0.15° forming a circular aperture (20° in diameter) alternated in time between moving (9 s) and stationary states (27 s) for 8 cycles on black background. At moving state, random dots traveled toward and away from fixation (8°/sec), alternating direction once per second. To localize MT, a motion-defined 90° wedge (one quarter of the field) within a circular aperture (20° in diameter) rotated slowly around the central fixation point. As in the hMT+ localizer stimulus, the dots within a wedge moved toward and away from fixation except that the rest of the dots were stationary. This motion-defined wedge rotated 20° every 2 sec and ran eight full cycles. To localize the MST, we tested for ipsilateral responses using stimuli restricted to either the left or right hemifield. The stimuli was a 15° circular aperture consisted of random dots alternating every 18 sec between a field of moving and static dots for a total of eight cycles. The circular aperture was presented at 12.5° eccentricity (relative to the central fixation point). Please also see the descriptions in an early work from Heeger's group for the localization of hMT+, MST, and MT [Huk et al., 2002]. To study the illusory rotation, three stimulus conditions were randomly interleaved within a block-design paradigm (Fig. 1C): (1) "The Pinna-Brelstaff figure" or illusory rotation (IR) (Fig. 1A), which elicited illusory rotation by physical expansion. (2) An "Expansion only" condition (EO, Fig. 1B), which exhibited neither illusory nor physical rotation and served as a control. (3) A real "Physical-rotation" condition (PR), identical to (2), except that the two rings were physically

rotated at 20°/s, which was the matching speed obtained in psychophysics experiments for generating vivid illusory rotation in all subjects.

fMRI Data Acquisition

All 17 subjects were scanned with a standard 32-channel phased-array head coil on a Siemens Tim Trio 3.0 T scanner (Erlangen, Germany), while maintaining fixation on a small spot (0.1° radius) in the middle of the screen on which the stimuli were displayed. Eye position was continuously monitored at 120 Hz during the scan using an MRI-compatible ISCAN ETL-200 eye tracker system to track pupil position and corneal reflection.

Three-dimensional whole-brain high-resolution T1-weighted images of each subject were acquired using the magnetization-prepared-rapid-acquisition-gradient-echo (MPRAGE) pulse sequence (TR = 2,530 ms; TE = 3.14 ms; TI = 1,100 ms; flip angle (FA) = 7°; FOV = 256 × 256 × 176 mm; matrix = 256 × 256; voxel size = 1.0 × 1.0 × 1.0 mm³). T2*-weighted functional data were acquired using a gradient echo, echo-planar imaging (GE-EPI) sequence sensitive to blood oxygen-dependent contrast. The total scanning time for each subject lasted up to 90 min including shimming, anatomical, and functional imaging. A total of 1,904 functional volumes were acquired in three sessions for each subject: 512 volumes for the retinotopic experiment, 1,152 volumes for the hMT+/MT/MST area localizers, 240 volumes for the Pinna illusion and two control conditions.

The detailed scan parameters for each imaging session were as follows: (1) Retinotopic session: TR = 2,000 ms, TE = 30 ms, FA = 77°, FOV = 172 × 160 mm, matrix = 86 × 80, slice thickness = 2.0 mm (voxel size = 2.0 × 2.0 × 2.0 mm³) and 31 slices oriented perpendicularly to the calcarine sulcus were acquired covering the entire occipital lobe. Four fMRI runs were conducted (two for polar angle mapping and the other two for the eccentricity mapping), and 128 volumes were recorded for each run (hereafter denoted as Dataset1); (2) MT, MST and hMT+ localizer session: TR = 1,000 ms, TE = 30 ms, FA = 62°, FOV = 220 × 200 mm, matrix = 110 × 100, slice thickness 3.0 mm (voxel size = 2.0 × 2.0 × 3.0 mm³) and 13 slices oriented parallel to the calcarine sulcus were acquired with the lowest slice near the ventral surface of the occipital lobe. Four runs were conducted (one for hMT+, one for MT, and two for MST), and 288 volumes were recorded for each run (denoted as Dataset2); (3) Pinna-Brelstaff figure and control session: TR = 3,000 ms, TE = 30 ms, FA = 84°, FOV = 220 × 220 mm, matrix = 88 × 88, slice thickness = 3.0 mm (voxel size = 2.5 × 2.5 × 3.0 mm³) and 49 slices oriented parallel to the AC-PC line covering the entire brain. 240 volumes were recorded for this session (denoted as Dataset3).

fMRI Data Analysis

Image processing and analysis were performed using Freesurfer V5.1.0 (<http://surfer.nmr.mgh.harvard.edu/>). We conducted a surface-based analysis in which cortical reconstruction and volumetric segmentation were done automatically by using the software [Dale et al., 1999; Fischl et al., 1999]. Preprocessing of functional image data included motion-correction, slice-timing correction, and registration onto the reconstructed individual cortical surface. To minimize individual variability in subsequent statistical analysis, individual surface was normalized to the “fsaverage” surface template in the Freesurfer. The functional surfaces were then smoothed with 5 and 7 mm FWHM Gaussian kernels for Datasets2/3 and Dataset1, respectively, and high-pass filtered at a frequency of 1/64, 1/72 and 1/60 Hz for Datasets 1, 2 and 3, respectively.

Activation maps for each dataset were obtained by the following analyses: (1) A standard phase-encoded retinotopic mapping procedure was applied to spatially delineate the boundaries of V1, V2, V3, V3A and V4 [Brewer et al., 2005; DeYoe et al., 1996; Engel et al., 1994; Hansen et al., 2007; Sereno et al., 1995]. We noticed that there is a debate on the differences between V4 and V4v [Brewer et al., 2005; DeYoe et al., 1996; Engel et al., 1994; Hansen et al., 2007; Sereno et al., 1995; Wandell et al., 2007]. However, our study did not intend to differentiate between the subareas of the ventral occipital, and for simplicity we referred the large activated area in the ventral occipital cortex to V4 in our study. (2) A phase-encoded mapping procedure was used to calculate the functional maps of MT. Standard general linear model (GLM) analysis was used for calculating hMT+ and MST activation maps, in accordance with previous studies [Amano et al., 2009; Huk et al., 2002]. (3) A block-design based GLM, in which three regressors of the three experimental conditions convolve with a gamma function ($\delta = 2.25$, $\tau = 1.25$), and six motion correction parameters was used to process Dataset3 of the Pinna-Brelstaff figure condition experiment. Activation maps of six contrasts—three stimulus conditions and three differential conditions (illusory rotation vs. expansion only, physical rotation vs. expansion only, and illusory rotation vs. physical rotation)—were generated. All activation maps were displayed and statistically analyzed in Caret (<http://www.nitrc.org/projects/caret>) [Van Essen et al., 2001].

To make a quantitative comparison of the percentage change of BOLD signals evoked by the visual stimuli, areas of V1-V4, hMT+, MT, and MST in standard space were labeled at Caret surface and converted to the volumes in individual space as masks. The percentage change of BOLD signals was defined by the mean response of all activated voxels relative to the baseline fluctuations during the stimulus interval period. The peak value of the mean BOLD response during the 15 s stimulus presentation within afore-defined V1-V4, MT, MST, and hMT+ in each subject were calculated for subsequent statistical comparison.

To map the brain areas related to rotation component of illusory and physical rotation stimulation, the activation maps of contrasts after condition-wisely subtracting expansion components (illusory rotation vs. expansion only and physical rotation vs. expansion only) were threshold at a statistical significance level of $P < 0.05$ and a cluster size of voxels $\geq 10 \text{ mm}^2$. In addition to traditional magnitude analysis, a good number of studies have used an analysis of activated volume (or voxel number) in 3D space [Goodyear and Menon, 1998; Kayser et al., 2005] and of the activated areal size [Ghosh et al., 2010]. Following these studies, we performed analyses of the spatial localization of activation and the corresponding areal size within hMT+. As the % BOLD signal change is normally related to the area size of activation, the surface-based analysis may provide an additional index to evaluate activation. We inflated the cortex at the “midthickness” level in Caret and quantified the size of activated areas at these two contrasts in every afore-defined visual regions. To further pin down the contribution of MST and MT to illusory and physical rotations, an area index was developed and defined as the difference of area size at MST and MT divided by the sum of area size at MST and MT:

$$\text{area index} = \frac{A(\text{MST}) - A(\text{MT})}{A(\text{MST}) + A(\text{MT})} \quad (1)$$

where $A(\text{MST})$ and $A(\text{MT})$ are the sizes of activated areas in MST and MT, respectively. Nevertheless, instead of arbitrarily assigning the overlapping areas of MT and MST to the nominal MT region [Amano et al., 2009; Huk et al., 2002], the area of overlap between MT and MST was treated separately in this study. The overlap index was defined as the ratio of overlap (RO) area in MT and MST:

$$\text{RO} = \frac{A(\text{overlapping})}{A(\text{MST}) + A(\text{MT}) + A(\text{overlapping})} \quad (2)$$

where $A(\text{overlapping})$ is the size of the activated overlapping area in MST and MT.

RESULTS

Angular Velocity Closely Correlates With the Strength of Illusory Rotation

The aim of the psychophysical tests was to determine the most suitable stimulus configuration for each subject to perceive the Pinna rotary illusion in the scanner. In our current study, we tested the classical Pinna-Brelstaff figure, which elicited illusory counter rotation of the concentric rings (Fig. 1A). The two rings in the Pinna illusory rotation expanded radially from the center toward the edge of the

screen within a constant time period of 1 s. We noticed that the perceived illusory rotation accelerated particularly when approaching the edge of the display. Therefore, we measured the perceived speed of illusory rotation during the first and second 0.5 s periods and found that it was indeed higher in the second half than in the first period. These results indicated that the perceived speed of illusory rotation increased with retinal eccentricity of the two rings. We thus used an averaged estimated speed for the 1 s presentation in each trial.

In order to find the optimal conditions we explored the two parameters most likely to influence the illusory rotation: (i) viewing distance, and (ii) speed of approach of the observer toward the display. To quantitatively measure the strength of the illusory rotation, we used a speed-matching task (see methods). As expected, all subjects reported that the physical rotation of inner and outer rings was robust and compelling. However, the strength of the perceived illusory rotation in the Pinna-Brelstaff figure varied considerably among subjects. When viewing the Pinna-Brelstaff figure, some reported stronger illusory rotation while others reported that the illusion was rather weak. For example, for a distance of 140 cm, the perceived speed of illusory rotation for all 17 subjects ranged from 9.2 deg/s to 31.6 deg/s with a mean of 25.7 ± 1.49 (mean $\pm$ s.e.m.) deg/s and a median of 27.2 deg/s. To ensure consistency across all subjects, we therefore averaged the maximal perceived speeds across all 17 subjects to generate a value representing the maximal perceived speed of the population. We then normalized the matching speed of each subject to this population value as an index of the perceived illusory strength of the rotation for that individual subject. This gives us a sense of how much an individual's report deviates away from the population. Figure 2A,B plots this index for 17 observer as a function of the simulated speed of approach under different simulated viewing distances. We found that for all eight viewing distances from 20 to 160 cm, illusory strength for all subjects increased linearly with increasing simulated speed of approach. This was reflected in the correlation coefficients of all eight plots ($r^2 > 0.98$ for all curves). In contrast, we found that the perceived illusory strength was not significantly different among different visual distances except for 20 cm ($P < 0.05$, one-way ANOVA), which might be due to the limited number of data points. When we plotted the simulated angular speed of approach as a function of perceived speed across viewing distances, we found that the angular velocity of the Pinna-Brelstaff figure on the retina was largely the same (Fig. 2C). This result further suggests that angular velocity on the retina was the key factor in eliciting vivid illusory rotation regardless of viewing distance. Together, the results from our psychophysical tests imply that, given the large visual distance in the scanner, a relatively high simulated speed of approach is needed to generate an optimal angular velocity for eliciting vivid illusory rotation.

Figure 2.

Population results of psychophysical tests. **A**, Perceived illusory strength is plotted as a function of the simulated speed of approach for all subjects. Individual curves refer to the simulated viewing distance. Error bars represent s.e.m. throughout. **B**, Perceived illusory strength is plotted as a function of simulated viewing distance for all subjects. **C**, Perceived speed of illusory rotation at various simulated distances plotted as a function of simulated angular speed of approach. Data were derived from all 17 subjects.

Activations in V1-V4 And hMT+ by the Pinna-Brelstaff Figure and Physical Rotation

In order to identify the human brain areas that mediate the Pinna rotary illusion, we first mapped V1, V2, V3, V3A, and V4 (see methods), using established retinotopic mapping procedures [Engel et al., 1994; Sereno et al., 1995; Wandell et al., 2007], before mapping hMT+ with random dot patterns [Amano et al., 2009; Huk et al., 2002; Kolster et al., 2010]. To examine the origin of the Pinna rotary illusion, we used the expansion-only condition as a control because both of the Pinna illusory and physical rotation conditions contained a component of physical expansion (Fig. 1C).

Stimuli of expansion-only, physical and illusory rotation conditions all yielded robust BOLD signals in the visual areas of V1, V2, V3, V3A, V4, and hMT+, when individual subjects were examined as independent samples. As the first step we compared % changes of BOLD signals of all voxels in a given ROI of V1-V4 and hMT+ for each stimulus condition averaged across individual subjects without presetting any response threshold. In this case, we found with a surprise that there was no statistical difference either among areas ($P = 0.94$, $N = 17$, two-way ANOVA), or among three stimulus conditions ($P = 0.75$, $N = 17$, two-way ANOVA) (Fig. 3A). These similar response amplitudes were mainly caused by the fact that these stimulus conditions were closely matched, and both of illusory and physical rotation conditions contained the physical expansion of concentric rings that was responsible for the strong retinotopic activations of V1-V4 and hMT+. Thus, the analysis by simply summing the BOLD signal across all voxels could not readily isolate rotation-specific signals, because the relatively smaller number of rotation-specific voxels were mixed with the rest voxels associated with retinotopic and other non-rotational activations.

To nevertheless isolate the response specific to the rotation component, we subtracted the common expansion component and set an activation threshold at a statistical significance level of $P < 0.05$, and also required a cluster level of voxels at $\geq 10 \text{ mm}^2$ (see method). In this case for the contrast map of physical rotation subtracting physical expansion, robust activation was seen mostly in hMT+ with only little activation in V1, V2, V3, V3A, and V4 in all 17 subjects. The results are reflected in the plot of accumulated activated areas shown in Figure 3B (left panel). To account for the difference in the size of the gyri and sulci in different visual areas and subjects, (e.g., the total area size in V1 was much larger than in hMT+), we computed an accumulated size ratio by normalizing the activated sub-region to its total area and again found that robust activation occurred mostly in hMT+ (Fig. 3C). To quantify the difference in the activation between hMT+ and other visual areas (V1-V4), we applied a one-way ANOVA analysis, and if there was a significant difference ($P < 0.05$), a Tukey HSD test was further performed to determine which specific area was significantly different

from the others. We found that in the physical rotation condition, the one-way ANOVA test produced a highly significant P -value of $1.2764\text{e-}016$, and the consequent Tukey HSD test also showed that it was the activated areas (computing from activated voxels) in hMT+ that were significantly larger than in other areas, i.e., V1-V4 ($P \ll 0.001$).

In the illusory rotation condition, we observed that the Pinna-Brelstaff figure also predominantly and consistently activated hMT+ in most subjects, but more sporadic and variable responses observed among subjects in visual areas V1-V4 (Fig. 3B, right panel). Indeed, the variance of the activated area size in hMT+ across subjects was not significantly different between the physical rotation and the Pinna-Brelstaff figure condition ($P = 0.73$, F-test), but turned out to be significantly different between the two conditions in the other areas (V1: $P = 0.0029$; V2: $P = 4\text{E-}6$; V3A: $P = 9\text{E-}9$; V3: $P = 2\text{E-}6$; V4: $P = 4\text{E-}13$, F-test). Nevertheless, a one-way ANOVA analysis indicated a significant difference in the activated area size among ROIs ($P = 3.9140\text{e-}004$), and the Tukey HSD test showed that the responses in hMT+ were significantly larger than for the majority of the other areas ($P = 0.001$, hMT+ versus V1; $P = 0.043$, hMT+ versus V2; $P = 0.001$, hMT+ versus V3A; $P = 0.001$, hMT+ versus V4), but were only marginally larger than for area V3 ($P = 0.053$, hMT+ versus V3). Hence, after condition-wise subtraction, both physical and illusory rotation stimuli mainly activated hMT+ with high significances when compared to the other visual areas (V1-V4), although this difference between areas was slightly weaker in the illusory rotation condition.

Moreover, within area hMT+, we observed that only small areas or patches were activated specifically by rotary motion. Indeed, the mean proportion of the rotation-activated areas to the whole hMT+ across 17 subjects was only $8 \pm 2\%$ and $11 \pm 2\%$ (mean $\pm$ s.e.m.), respectively, for illusory and rotation conditions. The average response magnitudes in both the illusory (0.83 ± 0.06 , mean $\pm$ s.e.m.) and physical rotation conditions (0.83 ± 0.05 , mean $\pm$ s.e.m.) appeared to be larger than in the expansion-only condition (0.78 ± 0.05 , mean $\pm$ s.e.m.) in hMT+, but no statistical difference ($P > 0.05$, $N = 17$, one-way ANOVA). This was because that the responsive voxels associated with rotation-sensitive neurons in small patches of hMT+ were diluted when the whole hMT+ was treated as the region of interest (ROI). Only after applying a subtraction procedure to remove the majority of voxels that were irrelevant to the rotation component and after applying a statistical criterion ($P < 0.05$) plus clustering requirement to exclude noise, the small proportion of activated voxels in hMT+ revealed themselves statistically higher for both illusory and physical rotations when compared to the expansion-only condition at different contrast maps. These results were presented in Figure 3D as average percentage changes of BOLD signals comparing to baseline at contrasts of both illusory and physical rotation versus

Figure 3.

fMRI results across all subjects. **A**, the response strength comparison ((% changes of BOLD signals in a given ROI). All voxels averaged in V1–V4 and hMT+ in response to expansion only, illusory and physical rotations without subtraction and presetting a response threshold. **B**, Accumulated analysis for the comparison of area sizes in V1–V4 and hMT+ activated by the physical and illusory rotation stimulus after subtraction of the expansion-only stimulus, respectively. Data was pooled from both hemispheres in each subject. *N*: the number of subjects. Different colors stand for different brain areas. Note that there were two

subjects, in which the activation of hMT+ by the physical rotation did not pass the threshold of the significant response level and which therefore were assigned a value of 0. Shaded area denotes s.e.m. **C**, Similar plot and denotations as in **B**, but the activated brain size was normalized to each brain area's own size, i.e., the size ratio, respectively. **D**, The % change of BOLD signals in three conditions (IR, PR, and EO). The % change of BOLD signals was computed from activated locations in hMT+ at contrasts of either IR or PR versus EO.

Figure 4.

Localization and comparison of hMT+, MST, MT. **A**, hMT+, MST, and MT in the left hemisphere averaged across subjects. The pseudo-color map overlay on each image indicates the activation masks. The color scale stands for the percentage of participants in the functional localization of hMT+, MST, and MT with consistent activation. Standard MT+ (MTp_fs) defined by Freesurfer is outlined in black, largely consistent with that localized by our hMT+ localizer paradigm. ITS: Inferior temporal sulcus. **B**, Comparison of surface area (mm²) of hMT+, MT and MST in both hemispheres for all 17 subjects on the standard brain atlas. *P* values were derived from the paired *t*-test. LH and RH stand for left and right hemispheres.

expansion-only conditions. The fact that hMT+ dominated the response to physical rotation and to the Pinna-Brelstaff figure was consistent with a previous study showing that the 'spinning wheel' illusion produced strong activations in hMT+, but not in areas of the ventral visual stream [Sterzer et al., 2002]. We therefore focused on subareas of hMT+ in the following analyses, by asking which subarea was mainly activated by the illusory rotation figure.

Activation of Subarea MST In hMT+ by the Pinna-Brelstaff Figure

The hMT+ contains at least two subareas involved in distinct functions according to previous studies: the medial

superior temporal area (MST) and the middle temporal area (MT) [Amano et al., 2009; Dukelow et al., 2001; Huk et al., 2002; Kolster et al., 2010]. To differentiate which part of hMT+ was responsible for mediating the illusory rotation, we identified its subareas MST and MT in all subjects by employing established methods [Amano et al., 2009; Becker et al., 2008; Huk et al., 2002; Kolster et al., 2010]. Population results of functional localization on the left hemisphere of the standard brain are shown in Figure 4A. The size of the responsive areas did not differ statistically between the left and right hemispheres for hMT+, MT, and MST (Paired *t*-test, *P* > 0.6, *N* = 17; Fig. 4B). Therefore, data from both hemispheres of individual subjects were pooled in the following analyses.

Figures 5 and 6 present our primary observations from two individual subjects. The top panels (Figures 5A–C and 6A–C) illustrate robust responses in the early and

Figure 5.

fMRI results from left hemisphere of one subject. **A–C**, Activation maps for three stimulus conditions (given on top) in the left hemisphere of one subject. Physical rotation stands for physical rotation. **D–F**, The corresponding difference maps after subtraction of the two stimulus conditions specified underneath. Both the physical and Pinna illusory rotations contained expansion components. Color bar indicates $-\log_{10}(P)$ value of paired *t*-test (*P* < 0.05). Areas MST and MT are outlined in white and black, respectively. The blow-up images are for better visualization.

Figure 6.

fMRI results from right hemisphere of another subject. Annotations of **A-F** are the same as in **Figure 5**.

intermediate visual areas (V1-V4, MT, and MST) activated by all three stimulus conditions, i.e., illusory rotation, physical rotation and expansion-only. However, the corresponding differential maps revealed rotation-component specific activations for both physical and illusory rotary motion predominantly lay in MST, but not in the other areas (Figures 5D-F and 6D-F). Note that the subject shown in Figure 5 also exhibited some extra activation far outside MST by physical or illusory rotation. The exact coordinates of the extra activated areas pointed to the intraparietal sulcus (IPS) within Brodmann 7, where it approached the base of the superior parietal lobule. As a downstream cortical region beyond MST, it was expected that the IPS region was activated under both physical- and illusory-rotation conditions, particularly considering the finding that IPS regions respond differentially to rotation and expansion [Konen and Kastner, 2008]. This activation was also observed in a few other subjects, but since these areas were located at a level beyond MST/MT and thus were outside the current research scope, we left them for future studies. We therefore focused on MST/MT in the following analysis.

We next compared the size of the activated regions in the sub-regions MT and MST without taking overlapping regions between these two sub-regions into consideration.

The activated area was significantly larger for both illusory and physical rotations in MST than in MT for all 17 subjects ($P = 0.004$, Wilcoxon rank sum test, $N = 17$) (Fig. 7A). We additionally calculated an area index to quantify this difference [Eq. (1) in the Method Section]. An index of 1 indicates that activation was confined entirely to area MST, while an index of -1 indicates that activation was completely within MT. The distribution of this index for all 17 subjects clearly showed that the activation occurred mostly in MST for both illusory and physical rotation. The average indices were significantly greater than 0 (one-sample Wilcoxon signed rank test, $P \ll 0.001$, $N = 17$) (Fig. 7B).

MST and MT are known to partially overlap when examined by fMRI [Huk et al., 2002] and subareas MST and MT were indeed not fully separable in most of our subjects. It is possible that some rotation component activations (both illusory and physical) may have been located in these overlapping regions, and thus excluding these regions could underestimate the activations that should have belonged to MT. To address this issue, we conducted a further analysis: First, we quantified the extent of overlap of MST and MT in each subject. We defined an overlap index where a value of 1 means complete overlap of the two subareas, and a value of 0 means complete separation. The mean value of the overlap index across all hemispheres was 0.18 ± 0.09 for illusory rotation and 0.28 ± 0.07 for physical rotation (mean $\pm$ s.e.m), indicating that the amount of overlap was small in all subjects. Second, we attributed the overlapping regions to area MT in accordance with a previous study [Huk et al., 2002] and found that MST was still the primary area activated during the illusory rotation condition (Fig. 7C; $P = 0.018$; Fig. 7D, $P = 0.017$, Wilcoxon rank sum test, $N = 17$). Finally, we determined that there was no significant correlation between the area index and the overlap index ($r = -0.1339$, $P = 0.66$, Spearman rank correlation), suggesting that the predominance of activation in area MST did not correlate with the extent of overlap between MST and MT. Therefore, we conclude that the cortical representation of the Pinna illusion resides mainly in subarea MST, just as it does for physical rotation.

Average Response Strength and Size Comparison in MST For Illusory and Physical Rotation

So far our results suggest that the perception of both physical and illusory rotation originates as early as in area MST. Now we ask whether the two types of rotation produced the same strength of BOLD signals within MST. The answer to this question is not immediately known. However, in other illusion studies of single-cell recordings in macaque V2 and V4, it has been reported that some cortical neurons respond even more strongly to illusory contour stimuli than to physical control stimuli [Cox et al.,

Figure 7.

Statistical summary of the activated area size for physical and illusory rotation in MST and MT. **A**, Scatter plot of area sizes of activations in MST (ordinate) and MT (abscissa) for both physical rotation $N = 17$ subjects. **B**, Distribution of area index. Color denotations of columns as in **A**. Gray and black arrows indicate

the mean (solid) and median (open) values for illusory and physical rotation, respectively. **C**, Scatter plot of area values of visual activation in MST and MT. **D**, Distribution of the area index. N : the number of subjects. In **C** and **D**, the overlapping area was attributed to MT.

2013; Pan et al., 2012; von der Heydt and Peterhans, 1989; von der Heydt et al., 1984]. We therefore compared response intensities elicited by the illusory and physical rotation stimuli in terms of the percentage of changes in BOLD signals. We found that the overall response intensities elicited by the illusory and physical rotation stimuli were not significantly different in subarea MST (0.81 ± 0.06 (mean $\pm$ s.e.m) for illusory rotation and 0.85 ± 0.07 for physical rotation, $P = 0.49$, $N = 17$, Wilcoxon rank sum test, Fig. 8A,B). When compared with expansion-only condition (0.79 ± 0.05), the response magnitudes under neither physical nor illusory rotation conditions were found significantly different ($P > 0.5$, $N = 17$, one-way ANOVA). These

results suggest that changes in activation magnitudes were not able to reflect the recruitment of rotation-sensitive neurons in MST during the stimulation. In fact, previous neurophysiological experiments have shown that there was only a small subgroup (5%) of MST neurons encoding pure rotary motion, while more neurons responded to spiral motion (containing rotation and expansion at the same time) [Duffy and Wurtz, 1991; Graziano et al., 1994; Saito et al., 1986; Tanaka et al., 1989; Tanaka et al., 1993]. Thus if BOLD contrasts reflect pooled signals from neural population activities [Logothetis and Wandell, 2004], the changes in the response amplitude might not be sensitive enough to represent the recruitment of the small subgroup of MST

Figure 8.

Statistical summary of the response size and intensity for physical and illusory rotation in MST. **A**, Scatter plot for the comparison of response amplitudes for both physical and illusory rotation in subarea MST. **B**, Percentage changes of BOLD signals for illusory and physical rotation stimuli in subarea MST. The gray lines indicate the median values while the small black boxes

represent the mean values. IR: illusory rotation; PR: physical rotation. **C**, Scatter plot for the comparison of activated brain sizes for the physical and illusory rotations in subarea MST. **D**, Boxplots of the activated brain sizes by both physical and illusory rotation with and without overlapping areas. The annotation is the same as in **B**. *N*, the number of subjects.

rotation-sensitive neurons. Also note that we only chose a fixed matching speed for physical rotation control stimulus. This speed might not be able to elicit maximal responses for all rotation-sensitive neurons in MST.

We also examined whether physical and illusory rotation stimuli activated similar or different area sizes in MST (Fig. 8C). The average size activated by the illusory figure was 34.01 ± 7.74 mm² (mean $\pm$ s.e.m), when the overlapping area was excluded, and 40.57 ± 8.15 mm², when it was included. In comparison, the brain area activated by the physical rotation stimulus was 46.53 ± 9.85 and 67.59 ± 12.9 mm², respectively. It turned out that the differences between the activated sizes, when comparing the

results for illusory and physical rotation, were not significantly different across 17 subjects ($P = 0.33$ and 0.09 , paired *t*-tests, for overlap areas excluded and included, respectively; $N = 17$, Fig. 8D).

Taken together, both the BOLD signal strength and the responsive area size elicited by the Pinna-Brelstaff figure and the matched physical rotation control were comparable after direct subtraction of the expansion-only condition. These results suggest that as in the case of the activation by physical rotation, the rotation-sensitive neurons in human MST likely mediate the illusory rotary perception in the presence of the Pinna-Brelstaff figure.

DISCUSSION

In the present study, we combined human psychophysics with fMRI methods to examine the representation of the Pinna rotary illusion in early and intermediate visual areas. Specifically, we found that in the dorsal visual stream subarea MST of hMT+ was predominantly activated by the Pinna-Brelstaff figure as compared to subarea MT. By contrast, the activation in other visual stages and the ventral stream, including V1-V4 in response to the Pinna-Brelstaff figure was neither consistent nor reproducible across subjects. Our findings demonstrate that illusory rotation is predominantly represented as early as in human MST in a way similar to real physical rotation with a matching rotary speed, implying that the Pinna rotary illusion is mediated by rotation-sensitive neurons in MST that normally encode physical rotation. Our work constitutes an important step to resolve the ‘where’ question, i.e., which part of the visual brain mediates the Pinna rotary illusion. This is a prerequisite for tackling the ‘how’ question, i.e., how cortical neurons in primate area MST integrate local visual cues to form a global percept.

Different Visual Areas May Represent Different Visual Illusions

Several human brain-imaging studies found that responses in human V1 could predict the effects of size illusions [Fang et al., 2008; Murray et al., 2006; Schwarzkopf et al., 2011; Sperandio et al., 2012], while responses from extrastriate visual cortices and beyond yielded equivalent representations for illusory and physical contours [Mendola et al., 1999; Montaser-Kouhsari et al., 2007; Stanley and Rubin, 2003]. These fMRI studies agree with electrophysiological single-unit recordings as subgroups of neurons in macaque V1, V2 and V4 have been shown to encode illusory contours in a way similar to physical contour stimuli [Lee and Nguyen, 2001; Pan et al., 2012; Peterhans and von der Heydt, 1989; von der Heydt and Peterhans, 1989]. Our current findings are based on the standard condition-wise subtraction method commonly used in block-design fMRI experiments. By using this strategy, a recent fMRI study demonstrated that in hMT+ the flash-drag effect produced similar activation patterns as a physical position shift [Maus et al., 2013]. Other human imaging studies have examined the phenomena of apparent motion, such as in the “Enigma” illusion [Zeki et al., 1993] and the “Rotating Snakes” illusion [Ashida et al., 2012; Kuriki et al., 2008]. All these studies found significant activation in hMT+, which is regarded as a specialized motion-processing area [DeYoe et al., 1996; Dumoulin et al., 2000; Tootell et al., 1995b; Watson et al., 1993]. Interestingly, hMT+ was activated even when subjects only imagined seeing motion [Kourtzi and Kanwisher, 2000; Senior et al., 2002]. These findings imply that hMT+ is responsible for motion perception, regardless of

whether the motion arises from a physical or illusory and mental origin.

Subareas MST and MT In hMT+

An important foundation on which our findings are based is the differentiation of subareas MST and MT, although subdivisions at high levels often spatially overlap with broad intrinsic functional connectivity and share similar activity patterns and functionality [Hutchison and Everling, 2013]. Using a 7T scanner, MSTd and MSTv have been successfully mapped in the macaque brain [Kolster et al., 2009]. However, MSTd and MSTv are not clearly separable in human subjects when using a 3T scanner [Kolster et al., 2010]. In our fMRI experiments, we therefore used the same differentiation method as that used in previous studies by other authors [Amano et al., 2009; Huk et al., 2002; Kolster et al., 2010; Smith et al., 2006]. We found our results to be consistent with these studies. Nevertheless, the differentiation was based on dual criteria: within hMT+, a strong retinotopic response was used to identify MT, whereas a strong response to stimulation in the ipsilateral visual field was used to localize MST. These criteria did not fully suffice in every subject to identify the residual region lacking retinotopic responses. Even so, when we added the overlapping region between the two sub-regions to area MT in accordance with a previous study [Huk et al., 2002], we obtained similar results with the same conclusions (Fig. 7C,D). The overlap observed between MST and MT originates from the fact that MST contains an area within which the response properties resemble those of MT [Graziano et al., 1994]. By using the same functional localizers, but population receptive field analysis, two subareas TO-1 and TO-2 can be isolated within hMT+ [Amano et al., 2009]. Subarea TO-2 is more sensitive to peripheral ipsilateral stimuli, suggesting a correspondence between TO-2 and MSTl [Graziano et al., 1994]. Moreover, another fMRI study using pursuit also reported the existence of MSTl in human observers [Dukelow et al., 2001]. We therefore conclude that both the Pinna-Brelstaff figure and the physical rotation predominantly activated MST rather than MT, in both hemispheres.

Processing Rotary Motion in Area MST

As no rotation- and expansion-sensitive neurons have so far been found in macaque V1-V4, it is reasonable to assume that the sporadic activation in human V1-V4 encoded neither physical nor illusory rotation motion. Instead the variation in the response strength of V1-V4 suggests that the retinotopic activations evoked by the local pattern of concentric rings may reflect the differences in the size of the receptive field and the spatial-frequency selectivity of each individual area. However, this may not be the case for area V3 as over 40% of macaque V3

neurons have been reported to be strongly direction selective [Gegenfurtner et al., 1997]. We thus speculated that the corresponding neurons in human V3 might give rise to stronger BOLD signals compared to V1-V4.

Again, by recording single-unit activity in MSTd and MSTl in macaque, few neurons have been found to be rotary-motion selective in MSTl [Tanaka et al., 1986; Tanaka et al., 1993], while a much larger proportion of neurons were responsive to rotation in MSTd [Duffy and Wurtz, 1991; Graziano et al., 1994; Saito et al., 1986; Tanaka et al., 1989; Tanaka et al., 1993]. Hence, the MST area mapped under both physical and illusory rotation in our study is most likely to be primarily MSTd. Neurophysiological studies have also demonstrated that macaque MST but not MT contains neurons selective for rotation motion that is typically experienced during natural navigation [Duffy and Wurtz, 1995; Graziano et al., 1994; Heuer and Britten, 2004; Orban et al., 1992; Tanaka et al., 1989; Tanaka and Saito, 1989; Yu et al., 2010]. More recently, simultaneous neurophysiological and psychophysical experiments on awake, behaving monkeys showed that these signals in area MST were involved in the animals' behavior, when heading information was extracted from the optical flow patterns (containing expansion component) [Andersen et al., 2000; Angelaki et al., 2009; Britten, 2008; Gu et al., 2008; Gu et al., 2012; Xu et al., 2014]. Results from physiological recordings in macaque MST are compatible with the observation that human MST responds selectively to optic flow such as expansion and rotation [Wall et al., 2008]. A computational model has proposed that the Pinna illusory rotation is mediated by human MST through recurrent interactions between areas V1, MT, and MSTd and a non-linear integration of space-variant flow patterns [Bayerl and Neumann, 2002]. It is worth noting that the Pinna illusory rotation is different from the rotating-snakes illusion, which contains no physical expansion and rotation and relies on microsaccades and blinks [Otero-Millan et al., 2012], in addition to the processing by direction-selective neurons in both V1 and MT [Conway et al., 2005]. Finally, another possibility to consider is that MST may also encode a variety of rotational velocities [Tanaka & Saito 1989], which is congruent with our psychophysics results. However, we chose a fixed 20 deg/s for our physical rotation as this was the matching speed for subjects under the visual distance in the fMRI scanner. This might explain why the changes of response magnitudes in the sub-region MST failed to reveal a difference under the illusory and the matched physical rotations. We speculate that a physical rotation with a faster speed may generate a larger response than the illusory rotation in the Pinna-Brelstaff figure does.

Rotary Motion Perception in Areas Beyond MST

Although evidence from previous neurophysiological experiments on macaques have indicated that area MST

(but not MT) is the first area along the dorsal visual pathway that its neurons begin to process complex optic flow patterns such as expansion and rotation information [Duffy and Wurtz, 1991; Graziano et al., 1994; Tanaka et al., 1986], there are also other brain areas downstream to MST to further process these signals. So far rotation neurons have been reported in a number of areas including the posterior parietal cortex (7a) [Siegel and Read, 1997], the VIP area in the intraparietal cortex (IPS) [Schaafsma et al., 1997] and the polysensory area in the superior temporal area (STS) [Anderson and Siegel, 1999]. In our current study as shown by Figure 5, we also noticed some extra activation in the parietal cortex across subjects. This activation beyond MST might be more associated with different attentional loads or perceived strengths of illusory rotary motion. Particularly, in our psychophysical experiments, we found that the perception of rotary motion was not homogeneous across subjects, i.e., some subjects perceived strong illusory rotation when viewing the Pinna-Brelstaff figure whereas others experienced only weak illusory rotation from the same figure. This may not be too surprising though, since the neural activity on a trial by trial basis in higher areas such as the posterior parietal cortex has been found to be more tightly coupled with perception than in area MST [Chen et al., 2013]. However, in our current block-designed fMRI experiments, we cannot specifically correlate the perceptual and attentional levels of individual subjects with the BOLD signals on a trial-by-trial basis.

CONCLUSION

The mismatch between perception and the physical world is typically regarded as evidence for a visual illusion, and illusions can help us to elucidate the neural mechanisms that underlie the creative nature of the human visual system. The stimulus size of either the concentric rings or the arrangement and orientation of the local inducers in the rings has been previously investigated psychophysically with regard to the perception of illusory rotation [Gurnsey and Page, 2006; Pinna and Brelstaff, 2000]. Due to the huge variation of receptive field sizes from V1 to MST, it is expected that different processing stages may have different visual activities, when local or global visual cues enter or match the receptive fields at each processing stage. Because the receptive fields of V1 and V2 neurons range from 0.1 to 2 degrees [Levitt et al., 1994], they respond maximally to local visual cues. In contrast, receptive fields of MT and MST neurons are much larger, in particular some MST neuron RFs range up to the full visual field [Desimone and Ungerleider, 1986; Duffy and Wurtz, 1995; Saito et al., 1986; Tanaka et al., 1986], thus MST is capable of encoding the global visual cues contained within the Pinna-Brelstaff figure. In summary, given that macaque MT neurons receive their inputs from direction selective V1 neurons [Movshon and Newsome,

1996] and project to MST, the processing of illusory rotation most likely arises along the hierarchy from V1 and MT to MST as previously proposed by a computational model [Bayerl and Neumann, 2002]. This is in line with a recent study of local versus global motion in MT showing that global motion perception depends on mechanisms qualitatively different from those in MT and thus motion perception reflects the action and interaction of multiple brain systems [Hedges et al., 2011]. Our findings support the notion that neurons in MST that normally encode real physical rotation may also mediate the illusory rotation of the concentric rings in the Pinna-Brelstaff figure. The exact neural/circuit mechanism underlying the perceived illusory rotation awaits further study.

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