

# Functional brain imaging of the Rotating Snakes illusion by fMRI

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The neural basis of illusory motion perception evoked from static images has not been established well. We examined changes in neural activity in motion sensitive areas of the human visual cortex by using functional magnetic resonance imaging (fMRI) technique when a static illusory-motion image ('Rotating Snakes') was presented to participants. The blood-oxygenation-level dependent (BOLD) signal changes were compared between the test stimulus that induced illusory motion perception and the control stimulus that did not. Comparison was also made between those stimuli with and without eye movements. Signal changes for the test stimulus were significantly larger than those for the control stimulus, if accompanied by eye movements. On the other hand, the difference in signal changes between test and control stimuli was smaller, if steady fixation was required. These results support the empirical finding that this illusion is related to some component of eye movements.

**Keywords:** Rotating Snakes illusion, motion, human fMRI, hMT+, primary visual cortex, eye movements, attention

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## Introduction

There are a variety of static images that evoke illusory motion perception to the observer (for review, see Kitaoka & Ashida, 2007), like Fraser–Wilcox illusion (Faubert & Herbert, 1999; Fraser & Wilcox, 1979; Naor-Raz & Sekuler, 2000). The 'Rotating Snakes' figure is one of such motion-illusion pictures designed by Kitaoka (2003). The Rotating Snakes figure used in this study consists of periodical arrangement of colored blobs along the circumference of concentric circles (see Figure 1a). Many observers perceive rotational motion for each concentric circle in the constant direction (i.e., black–blue–white–yellow–black: motion is seen in this direction). This illusion may be considered as an optimized version of the Fraser–Wilcox illusion (Backus & Oruç, 2005; Kitaoka, 2007; Kitaoka & Ashida, 2003).

Each element of luminance and/or color arrangement of this Rotating Snakes figure is estimated to evoke a small element of motion signal probably caused by either some nonlinearity and biases in the temporal response functions (Murakami, Kitaoka, & Ashida, 2006) or the difference in

the latency of brain activity for each luminance or color element (Backus & Oruç, 2005; Conway, Kitaoka, Yazdanbakhsh, Pack, & Livingstone, 2005).

The rotational motion perception yielded by the Rotating Snakes figure is continuous and persists during observation. It can be also intensified when the observer makes eye movements (Murakami et al., 2006) or by flashing the pattern (Conway et al., 2005), which implies that the part of the visual system that conveys transient visual signals plays a significant role in this illusory motion phenomenon.

The rotational motion perception is assumed to be generated by integrating local motion-signal elements at a later stage. In macaques, area MST (medial superior temporal) is considered as the site for such integration for rotation and other optic flow patterns (Saito et al., 1986; Tanaka, Fukuda, & Saito, 1989; Tanaka & Saito, 1989). In humans, a motion-sensitive area has been identified in a lateral part of the occipital cortex that is considered a human homolog of macaque MT (middle temporal area) and MST (Zeki et al., 1991) and is now often called a human MT complex (hMT+).

From the viewpoint of non-invasive functional brain-activity imaging in humans, it is not straightforward to

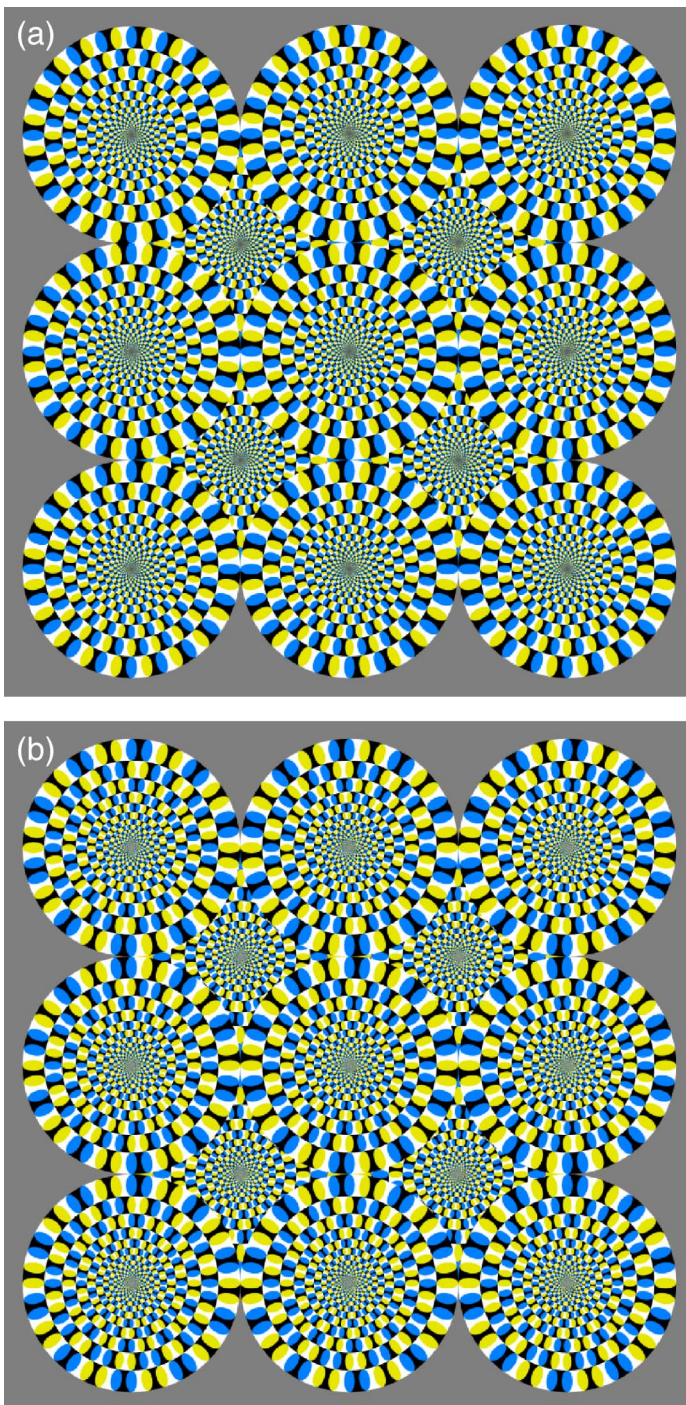


Figure 1. Stimulus figures. (a) Rotating Snakes illusion image (Kitaoka, 2003) used in the fMRI experiment as the ‘snakes’ stimulus. (b) An image generated for fMRI experiment as a ‘control’ stimulus. A unit of color elements (black–blue–white–yellow) is the same as the ‘snakes’ stimulus (panel (a)), but the arrangement was reversed between every flanking unit, so that no motion is perceived as a whole.

detect changes in brain activities resulting from such illusory motions, because motion signals, if any, should be much weaker than in the case of real motion stimuli. The

lower level of visual cortex tends to respond more or less directly to visual stimuli and any illusion-related signal could be much weaker than the overall responses to the pattern regardless of illusion. However, if the assumption is true that integration of motion signals at a higher level of visual cortex constitutes an overall motion perception, the illusion stimulus may allow us to observe changes in blood-oxygenation-level dependent (BOLD) signals in hMT+, even if changes in earlier areas like V1 are not strong enough.

There has not been a paper on human imaging studies on the illusory motion from the Rotating Snakes figure, but there are studies on at least three other kinds of illusory motions. A study by Zeki, Watson, and Frackowiak (1993), using the positron emission tomography (PET), found activation in V5 (hMT) when the participant was observing an op-art image called Enigma. Second, there are fMRI studies on implied motion (Kourtzi & Kanwisher, 2000; Krekelberg, Vatakis, & Kourtzi, 2005). They found a significant difference in the BOLD signal in hMT+ between the observations of static images with and without figures that imply visual motion. The most important difference between these implied motion stimuli and the Rotating Snakes figure is that the latter evokes a unidirectional motion perception, which is as vivid as actual motion and also measurable psychophysically, e.g., by cancellation techniques (Hisakata & Murakami, 2008; Murakami et al., 2006). Third, there are several fMRI studies discussing the correlations between hMT+ activities and the aftereffect of adaptation to visual motion (He, Cohen, & Hu, 1998; Huk, Ress, & Heeger, 2001; Tootell et al., 1995). The adaptation to the first-order motion evokes illusory motion percept to static test stimulus (Mather, Ferstraten, & Anstis, 1998). The motion is consistent enough to be canceled by the physical motion in the opposite direction of motion perception, and this characteristic is quite alike to the motion percept from ‘Rotating Snakes’ figure. Therefore, it is quite likely that the neural mechanisms for physical motion are deeply involved in the ‘Rotating Snakes’ illusion and thus it is possible to elucidate the relevance of hMT+ activities as a neural basis of the illusory motion perception from a static image.

The primary purpose of this study is to test whether some part of the human visual cortex, which selectively responds to motion stimuli, is activated during the observation of the Rotating Snakes illusion.

## Methods

### Stimuli and procedure

#### ‘Snakes’ and ‘control’ stimuli

Figure 1 shows the images used for the experiment. Figure 1a is an illusory image called the ‘Rotating Snakes’

figure (hereafter we simply refer to it as ‘snakes’ stimulus in this paper), which evokes the perception of global rotational motion. [Figure 1b](#) is the ‘control’ stimulus, which does not evoke motion perception globally. The smallest unit of the component for those figures was an arrangement of ‘black–blue–white–yellow’ patches in this order. In the ‘snakes’ stimulus, this order of color patches was arranged in the same direction and yields rotational motion in each circle. In the ‘control’ stimulus, the order of color sequence was reversed between adjacent units, so that the local motion signal, which may be evoked from the sequence of four colors, will be nulled in a relatively small area of the visual field. In fact, most observers do not perceive any rotational motion in the ‘control’ stimulus. The outermost diameter for each circle subtended 4.77 deg in visual angle, and the whole size of the stimulus image subtended 15 deg  $\times$  15 deg.

### Attentional task

Since BOLD signal change is known to be strongly affected by the state of attention, especially in the extrastriate cortex (Huk et al., 2001), we had to control the participants’ state of attention for the evaluation of the net BOLD signal changes during the observation of the ‘snakes’ and ‘control’ stimuli.

Participants were instructed to fixate at the fixation point whenever it was displayed. Every 0.5 s, the fixation point color changed to one of these colors, red, yellow, green, cyan, blue, and purple, in a random order. The participant’s task was to report the total number of the emergences of the blue fixation point during one run. In each run, the blue point appeared 100 times, on average. The participant’s task therefore consisted of monitoring the fixation point, detecting each blue emergence, and maintaining/updating the number of occurrences in the participant’s working memory. This was a very attention-demanding task, especially when the fixation point made frequent jumps to guide eye movements, but all participants were able to perform this task at the precision of more than 98%, meaning, on average, 2 misses every 100 occurrences in each run lasting 6 minutes.

### Experimental conditions

In the guided-eye-movement (GEM) condition, the fixation point horizontally moved among the centers of the three concentric circles in the middle row. The sequence of jumps was given as follows: center, left, center, right, and center. The position change occurred every 3 s in synchrony to the beginning of each scan.

In the no-eye-movement (NEM) condition, the fixation point was always located at the center of the screen, and the participants were instructed to conduct the attentional task presented at the fixation point.

### Stimulus presentation

Participants viewed visual stimuli projected on a screen in the MRI bore through an oblique mirror mounted on the head coil. The stimulus image was generated by a personal computer and rear projected with a liquid-crystal-display projector (DLA-G150CL, Victor, Japan). The spatial resolution of the projector was 1024 pixels  $\times$  768 pixels and the refresh rate was 60 frames per second. The distance from the participant’s eye to the screen was 37 cm and the screen size was 13.1 cm  $\times$  10 cm (20 deg  $\times$  15 deg in visual angle). Participants who use glasses used plastic correction lenses in the scanner.

The visual stimuli were presented in a block sequence. The presentation of either ‘snakes’ or ‘control’ (task) stimulus for 15 s was paired with 15 s of uniform gray screen presentation (rest). This rest–task stimulus pair was repeated in the order of ‘snakes’, rest, ‘control’, rest, ‘control’, rest, ‘snakes’, rest (the so-called, ABBA order), and this sequence was repeated for 3 times in each run. Before starting the stimulus presentation, we presented the ‘rest’ screen for 12 s. The fMRI images taken during this period were discarded before statistical analyses. The total length of each run was approximately 6 minutes.

### ROI localizing experiments

#### MT localizer

Stimuli were a pair of motion and rest stimuli, which was presented in a block paradigm. Participants conducted the fixation task through the run. The participant’s task was the same as in the main experiment (blue-fixation-point-counting task) except that the rate of color change was once per second. The motion stimulus consisted of a combination of rotation, contraction, and expansion of randomly distributed dots (Morrone et al., 2000). The stimulus subtended 15 deg  $\times$  15 deg centered on the screen, and the stimulated area in the visual field was the same as that for the ‘snakes’ and ‘control’ stimuli. The motion and rest blocks were presented for 15 s per block and this pair was repeated for 12 times. We took the BOLD contrast between motion and rest blocks and defined the hMT+ region by identifying voxels that showed statistically significant BOLD signal changes at the significance level of  $q < 0.05$  in false detection ratio (FDR).

#### Center-periphery-mapping experiments

Since the illusory motion perception occurs mainly in the peripheral visual field, we took a part of the primary visual cortex (V1), which represents the peripheral visual field as another ROI. Participants conducted the fixation task as in the other experiments. A black-and-white flickering checkerboard pattern (10 Hz) appeared either at the center or periphery of the visual field. The diameter of the central disk for the center field was 4.5 deg and the outermost diameter of the peripheral stimulus was 15 deg.

Voxels were identified by the same threshold as in the hMT+ localizer experiment ( $q(\text{FDR}) < 0.05$ ).

## Data acquisition and analysis

### Functional MRI

All fMRI images were taken under identical parameters. We used 1.5 [T] Shimadzu-Marconi MRI scanner equipped at Brain Activity Imaging Center in Advanced Technology Research Institute (ATR-BAIC, Japan). Participants used a bite bar to restrict the head motion. We used a normal head coil to measure the BOLD signal from the participant's head.

An anatomical image of whole brain in each participant was taken with the T1-weighted protocol (RF-FAST sequence, TR = 12 ms, TE = 4.5 ms, flip angle = 20 deg) at the spatial resolution of  $1 \times 1 \times 1 \text{ mm}^3$ . ROI analyses were made after the alignment of each fMRI image to this anatomical image.

Functional images were taken by EPI technique with T2\*-weighted protocol (FE-EPI sequence, TR = 3000 ms, TE = 49 ms, flip angle = 90 deg). The in-plane resolution was  $3 \times 3 \text{ mm}^2$  (FoV =  $192 \times 192 \text{ mm}^2$  at  $64 \times 64 \text{ pixel}^2$ ), and 30 slices, each 3 mm thick, were taken parallel to the AC-PC line in axial slice so that ventral half of the cerebral cortex (including the whole occipital cortex) were to be covered.

We used the Brain Voyager QX software (Brain Innovation, Netherlands) for the processes and analysis of MRI images. As preprocess, we applied motion correction, temporal high-pass filtering (cutoff = 3 cycles/run), and spatial Gaussian filtering (FWHM = 6 mm). ROI analysis was applied after the coregistration process. We used individual participant's head coordinates instead of the normalized one, because it has been reported that hMT+ location differs significantly among participants (Watson et al., 1993). We first calculated the average of event-related response (ER average) within each participant's ROI and then averaged the ER average among participants. The ER averages were taken among voxels that showed non-negative BOLD response during the stimulus blocks ('snakes' and 'control') as compared with the baseline activity during rest blocks. Thus, the selection of voxels was based on whether they exhibited any responses to visual stimulation. The same procedure was applied to the V1 ROI.

In order to assess the differences between two experimental conditions precisely, such as 'snakes' vs. 'control', we also statistically evaluated the difference of two ER-averaged BOLD signal curves within each participant. This evaluation was conducted because the slight differences in BOLD signal levels between 'snakes' and 'control' stimuli, which were small but consistent within participants, would be reduced by the difference in baseline BOLD signal values among participants. Therefore, we first took the difference of BOLD signal values between 'snakes' and

'control' conditions within each participant, and then averaged the BOLD signal differences across stimulus presentation period (scans 1–5 with respect to the onset of test stimulus) within each participant. We finally applied a two-tailed *t*-test to the mean across participants to see whether the mean of these differences across participants was significantly different from zero (null hypothesis).

### Eye-movement data

Eye movements were measured for the left naked eye by the limbus-reflection-based MR-compatible eye tracker (MR-eye tracker, Cambridge Research Systems, U.K.) and digitized (AIO-160802AY-USB, Contec, Japan) at 500 Hz. We calibrated the eye tracker before starting each fMRI run. The data shown in this paper are typical data from a participant, derived by averaging horizontal eye-position traces across 12 test blocks.

### Participants and samples

Eleven participants including the four authors took part in the experiments (age ranged 20–45 years old). All of them gave informed consent in a written form. Each participant conducted the same condition twice.

For each stimulus condition, the BOLD signal changes were averaged across all runs and hemispheres within each participant. Therefore, there were eleven samples for hMT+ and V1 ROIs.

The imaging study was approved by the ethical committee of ATR-BAIC and conducted in accordance with the declaration of Helsinki.

## Results

### No-Eye-Movement (NEM) condition

In this condition, participants maintained fixation at the stationary central point. The top and bottom panels of [Figure 2](#) show the grand average response time course for hMT+ ROI and V1 ROI, respectively. In hMT+, there were slight differences in the BOLD responses between 'snakes' and 'control' conditions, but the time-collapsed average of differences was not significantly above zero ( $t(10) = 1.17$ ,  $p = 0.271$ ; [Figure 5](#)). V1 showed no significant difference ( $t(10) = 0.681$ ,  $p = 0.511$ ).

### Guided-Eye-Movement (GEM) condition

The top and bottom panels of [Figure 3](#) show the result for guided-eye-movement (in short, GEM) condition, for hMT+ ROI and V1 ROI, respectively. The meanings of axes and symbols are the same as in [Figure 2](#).

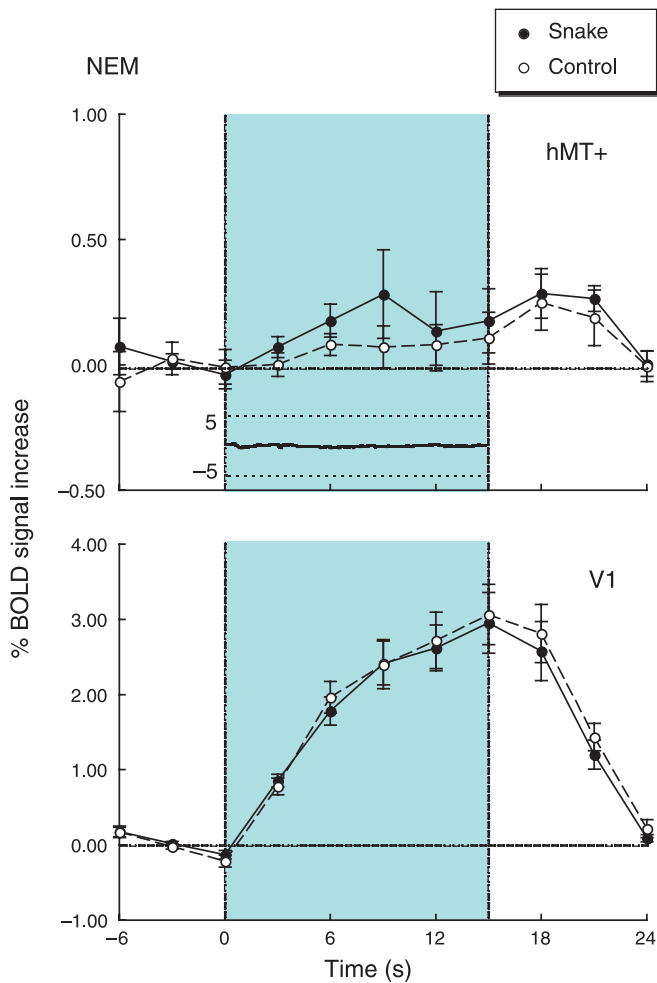


Figure 2. BOLD signal changes in hMT+ and V1 ROIs averaged across eleven participants under the no-eye-movement (NEM) condition. Error bars indicate the standard error of mean. Horizontal and vertical axes represent time with respect to the onset of task block and relative BOLD signal increase (%), respectively. Shaded interval represents the period during which the test stimulus (either ‘snakes’ or ‘control’) was presented. Filled and open symbols show the relative BOLD signal changes for ‘snakes’ and ‘control’ stimuli, respectively. Inset of the top panel shows the trace of eye movements during the period of stimulus presentation from one participant, aligned to the time course of BOLD signal changes. Vertical axis indicates horizontal eye position in visual angle (deg).

The grand average across participants showed consistent differences in the BOLD signal increase between ‘snakes’ and ‘control’ stimuli. The BOLD signal difference averaged across participants was significantly above zero ( $t(10) = 3.42$ ,  $p = 0.00659$ ; Figure 5). This result indicates that the neural activity of hMT+ differs between ‘snakes’ and ‘control’ stimuli when the participants were moving their eyes in a guided sequence, even under the condition with an attention-demanding task. V1 showed no such difference ( $t(10) = 0.591$ ,  $p = 0.567$ ).

## Supplemental condition

As we have observed, the condition with eye movements show consistent changes in BOLD signals between ‘snakes’ and ‘control’ stimuli. When we consider the natural viewing condition, we move our eyes spontaneously, and we do not conduct any attention task. We therefore conducted a supplemental experiment under a more natural viewing condition.

In this condition, the participants moved their eyes spontaneously without conducting the attention task. However, in order to equate the eye-movement-related activities across stimulus blocks, we asked the participants to move their eyes in the same way as the GEM condition. To be more specific, the participants were instructed to

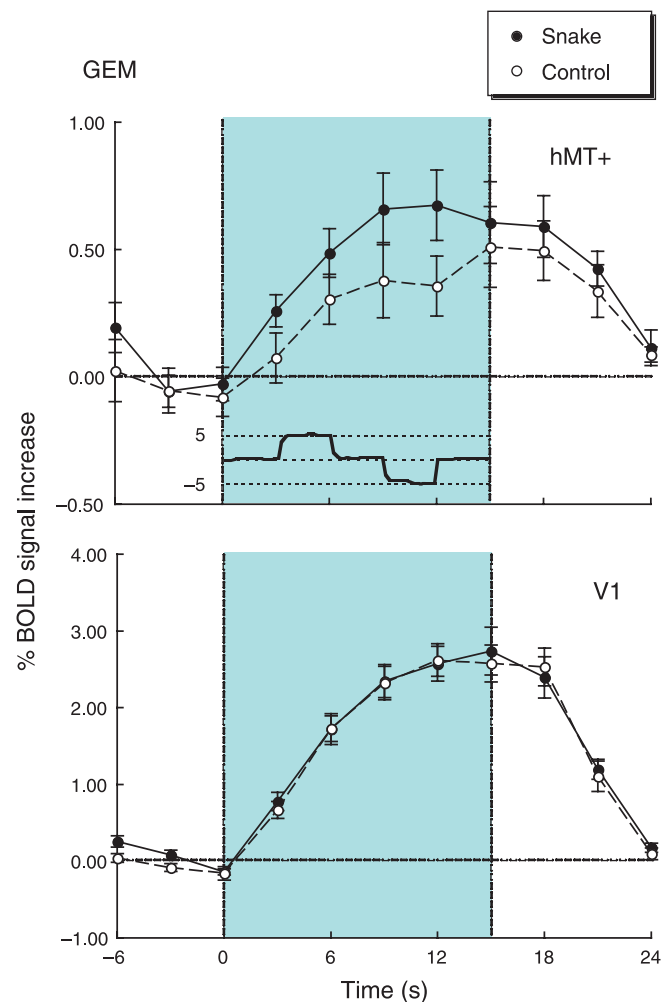


Figure 3. BOLD signal changes in hMT+ and V1 ROIs averaged across eleven participants under the guided eye-movement (GEM) condition. The meanings of axes, shades, and symbols are the same as those in Figure 2. The response from hMT+ changed dramatically by participant’s eye movements. Difference in responses between ‘snakes’ and ‘control’ conditions is statistically significant. See text for details.

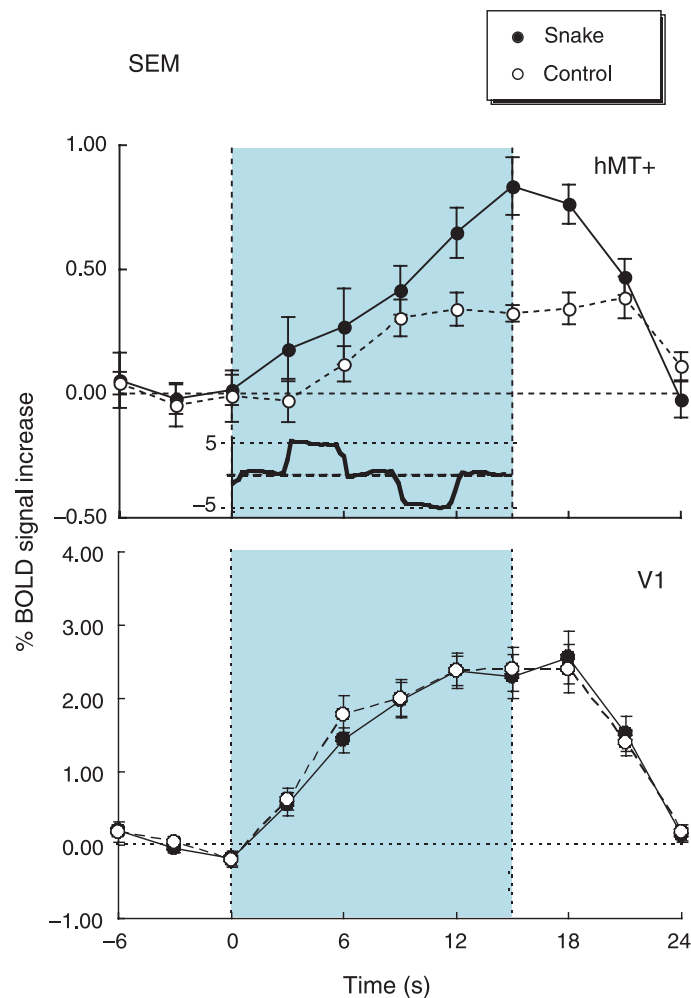


Figure 4. BOLD signal changes in hMT+ and V1 ROIs averaged across eight participants under the spontaneous eye-movement (SEM) condition. The meanings of axes, shades, and symbols are the same as those in Figure 2. There is remarkable increase in the hMT+ response between ‘snakes’ and ‘control’ stimulus conditions, but not in V1.

move their eyes to the center of three concentric circles in the middle row, synchronous to the onset of scan (judging from short pause of scanner noise between scans) every 3 s. They were also instructed to move their eyes in the same order as in the GEM condition: center, left, center, right, and center. The participants’ eye movements were monitored during the scan, whenever available.

Eight of the participants in the NEM and GEM conditions above were also tested with this condition.

### Spontaneous-Eye-Movement condition

The top and bottom panels of Figure 4 show the result of average across all participants for the hMT+ ROI and V1 ROI, respectively, under the spontaneous-eye-movement (in short, SEM) condition. The difference

between snakes and control stimuli is now remarkable in the latter half of the stimulus presentation period. The difference is significant by the statistical assessment of averaged BOLD signal differences ( $t(7) = 4.03$ ,  $p = 0.00495$ , Figure 5). Results from the V1 showed no significant difference between the stimulus conditions ( $t(7) = 0.186$ ,  $p = 0.857$ ).

This result implies that in the natural viewing condition, there could be significant differences in neural activity in hMT+, which may correspond to the slow but consistent motion perception in the Rotating Snakes figure, compared to the condition with similar images but without a motion illusion.

## Discussions

### Summary of achievements

We have succeeded in recording significant activation in a motion-sensitive area in the human extrastriate visual cortex during the observation of the ‘Rotating Snakes’ figure. Figure 5 shows the average of relative BOLD signal changes during scans 1–5 with respect to the onset of visual stimulus, which represents the result of our fMRI experiment in a summarized form. V1 shows no statistically significant differences in the brain activities between ‘snakes’ and ‘control’ stimuli, whereas hMT+ shows significant differential activities in some conditions. The

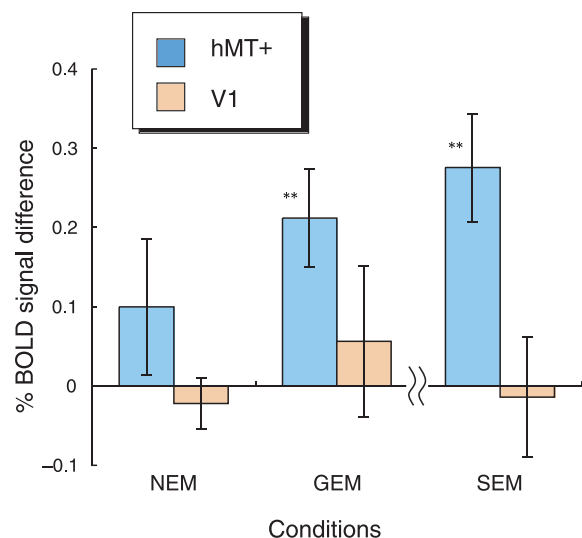


Figure 5. Mean differences in BOLD signal changes between ‘snakes’ and ‘control’ stimuli (‘snakes’ – ‘control’) during scans 1–5. Different color bars on the left and right for each condition indicate results from hMT+ and V1 ROIs, respectively. Error bars indicate standard errors across participants. Asterisks represent the statistical difference from zero ( $p < 0.01$ ).

GEM condition showed a significant difference between ‘snakes’ and ‘control’ stimuli under strict control of attention, while the condition without attentional task (SEM) showed a larger difference.

In the present fMRI study, we found that when the participants were instructed to make saccadic eye movements with attention task (GEM condition), the cortical area hMT+ exhibited greater BOLD responses to the stationary stimulus that evokes subjective impression of rotational motions, compared with the responses to the control stimulus that evokes no motion perception. Such a difference was not significant in the condition without eye movements (NEM condition). This pattern of results is consistent with previous notions that this motion illusion is degraded over a long period of maintained fixation (Backus & Oruç, 2005; Murakami et al., 2006) and that participants who make a greater amount of fixational eye movements indeed perceive greater magnitudes of illusion (Murakami et al., 2006). Altogether, our brain imaging study and these psychophysical investigations strongly suggest the relevance of eye movements in the generation of this motion illusion in static visual images.

## Attention and eye-movement factors

The SEM condition was optimized for illusion strength, at the expense of strict experimental controls. This condition is the closest to the natural viewing condition in which we normally observe the ‘Rotating Snakes’ illusion, and we wanted to see how far the hMT+ activity could increase under conscious perception of the illusory motion of the ‘snakes’ stimulus in comparison to the ‘control’ stimulus. Indeed, observation of the ‘snakes’ stimulus led to the greatest activation in hMT+ of the three conditions. This indicates that the results could be affected by two major confounding factors. Voluntary attention is one such factor, since the greater activation to the ‘snakes’ stimulus might be due to a greater attentional deployment to this stimulus for any reason, rather than a greater visual response to the perceptually rotating image (Huk et al., 2001). Another factor is the preparation/execution of voluntary saccades without onsets of saccadic targets. In the following subsections, we would like to attempt to discuss the possible inference from our results.

### Attentional factor

The result of the SEM condition suggests some effect of attention in hMT+ as previously discussed (Huk et al., 2001). Under this condition, the participants were actually able to perceive the illusory motion and direct attention in the absence of the attention task. This calls for a caveat that the difference in activities found in the GEM condition may also reflect the participants’ directing attention to the illusory motion when the task was not fully demanding. However, we do not think this is very

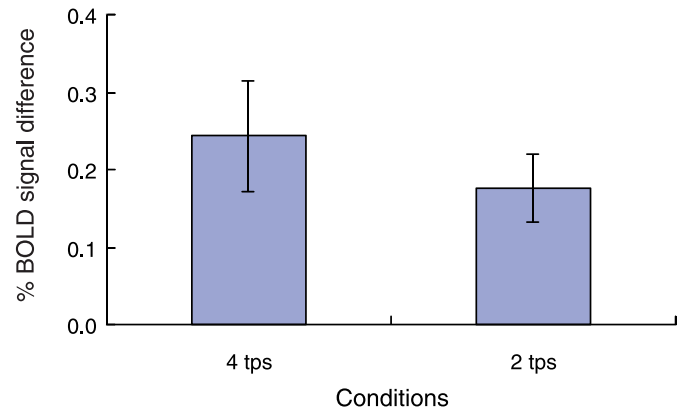


Figure 6. Difference in BOLD signal increase in hMT+ ROI under GEM condition with two temporal rates: from left, 4 times per second (tps; rapid condition) and 2 tps (original condition). Results of four runs (two participants and two runs for each) were averaged during scans 1–5 and error bars indicate standard errors across the four runs.

likely. First, the task of counting plus tracking of the fixation mark was obviously more demanding than the simple counting under the NEM condition where the participants could have had more available resources for directing attention covertly or even overtly. The fact that we observed less activity differences in the NEM condition than in the GEM condition is an indirect support that the participants were occupied with the task.

In addition, we repeated the GEM condition with a harder attentional task for the assessment of possible attentional confounds in the GEM condition and found that the task difficulty did not affect the existence of the difference in hMT+ activation between the ‘snakes’ and ‘control’ stimuli. We changed the color of the fixation point at four times per second, twice as fast as the original condition. Two participants who had also participated in the main experiments served in this experiment. Differences in BOLD signal increase between snakes and control images were calculated from two runs in hMT+ ROI under the GEM condition (Figure 6).

The blue-counting task in this rapidly color-changing condition was more attention-demanding than the original, but the participants made a great effort to accomplish it since the performance of counting was almost the same as the original one. If the BOLD signal differences between the ‘snakes’ and ‘control’ stimuli that we observed in the main experiment were primarily due to the attentional modulation, the use of this rapidly color-changing task may reduce such differences, because this task employs more attentional resource to the blue-counting task at the fixation point than the original task did. However, the effect of ‘snakes’ is clearly intact with the increased attentional load.

Altogether, it is most likely that the differences between ‘snakes’ and ‘control’ stimuli in GEM condition in hMT+

(Figure 5) were primarily elicited by the bottom-up signals from the visual stimuli.

### Eye movements

As the participant was requested to execute preplanned trains of saccades only with a guide of sound in the SEM condition, more computation related to oculomotor actions might be needed during observation of the ‘snakes’ stimulus for any reason (for example, it might become a harder job to determine future saccadic goals when every circle appears to rotate slowly). In the GEM condition, the participant’s saccades were guided by positional changes of the fixation point, which itself also changed its color and served as the attention-controlling stimulus. The participant was instructed to follow the position of the fixation point and to count how many times the fixation point changed to blue. In both conditions, we obtained a similar pattern of results, namely, the ‘snakes’ was better than ‘control’ at activating hMT+. If some preparatory process for the initiation of saccade is related to the hMT+ activity, we might see some difference in BOLD signal patterns between conditions (but not between stimuli).

There are several psychophysical studies that suggest possible existence of different mechanisms for the initiation of the two types of saccades, namely stimulus-triggered and internally generated saccades (Deubel, 1995; Erkelens & Hulleman, 1993). However, most physiological studies suggest the contribution of frontal eye fields (FEF) or intraparietal areas to the programming of saccade, and no human studies suggest the possibility of hMT+ contribution (Acs & Greenlee, 2008; Connolly, Goodale, Menon, & Munoz, 2002). Therefore, it may be unlikely that the difference in hMT+ activity between SEM and GEM conditions is due to differences in the way of initiating saccades, but if any, the difference could be due to the characteristics of retinal slip produced by eye movements.

### Summary

Eye movements may evoke transient signal from a static figure, which will evoke motion signals for the four-colored blobs in the ‘Rotating Snakes’ figure (Backus & Oruç, 2005; Conway et al., 2005). Also, fixation becomes less stable after a saccade, which may increase the eye drift to cause more motion illusion (Murakami et al., 2006). In either case, such motion signals for each element will be integrated as motion signals in hMT+ in each figure, if the blobs are arranged in a way to constitute a global motion. For the ‘snakes’ stimulus, this integration of motion signals facilitates global coherent motion along the circumference of each circle, whereas the ‘control’ stimulus leads to local cancellation in adjacent pairs of opposite motions. Therefore, the ‘snakes’ stimulus yields stronger rotational motion signals than the ‘control’

condition, even while the participant is performing an attentional task (GEM conditions in Figure 5). If there is additional attentional resource, the global motion signals will be enhanced by the attentional modulation of hMT+ activity (SEM conditions in Figure 5). Such involvement of attentional modulation for the illusory motion perception evoked by eye movements may be supported by the fact that the illusion becomes more visible when the participant notices it, and also there are large individual differences in the strength of illusory motion percept.

### Neural basis of illusory motion perception

Since V1 is known to be a motion sensitive area in the human visual cortex (De Valois, Yund, & Hepler, 1982; Hubel & Wiesel, 1977; Sasaki, Murakami, Cavanagh, & Tootell, 2002; Tootell et al., 1998), one may expect the existence of the origin of motion signals in V1. In fact, single-cell recording of monkeys has revealed directional responses to flashed patterns of a grayscale version of the Rotating Snakes figure, in both V1 and MT (Conway et al., 2005). However, the present study revealed that V1 showed no significant difference in BOLD signal increase during the observation of illusory motion perception in comparison to that during the observation of control stimulus. We suggest that this was mainly because the local structures of the stimuli (i.e., unit color sequence) were identical between the ‘snakes’ and ‘control’ stimuli. It should be noted that localization of visual field representation is much stronger in V1, compared to the higher order visual cortex. This is proved by the clarity of retinotopic maps obtained in various previous studies. Our ‘snakes’ and ‘control’ stimuli consist of the same unit of color blobs each of which subtends approximately 0.7 deg at the maximum, and this could evoke motion signals locally. It is therefore possible that the control stimulus activated motion sensitive cells as much as the snake stimulus in V1 where the receptive fields are small. It is also possible that V1 neurons process many other features of the stimuli like color or edge structures so that our scanner may not have been sensitive enough to pick up small differences due to the illusory motion. Future improvement of imaging technology might make it possible to clarify this issue.

On the other hand, motion sensitive areas in extrastriate cortex, hMT+ in the present study, are known to show considerable spatial summation property (Tootell et al., 1995) that is consistent with the primate neurophysiological investigations showing a relatively large receptive field size in extrastriate neurons compared to the lower level of visual areas (Albright & Desimone, 1987). Furthermore, hMT+ responds to global motion structures such as expansion/contraction and rotation (Morrone et al., 2000; Smith, Wall, Williams, & Singh, 2006; Wall,



Lingnau, Ashida, & Smith, 2008). Therefore, hMT+ seems a likely candidate for the neural support of global rotational motions we see in the figure.

## Conclusion

This is the first report of the successful recording of the increase in neural activity in the motion sensitive area of the human visual cortex, hMT+, by BOLD fMRI during the observation of ‘Rotating Snakes’ figure. The activation of hMT+ was enhanced when the observation was accompanied by eye movements, which indicates that the eye movements play a significant role in the illusory motion percept from the ‘Rotating Snakes’ figure.

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